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Complex timing of Marsh Harrier *Circus aeruginosus* migration due to pre- and post-migratory movements

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We tracked three juvenile and 14 adult Marsh Harriers *Circus aeruginosus* from southern Sweden via satellite to investigate migration strategies. Four individuals were tracked for at least two years. All three juveniles and four of the adults made west-oriented pre-migratory movements well before the onset of autumn migration, and trans-Saharan migrants visited post-migratory stopover areas in tropical Africa. By these movements, the harriers presumably exploit short-term regional variation in food abundance. Autumn and spring migration occurred in a relatively narrow corridor, without distinct differences between sexes in timing, speed, distance, and duration of migration, except that females tended to migrate faster in spring than did males. Juveniles migrated shorter distances than adults, and migration speeds were lower. Spring migration was similar to autumn migration in terms of speed and duration. Juveniles did not cross the Sahara Desert and three birds, one female and two juveniles, wintered in Europe, which is in accordance with a recent increase in the number of (juvenile) Marsh Harriers wintering in northwestern Europe. All birds that crossed the Sahara wintered in tropical West Africa. Harriers showed site fidelity to breeding, wintering and stopover areas. The overall migration speed of Marsh Harriers was similar to that of Ospreys *Pandion haliaetus* and Honey Buzzards *Pernis apivorus*, two other trans-Saharan migrants. Ospreys use fly-and-forage migration to promote resulting speed, whereas Honey Buzzards are particularly apt to exploit thermal soaring. How Marsh Harriers balance foraging versus travelling to accomplish their rapid migration speeds remains to be resolved.

Key words: migration, satellite tracking, pre-migratory movements, post-migratory movements, Marsh Harrier

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INTRODUCTION

Migrating birds exploit temporary and variable energy resources not only to breed but also to survive through the non-breeding period. Many bird species breeding at northern latitudes undertake long-distance migration to reach areas at lower latitudes with temporarily high food abundance during the unproductive winter season in the north. These long journeys are challenging and could affect mortality and future breeding attempts by reducing the birds' physical condition and delaying the arrival time to the breeding grounds (e.g. Alerstam 1990, Berthold 2001).

Marsh Harriers *Circus aeruginosus* from the northernmost part of the European breeding range are long-distance migrants, wintering mainly in tropical Africa, whereas the population in southern parts of Europe are mostly sedentary (Cramp & Simmons 1980, del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001). Most of the Marsh Harriers from Scandinavia migrate to wintering grounds in West Africa along routes through France and Spain, with a minority of ringed birds recovered in Europe during winter (Fransson & Pettersson 2001, Bønløkke *et al.* 2006). Birds ringed in the eastern part of Sweden also pass the Mediterranean via Italy (Fransson & Pettersson 2001). Differences in age ratios indicate that young birds migrate less far in their first year and are more prone to remain in Europe in winter (Castelijns & Castelijns 2008).

Satellite telemetry is a powerful method to study the migration performance of individual birds in detail. We equipped Marsh Harriers from a breeding population in southern Sweden with satellite transmitters in order to reveal spatial and temporal patterns of migration. The aim of this paper is to evaluate the timing of migration, determine if there are differences between age classes or sexes, analyse the speed of migration and determine if the migration speed is the same during spring and autumn. It appeared that Marsh Harriers made movements in autumn, both before and after migration, which were not solely linked to migration itself. We analyse the temporal pat-

tern of Marsh Harrier migration including these pre- and post-migratory movements. Spatial and geographic patterns of migration will be analysed in detail in a separate paper (Klaassen *et al.* in prep.).

We predict that male and female Marsh Harriers, because of the sex dimorphism (e.g. Cramp & Simmons 1980), may have different migration strategies and that the overall migration speed is faster in spring than in autumn for both sexes as seen in many long-distance migrating species (e.g. Berthold 2001, Alerstam *et al.* 2006). The smaller and lighter males might have a higher travel speed due to higher proportion of flapping flight, because smaller harrier species like Montagu's Harrier *Circus pygargus* and Pallid Harrier *Circus macrourus* have slightly higher proportion of flapping flight than Marsh Harriers during their daily migration flight (Spaar & Bruderer 1997).

Spaar & Bruderer (1997) showed that Marsh Harriers flew at lower altitudes during spring compared to autumn and spent more time flapping than soaring and thus might attain higher travel speed during spring migration. This does not necessarily mean that the overall migration speed is higher in spring, because energy consumption increases considerably with the use of flapping flight and the birds have to spend more time on stopover to refuel (e.g. Hedenström 1993). Spaar & Bruderer (1997) also associated the increased flapping proportion in spring to headwind conditions, which is a common situation in the Sahara Desert with prevailing northeasterly winds (Klaassen *et al.* in prep.).

Finally, to put the migratory performance of Marsh Harriers into perspective, we compare overall migration speeds of Marsh Harriers with those of two raptors tracked by satellite telemetry on their migration between northern Europe and West Africa (Kjellén *et al.* 2001, Hake *et al.* 2003). These species differ considerably in their migration strategy, in which the Osprey *Pandion haliaetus* represents a fly-and-forage migrant (Strandberg & Alerstam 2007, Klaassen *et al.* 2008), and the Honey Buzzard *Pernis apivorus* a soaring migrant (Hake *et al.* 2003). Spaar & Bruderer

(1997) showed that Marsh Harriers prolonged their daily migration by using flapping flight during mornings and evenings, which has not been the case for Ospreys or Honey Buzzards (Kjellén *et al.* 2001, Hake *et al.* 2003). This might compensate for the relatively low flight speed in soaring flight for the Marsh Harrier compared to the other two raptor species (Spaar 1997, Kjellén *et al.* 2001), even if harriers seem to maximize cross-country speed (Spaar & Bruderer 1997). Hence, we predict that the overall migration speed is lower for Marsh Harriers than for Ospreys and Honey Buzzards because the harriers' flight is probably more energy demanding, without the ability to exploit thermal soaring to its full extent.

