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# Satellite tracking of Swedish Ospreys *Pandion haliaetus*: autumn migration routes and orientation

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Autumn migration routes and orientation of Swedish Ospreys *Pandion haliaetus* were studied by satellite tracking of 18 birds. Of these, 13 could be followed during the entire migration (6 females, 5 males and 2 juveniles). Most birds migrated across western and central Europe to winter in tropical West Africa. However, one juvenile flew to Cameroon and one female used a very easterly route and reached Mozambique. On average, the birds travelled a total distance of about 6700 km, with little variation except for the female wintering in Mozambique, who travelled more than 10000 km. Of 21 stopovers (of > 1 day), only five were made south of 45°N; three of these in Africa. Females departed before males and juveniles and flew to a stopover site they probably were familiar with. After 3–4 weeks there, they continued to their wintering grounds. Also males and juveniles usually made one or more stopovers. Adults seemed to travel to a known wintering site, where they remained stationary, whereas juveniles were more mobile after reaching tropical regions, probably looking for good wintering sites. Males generally left the breeding area in directions similar to the mean migratory direction, whereas a few females departed in diverging initial directions. Apart from these diversions, adult Ospreys followed very straight migratory routes, with overall mean directions of 185–209° and with mean angular deviations of 6–33°. Some juveniles also departed in diverging directions. Moreover, young birds tended to show a larger variability in orientation. Thus, the Ospreys kept a fairly straight direction and did not avoid geographical obstacles such as mountain ranges and desert areas. However, they seemed reluctant to cross large water bodies. There was no correlation between angular deviation and length of the migrational segment, indicating that the principles of orientation by vector summation may not be valid for Osprey migration. Moreover, the geographic direction of migration did not vary in accordance with variations in the magnetic declination, suggesting that the Ospreys did not orient along magnetic loxodromes.

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The Osprey *Pandion haliaetus* has a wide distribution in the northern hemisphere, but also breeds in the tropics. Most, however, breed in temperate areas, mainly between latitudes 40° and 70°N, and are long-distance migrants to tropical regions (Cramp and Simmons 1980, Poole 1989). Ringing recoveries show that most Ospreys breeding in northern Europe migrate across western and central Europe to winter in tropical West Africa, from Mauretania eastwards to Cameroon (Österlöf 1977, Saurola 1995). However, there are also a number of records from East Africa and at least four from South Africa, mainly of birds ringed in Finland, but also of Swedish birds (Saurola 1994, Stolt et al. 1998). Moreover, one bird ringed as a chick in northern Norway was found in India during the winter (NOF 1988), showing that the migration of the species is complex and not fully understood.

Sweden holds a large proportion of the European breeding population, with an estimated 3200 pairs (SOF 1990), and this population is a potentially important source of birds for the re-establishment of populations in other parts of Europe, including Scotland (Dennis 1995) and Germany (Schmidt and Kapfer 1994). Recently, there has been a tendency towards a population decline in some areas in southern Sweden (M. Hake unpubl.). Although this may be due to low reproductive performance (M. Hake unpubl.), it also may be connected to threats Ospreys face during the non-breeding season, as they spend most of the year away from the breeding grounds. Threats may include pollution and acidification of freshwater habitats, as well as hunting, fishing and fish-farming (e.g. Eriksson 1984, Poole 1989, Eriksson and Wallin 1994).

As of 1995, more than 15000 Ospreys have been ringed in Sweden, mainly as chicks. From about 2000 ringing recoveries, it seems obvious that the majority of Swedish Ospreys migrate across western Europe to winter in tropical West Africa (Österlöf 1977, Saurola 1994, Stolt et al. 1998). However, ringing data provide limited information about actual migration routes or stopover and wintering sites. Moreover, little is known about orientation during migration. As the Osprey is less concentrated to migration "hot-spots" than other species (e.g. Alerstam 1990a, Kjellén 1997), it is considered to migrate on a broad front. Therefore, it seems likely that Ospreys should readily cross geographical obstacles, such as larger water bodies, deserts and mountain ranges. Although some ringing recoveries support this, little is known also about this aspect of the Osprey's migration. Hence, detailed information about migration routes and stopover and wintering sites of the Swedish population is important not only for identifying potential risk areas en route, but also to enhance our understanding of the evolution of migration strategies in this species and in birds in general.

During the last decade, satellite telemetry has proved to be a very valuable tool for detailing movements of large bird species such as storks (e.g. Berthold et al. 1992, 1995) and raptors (e.g. Meyburg et al. 1995a, b). Ospreys have been provided with satellite transmitters in USA as well as in Germany and Sweden. During 1995–1996, five and 17 birds were tracked to their tropical wintering sites from breeding grounds in Germany and USA, respectively. However, the results of these efforts have not been published (B. Meyburg pers. comm., M. Martell et al. unpubl.). The autumn migration of two Swedish Osprey females fitted with satellite transmitters during breeding has previously been described (Kjellén et al. 1997).

