

Migration and wintering areas of adult Montagu's Harriers (*Circus pygargus*) breeding in Spain

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Abstract Between 2006 and 2008, 14 Montagu's Harriers (*Circus pygargus*) were tagged with satellite transmitters at their breeding grounds in NE Spain, recording a total of 18 autumn and 10 spring journeys. In both autumn and spring migrations, harriers migrated between Europe and West Africa along a relatively narrow corridor between the coast of Morocco and Western Sahara and the western border of Algeria. Birds tended to follow a slightly more westerly track during spring migration compared to autumn migration. Harriers started autumn migration in late August–early September, arriving at their wintering grounds in early–mid-September, after travelling between 8 and 25 days, and covering a mean of 187 km a day. Spring migration started in mid-March, with birds arriving at the breeding grounds in mid-April after covering a mean of 114 km a day. On average, spring migration lasted longer, with birds covering longer distances than during autumn migration, and distances travelled in a day tended to be shorter. Significant differences in the routes followed by harriers were observed among seasons and individuals,

with the same individuals following different routes in different years. Wintering areas were located in northern Senegal and the southern border of Mauritania with Mali, with some birds breeding in the same colony in Europe separated more than 1,200 km during the wintering season. Birds showed a relatively high fidelity to their wintering areas. Several birds moved from one area to another during the wintering period, which resulted in larger wintering areas, whereas others remained in the same area during the whole wintering season.

Keywords Autumn migration · Migration routes · Migration timing · Repeated migrations · Satellite tracking · Spring migration

Zusammenfassung Zwischen 2006 und 2008 wurden 14 Wiesenweihen (*Circus pygargus*) in ihren Brutgebieten in Nordostspanien mit Satellitensendern versehen und insgesamt 18 Herbst- und zehn Frühjahrszugwege aufgezeichnet. Sowohl auf dem Herbst- als auch auf dem Frühjahrszug zogen die Weihen zwischen Europa und Westafrika in einem relativ engen Korridor zwischen der Küste Marokkos und der westlichen Sahara und der Westgrenze von Algerien. Die Vögel tendierten dazu, auf dem Frühjahrszug einem etwas westlicheren Kurs verglichen mit dem Herbstzug zu folgen. Die Weihen begannen mit dem Herbstzug Ende August bis Anfang September und kamen in ihren Überwinterungsgebieten Anfang bis Mitte September an, nachdem sie zwischen acht und 25 Tage geflogen waren und im Mittel 187 km pro Tag zurückgelegt hatten. Der Frühjahrszug setzte Mitte März ein, und die Vögel trafen Mitte April in ihren Brutgebieten ein, wobei sie im Mittel 114 km pro Tag flogen. Der Frühjahrszug dauerte im Durchschnitt länger als der Herbstzug, die Vögel legten größere Entfernungen zurück,

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und die an einem Tag zurückgelegte Entfernung war tendenziell kürzer. Zwischen verschiedenen Saisons und Individuen wurden signifikante Unterschiede in den von den Weihen geflogenen Routen beobachtet, und dieselben Tiere nutzten verschiedene Routen in verschiedenen Jahren. Die Überwinterungsgebiete lagen in Nordsenegal und an der Südgrenze Mauretaniens zu Mali. Einige Vögel, die in Europa in derselben Kolonie brüteten, überwinterten mehr als 1,200 km voneinander entfernt. Die Weihen zeigten eine relativ ausgeprägte Treue zu ihren Überwinterungsgebieten. Einige Vögel zogen während der Überwinterungsperiode von einem Gebiet zu einem anderen, was in insgesamt größeren Überwinterungsgebieten resultierte, wohingegen andere während der gesamten Wintersaison im selben Gebiet blieben.

Introduction

In recent years, the development of satellite telemetry has enabled tracking the migrations of medium-sized bird species. The use of this technology has revealed the poorly known migratory routes of several species, including Eurasian Hobby *Falco subbuteo* (Strandberg et al. 2009) and Eleonora's Falcon *Falco eleonora* (Gschweng et al. 2008; López-López et al. 2009, 2010), and enabled a whole new range of studies in other migratory species (e.g. Alerstam et al. 2006; Gill et al. 2009; Klaassen et al. 2008; Limiñana et al. 2008; Strandberg et al. 2008). By tracking the complete migration cycle of individuals, satellite telemetry allows the study of individual variation in migration strategies, and may provide valuable insights into the causes and consequences of migration and settlement decisions.

