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Mapping the migratory routes and wintering areas of Lesser Kestrels *Falco naumanni*: new insights from satellite telemetry

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Recent improvements in satellite tracking, such as the miniaturization of transmitters, have enabled the study of movements of an increasing number of bird species. The Lesser Kestrel *Falco naumanni* has been the subject of numerous studies but detailed information on its migration routes and wintering areas is still lacking. Here, we provide a detailed description of migration routes, timing of migration and wintering areas of Lesser Kestrels. Five adults fitted with satellite transmitters in southeastern Spain were tracked during autumn and spring migration journeys and on their wintering grounds. The overall migration duration was longer in spring than in autumn, although birds also showed longer stopovers in this season and hence the number of travelling days was lower. Lesser Kestrels covered longer daily distances in spring due to a higher frequency of nocturnal migration, rather than differences in flight speed, which did not differ between seasons. Wintering areas of Lesser Kestrels from the same breeding colony were widely spaced throughout the western Sahel along the borders of Mauritania, Mali and Senegal, approximately 2800 km from their breeding sites. The autumn migration duration of Lesser Kestrels derived from recent studies using geolocators was underestimated compared with that recorded by satellite telemetry. Given the current rapid habitat loss in the Sahel, a better understanding of migratory routes and wintering areas of other populations of this species would be important to assess its influence on population trends.

Keywords: migration strategies, nocturnal migration, Sahel, stopover, time-budget.

Knowledge of complete life cycles of migratory birds is necessary for effective management and conservation actions (Martin *et al.* 2007, Newton 2008). Numbers of most Afro-Palaearctic migratory birds have been declining over the last few decades (Sanderson *et al.* 2006) and the causes of these declines may lie outside the breeding ranges. For example, declines in some populations of raptors in West Africa have been attributed to land-use changes, pesticide use and illegal hunting (Thiollay 2006). However, there is usually limited knowledge on the ecology and conservation problems of these species on their wintering grounds and passage areas, due largely to the difficulties in tracking migratory species over long distances.

The Lesser Kestrel *Falco naumanni* is a small migratory raptor distributed across the Palaearctic region, with populations breeding from the Iberian Peninsula to China (Negro 1997). It is thought that western European populations of the species winter in West Africa (Rodríguez *et al.* 2009, Catry *et al.* 2011), whereas those from eastern Europe, the Middle East and Asia winter in eastern

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and southern Africa (Negro 1997, Rodríguez *et al.* 2011). The current European population is estimated at 25 000–42 000 pairs, with half of these breeding in Spain. Populations have declined during past decades, the main cause suggested as being habitat loss at both their breeding and their wintering grounds as a consequence of agricultural intensification, urbanization and intensive pasture management (BirdLife International 2011). Environmental conditions in the wintering areas may influence population trends of the species, for example affecting juvenile survival (Mihoub *et al.* 2010). Populations have recovered in recent years (particularly in southwestern Europe) following the implementation of conservation measures (Íñigo & Barov 2010) and therefore the species has been recently listed as of 'Least Concern' globally (Birdlife International 2011). However, it is also listed under Annex I of the European Bird's Directive (2009/147/CE) and hence conservation actions within its entire distribution range should be undertaken. A detailed knowledge of the areas used throughout the year is of importance in developing a conservation strategy, as well as fulfilling the European Directives on biodiversity conservation.

In recent years, knowledge of migration and wintering of the Lesser Kestrel has been improved greatly using geolocators (Rodríguez *et al.* 2009, Catry *et al.* 2011). However, this technique may result in large errors (up to a few hundred kilometres) in the estimation of a bird's location (Phillips *et al.* 2004, Catry *et al.* 2011). Moreover, it is impossible to map the exact migration routes of this species using geolocators, as these movements coincide with the equinoxes (especially in autumn), which inhibit latitudinal positioning (Rodríguez *et al.* 2009, Catry *et al.* 2011). Recent developments in satellite tracking have provided new insights into the study of migration ecology of medium-sized birds, including the identification of wintering areas and migration routes (e.g. Limiñana *et al.* 2007, 2012, Gill *et al.* 2009, López-López *et al.* 2009, 2010, Strandberg *et al.* 2009b, Mellone *et al.* 2011b). Hence, this technology can provide valuable information that otherwise would be very difficult to obtain, due to the difficulties of tracking long-distance migratory birds. Here, we use satellite telemetry to provide more accurate information on the migratory routes of Lesser Kestrels than those previously obtained using geolocators, and to generate information on wintering areas, migration timing and travel distances.