In this study, we report on the routes and orientation of 13 Ospreys, including the two mentioned above, migrating between Sweden and tropical Africa, along with information on six birds which did not complete the entire migration.

## Methods

During 1995–1998, we fitted satellite transmitters on 18 Ospreys in an area close to Grimsö Wildlife Research Station (59°43′N, 15°30′E) in South Central Sweden, about 200 km west of Stockholm. Twelve breeding adults (six of each sex) were caught during the first half of July, with a clap-net on the nest, or with a net ($10 \times 4$ m) placed above a Goshawk *Accipiter gentilis* mount close to the nest. The transmitters were attached as backpacks, and the birds were released within one hour of capture. One of the females (Fe 49–96, see Table 1), which disappeared in Spain during migration in September 1998, was followed in both 1996 and 1998 (see Table 2). Six juveniles were provided with transmitters just before fledging in late July. We used transmitters with conventional batteries (Microwave Nano PTT 100), weighing 30 g (about 2% of the body weight of the birds), on four females, three males and six juveniles. During 1997–1998, however, two females and three males were provided with solar-powered transmitters, weighing 35 g. Although a few birds apparently died during migration, we have no reason to believe that their deaths were caused by the extra load. At least six adults subsequently returned to breed in the same nest, and we then recaptured them and removed the transmitter. After refurbishing, these transmitters were re-used the following seasons. In all cases, the harnesses were intact and the Ospreys showed no signs of injury.

The transmitters were tracked by CLS/Service Argos in Toulouse, France. The batteries of the 30 g transmitters had an expected life-time of at least 500 hours. The transmitters were programmed to transmit during 10 h every third day to cover the autumn migration and parts of the wintering period. Depending on satellite orbits and local conditions we received 0–15 positions during one 10-h period. The solar-powered transmitters, on the other hand, were more or less constantly active, provided that there was enough sunshine. Although these transmitters sometimes failed at northerly latitudes, they often provided a great number of positions each day.

Locations provided by the Argos system are divided into different classes (labelled A, B and 0–3) depending on validation, number of messages received and location accuracy. We normally used all validated locations in this analysis, taking location accuracy into account only when relevant (see below). For three classes of locations (1–3), the accuracy is within 1 km, while the accuracy for A, B and 0 is unspecified. The high-quality locations make up about 10% of our data set. During periods when the Ospreys were stationary within a limited area, e.g. the breeding area, it was obvious that locations of unspecified accuracy were often 5–10 km from the correct position, and in extreme cases the deviation was 20–100 km. However, it seems appropriate to use all available locations in the analysis of migratory movements over substantial distances, as the location error will, in such cases, only affect the result to a minor degree. In contrast, when considering local movement patterns within limited areas, it is essential to rely primarily on the high-quality locations.

As the transmitters were not normally active every day, we did not always know the exact date of departure from the breeding grounds and arrival at the wintering sites. If these dates were not known, we used the average speed on travelling days (see Kjellén et al. 2001) to calculate the most likely dates of departure and arrival. The total durations of stopovers were determined by the same method. An area was considered to be a stopover site if the bird staged for at least 24 h and moved less than 100 km.

Distances and directions are based on standard calculations for loxodromes (rhumblines). The total distance migrated was obtained by using a maximum of one position per 24-h period and adding the daily distances flown. Furthermore, for plotting, the locations were transformed to coordinates in the Mercator projection (Gudmundsson and Alerstam 1998). This map projection has the advantage of showing loxodromes as straight lines, and is therefore traditionally used for nautical charts. However, it is true neither with respect to distance nor area, exaggerating geographical dimensions of high latitudes in com-

Table 1. Autumn migration of thirteen Ospreys followed from the Swedish breeding grounds to Africa during 1995–1998. Approximate coordinates (decimal values) are given for stopover and wintering sites. Indices for the different individuals refer to the identification number of the transmitter and the year it was used (e.g. Fe 43–95 = female with transmitter no. 43, attached in 1995).