The Montagu's Harrier (*Circus pygargus*) is a migratory Palaearctic species with a large breeding distribution, ranging from western Europe to central Asia (Cramp and Simmons 1980). Although their migratory routes and wintering grounds have been studied by ring recoveries and observations at bottleneck points (e.g. García and Arroyo 1998), in the last years, the use of lightweight satellite transmitters has enabled more detailed studies on Montagu's Harrier migration (Limiñana et al. 2007, 2008; Trierweiler et al. 2007). However, relevant information, such as the repeatability of wintering areas in successive years and between-year differences in migration timing and routes, are still lacking. From a conservation point of view, knowledge of these aspects is of paramount importance, since changes (e.g. in climate or land use) in both breeding and wintering areas may affect these parameters and, consequently, have an effect on species persistence.

Here, we use satellite tracking data of individual Montagu's Harriers to describe and compare autumn and spring migration routes of this species, and to explore individual variations in migration strategies like between-year differences in spring and autumn migration routes and timing. We also provide data on size, location and between-year variation in the location of wintering grounds used by the same individuals.

Methods

Tagging data

In 2006, ten adult Montagu's Harriers (six males and four females) were captured and equipped with 9.5-g Solar PTT satellite transmitters (Microwave Telemetry), at their breeding sites in Castellón province (NE Spain). Five of these birds were tracked up to the 2008 post-breeding migration (thus, we have information on repeated autumn and spring journeys for them). Four other adult birds (one male and three females) were fitted with satellite transmitters in the 2008 breeding season in the same area, and subsequently tracked during their migration to Africa. Overall, we recorded a total of 18 autumn and 10 spring journeys, corresponding to nine birds, which are analysed here. Satellite transmitters were programmed on a duty cycle of 6 h on/16 h off for the first 3 months and then the duty cycle was changed to 10 h on/56 h off for the subsequent months (Limiñana et al. 2007, 2008). Only Argos data belonging to Location Classes (LCs) 3, 2, 1 and 0 were used to draw the migratory routes, as these are the most accurate locations obtained from Argos System (e.g. Costa et al. 2010; Soutullo et al. 2007). All data were retrieved and managed using the STAT software (Coyne and Godley 2005).

Data analyses

Positions recorded during autumn and spring journeys for each individual and year were mapped using ArcView 3.2. Points were converted into polylines using the Animal Movement extension for ArcView (Hooge and Eichenlaub 1997). Following the polylines, we estimated the longitudinal positions every 2° of latitude, from 43°N to 15°N for every travel (see Strandberg et al. 2009). We used 2°, because this distance corresponds to approximately 220 km, which is about the maximum distance covered in a day by harriers during the autumn migration (Limiñana et al. 2007). Consequently, each of these segments was treated as independent with regards to decisions depending on wind and weather conditions. Differences between autumn and spring migration routes were estimated using

the General Linear Model module of SPSS 15.0. We used interpolated longitude of these positions as the response variable, and latitude, year, individual and season as explanatory variables.

For each individual and season, we calculated date of migration onset, end and duration, migration distance (i.e. distance between migration onset and end), and average distance covered in a day (see Limiñana et al. 2007, 2008 for details on parameter calculations). As a post-breeding pre-migratory stage has been previously described for Montagu's Harriers (Limiñana et al. 2008; Trierweiler et al. 2007), we also calculated the onset and duration of this stage. For individuals for which data for more than 1 year were available for migration parameters, we calculated an average value and used these figures for further analyses. We used Wilcoxon tests to compare spring and autumn migration timing (speed, distance and duration). Due to the small sample size, no between-sex comparisons were conducted.

We also estimated the size of the individual wintering areas as the 95% fixed kernel (e.g. Kenward 2001) encompassing all the locations obtained from the end of each autumn migration and the onset of the following spring one (we only considered LCs 3, 2 and 1 for these calculations). Additionally, we calculated the distance between the location where autumn migration ended and the beginning of the next spring migration. We also calculated the distance between the centroids of wintering areas used in consecutive years by the same individual, to evaluate the fidelity to these areas. Centroids were calculated using the "Center of Mass v.1.b" extension for ArcView (Jenness 2006). Calculations on wintering areas were only done for the five individuals for which data on two wintering seasons were obtained (i.e. excluding the four birds tagged in 2008).