METHODS

Tagging and satellite data

Six adult Lesser Kestrels (three males and three females) were captured at 'Los Alhorines' (Villena, southeastern Spain). This Lesser Kestrel population was established in the study area after a reintroduction project carried out between 1997 and 2002 (Alberdi 2006). In 2000, three pairs bred for the first time in our study area and currently the number of breeding pairs is around 50–60. All pairs breed naturally in the roofs of abandoned or semi-abandoned farmhouses. The number of farmhouses occupied by breeding Lesser Kestrels varies between years, with the number of breeding pairs per house ranging between 1 and 11 (Romero 2011).

Birds were trapped from 16 to 23 June 2010 next to nesting houses during the late incubation stage or when they had small nestlings, using dho-gaza nets and a stuffed Eagle Owl *Bubo bubo* as a decoy. Birds were sexed (based on the pattern of colours of the plumage), weighed and ringed, and a 5-g solar-powered PTT-100 satellite transmitter (Microwave Telemetry Inc., Columbia, MD, USA) was fixed as a backpack using a Teflon harness (Limiñana *et al.* 2007). Birds were released a maximum of 40 min after capture. Satellite transmitters were programmed with an 8-h ON/15-h OFF duty cycle. Tagged Lesser Kestrels were named using the ID number (#ID) of the PTT deployed (Table 1). Birds' locations were obtained using the ARGOS system and managed using the Satellite Tracking and Analysis Tool (STAT, Coyne & Godley 2005). Locations were retrieved in geographical coordinates and converted to UTM coordinates for further calculations.

Migration routes

The satellite-tracking Argos system assigns a measure of reliability known as location class (LC) to each position estimate (Argos 2011). LCs 3, 2 and 1 have nominal errors up to 1.5 km, for LC 0 accuracy is > 1.5 km, whereas for LCs A and B no accuracy can be estimated (Argos 2011). The recorded positions belonging to location classes 3, 2, 1 and 0 were always used in the analyses, as these are the most reliable (e.g. Limiñana *et al.* 2007, Soutullo *et al.* 2007). We also used LCs A and B when they were reliable according to normal travel rates (speed and direction; see Strandberg *et al.* 2009b, López-López *et al.* 2010, Trierweiler 2010). We

Table 1. Migration timing and distances of five satellite-tracked Lesser Kestrels breeding in southeastern Spain (sex is indicated in parentheses together with ID#). For flight speed, only travelling segments are considered, values are mean ± sd and range in parentheses. Migration distance refers to the sum of migration segment length (one point per day). Distance/day is the migration distance divided by the number of travelling days (given in parentheses), i.e. excluding days spent in stopovers. Size of wintering grounds (95% fixed kernel) is also indicated.