| Sex/Age<br>Ind.-Year | Migration period<br>(average breeders) | Dates and sites of stopovers (coordinates) | Wintering site (coordinates) | Distance flown, km (average) |
|---|---|---|---|---|
| Fe 43–95 | 28 Aug–24 Sep | 31 Aug–3 Sep W Czech Rep. (49.8N, 12.8E) | S Ivory Coast (05.2N, 06.2W) | 6550 |
| Fe 44–95 | 5 Aug–24 Oct | 13 Aug–10 Sep W Kazakhstan (49.3N, 49.8E)<br>27–30 Sep N Ethiopia (12.2N, 37.2E)<br>5–15 Oct Central Uganda (01.9N, 32.9E) | W Mozambique (15.6S, 32.4E) | 10 060 |
| Fe 48–96 | 15 Aug–15 Sep | 21–30 Aug NE Germany (About 51.0N, 7.5E) | The Gambia (13.5N, 15.8W) | 5810 |
| Fe 49–96 | 22 Aug–27 Sep | 25 Aug–5 Sep SW Norway (58.9N, 06.1E) | W Senegal (14.8N, 17.3W) | 5980 |
| Fe 51–97 | 28 Jul–17 Sep | 2–29 Aug N Germany (53.5N,10.7E) | S Senegal (12.9N, 16.7W) | 6090 |
| Fe 49–98 | 7 Aug–30 Sep | 9–13 Aug SE Sweden (About 57.0N, 16.0E)<br>15–16 Aug NE Germany (53.9N, 13.3E)<br>20 Aug–12 Sep E Austria (47.8N, 17.5E) | E Guinea Bissau (12.1N, 14.5W) | 6910 |
| Total Fe | (12 Aug–27 Sep, n = 6) | | | (6900) |
| Ma 50–96 | 4–17 Sep | – | Guinea Bissau (11.5N, 16.0W) | 6040 |
| Ma 55–97 | 3 Aug–26 Sep | 10 Aug–1 Sep E France (48.2N, 04.5E)<br>3–12 Sep Central France (46.8N, 03.8E) | SW Mali (11.5N, 08.3W) | 5930 |
| Ma 51–98 | 12 Sep–5 Nov | 19 Sep–2 Oct W Poland (51.1N, 15.6E)<br>5–8 Oct Central Austria (47.2N, 13.3E)<br>19–25 Oct N Tunisia (36.0N Oct. 5E) | Ivory Coast (07.3N, 05.5W) | 7230 |
| Ma 52–98 | 3 Sep–18 Oct | 5–6 Sep N Germany (54.8N, 11.5E)<br>10–14 Sep E Germany (51.6N, 14.0E)<br>16–18 Sep W Czech Rep. (49.7N, 13.4E)<br>23–30 Sep S France (43.8N, 01.3E) | The Gambia (13.6N, 16.5W) | 6570 |
| Ma 54–98 | 17 Sep–29 Oct | 23 Sep–6 Oct N Germany (52.0N, 10.7E) | W Sierra Leone (08.8N, 13.2W) | 6320 |
| Total Ma | (9 Sep–13 Oct, n = 4) | | | (6420) |
| Juv 53–96 | 3 Sep–26 Oct | 15 Sep–6 Oct S Spain (36.4N, 06.0E) | Central Guinea (11.0N, 10.8W) | 7270 |
| Juv 55–96 | 3 Sep–5 Oct | – | W Cameroon(?) (05.6N, 09.9E) | 7140 |
| Total Juv | (3 Sep–15 Oct, n = 2) | | | (7200) |
| Total average | 23 Aug–6 Oct | | | 6760 |

Table 2. Autumn migration of the six Ospreys that failed to complete their migration in 1996–1998. Approximate coordinates are given for stopover sites and sites where signals were lost. Indices for the different individuals refer to the identification number of the transmitter and the year it was used.

| Sex/Age Ind.-Year | Start of migration | Dates and sites of stopovers (coord.) | Site and date of disappearance (coordinates) | Distance flown, km |
|---|---|---|---|---|
| Fe 53–98[a] | 8 Aug | 10 Aug–15 Sep SW Norway (58.9N, 06.1E) | | |
| | | 23–29 Sep Central Spain (40.4N, 04.5E) | Central Spain (40.4N, 04.5E), 29 Sep | 2600 |
| Ma 51–96 | | – | Breeding area (59.6N, 15.4E), 23 Aug | 0 |
| Juv 52–96 | 18 Aug | 20 Aug–8 Sep SE Sweden (58.8N, 17.5E) | | |
| | | 12 Sep–7 Oct N Slovakia (49.4N, 19.5E) | N Slovakia (49.4N, 19.5E), 7 Oct | 1800 |
| Juv 54–96 | 29 Aug | – | SW Sweden (57.3N, 12.3W), 31 Aug | 330 |
| Juv 13–98 | 23 Aug | 26 Aug–22 Sep N Poland (53.9N, 18.4E) | N Poland (53.9N, 18.4E), 22 Sep | 650 |
| Juv 48–98 | 3 Sep | 5 Sep–6 Oct W Norway (61.8N, 05.3E) | W Norway (61.8N, 05.3E), 6 Oct | 780 |

[a] Previously followed in 1996 (Fe 49–96, see Table 1).

parison with equatorial areas (Alerstam 1996). As a basis for evaluating topographical features along the flight routes and at stopover sites, the Times Atlas of the World was used (scale of map generally 1: 2500000–5000000).