Results

Migration routes and timing

Prior to departure to their wintering areas, almost all harriers performed some pre-migratory movements, mainly in a N–NW direction from their breeding sites. No evidence of pre-migratory movements before the spring migration was observed (Table 1; see also Limiñana et al. 2008). In both autumn and spring migrations, adult Montagu's Harriers migrated from Europe and West Africa along a relatively narrow corridor between the coast of Morocco and Western Sahara and the western border of Algeria (Fig. 1). All birds migrated across the Strait of Gibraltar area in autumn and returned to the breeding areas using this same area to cross the Mediterranean Sea.

Timing of migration was more variable in autumn than in spring, both for the onset and the end (even if the four birds for which only data on autumn migration timing is available are not taken into account; Table 1). Harriers started autumn migration in late August–early September, generally from a pre-migratory staging area, arriving at their wintering grounds in early–mid-September, after travelling on average 16 days, and covering on average 187 km a day (Table 1). Spring migration started in mid-March, with birds arriving at the breeding grounds in mid-April (after an average of ca. 1 month of travel), and covering a mean of 114 km a day during migration. On average, the spring migration lasted longer ($Z = 2.023$, $P = 0.043$, $n = 5$), with birds covering longer distances than during the autumn migration ($Z = 2.023$, $P = 0.043$, $n = 5$), and the distance travelled in a day tending to be shorter ($Z = 1.753$, $P = 0.080$, $n = 5$; Table 1).

Significant differences in routes used by harriers were observed among seasons and individuals, with the same individuals following different routes in different years (Fig. 2). Yet, when individual paths are pooled, migration route used by harriers from our breeding population did not vary between years (Fig. 1; Table 2). On average, birds tended to follow a slightly more westerly track during spring migration compared to autumn migration (Figs. 1 and 2). The largest differences in mean longitudes between autumn and spring migrations were observed between 23 and 27°N in northern Mauritania. The largest difference between autumn and spring routes took place at 23°N where mean distance between routes reached up to 145 km (maximum actual differences for the same individual ranged from 385 km for bird #39715 to 719 km for bird #39710; Fig. 2).

Wintering areas

Wintering areas of Montagu's Harriers tracked in this study were located between northern Senegal and the southern border of Mauritania with Mali (Fig. 1). All birds established in a narrow latitudinal range, but a longer longitudinal one, with some birds breeding in the same colony wintering more than 1,200 km apart. Birds with repeated data on wintering grounds showed a relatively high fidelity to the wintering areas. Centroids of consecutive wintering areas of the same bird ranged from 18 to 93 km (with an average of 53 ± 37 km, which represents ca. 10% of the maximum longitudinal scatter of winter positions for the studied individuals; Table 3).

Individual wintering areas (estimated as the 95% fixed kernel) were relatively large (an average of $12,290 \pm 15,409$ km²). However, great variability was observed between individuals and years. Several of the individuals moved from an area to another during the wintering period,

Table 1 Timing of spring and autumn migrations of adult Montagu's Harriers (*Circus pygargus*) breeding in NE Spain tracked between 2006 and 2008

ID#	Sex	Onset	Duration (days)	End	Distance (km)	Distance/day (km/day)		
Spring migration								
34474	M	13 Mar	29.5	12 Apr	2,883	97.7		
39706	F	26 Mar	38.0	27 Apr	3,315	87.2		
39707	F	13 Mar	27.5	09 Apr	2,657	96.6		
39710	M	16 Mar	17.5	02 Apr	2,880	164.6		
39715	M	13 Mar	23.5	05 Apr	2,916	124.1		
Mean		16 Mar	27.2	11 Apr	2,930	114.0		
SD		5.6	7.6	9.7	239	31.4		
ID#	Sex	Pre-migration onset	Pre-migration duration (days)	Onset	Duration (days)	End	Distance (km)	Distance/day (km/day)
Autumn migration								
34466	F	01 Jul	62	01 Sep				
34474	M	09 Jul	38.7	17 Aug	21.3	07 Sep	2,752	129.2
39706	F	19 Aug	25	07 Sep	25.3	02 Oct	2,855	113.1
39707	F	08 Jul	41	24 Aug	17.0	07 Sep	2,491	146.6
39710	M	27 Jul	29.7	21 Aug	16.3	06 Sep	2,489	152.7
39714	M	07 Jul	52	28 Aug				
39715	M	22 Jul	3	29 Jul	13.5	12 Aug	2,309	171.0
80404	F	– ^a	– ^a	08 Sep	8.0	16 Sep	2,365	295.6
80405	M	– ^a	– ^a	08 Sep	11.0	19 Sep	2,660	241.8
80406	F	23 Jul	44	24 Aug	23.0	16 Sep	2,665	115.9
80407	F	10 Jul	53	30 Aug	8.0	07 Sep	2,508	313.6
Mean		17 Jul	38.7	26 Aug	15.9	10 Sep	2,566	186.6
SD		14.9	17.7	11.8	6.4	13.8	180	77.2