		Autumn migration						Spring migration						Wintering grounds
Bird ID#	Weight (g)	Migration onset	Migration duration (days)	Migration end	Migration distance (km)	Distance/day (km/day)	Fight speed (km/h)	Migration onset	Migration duration (days)	Migration end	Migration distance (km)	Distance/day (km/day)	Fight speed (km/h)	Size (km^2)
51899 (M)	112	21/09/2010	14	5/10/2010	3606	277.4 (13)	22.3 ± 14 (6.8–51.8)	17/03/2011	14	31/03/2011	3123	390.4 (8)	34.5 ± 26.4 (5.9–82.7)	210
51900 (M)	128	11/10/2010	12	23/10/2010	3536	294.7 (12)	26.4 ± 13.4 (6.1–49.9)	5/02/2011	17	22/02/2011	3253	361.4 (9)	38.9 ± 18.5 (12.9–73.2)	8267
51901 (M)	116	7/10/2010	15	22/10/2010	3396	261.2 (13)	34 ± 14.5 (11.4–59.3)	28/02/2011	33	2/04/2011	3021	431.6 (7)	33.7 ± 22.1 (11.1–59.6)	9373
51902 (F)	160	18/09/2010	11	29/09/2010	2985	331.7 (9)	26.5 ± 13.4 (5.1–51.6)	22/02/2011	34*	28/03/2011*	3523*	220.2 (16)*	26.6 ± 16.2 (6.4–48.4)	830
51903 (F)	127	24/10/2010	12	5/11/2010	3244	294.9 (11)	27.2 ± 17.7 (5.6–66.5)	18/02/2011	–	–	–	–	34.7 ± 14.2 (13.3–52.9)	43 856
Mean		4/10/2010	12.8	17/10/2010	3353	292 (12)	26.6	23/02/2011	24.5	21/03/2011	3230	351 (10)	33.9	
sd		14.9	1.6	14.9	248	26.2	14.7	14.6	10.5	18.4	217	91.8	19.3	

*This bird stopped transmitting on 27/03/2011 at 72 km before reaching the breeding area and was found dead in early April at the breeding grounds. Therefore, we estimated migration end (from flight speed), and migration distance (assuming a straight segment between last known position and place where it bred the past year).

excluded from the analyses those locations separated by less than an hour from the previous one to avoid biases associated with the non-independence of locations (Limiñana *et al.* 2007). When more than one location was available within a given hour, we used that of the highest quality.

To identify the onset and the end of autumn and spring migrations, we used standardized methods; migration onset was defined as an abrupt change in movement patterns before and after the migration onset (Limiñana *et al.* 2008) and migration end was defined as the stabilization in the distance travelled from tagging site (autumn migration) or wintering areas (spring migration; Limiñana *et al.* 2007). Locations obtained between these two dates, for every bird and season, were plotted in ARCVIEW 3.2 and used for subsequent analyses. We also inspected the data for stopovers during migrations, which were identified when a bird moved < 20 km for at least 1 day showing non-directional movements. For both migratory periods we calculated (1) the migration duration; (2) the distance covered during migration, following the procedure described in Strandberg *et al.* (2008), selecting one location per day during the migration period, excluding stopovers, to avoid biases associated with the different number of locations per day among individuals, and adding up the length of these resulting segments; (3) the average distance covered in a day as migration distance/number of travelling days (i.e. excluding stopovers); and (4) the distance covered hourly, i.e. flight speed, considering only locations obtained within < 4 h of difference following Limiñana *et al.* (2007) and using only flight speed values higher than 5 km/h, as these segments were considered to represent birds in active flight (Strandberg *et al.* 2009b, López-López *et al.* 2010).

To analyse migratory behaviour in relation to time of day (time budget), we also used intervals between locations ('segments') shorter than 4 h, which were classified as occurring during day or night according to the status at median time (nocturnal segments were those for which at least half the time length occurred after sunset or before sunrise, whereas the remaining segments were considered to be diurnal; López-López *et al.* 2010). The exact time of sunrise and sunset (when the sun is 0.833° below the horizon) for the midpoint of each segment were calculated using the Sunrise/Sunset spreadsheet downloaded at http://www.ecy.wa.gov/programs/eap/models.html, which is based on the calculation procedure by the National

Oceanic and Atmospheric Administration (NOAA). Also, every segment was classified as 'travelling' or 'stationary', according to the above-mentioned threshold of 5 km/h (Strandberg *et al.* 2009b, López-López *et al.* 2010). We compared the proportion of travelling and stationary segments during day and night between seasons using a contingency table (López-López *et al.* 2010). Finally, we assessed differences in flight speed between night and day, and between autumn and spring (and the interaction of both variables), considering only the travelling segments, using a generalized linear mixed model with flight speed as dependent variable, 'day/night' and 'autumn/spring' as fixed factors, and 'individual' as a random factor in the model, using a normal error distribution. All statistical analyses were carried out in SPSS v.15 (SPSS Inc., Chicago, IL, USA) and statistical significance was accepted at $P < 0.05$.