Mean and scatter of directional data were calculated as mean vector directions, mean vector lengths ($r$) and angular deviations according to Batschelet (1981). Movements over a minimum distance of 100 km and a minimum time of 9 h were considered as segments (excluding irregular changes in positions during stopover periods). The duty cycles of the transmitters and the availability of positions determined how many segments the migratory journey could be divided into for the different Ospreys. Only locations of high quality were used in this analysis.

## Results

### Migration routes

Of the 18 Ospreys provided with transmitters, six females (Fig. 1), five males (Fig. 2) and two juveniles (Fig. 3) completed their autumn migration (with the possible exception of Juv 55–96, see Table 1). Five Ospreys faced transmitter failure or died (Table 2). One adult male, who probably died, disappeared in the breeding area in late August. His transmitter was located three km north of the nest, but the bird was not found. Moreover, one adult female (Fe 49–96) was lost in Spain in September 1998, when being followed for the second time (Table 2). Only two of six juveniles reached Africa (Tables 1 and 2, Fig. 3). All of them left the breeding area, but the signals from four of them were lost during the autumn. One was lost in southern Sweden, shortly after departure from the nest. The other three juveniles departed to Norway, Poland and Slovakia (Table 2, Fig. 3), where contact was lost after extended stopover periods. The bird in Norway was found moribund, and a veterinary X-ray showed damages probably caused by collision with a power line. The cause of disappearance is not known for the other three, but it seems likely that they died. The juvenile who reached Cameroon was killed by local people at a small stream and the transmitter sent back to us by a French missionary. Assuming that all lost birds died, the mortality was close to significantly higher in juveniles than in adults, although sample sizes were small ($p = 0.06$, Fisher's exact test).

All adults with satellite transmitters produced fledged young, except Ma 55–97 (Table 1), whose breeding was terminated in late July. The majority of the birds migrated across western Europe, and crossed the Mediterranean Sea close to Gibraltar. However, two females, one male and one juvenile migrated along more easterly routes, crossing the Mediterranean Sea either via Sardinia-Corsica (Fe 43–95 and Juv 55–96) or Sicily-Malta (Fe 49–98 and Ma 51–98, Figs 1–3). One bird (Fe 44–95) did not cross the Mediterranean Sea at all, but used a very easterly route across the Caucasus and the Red Sea (Fig. 1).

Most birds wintered in tropical West Africa, from The Gambia to the Ivory Coast, although one juvenile (55–96) reached Cameroon and one female (44–95) spent the winter in Mozambique (Table 1, Figs 1 and 3). Despite the very easterly wintering site of this female, there was a tendency, although not statistically significant, that females more often wintered farther west than males ($U = 6$, $p = 0.06$, $n_1 = 5$, $n_2 = 6$, Mann-Whitney U-test). The total migration distance generally varied less than 1000 km around a mean of 6760 km (Table 1). The exception was Fe 44–95, who wintered in Mozambique and covered more than 10000 km.

Most of the birds made one or more stopovers (Tables 1 and 2). Of 21 recorded stopovers only five were south of 45°N; southern France, southern Spain, Tunisia, Ethiopia and Uganda. Generally, females left the breeding grounds before the males (cf. Kjellén et al. 2001 for details) and flew to a stopover site, where they remained stationary for 3–4 weeks before continuing migration (Table 1). This also includes Fe 43–95, who left the male and two newly fledged young already on 3 August, and then staged in an area with good fishing lakes about 30 km NW of the nest site (see Kjellén et al. 1997). An interesting detail is that she subsequently chose this area for nesting in 1996–2000 (pers. obs.). Fe 48–96 probably also made a more extensive stopover (Table 1), but this could not be confirmed as the locations provided on 15 through 21 August were of insufficient accuracy.

Most males and juveniles made stopovers on migration. The exceptions were Ma 50–96 and Juv 55–96, who made no obvious stopovers at all. Ma 55–97, whose breeding failed, behaved very similar to the females, as he left the breeding area early and made an extended stopover in east-central France (Table 1). Three of five juveniles that could be followed for more than two weeks after departure seemed to adopt a similar strategy to the females, travelling to an initial stopover site not too far away where they remained for a longer period (Table 2, Fig. 3).

After reaching Africa, adults seemed to travel directly to a previously used wintering site, where they remained for the winter. The two juveniles were more mobile after reaching the tropics. The one that reached Cameroon travelled more slowly and veered from a southerly to an easterly course after arriving in Nigeria. The surviving juvenile slowed down and made a sharp turn in a similar way before settling in Guinea (Fig. 3). In addition, it made a number of movements of up to 480 km from the main wintering site during December–April.