For individuals performing more than one migration (either spring or autumn), values provided represent means (see text)

^a No accurate data were available

which resulted in larger wintering areas, whereas others remained in the same area during the whole wintering season (Table 3). For example, during the 3 years it was tracked, bird #39710 established in the same area when arriving from Europe and, also in the 3 years, it moved westerly to another area and then to a different area from where it started the northwards migration to Europe (with first and last positions separated by more than 450 km in both winters; Table 3).

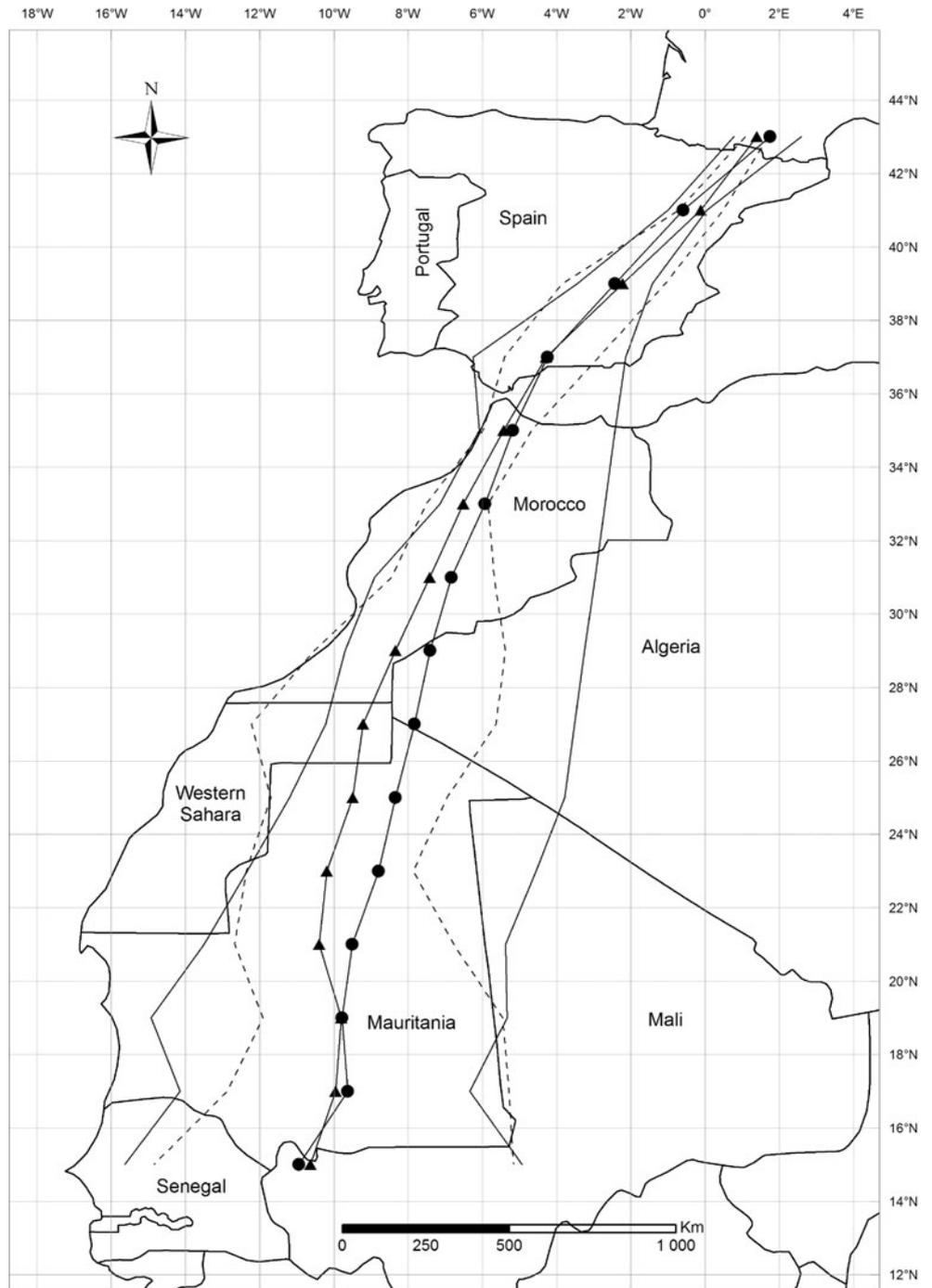
Discussion

For Montagu's Harriers, the spring migration seems not to be a simple reverse autumn migration in terms of routes and timing, as has also been shown in other migratory raptor species (e.g. Alerstam et al. 2006; Klaassen et al. 2010). Overall, Montagu's Harriers tended to follow a slightly more westerly track during spring migration

compared to the autumn track (Fig. 1). This is in contrast with the results previously observed for the European population of Montagu's Harriers, which suggested (at least partially) a loop counter-clockwise migration, with birds crossing to Africa in autumn through the Strait of Gibraltar and returning to the breeding grounds in spring through Italy (Agostini and Logozzo 1997; García and Arroyo 1998). However, the latter studies focused on the European population of the species (not on the tracking of individual harriers), which may conceal individual patterns of migration. Although our birds always travelled across the Gibraltar Strait area, at a larger scale it is possible that more complex patterns of Montagu's Harrier migration arises, as the central Europe population can choose to travel into Africa through Spain or Italy (Trierweiler et al. 2007).