Wintering grounds

To identify the individual wintering areas and their extent, we calculated the 95% fixed kernel encompassing the locations obtained for every individual from the end of the autumn migration to the onset of the spring migration, considering only LCs 3, 2 and 1 (Limiñana *et al.* 2011, Mellone *et al.* 2011c) and using the Animal Movement Extension for ARCVIEW 3.2 to compute the kernels (Hooge & Eichenlaub 1997). To calculate the actual size of individual home-ranges, we converted the kernel polygons in geographical coordinates to an equal-area cylindrical projection using the Projector! extension for ARCVIEW 3.2.

RESULTS

Migration routes and timing

In autumn, information on migration was obtained for five of the six tagged Lesser Kestrels. A female bird (not shown in Table 1) stopped transmitting in early August before the onset of autumn migration. The tagged birds began to migrate between late September and late October (mean date of autumn migration onset = 4 October; Table 1). Birds crossed the Mediterranean on a broad front, travelling around 180 km over water to reach the northern coast of Africa (Fig. 1). Kestrels arrived at their wintering grounds, which were about 2800 km from their breeding grounds, after covering between 3000 and 3600 km in 11–15 days (Table 1). Individual average daily distances ranged between 261 and 332 km, and mean flight speed was around 27 km/h, with a maximum of 67 km/h recorded. Observed stopover information was as follows: #51899 stopped for 1 day in southern Mauritania (16.2°N), #51901 for 2 days in southern Spain (37.3°N), #51902 for 2 days in northern Morocco (33.5°N) and #51903 stayed in a small area within the Sahara Desert in Mauritania (20.4°N) for a day (Fig. 1).

In spring, only four birds reached the breeding grounds, as a female stopped transmitting in northern Morocco (#51903; Fig. 1). Another female (#51902) was found dead several days after reaching the breeding area, although its last location was recorded 72 km away (see Table 1); according to the observed flight speed, we considered that this bird should have arrived at the breeding area the day after that at which the last location was recorded. Lesser Kestrels left their wintering grounds between early February and mid-March (mean date of spring migration onset = 23 February; Table 1). In this season, birds crossed the Mediterranean mainly by the Strait of Gibraltar, and covered between 3000 and 3500 km in 14–34 days (Table 1). Daily distances ranged between 220 and 431 km, achieving a mean flight speed of approximately 34 km/h (with a maximum of 83 km/h; Table 1). In spring, all birds undertook stopovers of different duration (all longer than in autumn) in northern Morocco, before crossing the Mediterranean (between 34.1 and 35.7°N). The longest stopover was performed by #51901, which stayed for 26 days (between 5 and 30 March) in this area. #51903 also stopped for 2 days in Mauritania (22.6°N), near the place it used as a stopover in autumn (Fig. 1) and #51902 performed the shortest stopover during this season, stopping for 1 day in the Sahara (Fig. 1). In these two cases it was impossible to exclude the possibility that birds may have stopped due to unfavourable weather conditions as opposed to taking advantage of foraging opportunities (Strandberg *et al.* 2010).

To analyse time budgets, we used a total of 165 segments in autumn and 99 in spring (Fig. 2). In autumn, Lesser Kestrels migrated mainly during the day, although some travelling segments also occurred at night (Fig. 2) and most migratory movements occurred between 09:00 and 15:00 h (local time; Fig. 3), although the maximum recorded speeds were recorded at night (Fig. 3). In