METHODS

From 2004 to 2007 we equipped 17 Marsh Harriers (14 adults and three juveniles) with satellite transmitters near Kristianstad (56°N, 14°E) in southern Sweden. Fourteen breeding adults (eight females and six males) were caught on the nest with a Bal-chatri trap. Transmitters were attached as backpacks, and the birds were released near the nest within one hour of capture. Three juveniles were provided with transmitters just before fledging in early July. We used Solar PTT 100s (Microwave Telemetry, Inc.), mass 18 g (on average 2.7% of the harriers' body mass). The two birds caught in 2007 received 22 g (3.3% of mass) SolarArgos/GPS PTT 100s (Microwave Telemetry, Inc.).

Transmitters were tracked by CLS/Service Argos in Toulouse, France and programmed to operate on a transmitting cycle of 10 h on and 24 h off. Depending on satellite orbits and local conditions, we received 0–15 positions during one 10-h period.

In total, we recorded 20 autumn migration tracks and 13 spring migration tracks of which 17 and 12 tracks, respectively, were complete (Online Appendix 1 and 2). These tracks were made by 14 of the 17 Marsh Harriers provided with transmitters (contact was lost with three birds before they arrived at their wintering grounds). Repeated jour-

neys were recorded for F3 (female no. 3), M2 and M3 (males no. 2 and 3) with three complete autumn and spring tracks for the female (Online Appendix 1 and 2).

Our complete Marsh Harrier data set contained approximately 12 000 positions, consisting of 21% high quality locations (ARGOS-class 1–3), 48% moderate quality locations (ARGOS-class A and 0), and 31% low quality locations (no accuracy estimate, ARGOS-class B; <http://www.argos-system.org>). In order to reduce a possible effect of low quality locations we always selected the best quality position for every 10-hour transmitting period. Thus, for the present analyses we only used 17% of all received locations. Out of these, 52% were class 1–3 locations and only 5% were class B locations. As the transmitters did not transmit continuously, and because sometimes no positions were obtained during 10h sending cycles, we did not always know the exact date of departure or arrival from/to breeding grounds, stopover areas and wintering areas. If these dates were not known, we used the average speed on travelling days (see Kjellén *et al.* 2001) to calculate the most probable dates.

Migration never started before the end of August. We conclude this from the fact that individuals that initiated migration directly from their nesting area never left before this date. Well before the onset of migration, all juvenile and four adult birds made pre-migratory movements to stopover sites in northern Europe. An area was considered to be a stopover site if the bird moved less than 25 km day⁻¹ (we assume that birds spent relatively little time on migration on days with <25 km of movement). Thus, days at which harriers travelled more than 25 km were defined as travel days. The onset of migration was very obvious since, in all cases, autumn migration was initiated by a south-westward movement of >100 km. Harriers also made long-distance movements after they had arrived at their wintering grounds. We defined these movements as post-migratory if they were preceded by a stationary phase of at least 7 days (one week) within the wintering range south of the Sahara.

Distances and directions of movements are based on standard calculations for loxodromes (rhumb lines). The total distance migrated was obtained by using a maximum of one position per 24-h period (excluding stopover days) and adding up the daily distances travelled. Furthermore, for plotting, locations were transformed to coordinates in the Mercator projection (Gudmundsson & Alerstam 1998).

We tested the differences concerning timing, duration, distance and speed of migration between the sexes and age categories in GLM mixed models (SPSS 16.0), with individual as a random factor. We used paired *t*-tests (SPSS 16.0) to compare the individuals' autumn and spring migration with respect to timing, duration, distance and speed. Two adult Marsh Harriers were tracked during more than one complete migration cycle (autumn plus spring season). We used mean values of the repeated seasons for each of these individuals in the comparison.

We compared the total autumn migration speed of Marsh Harriers in relation to distance with the corresponding results for Ospreys and Honey Buzzards which have been studied previously by satellite (e.g. Kjellén *et al.* 2001, Hake *et al.* 2003). The comparison refers to individuals migrating between Sweden and West Africa, and we excluded post-Saharan movements after more than a week of initial sedentariness for the juvenile Honey Buzzards (adults do not move around in winter as the juveniles do), as well as the post-migratory period for the Marsh Harriers (Ospreys do not show any such movements). We tested the difference in mean distance using a one-way ANOVA (SPSS 16.0).

RESULTS

General routes and wintering areas

Migration between southern Sweden and tropical West Africa occurred along a relatively narrow corridor (Fig. 1). Three birds did not cross the Mediterranean Sea; one adult female (F4) and two juveniles (J1 and J2) wintered in Europe. The third

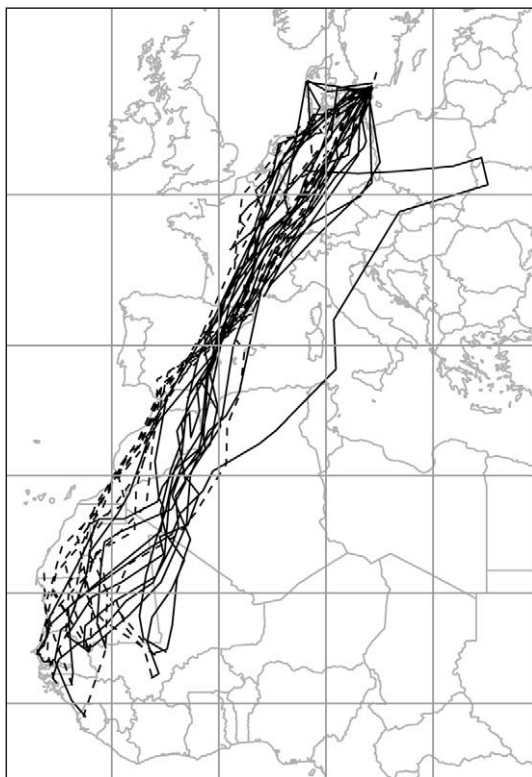


Figure 1. Migration routes of Marsh Harriers recorded by satellite tracking for autumn and spring (dashed tracks) journeys 2004–2008.

juvenile (J3) did not cross the Sahara Desert but stayed in northern Algeria. All birds that crossed the Sahara wintered in tropical West Africa.