The tendency towards a narrow loop migration pattern observed for Montagu's Harriers in this study has also been recorded in Marsh Harriers (*Circus aeruginosus*) migrating

Fig. 1 Interpolated mean migration routes of adult Montagu's Harriers (*Circus pygargus*) in autumn (filled circle) and spring (filled triangle). For each season, the migration corridor is indicated (autumn solid lines, spring dashed lines). Routes are interpolated every 2° from 43°N to 15°N



between Sweden and western tropical Africa (Klaassen et al. 2010). The study on Marsh Harriers concluded that seasonal differences in the dominant winds along passage areas explained the migration pattern observed, which probably applies to the migration pattern observed in Montagu's Harriers, as migration timing roughly coincides for both species (Limifiana et al. 2007; Strandberg et al. 2008; this study), and they use similar passage areas (Klaassen et al. 2010). However, the greatest longitudinal

differences between autumn and spring for Montagu's Harriers were recorded between 23 and 27°N. If wind is the only force shaping the migratory routes of harriers, we would expect a greater difference at around 20°N, due to easterly winds at this latitude during spring (see Klaassen et al. 2010). Hence, migratory movements in this species are likely to also be considerably affected by other factors, which should be investigated more in depth including the tracking of juvenile birds, since this may provide valuable

Fig. 2 Repeated migratory routes of five adult Montagu's Harriers breeding in eastern Spain. Autumn tracks are indicated with *solid lines* and spring tracks with *dashed lines*. The number above each map indicates the ID number of the PTT on the bird (see Table 1)