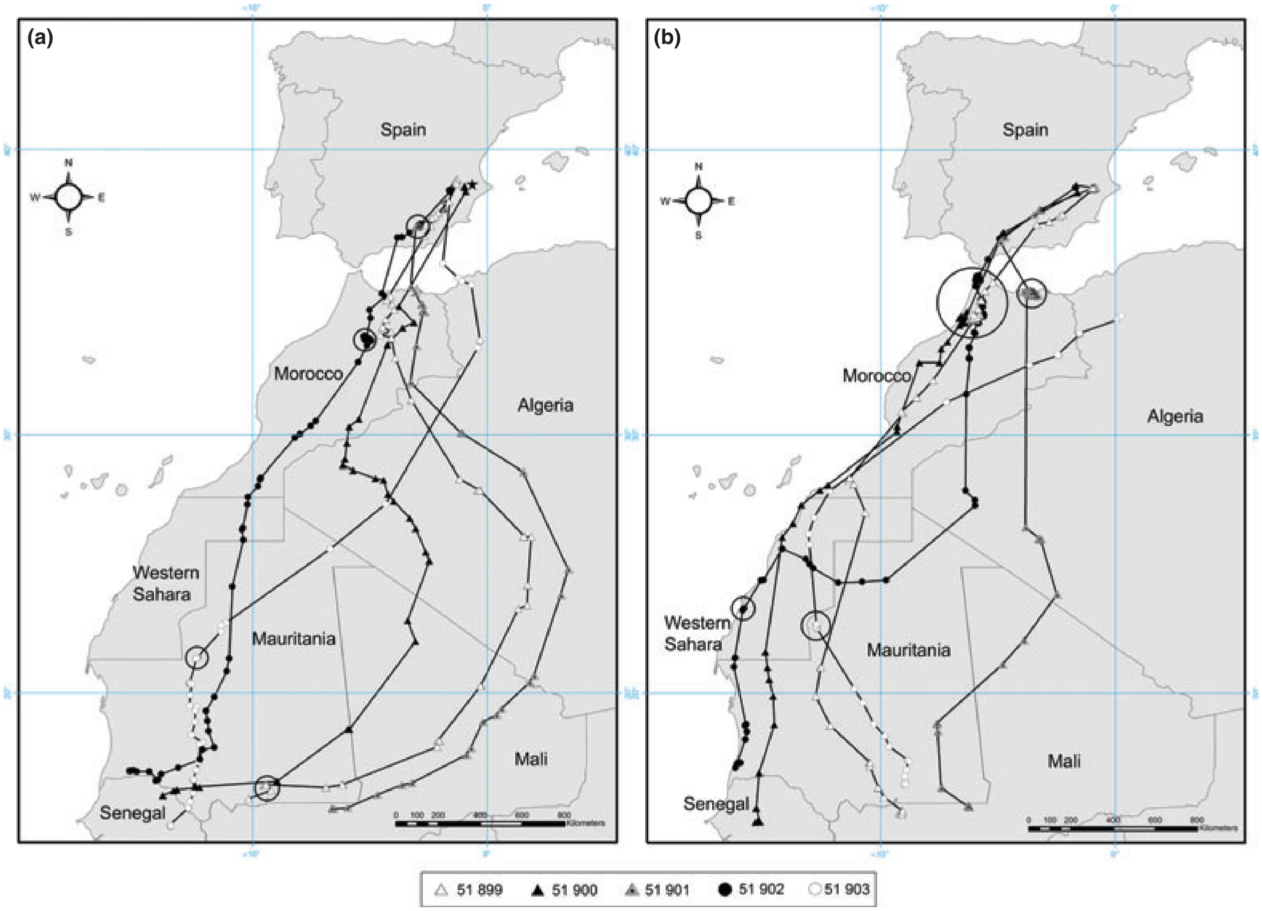

Figure 1. Autumn (a) and spring (b) migration routes of five adult Lesser Kestrels tracked using satellite telemetry between their breeding colonies in Villena (eastern Spain) and sub-Saharan Africa (Mercator projection). The tagging site is indicated with a star (in panel a) and stopover sites are shown within circles.

spring, Lesser Kestrels travelled more consistently at night, with the proportion of nocturnal travelling segments being significantly higher than in autumn ($\chi^2_1 = 6.15$, $P = 0.013$), whereas the proportion of diurnal travelling segments was not significantly different between seasons ($\chi^2_1 = 2.95$, $P = 0.09$). Although flight speed showed a tendency to be higher at night, especially during spring (Fig. 3), this pattern was not significant ($F_{1,153} = 2.627$, $P = 0.107$). Similarly, seasonal differences in flight speed were not significant ($F_{1,153} = 2.358$, $P = 0.127$), nor was the interaction between day/night and spring/autumn ($F_{1,153} = 2.193$, $P = 0.141$).