## Orientation

Adults generally seemed to keep a fairly straight direction on the southbound migration, with only one individual turning back northwards. Ma 51–98 crossed the Mediterranean Sea from Sicily via Malta to Libya, but then flew northwest to make a 6-d stopover in northern Tunisia before crossing the Sahara (Table 1, Fig. 2). Apart from the deviation by this male, two females (44–95 and 49–96) showed a high degree of directional deviation when leaving the nest sites for stopovers in Kazakhstan and Norway, respectively (Fig. 1). Excluding these deviations, directions generally varied between 160 and 240° in all adults.

Some migration segments were apparently directed towards specific stopover goals, like the male's reversal in North Africa and the initial movements east and west by the two females. Excluding these segments, the migration routes of the adult Ospreys were remarkably straight with similar overall mean directions towards 185–209°, and with mean angular deviations of 6–33° (corresponding to mean vector lengths $r = 0.84–0.99$) (Table 3). Mean direction was 205° for females and 200° for males. This difference is primarily caused by more females wintering farther west. Female 44–95 did not change the picture much as she, after the initial movement to Kazakhstan, kept an average direction of 195° when travelling to Mozambique.

Some juveniles initially migrated in directions clearly deviating from the normal migration course (Fig. 3). The six juveniles provided with transmitters left the breeding area in the directions 136, 165, 178, 192, 215

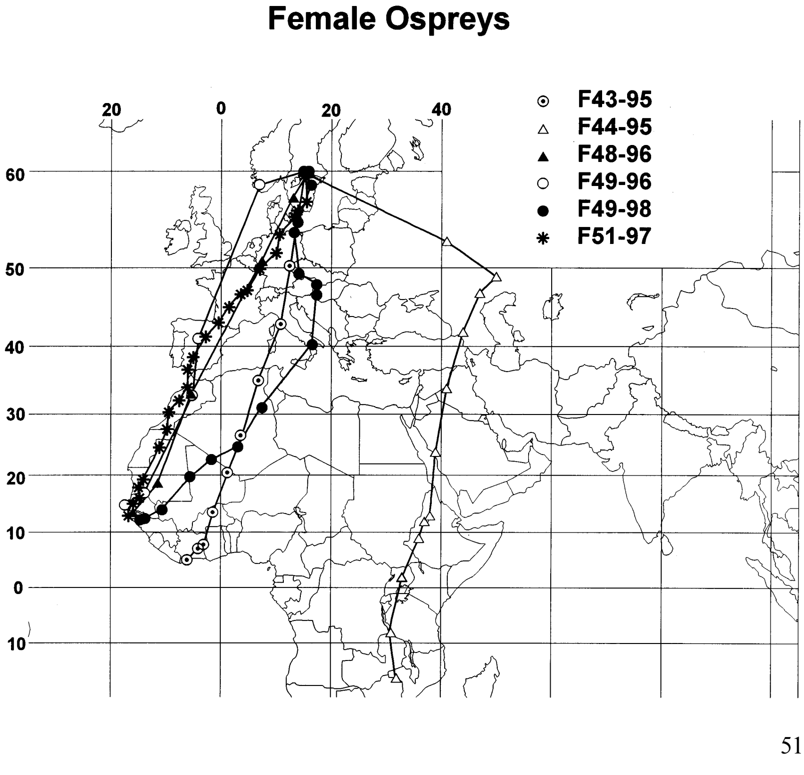

Fig. 1. Map (Mercator projection) of the migration routes of six female Ospreys tracked by satellite from the breeding site in Sweden to the winter quarters in Africa.

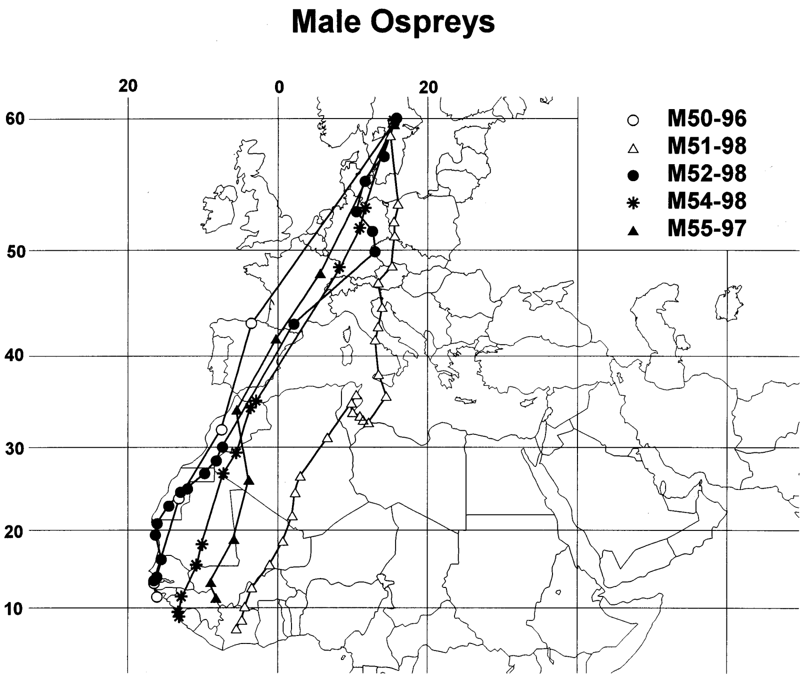

Fig. 2. Map (Mercator projection) of the migration routes of five male Ospreys tracked by satellite from the breeding site in Sweden to the winter quarters in Africa.