Routes in spring were similar to the routes in autumn, although birds followed on average a more westerly track, particularly in Africa (Klaassen *et al.* in prep.). M5 needed a second attempt to cross the Sahara Desert in spring 2007, after a sandstorm had forced him to abolish his first attempt. In 2008, M2 tried to cross the Sahara Desert three times in spring, but failed to do so and finally retreated to the Senegal River basin.

Timing of migration

Autumn migration started mainly in September, either from the breeding area or from a pre-migra-

tory area in northern Europe (see below about pre- and post-migratory movements), with departures ranging from 27 August to 7 October (median: 8 September). Trans-Saharan migrating harriers passed the Mediterranean Sea from 12 September to 24 October (median: 25 September) and arrival dates at the wintering or post-migratory stopover areas ranged between 9 September and 4 November (median: 6 October, Table 1, Online Appendix 1).

Spring departure from the wintering grounds occurred between 11 February and 17 April for adults (median: 12 March, Table 1, Online Appendix 2), with the trans-Saharan migrants crossing the Mediterranean Sea between 18 March and 29 April (median: 25 March). The only one of the three juveniles surviving the winter started migrating north on 30 April.

We did not find significant differences in timing (departure and arrival dates) between females, males and juveniles during either autumn migration (GLM mixed models, departure: $F_{2,11} = 0.43$, $P = 0.66$; arrival: $F_{2,9} = 0.51$, $P = 0.62$) or spring migration (departure: $F_{1,8} = 0.19$, $P = 0.67$; arrival: $F_{1,6} = 1.71$, $P = 0.24$, see also Fig. 2). The

early departure of M3 from its wintering ground was considered to be an outlier (departed from the wintering area in mid-February, well before other Harriers), and therefore excluded from the statistical tests for spring departure (departure date from the stopover site in Morocco was used instead, Online Appendix 2). Note that juveniles were not included in the analyses of spring departure and arrival times (too few data). Excluding the juveniles from the autumn tests did not change the outcome.

Speed, distance and duration of migration

Autumn migration from the breeding ground or pre-migratory stopover took on average 28 days (stopover plus travel days), of which 23 were travel days (Table 1). Calculated from the breeding area, autumn migration took an average of 50 days. Travel distances averaged 4504 and 4243 km, calculated from the breeding area and pre-migratory stopover area, respectively. The corresponding overall migration speeds were 127 and 166 km day⁻¹, respectively. The average speed on travel days was 204 km day⁻¹.

Table 1. Timing, duration, distance and speed of autumn and spring migration for Marsh Harriers recorded by satellite tracking in 2004–2008. Duration = mean number of migration days including stopovers. Distance = mean distance travelled on migration days (stopover movements excluded). Speed = mean total distance travelled between transmitting periods divided by mean total number of migration days. Speed on travel days = mean total distance divided by the number of travel days (autumn: counted from the breeding area to the post-migratory stopover area).

Category	Median departure date ^a	Median departure date ^b	Arrival date	Duration (days), distance (km), speed (km day ⁻¹) ^a			Duration (days), distance (km), speed (km day ⁻¹) ^b			No. of travel days	Speed on travel days (km day ⁻¹)	Max. speed
Autumn												
Females	5 Sept	8 Sept	4 Oct	32	4480	159	27	4426	173	21	221	543
Males	29 Aug	10 Sept	14 Oct	70	5705	116	33	5252	167	28	204	514
Juveniles	16 Aug	19 Sept	29 Sept	45	1757	55	11	1476	136	11	146	332
All birds	30 Aug	8 Sept	6 Oct	50	4504	127	28	4243	166	23	204	504
Spring												
Females	12 Mar	-	7 Apr	27	4865	193	-	-	-	21	233	520
Males	6 Mar	-	13 Apr	46	6166	139	-	-	-	30	219	490
All birds	12 Mar	-	11 Apr	34	5096	161	-	-	-	24	218	486

^a Departure from breeding area/wintering area.

^b Departure from pre-migratory stopover area in autumn (including departures from breeding area for birds not performing a pre-migratory movement).

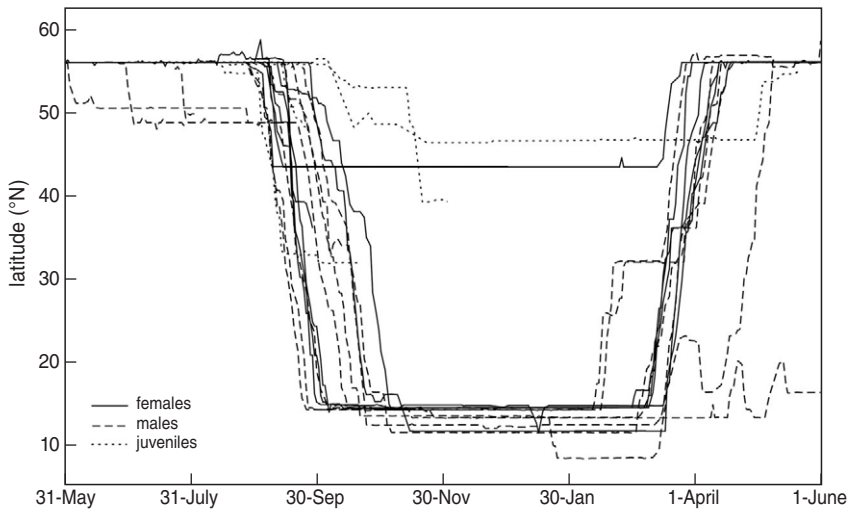


Figure 2. Temporal pattern of latitudinal movement of Marsh Harriers recorded by satellite tracking 2004–2008. For birds still transmitting at the end of study period the curves are interrupted at 31 May 2008.