Wintering grounds

All tracked birds wintered in the western Sahel region, along the borders of Mauritania with Mali and Senegal (Fig. 4), where they arrived between late September and early November (mean date = 17 October; Table 1). For three birds (#51899, #51900 and #51902), all wintering locations were recorded only within a single country (Mali, Senegal and Mauritania, respectively). Bird #51901 moved between Mauritania and Mali, whereas for #51903 most of the locations were recorded in Mauritania, although several locations also occurred in Senegal. Although birds wintered in a narrow latitudinal belt (from 14 to 17°N), there was a large longitudinal variation in wintering areas of Lesser Kestrels (from 4 to 16°W). The size of individual wintering areas (95% fixed kernel) ranged from 210 to 43 856 km^2 (Table 1).

DISCUSSION

Knowledge of the complete annual cycle of the Lesser Kestrel has been recently improved using data from geolocators (Rodríguez *et al.* 2009, Catry *et al.* 2011) but the exact migration routes of individual birds cannot be established using this technology. The Lesser Kestrel is one of the few species that has been tracked using both geolocators and satellite transmitters (see also Phillips *et al.* 2004) and thus results obtained with these two technologies can be compared to evaluate their usefulness in a wider context. Geolocators do not provide adequate data to estimate migration parameters in detail, e.g. flight speed, time budget or individual variation of routes. Therefore, the only comparable parameters here are the overall migration duration (departure and arrival dates) and daily travel distances.

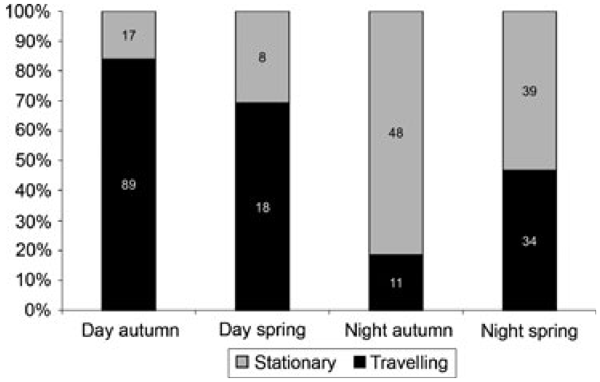

Figure 2. Time budget of Lesser Kestrels during autumn and spring migrations. Only segments between 1 and 4 h were used, which were classified as travelling or stationary (using a threshold of 5 km/h; see text). Numbers on bars indicate the sample size of each category.

Geolocators may have underestimated the overall duration of the migratory journey of Lesser Kestrels, especially in autumn (Fig. 5). For this season, we obtained an average duration of 12.8 days (sd = 1.6, *n* = 5), whereas birds tracked in previous studies using geolocators and covering roughly the same migration distance, only took 5 days from southwestern Spain (sd = 1, *n* = 3; Rodríguez *et al.* 2009) and 4.8 days from southern