and 277°, respectively. The two juveniles that reached Africa showed a relatively large directional scatter also along their migration routes (their variable directions after reaching the wintering latitudes were excluded from the calculations presented in Table 3) compared to most adults. Mean directions for the two juveniles were 189° and 195°, and angular deviations 24° and 31°, respectively. Thus, there may be a tendency for the juveniles to show more variable orientation than adults, which most often had deviations between 10 and 20° (Table 3).

If the Ospreys were guided by the principles of vector orientation, as discussed by Rabøl (1978), Mouritsen (1998) and Alerstam (2000), one would expect a reduced directional scatter with increased segment length. However, there was no significant correlation between angular deviation and segment length, either when considering all individuals ($r_s = -0.03$, $n = 13$, n.s., Spearman rank correlation test) or when excluding the juveniles ($r_s = -0.17$, $n = 11$, n.s.).

## Discussion

### Migration routes

Ringing recoveries show that the great majority of Swedish Ospreys winter in West Africa south of the Sahara. Before this study began, a total of more than 15000 birds ringed, primarily as nestlings, had resulted in about 230 recoveries in western Africa compared to only two in eastern Africa (Österlöf 1977, Stolt et al. 1998). Nevertheless, one of the birds in this study wintered in Mozambique, which suggests that care must be taken when interpreting the results of ringing recoveries. There seems to be no doubt, however, that the density of wintering Ospreys from north European breeding grounds is lower in eastern than in western Africa. The less frequent overall occurrence of wintering Ospreys in eastern Africa may possibly be due to the risk of piracy from the African Fish Eagle *Haliaeetus vocifer*, which is more numerous in this region (e.g. Brown et al. 1982).

In Senegal and The Gambia, most wintering Ospreys stay within very small areas, and a high proportion return to the same site in consecutive winters (Prevost 1982). This study supports this pattern, as all our adults went straight for a certain, presumably previously used, wintering site. Moreover, all the adults were very stationary during the winter, generally moving less than 10 km from the centre of the home range. Juveniles seemed to search for a suitable wintering site at fairly low speeds over rather large areas. This behaviour involved major changes in the general direction of migration when reaching the tropical region (Fig. 3). Young Ospreys probably arrive comparatively late in the wintering area, only to find most good territories occupied by adults. Juveniles do not return to the breeding grounds during their second, and often not even during their third calendar year (Österlöf 1977, Cramp and Simmons 1980). As indicated by the juvenile staging in Guinea, it seems likely that they instead move around during this time, searching out a more favourable site to use during forthcoming winters.

During the migration, all except two of the birds made one or more stopovers, primarily in northern and central Europe. Most lakes in the breeding area at Grimsö are oligotrophic and hold relatively small fish stocks compared to lakes in other areas in northern Europe (M. Hake unpubl.). Hence, although some of the birds obviously were able to prepare for migration in the breeding area (cf. Kjellén et al. 2001), others may have found it favourable to use more profitable sites not too far from the breeding area before covering any longer distances. These birds may have staged in northerly areas because they had previous experience from visiting certain sites. This was apparently the case for some of the females, but may also have been true for some males, as indicated by Ma 55–97 (see below). Alternatively, good feeding sites were more easy to find at northerly latitudes.

Males generally used fewer days for stopovers than females (Kjellén et al. 2001). The failed breeder (Ma 55–97), however, adopted a strategy similar to the females. Possibly he was familiar with the stopover sites used in 1997, as we know that he visited one of these sites in France also the following autumn (observed by French ornithologists, Rolf Wahl pers. comm.). This male departed unusually late from his wintering site in spring 1998 (unpubl. data), and arrived in the breeding area too late to breed. Thus, it seems that his autumn migration behaviour in 1998 was the same as in 1997. Males whose breeding failed generally left the breeding area earlier than successful males (Kjellén et al. 2001), which indicates that our males actually preferred a migration strategy similar to the one adopted by the females. The Osprey shows a high degree of sexual dimorphism, with the female being larger than the male (e.g. Poole 1989). Consequently, females seem to dominate males. During breeding, males do most or all fishing and nest construction (e.g. Poole 1989, M. Hake unpubl.). Therefore, males are forced to postpone moult until after the breeding season, whereas females normally moult several flight-feathers while breeding (M. Hake unpubl.). As males care for the young after the females have departed, they may be forced to adopt a less favourable migration strategy. Nevertheless, the males spent fewer days at stopover sites than the females, particularly Ma 50–96, indicating that they were capable of preparing for the southbound migration in the breeding area.