No significant differences in the duration, distance, migration speed, number of travel days, and speed on travel days could be detected between adult males and adult females (GLM mixed models, $F_{1,5-12} = 0.01-2.37$, $P = 0.17-0.93$) during autumn migration. Juvenile birds migrated shorter distances than adult birds (1757 versus 5093 km, GLM mixed models, $F_{1,11} = 17.06$, $P = 0.002$), and thus the total duration of migration tended to be shorter for juveniles than for adults ($F_{1,13} = 4.49$, $P = 0.05$), and also the number of travel days tended to be less ($F_{1,11} = 4.74$, $P = 0.05$). In addition, juveniles migrated a shorter distance on travel days (mean for adults: 213 km day^{-1} , mean for juveniles: 146 km day^{-1} , GLM mixed models, $F_{1,14} = 6.50$, $P = 0.02$).

Spring migration was in general very similar to autumn migration (see Table 1). There were no significant differences between females and males in the distance, migration speed, number of travel days, and speed on travel days (GLM mixed models, $F_{1,2-11} = 0.00-3.37$, $P = 0.12-0.97$, Fig. 2) during spring migration. However, the duration of spring migration tended to be shorter for females ($F_{1,4} = 7.36$, $P = 0.05$).

No significant differences were revealed when comparing autumn and spring migration on an individual basis (only adult birds) with respect to duration, distance, migration speed and travel speed (paired t -tests, $t = -1.17-1.18$, $P = 0.28-0.89$, $n = 8$ individuals).

Pre- and post-migratory movements

Five of 12 adult Marsh Harriers made movements away from the breeding area prior to autumn migration (Fig. 3, Table 2). Both individuals for whom we obtained two autumn migrations made pre-migratory movements in successive years. The individuals making pre-migratory movements included cases of both failed (3) and successful (2) breeders, and both males (2) and females (3). The pre-migratory movements were oriented to the west (Fig. 3) to stopover areas in Sweden, Denmark, Germany and France. An exception was the second pre-migratory movement of M2, who in both years flew via an initially western route through Denmark and Germany (to France in 2006), but shifted direction east to Ukraine in 2007 (Fig. 3B). F6 made a pre-migratory stopover in Sweden, 95 km northwest of her nest, but

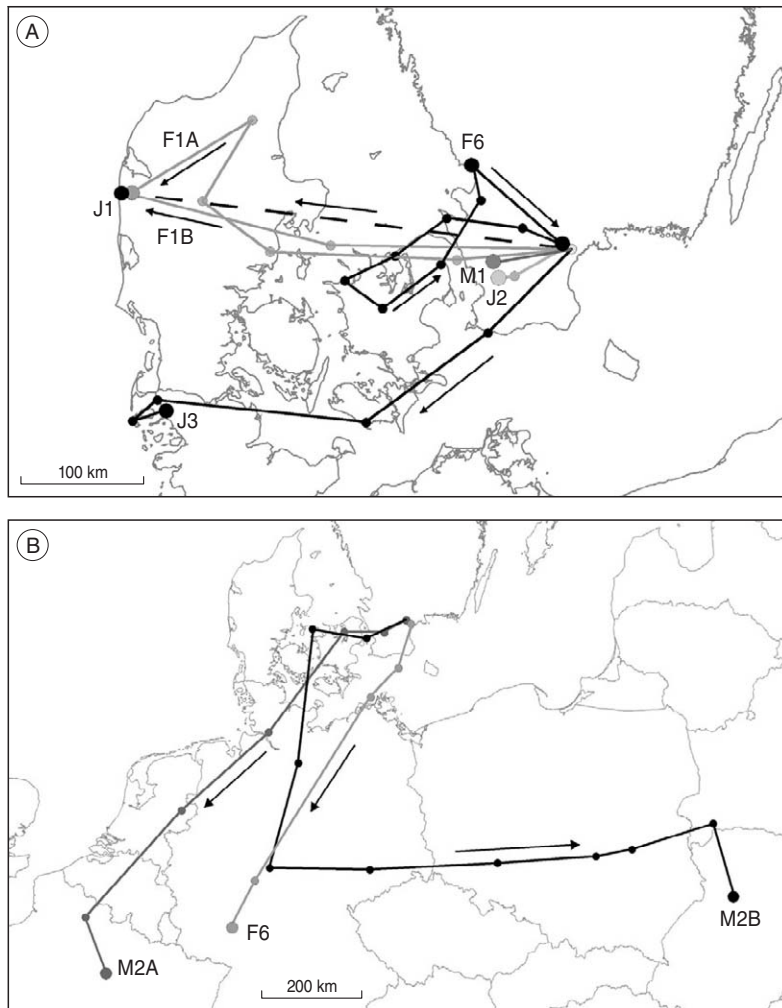


Figure 3. Shorter (A) and longer (B) pre-migration autumn movements of Marsh Harriers recorded by satellite tracking 2004–2008. (A) F1A = 2004; F1B, M1, J1 (track dashed because the route taken is unknown), J2 and J3 = 2005; F6 = 2007. Note that F6 returned to the breeding area before departing on autumn migration. (B) F2 = 2004; M2A = 2006; M2B = 2007. The female (F2) stopped transmitting after a few stationary days either before reaching, or just reaching, the pre-migratory stopover area. Arrows show flight direction along tracks, larger dots shows the stopover areas and smaller dots show higher quality positions along the flyway.

returned to the nesting place one month before she initiated her migration. Pre-migratory movements were relatively short (mean = 345 km), excluding the exceptional movement of M2 (1148 km in 2006 and 1958 km in 2007, Table 2).

The three juveniles moved to pre-migratory stopover areas in Sweden, Denmark and north-western Germany in mid-August (Fig. 3A, Table 2). One of these birds (J1) did not give any positions from this area until 30 September (Online Appendix 1) but may have reached it much earlier.

Table 2. Pre- and post-migratory movements and stopovers of Marsh Harriers recorded by satellite tracking during autumn and winter 2004–2008. days = number of days at pre- and post-migratory site, respectively.