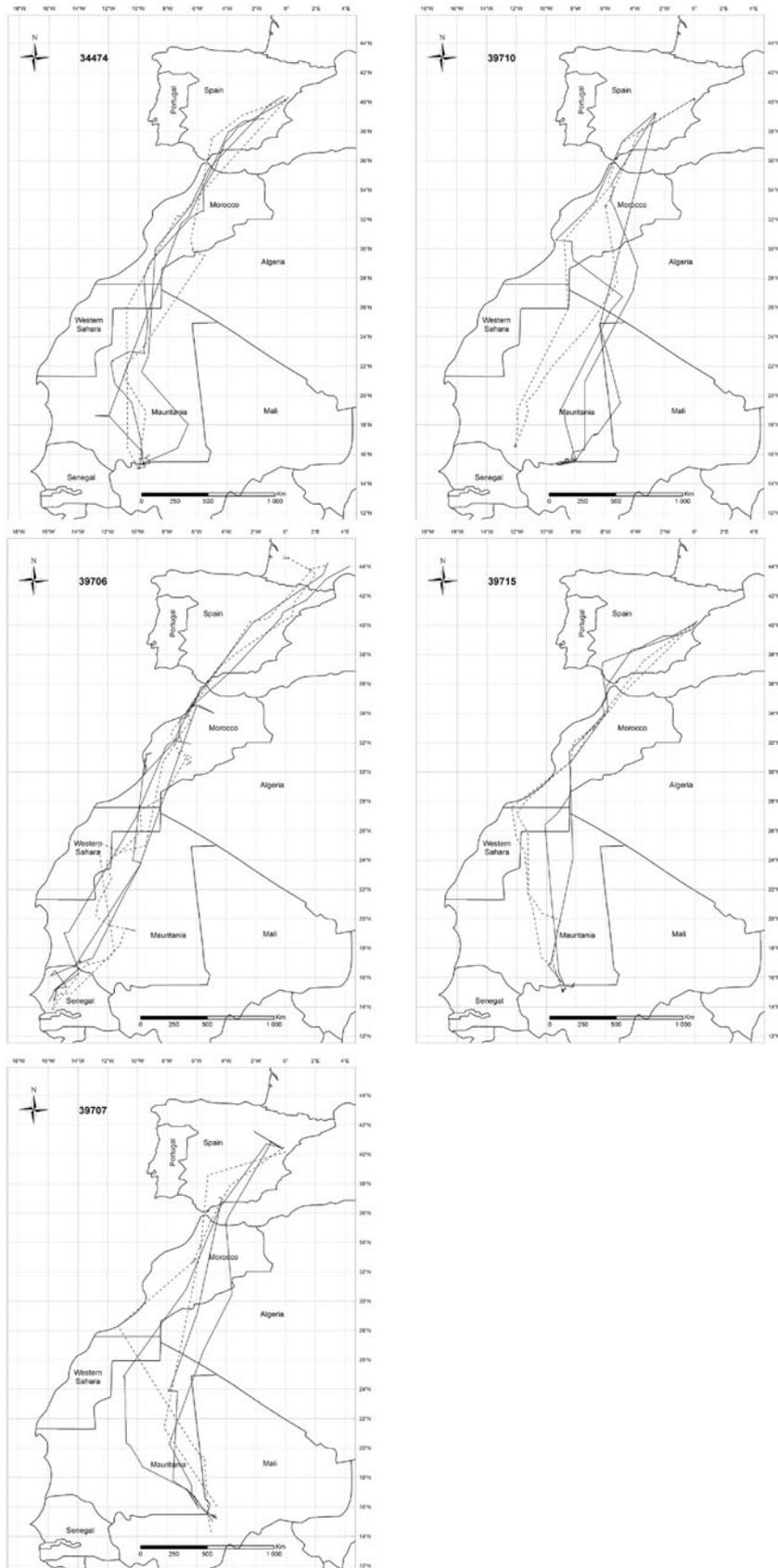


Table 2 ANOVA table of the General Linear Model linking migration longitude with migration latitude, season, year and individual tracked (ID)

Source	Type III sum of squares	df	Mean square	F	P value
Response variable: longitude					
Corrected model	3,581.281	171	20.943	18.232	<0.001
Intercept	6,659.572	1	6,659.572	5,797.509	<0.001
Latitude	1,284.493	14	91.749	79.873	<0.001
Season	12.565	1	12.565	10.939	0.001
ID	385.125	8	48.141	41.909	<0.001
Year	2.949	2	1.475	1.284	0.279
Latitude × season	11.304	14	0.807	0.703	0.770
Latitude × ID	349.026	92	3.794	3.303	<0.001
Latitude × year	25.215	27	0.934	0.813	0.731
Season × ID	52.218	4	13.055	11.365	<0.001
Season × year	0.850	1	0.850	0.740	0.391
ID × year	57.529	8	7.191	6.260	<0.001
Error	211.360	184	1.149		
Total	22,478.220	356			
Corrected total	3,792.640	355			

Significance of parameters main effects and all 2-way interactions are shown
 $R^2 = 0.944$ (Adj $R^2 = 0.892$)

Table 3 Characteristics of wintering areas in tropical western Africa of adult Montagu’s Harriers tracked between 2006 and 2008