Fe 43–95 left the nest already on 3 August (Table 1), and the positions up to 28 August indicated that she primarily frequented an area with good fishing lakes about 30 km NW of the breeding site (Kjellén et al. 1997). All other females moved considerably farther before staging. Three of the females made stopovers more or less en route south (Table 1, Fig. 1), whereas two of the females moved to stopover sites well off the main route to Africa (Norway and Kazakhstan). Fe 49–96 was ringed as a nestling in southern Norway (59.17N, 9.87E) in 1992 (Odd Frydenlund-Steen in litt.), which indicates that she may have found a good stopover site at the Stavanger Fiord in Norway during dispersal in her first autumn. We supplied this female with a new transmitter in 1998, and she left for the same area in Norway, spending over a month there before resuming migration south. Unfortunately she

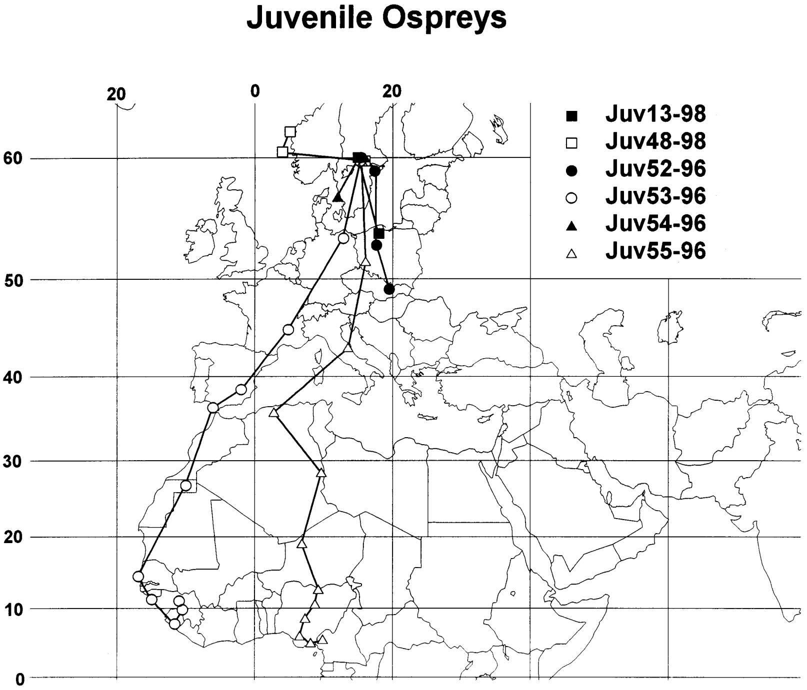

Fig. 3. Map (Mercator projection) of the migration routes of two juvenile Ospreys tracked by satellite from the breeding site in Sweden to the winter quarters in Africa. Four young birds that perished early during autumn migration are also included on the map.

Table 3. Mean and scatter of directions of Ospreys, based on directions of segments of their migratory routes from Sweden to Africa, as recorded by satellite tracking.

| Ind. | No. of segments | Mean segment length (km) | Mean direction (degrees) | *r* | Angular deviation (degrees) |
|---|---|---|---|---|---|
| Fe 43–95 | 9 | 725 | 204 | 0.95 | 17 |
| Fe 44–95 | 12 | 830 | 185 | 0.87 | 29 |
| Fe 44–95[a] | 10 | 748 | 195 | 0.98 | 11 |
| Fe 48–96 | 5 | 1163 | 209 | 0.99 | 6 |
| Fe 49–96 | 5 | 1189 | 217 | 0.90 | 26 |
| Fe 49–96[b] | 4 | 1363 | 207 | 0.95 | 19 |
| Fe 51–97 | 22 | 271 | 209 | 0.95 | 17 |
| Fe 49–98 | 14 | 489 | 205 | 0.84 | 33 |
| Ma 50–96 | 5 | 1207 | 197 | 0.96 | 17 |
| Ma 55–97 | 8 | 733 | 194 | 0.96 | 17 |
| Ma 51–98 | 24 | 292 | 199 | 0.84 | 33 |
| Ma 51–98[c] | 22 | 306 | 197 | 0.96 | 16 |
| Ma 52–98 | 17 | 382 | 206 | 0.90 | 25 |
| Ma 54–98 | 11 | 570 | 203 | 0.99 | 9 |
| Juv 53–96 | 8 | 842 | 195 | 0.85 | 31 |
| Juv 55–96 | 9 | 752 | 189 | 0.91 | 24 |
| Mean | 11 | 727 | 201 | 0.94 | 19 |