Individual	Pre-migration				Post-migration						
	Movement period	Distance (km)	Stopover area (mean coordinates)	Days	Depart. date	Arrival date	Movement period	Distance (km)	Stopover area (mean coordinates)	Days	Final destination
F1 ^b	3–4 Aug-04	382	Denmark (56.4N, 8.3E)	36	8 Sept	7 Oct	13–17 Jan-04	811	Mali (15.0N, 10.4W)	991	Mali (15.0N, 10.4W)
F1	31 Aug–1Sept-05	383	Denmark (56.4N, 8.3E)	15	15 Sept						
F2	24–29 July-04	799	Germany (49.9N, 8.3E)	-	-						
F3						4 Oct	13 Oct-05	49	Mauritania (15.2N, 12.5W)	10	Senegal (14.8N, 12.3W)
F3						1 Oct	21 Oct-06	51	Mauritania (15.1N, 12.6W)	21	Senegal (14.8N, 12.3W)
F3						4 Nov	5 Nov-07	51	Mauritania (15.1N, 12.6W)	2	Senegal (14.8N, 12.3W)
F6 ^c	2–5 & 26 Aug-07	302+94	Sweden (56.4N, 13.0E)	22+32	26 Sept	24 Oct	9–12 Nov-07	623	Mauritania (16.4N, 12.0W)	17	Guinea Bissau (11.9N, 15.2W)
M1	3 July-05	67	Sweden (55.9N, 13.2E)	52	23 Sept	25 Oct	2–4 Nov-05	538	Mauritania (16.6N, 13.8W)	9	Guinea Bissau (11.8N, 13.8W)
M2	26 June-3 July-06	1148	France (48.9N, 4.0E)	53	24 Sept	14 Oct	22–25 Nov-06	200	Senegal (14.6N, 17.0W)	40	Senegal (13.6N, 15.7W)
M2	1–14 June-07	1958	Ukraine (50.5N, 25.1E)	75	27 Aug	3 Oct	14–15 Nov-07	182	Senegal (14.6N, 17.0W)	43	Senegal (13.6N, 15.7W)
M3						26 Sept	25 Oct-06	120	Mali (14.7N, 5.0W)	30	Mali (14.5N, 5.9W)
M3						24 Sept	24 Oct-07	105	Mali (14.5N, 5.1W)	31	Mali (14.5N, 5.9W)
M5						21 Oct	21–24 Jan-06	632	Senegal (13.8N, 15.4W)	93	Sierra Leone (8.8N, 12.7W)
M6 ^d						24 Oct	17 Dec-07	35–70	Mali (12.7N, 5.6W)	55	Mali (12.3N, 6.1W)
J1	-	379	Denmark (56.4N, 8.2E)	-	-						
J2	18 Aug-05	51	Sweden (55.8N, 13.5E)	51	7 Oct						
J3	15–18 Aug-05	396	Germany (54.7N 8.8E)	16	2 Sept						

^a F = adult female, M = adult male, J = juvenile.
^b Made a return trip to the Niger River near the Guinea-Mali border 13–17 January 2004.
^c Made a return trip to the breeding area 2–26 August with a longer stopover in southern Sweden at 56.4°N, 13.0°E during the period 5–26 August.
^d Made several trips between the post-migratory area and winter area 18–26 November before moving permanently to the winter area 17 Dec.

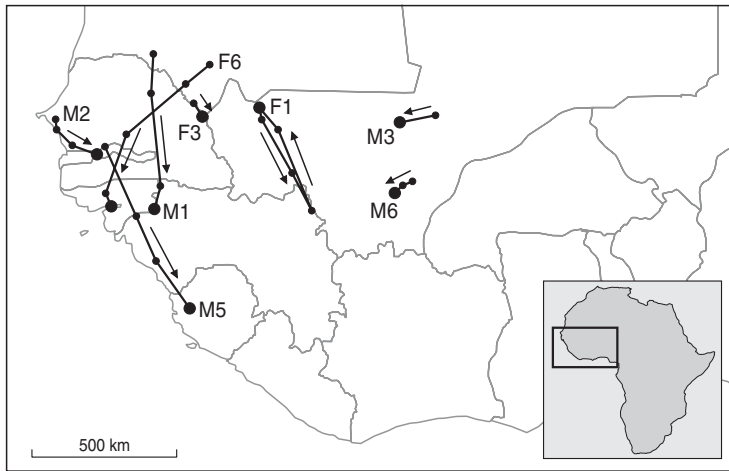


Figure 4. Post-migration autumn/winter movements south of the Sahara Desert of adult Marsh Harriers recorded by satellite tracking 2004–2007. F1 = 2004; M1 = 2005; F3 = 2005, 2006 and 2007; M5 = 2006; M2 and M3 = 2006 and 2007; F6 and M6 = 2007. Note that repeated tracks occurred for the three individuals F3, M2 and M3.

In autumn, all eight trans-Saharan migrants made a post-migratory stopover just after the crossing of the Sahara Desert (between latitudes 16.6°N and 12.6°N, Table 2, Fig. 4). F3 was delayed in her third tracking season and then only visited her 'traditional' post-migratory area for one night. Post-migratory movements were made in October–November (nine cases), but also in winter (three cases, see Table 2, Fig. 4). Two of the adults behaved differently from the rest: the post-migratory movement of F1 consisted of an 811 km long round trip before returning to the initial area in mid-winter and M6 made several round trips (from 18 November) after being stationary for almost two months. Finally, he moved 90 km west of his initial staging area on 13 January.

Two of the juvenile Marsh Harriers departed southwards from longer stopovers in northern Europe as late as mid-November. Although the timing of these movements was more similar to the timing of post-migratory movements of the adult birds, we did not include these in Table 2, given the problems to distinguish between post-migratory movements and pure migratory movements in juvenile birds (further studies needed!).