ID#	Size of wintering areas (km ²) ^a	Distance between the centre of consecutive wintering sites (km)	Distance between arrival in autumn and next spring departure (km) ^a
34474	1,163.1 ± 1,590.4	36.25	27.65 ± 37.79
39706	6,455.3 ± 7,926.8	92.67	246.13 ± 258.36
39707	15,282.6 ± 12,501.2	93.44	128.23 ± 4.84
39710	37,508.1 ± 7,453.9	18.09	451.32 ± 0.93
39715	1,040.4 ± 1,061.1	25.11	35.84 ± 4.42
Mean ± SD	12,289.9 ± 15,409.1	53.11 ± 37.03	177.83 ± 187.82

Size of wintering areas are 95% fixed kernels

^a Mean values for winters 2006/2007 and 2007/2008

information on navigation and orientation mechanisms used by the species during migration. This will help in clarifying if adult and juvenile birds use different orientation and navigation mechanisms to reach their wintering or breeding areas, and how both are affected by general wind patterns (Mouritsen 2003).

Previous satellite tracking studies of long-distance migratory birds have shown evidence of both spring migration lasting shorter than autumn migration (e.g. Fuller et al. 1998 and McGrady et al. 2002 for Peregrine Falcon *Falco peregrinus*, Alerstam et al. 2006 for Osprey *Pandion haliaetus*), and vice versa (e.g. Fuller et al. 1998 for Swainson’s Hawk *Buteo swainsoni*, and Shamoun-Baranes et al. 2003 for White Stork *Ciconia ciconia*). For other species like Marsh Harrier, no differences between spring

and autumn migration in terms of duration have been found (Strandberg et al. 2008). In our study, Montagu’s Harriers spent more time completing the spring migration than the autumn migration, but the variability in the timing of the autumn migration was higher. This may have several consequences for individual fitness. On the one hand, the harriers’ departure to the wintering sites will depend on their performance during the breeding season. Birds that fail to reproduce or those that breed earlier (those in better condition on arrival at the breeding grounds) will be ready to depart earlier, while successful breeders that nested later will be among the last to depart. Both pre-migration and migration duration will be then affected by breeding performance, with late breeders having less time to prepare for migration. This probably increases the risk of mortality

during the migration, and relegates them to poorer wintering sites (Gunnarsson et al. 2005). Consequently, a higher variability in autumn migration and pre-migration is actually to be expected. On the other hand, despite differences in habitat quality during the wintering season, when breeding habitat is saturated or the worst territories are of much lower value than the rest, competition would lead to the majority of the population departing within a fairly short interval, to be able to secure an adequate breeding territory. Therefore, a smaller variability in the timing of spring migration is not surprising either. Regarding migration timing, the shortest time invested to complete the autumn migration may be an indication that securing a better site to spend the winter may be as important as choosing a good breeding site, since it may have carry-over effects on the following breeding season (e.g. Norris 2005).

No apparent stopovers along the route were observed for harriers in this study. Since Montagu's Harriers can find their food in a wide variety of habitats, birds do not need to make long stopovers in fixed areas. In contrast to autumn, pre-migratory movements were not observed before the spring migration, although movements of several individuals were observed within the wintering areas. These movements may be due to changes in food availability throughout the wintering season, forcing birds to move to search for food (Trierweiler and Koks 2009). This may explain why birds do not perform pre-migratory movements prior to the spring migration: it is not necessary for birds to move to other areas before departing in spring because they are free to move over larger distances during the whole winter in response to food availability (during the breeding season, their movements are restricted to areas close to their nesting site).

The results presented in this study suggest a complex pattern in migration strategies of Montagu's Harriers. On the one hand, the existence of pre-migratory and even post-migratory movements may affect the total time spent by harriers in completing the autumn and spring migrations, and both may have important implications for future breeding of the individuals. On the other hand, it seems that adult European Montagu's Harriers arrive at their wintering areas (which seem to be roughly the same every year) following different paths and crossing a large number of countries (see also Trierweiler et al. 2007; Trierweiler and Koks 2009). Hence, different conservation problems for the species may arise during the breeding and wintering seasons, as well as during the migration journeys (Newton 2004). In fact, wintering populations of several migrating raptors species using the European–African flyway have decreased in numbers in recent years (Thiollay 2006). In the face of climate change, it is very important to determine the effect of wind on migratory journeys of the species, since rapid changes due to climate change may affect the

dominating winds and, thus, modify migration patterns. Also, future research on conservation of this species should be directed to assess the importance of passage and wintering areas, as well as linking wintering and breeding ecology.

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