[a] Excluding two initial segments towards Kazakhstan.
[b] Excluding one initial segment towards Norway.
[c] Excluding two segments towards W/NNE to stopover site in Tunisia.

was later lost in central Spain (Table 2). As the female who left for Kazakhstan flew directly there, it seems likely that she too had previous information on her stopover site, possibly gained during dispersal as a juvenile from a nest site in easterly regions. This is supported by the winter site chosen by this female, as there seems to be a gradient in migration routes, with birds breeding in more easterly regions wintering further east (Österlöf 1977, NOF 1988, Saurola 1994). On the other hand, female 49–98, which was ringed as a nestling at Vaasa (62.60N, 24.30E) in W Finland in 1993 (Finnish Ringing Centre in litt.), did not make any detour during autumn migration. However, as she was hatched about 600 km north of her later breeding area, this is not too surprising.

## Orientation

Ospreys are strong flyers and therefore should hesitate less than other raptors before crossing geographical obstacles, such as large bodies of open water or mountain ranges. This is supported by this study, as several birds flew over mountain ranges like the Alps, Caucasus and the Atlas mountains. Also, several sea crossings, e.g. of the Baltic, Mediterranean and Red Seas, were documented. This may explain why Ospreys are less concentrated at migration hot spots like Falsterbo or Gibraltar compared to species that rely more on thermals during migration (Alerstam 1990a, Kjellén 1997). Nevertheless, our birds did not seem to pass extensive water areas at random points. Eight of the birds crossed the Mediterranean Sea from Southern Spain, although not necessarily at Gibraltar, and four flew south via Italy (Figs 1–3). A similar behaviour was recorded for Ospreys followed by satellite from Germany and USA (B. Meyburg pers. comm., M. Martell et al. unpubl.), indicating that Ospreys to some degree avoid risks connected with the crossing of larger water bodies.

Some juveniles departed in directions diverging from the general migration course (Fig. 3). Moreover, most of them made long stopovers shortly after leaving the breeding area. This may be an example of juvenile dispersal, and also a demonstration of how birds may find stopover sites used later in life. It seems natural that orientation in young Ospreys, lacking previous experience, should be less precise than that of adult birds, which have made the trip before. This seems to be the case for Swedish Honey Buzzards *Pernis apivorus*, where juveniles show a considerably greater scatter during autumn migration than adults, which mainly proceed directly towards the Strait of Gibraltar (Søgaard and Østerby 1989, Stolt et al. 1992).

Autumn ringing recoveries show a pattern of wide-angle orientation, where not only juveniles but also adults from Sweden fan out widely across Europe on a broad-front migration en route to mainly West African winter quarters (Österlöf 1977, Alerstam 1990a, b). This study indicates that postbreeding dispersal of juveniles in various directions and goal-orientation by adult females towards specific stopover sites (which may have been located and imprinted during the juvenile dispersal phase) may be the most important reasons for the wide scatter of ringing recoveries of Ospreys during the autumn. Other segments of the migratory routes are remarkably straight and concentrated around a mean direction towards SSW (Table 3).

While the magnetic declination is close to 0° in Sweden, it is about 10°W in the main West African winter quarters (Senegal-Ivory Coast). Consequently, if the Ospreys oriented along a constant magnetic compass course, their geographic direction is expected to shift gradually by about ten degrees towards the left throughout their autumn migratory journey. There is no such tendency of a leftward course change, making orientation along magnetic loxodromes unlikely.

Rabøl (1978) and Mouritsen (1998) demonstrated how migrants drawing their orientation during each flight step from a circular probability distribution with a fairly large scatter will, by the effect of vector summation over many flight steps, produce resulting long-distance migratory directions with a much more restricted angular scatter. With a directional concentration of each step corresponding to a mean vector length $r$, the bird would follow a circuitous route on average $1/r$ times longer than the straight-line distance to the destination (cf. Alerstam 2000). One day's movement over a distance of 200–400 km (Kjellén et al. 2001) may represent an orientational vector step for the Osprey. Table 3 indicates that the directional concentration between steps of such distances (recorded for three adults) corresponds to $r = 0.90–0.96$. For the two juveniles, a corresponding directional step concentration of $r = 0.7–0.8$ may be provisionally inferred from Table 3 (assuming that their mean segment length corresponds to three orientation steps), in conjunction with the appendix table in Mouritsen (1998). For a migratory journey requiring $n$ steps ( = travelling days) with exactly straight-line orientation, juvenile Ospreys would, with the orientation precision between steps as indicated above, use $1.2n$ to $1.4n$ steps to complete the journey, while adult Ospreys would complete it by $1.04n$ to $1.1n$ steps. These estimates remain provisional and uncertain given the limited data available and the lack of a distinct negative correlation between directional scatter and segment length that is expected from the vector summation model (Mouritsen 1998, Alerstam 2000).

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