The adult Marsh Harriers which were tracked for more than one season showed a strong site fidelity to breeding, wintering and post-migratory areas. In fact, exactly the same stopover and wintering areas were used, whereas the location of the nest could differ 0.1–7 km from the previous year. However, in 2008, M3 nested 87 km north of the previous two years' breeding sites.

Migration distance and speed among long-distance migrating raptors

We compared the total autumn migration speed of Marsh Harriers in relation to distance with the corresponding results for Ospreys and Honey Buzzards. All birds, except for an exceptional adult male Osprey, migrated at speeds of 100–250 km day⁻¹ over distances of approximately 5000–8000 km. The average autumn migration speed of these medium-sized long-distance migratory raptors is similar among the species: Honey Buzzard = 163.3 km day⁻¹, \pm 32.3 SD; Osprey = 172.5 km day⁻¹, \pm 69.2 SD; and Marsh Harrier = 171.8 km day⁻¹, \pm 36.6 SD.

There was a significant difference in migration distance between the three raptor species (one-way

ANOVA, $F_{2,46} = 12.97$, $P < 0.001$) but no significant difference in total migration speed ($F_{2,46} = 0.13$, $P = 0.88$). The Marsh Harriers migrated a shorter distance (mean: 5372 km, ± 388 SD) than the other two raptors (Honey Buzzards: 6211 km, ± 637 SD, Osprey: 6400 km, ± 621 SD), which holds even if we include the pre- and post-migratory movements in the migration distance comparison (5668 km, $F_{2,46} = 5.13$, $P = 0.01$).

DISCUSSION

Timing of migration

Ring recoveries show that adults tend to initiate autumn migration slightly earlier than juveniles (Fransson & Pettersson 2001), whereas migration counts at Falsterbo show the opposite with adult males having the latest median departure date (Kjellén 1992). Our results suggest no distinct differences in timing of autumn migration among the different sex and age categories of Marsh Harriers. Juveniles that leave Sweden before the end of August are most probably heading for a pre-migratory stopover site or dispersal area as commonly seen in other species such as Common Buzzard *Buteo buteo* (Olsson 1958) and Osprey (Österlöv 1977). The three juvenile Marsh Harriers tracked in this study came from different nests but all moved in a westerly direction prior to migration, which is in accordance with adults' (initial) pre-migratory movement directions from the breeding area.

Individuals we tracked on repeated journeys showed a considerable variation in the timing of migration between years. There were cases with birds departing and arriving >30 days later/earlier than the previous year and other cases of birds with almost identical timing between two years. The variation in timing during autumn migration might be explained by breeding success even if it is not directly evident in the data set. A delayed current breeding season (by laying of a second clutch after first failure) resulted in both delayed departure from breeding area (F1 season two) and delayed arrival to post-migratory area (F3 season

three, Online Appendix 1). The strategy of having a pre-migratory phase after breeding could counterbalance a delay in time, as seen for F1, who corrected the migration timing by reducing the length of the pre-migratory stopover period.

Speed, distance and duration of migration

The shorter distance of the juveniles' migratory journeys compared with those of adults was not completely unexpected in the light of the recent strong increase of juvenile Marsh Harriers wintering in northwestern Europe (Castelijns & Castelijns 2008). There is probably a trade-off between benefits associated with a shorter migration distance, and the costs associated with the harsher winter climate (caused by the generally lower prey availability at higher latitudes during winter).

There was individual variation in duration and speed between autumn and spring migration, but no general differences could be found. The specific weather situation during the desert passage probably has a great effect on survival and also influences the breeding success via delayed arrival to the breeding grounds as shown by our tracked Marsh Harriers and satellite tracked Montagu's Harriers (Trierweiler *et al.* unpubl. data). A recent increase (since the 1960s) in frequency of occurrence and annual duration of dust storms in the Sahara Desert and the bordering Sahel zone (Middleton & Goudie 2001) might have an impact on the survival of migrating birds. Future studies to examine effects of conditions in the Sahara Desert with survival and breeding success of long-distance migrants are thus of great importance.

Pre- and post-migratory movements

Pre-migratory movements away from the breeding area were not related to unsuccessful breeding attempts in our data set (but see above about timing of migration). Instead, the behaviour seems to be an individual characteristic, with birds undertaking a movement one year being prone to do so also in other years (F1 and M2). The pre-migratory return trip to the nest performed by F6 (Fig. 3A) supports our view that these movements should not be regarded as migratory movements.

Adult birds that did not engage in pre-migration to a distant site either stayed in the breeding territory or moved several km from the nest to a pre-migratory site, where they were stationary prior to migration. F1 exemplifies fidelity to the pre-migratory area from year to year, while M2 exemplifies use of different areas between the years. This kind of pre-migratory movement has not been recorded among other raptor species like Honey Buzzard, Common Buzzard and Eurasian Hobby *Falco subbuteo*, in spite of extensive satellite tracking (Hake *et al.* 2003, Strandberg *et al.* unpubl. data). Instead, satellite tracked Ospreys have shown a similar behaviour, moving to a pre-migratory stopover site in northern Europe (in some cases situated perpendicularly to the migration direction) where they spent some time before initiating migration (Hake *et al.* 2001, Alerstam *et al.* 2006). In contrast to the Marsh Harriers, Ospreys did not make post-migratory stopovers south of the Sahara, but continued directly to their winter site. Juvenile Honey Buzzards seem to make post-migratory stopovers in tropical Africa (Hake *et al.* 2003), and prolonged tracking of young birds in the wintering grounds, during up to almost two years, showed that they continued to travel and pause irregularly throughout their pre-mature life (Strandberg *et al.* unpubl. data).

The pre-migratory movements seem to be a strategy developed in the genus *Circus* and has also been shown for the Montagu's Harrier (Liminana *et al.* 2008, Trierweiler *et al.* 2008). Possible explanations for these movements of harriers are the reduction of competition with young (most often only cared for by one of the parents during the fledging period), finding resources for moult or recovery from breeding efforts, and for the preparation of migration. However, the idea that pre-migratory stopovers are important for moult is not supported by our own field observations in West Africa (Nov–Dec 2006). M2 (at his post-migratory stopover site) was in a state of intensive primary moult, despite his long pre-migratory stopover period. In fact, most adult Marsh Harriers (including females) observed during our visit to West Africa were in active flight

feather moult (Strandberg & Olofsson, unpubl. data). Females typically start flight feather moult during the breeding season (all tracked females had 4 to 10 newly grown flight feathers in June and early July) and, thus, seem to suspend their moult during migration.

Steenhof *et al.* (2005) reported pre-migratory movements (called breeding dispersals) for adult female Prairie Falcons *Falco mexicanus* breeding in Idaho (USA). In late summer, these birds moved in a northeasterly direction, prior to their migration to southern wintering grounds. This phenomenon was regarded as a strategy to exploit seasonally abundant prey resources. The same could be true for Marsh Harriers, with the majority of their pre-migratory movements directed to areas along the North Sea coast (Denmark, Germany and The Netherlands), where large numbers of migrating shorebirds and passerines (e.g. Starlings *Sturnus vulgaris*) gather and could form an easily accessible food source.

All trans-Saharan migrating Marsh Harriers visited a post-migratory stopover area or at least made a post-migratory movement (F1) in tropical Africa. These movements probably are related to changing food abundance as the areas where the harriers first stop after migration become drier. The arrival at the savannas south of the Sahara coincides with the peak in locust and Red-billed Quelea *Quelea quelea* occurrence, which are common prey after the rain season (Thiollay 1989, Strandberg & Olofsson unpubl. data). When locusts become scarcer and Queleas concentrate in wetlands or migrate elsewhere, other more southern and western locations may become more suitable for the harriers. The late and short visit in 2007 of F2 to her previous post-migratory area addresses the difficulties of defining and showing the Harriers' fidelity to these areas. We might have missed areas used by the tracked Marsh Harriers depending on arrival time and the food abundance associated with it. A similar post-migratory pattern is shown by Montagu's Harriers *Circus pygargus*, tracked from northern Europe, using several different areas south of the Sahara Desert during their post-migratory period (Trierweiler *et al.* 2008).

Migration distance and speed among long-distance migrating raptors

The comparison of migration distance and speed of Marsh Harriers with that of Ospreys and Honey Buzzards showed a significant difference in migration distance with Marsh Harriers travelling the shortest distance. The difference in distance is probably caused by the differences in habitats used throughout the winter, with Ospreys wintering mostly in coastal areas, Honey Buzzards in forested areas, and Marsh Harriers in more northerly savannas and wetlands.

Migration speed is highly affected by the flight strategy used (e.g. Hedenström 1993). The three species generally follow similar migration routes and probably all use thermal soaring flight to a great extent. Only adult Honey Buzzards seem to avoid water crossings to exploit the thermal convection to its full extent (Hake *et al.* 2003). It is noticeable that the Marsh Harriers reach similarly fast migration speeds as Ospreys that use fly-and-forage migration to promote resulting speed (Strandberg & Alerstam 2007, Klaassen *et al.* 2008) and as Honey Buzzards, which are particularly apt to exploit thermal soaring. How the Marsh Harriers balance foraging versus soaring to accomplish their fast migration speeds remains a fascinating question for the future, which cannot yet be solved using conventional satellite tracking, as temporal and spatial resolution are not sufficient for such detailed analyses.

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SAMENVATTING

De trekbewegingen van drie juveniele en 14 adulte Bruine Kiekendieven *Circus aeruginosus* vanuit broedgebieden in Zuid-Zweden werden in kaart gebracht met

behulp van satelliettelemetrie. Vier vogels werden gedurende meerdere jaren gevolgd. Alle juveniele en vier adulte vogels verlieten het broedgebied lang voordat ze daadwerkelijk aan hun herfsttrek begonnen. Daarnaast vlogen de vogels die ten zuiden van de Sahara overwinterden, niet direct naar hun uiteindelijke overwinteringsgebied, maar stopten een tijdje net ten zuiden van de Sahara. De functie van deze opmerkelijke bewegingen is waarschijnlijk het exploiteren van de ruimtelijke variatie in voedselbeschikbaarheid. Zowel de herfst- als voorjaars trek vond plaats binnen een nauwe baan, waarbij er geen duidelijke verschillen in timing, snelheid, afstand en duur van de trek tussen de seksen bestond. Vrouwtjes neigden er echter wel toe de voorjaars trek sneller te voltooien dan mannetjes. De afstanden waarover juveniele vogels trokken, waren korter en hun treksnelheid was lager dan bij adulte vogels. Snelheid en duur van de voor- en najaars trek waren gelijk. Geen van de juveniele vogels passeerde de Sahara. Twee juveniele vogels en één adult vrouwtje overwinterden in Europa, wat overeenkomt met het beeld van de recente toename van het aantal in West-Europa overwinterende (juveniele) Bruine Kiekendieven. Alle individuen die de Sahara overstaken, overwinterden in tropisch West-Afrika. De kiekendieven waren bijzonder plaatstrouw aan broedgebied, pleisterplaatsen tijdens de trek en overwinteringsgebieden. De overall treksnelheid was gelijk aan die van Visarenden *Pandion haliaetus* en Wespindieven *Pernis apivorus*, twee andere trans-Sahara trekkers. Bruine Kiekendieven trekken echter over kortere afstanden dan de twee andere roofvogels. Visarenden foerageren tijdens het trekken om de treksnelheid te verhogen, terwijl Wespindieven gespecialiseerd zijn in het benutten van thermiek. Hoe Bruine Kiekendieven de afweging maken tussen voedsel zoeken en het benutten van gunstige trekomstandigheden blijft voornamelijk een vraag.

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Appendix 1. Timing, duration, distance and speed of autumn migration for Marsh Harriers recorded by satellite tracking 2004–2008. In first column: Departure and arrival dates for grouped females, males, juveniles, and all birds are median dates. Duration = individual and mean (for males, females, juveniles and all birds pooled) number of migration days including stopovers. Distance = individual and mean distance travelled on migration days (stopover movements excluded). Speed = individual and mean total distance travelled between transmitting periods divided by mean total number of migration days. Speed on travel days = individual and mean total distance divided by the number of travel days (counted from the breeding area to the post-migratory stopover area). Duration, distance and speed from pre-migratory area include departures from breeding area for birds not performing a pre-migratory movement. Numbers in italics represent incomplete migration periods – these were only included in the calculation of median departure dates.

Individual ^a	Departure breeding area date	Departure pre-mig. area date	Arrival post-mig. area date	Duration (days), distance (km), speed (km day ⁻¹) from breeding area			Duration (days), distance (km), speed (km day ⁻¹) from pre-mig. area			No. of travel days	Speed on travel days (km day ⁻¹)	Max. speed
F1 ^b	3 Aug 2004	8 Sept 2004	7 Oct 2004	66	6231	94	30	5849	195	32	195	375
F1 ^b	31 Aug 2005	15 Sept 2005	-	28	2895	103	13	2511	193	9	322	781
F2 ^b	24 July 2004	-	-	6	799	133	-	-	-	5	160	263
F3 ^b	5 Sept 2005		4 Oct 2005	30	5719	191				24	238	697
F3 ^b	8 Sept 2006		1 Oct 2006	24	5470	228				20	274	809
F3 ^b	11 Sept 2007		4 Nov 2007	55	5572	101				32	174	420
F4 ^b	5 Sept 2006		13 Sept 2006	9	1692	188				9	188	463
F4 ^b	29 Aug 2007		9 Sept 2007	12	1585	132				7	226	488
F5 ^b	13 Sept 2006		-	14	1260	90				14	90	319
F6 ^d	26 Sept 2007		24 Oct 2007	29	5093	176				20	255	548
M1	3 July 2005	23 Sept 2005	25 Oct 2005	115	5317	46	33	5250	159	28	190	563
M2	26 June 2006	24 Sept 2006	14 Oct 2006	111	5553	50	21	4404	210	26	214	535
M2	1 June 2007	27 Aug 2007	3 Oct 2007	125	7725	62	38	5766	152	36	215	573
M3 ^b	30 Aug 2006		26 Sept 2006	28	5186	185				25	207	456
M3	28 Aug 2007		24 Sept 2007	28	5236	187				21	249	553
M4 ^b	14 Sept 2006		-	4	880	220				4	220	525
M5 ^b	19 Sept 2006		21 Oct 2006	33	5408	164				30	180	563
M6 ^b	7 Sept 2007		24 Oct 2007	48	5511	115				32	172	355
J1 ^c	July to Sept	Mid Oct 2005	Mid Nov 2005	-	1662	-	-	1282	-	-	-	-
J2	18 Aug 2005	7 Oct 2005	16 Oct 2005	60	639	11	10	589	59	6	107	206
J3	15 Aug 2005	2 Sept 2005	13 Sept 2005	30	2969	99	12	2558	213	16	186	458
Females	5 Sept	8 Sept	4 Oct	32	4480	159	27	4426	173	21	221	543
Males	29 Aug	10 Sept	14 Oct	70	5705	116	33	5252	167	28	204	514
Juv.	16 Aug	19 Sept	29 Sept	45	1757	55	11	1476	136	11	146	332
All birds	30 Aug	8 Sept	6 Oct	50	4504	127	28	4243	166	23	204	504

^a F = adult female, M = adult male, J = juvenile.

^b The bird had a successful breeding season prior to migration.

^c No positions 11 July – 29 Sept, 5–18 Oct, 19–24 Oct, 9–21 Nov and 23 Nov – 23 Dec. The bird made movements during these periods.

^d Made a pre-migratory return trip to the breeding area 2–26 Aug, not included in the table.

Appendix 2. Timing, duration, distance and speed of spring migration for Marsh Harriers recorded by satellite tracking 2004–2008. Explanations of column and row headings are found in Appendix 1.

Individual	Departure wintering area date	Arrival breeding area date	Duration (days), distance (km), speed (km day ⁻¹) from wintering area			No. of travel days	Speed on travel days (km day ⁻¹)	Max. speed
F1	17 Mar 2005	4 Apr 2005	19	5377	283	17	316	670
F3	9 Mar 2006	29 Mar 2006	21	5392	257	20	270	737
F3	1 Mar 2007	11 Apr 2007	42	5499	131	22	250	389
F3	10 Mar 2008	11 Apr 2008	33	5504	167	26	212	412
F4	15 Mar 2007	25 Mar 2007	11	1552	141	11	141	400
F6	17 Mar 2008	18 Apr 2008	33	5866	178	28	210	513
M1	3 Mar 2006	-	11	1263	115	11	115	178
M2	6 Mar 2007	18 Apr 2007	44	5870	133	44	133	304
M2 ^a	17 Apr 2008	-	-	-	-	-	-	-
M3 ^b	11 Feb 2007	9 Apr 2007	58	6112	105	28	218	498
M3 ^b	15 Feb 2008	28 Mar 2008	43	5494	128	19	289	527
M5 ^c	14 Mar 2007	9 May 2007	57	7901	139	38	208	579
M6	16 Mar 2008	13 Apr 2008	29	5452	188	22	248	542
J1 ^d	30 Apr 2006	13 May 2006	14	1136	81	9	126	264
Females	12 Mar	7 Apr	27	4865	193	21	233	520
Males	6 Mar	13 Apr	46	6166	139	30	219	490
All birds	12 Mar	11 Apr	34	5096	161	24	218	486

^a Made three return trips back to the wintering area at the Senegal-Gambia border 11 April, 21–26 April and finally to the Senegal River 5–15 May.

^b Made a long stopover in Morocco 26 February to 26 March 2007 and 20 February to 16 March 2008.

^c Made a return trip to the Senegal river, S Mauritania, from where it migrated north 13 April.

^d Arrived at presumed summer area in southern Denmark 13 May.