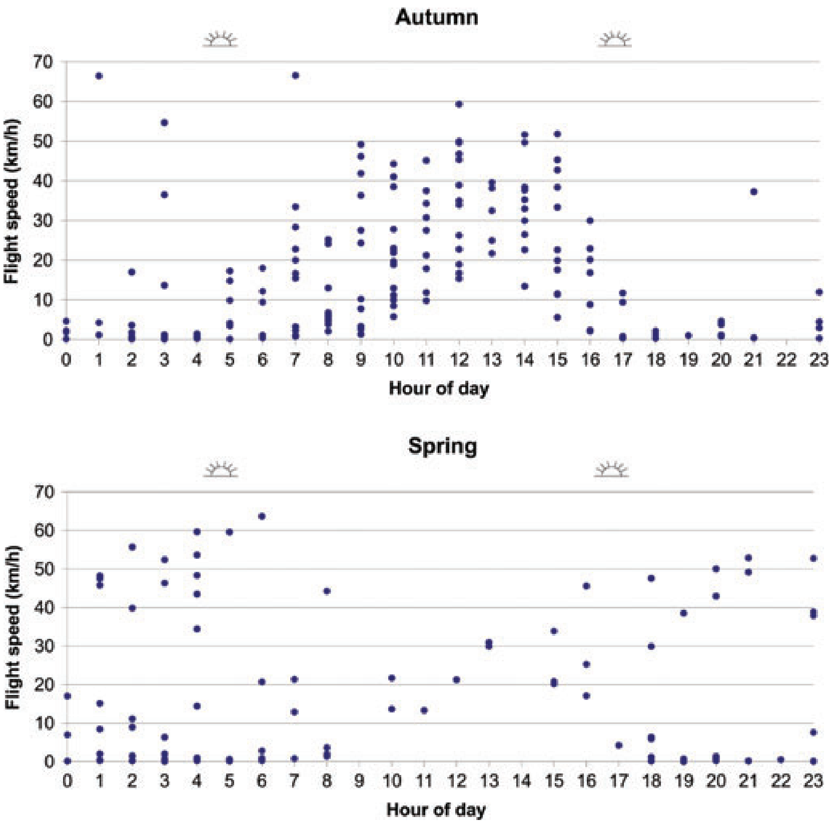

Figure 3. Autumn and spring flight speeds according to hour of day (local time) of five Lesser Kestrels tracked by satellite telemetry using migration segments between 1 and 4 h. Local time was calculated by correcting GMT times for the longitudinal time difference. Data from the five birds are pooled.

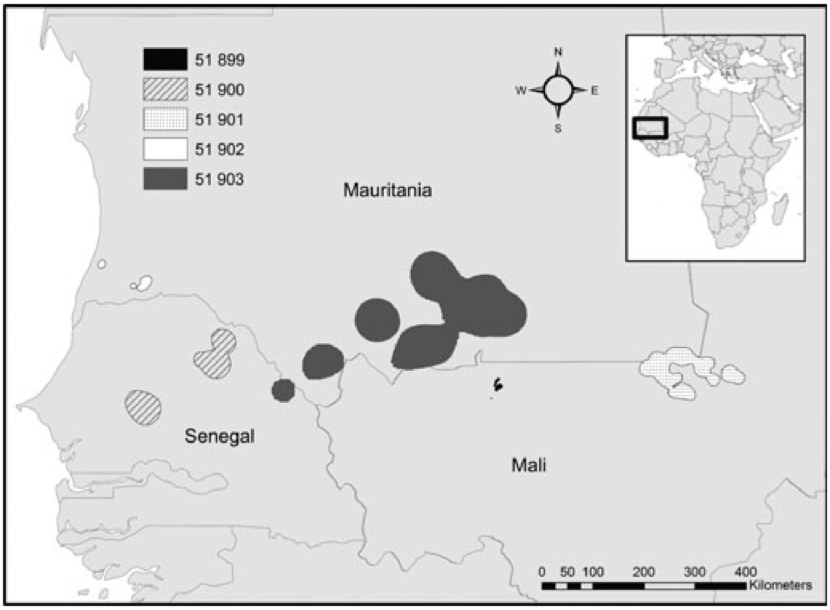

Figure 4. Wintering grounds (95% fixed kernels) of five adult Lesser Kestrels in the Sahel tracked by satellite telemetry.

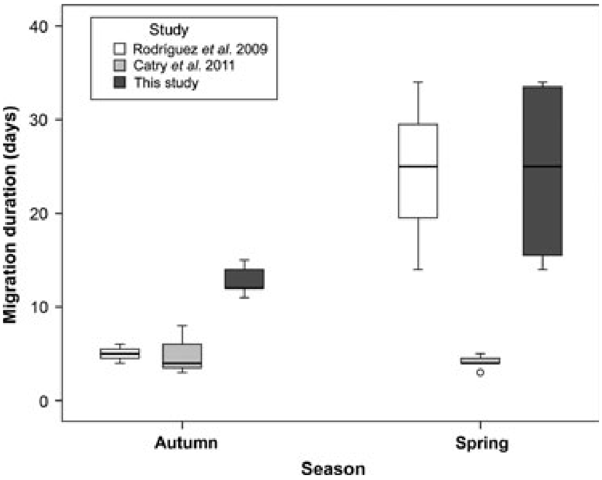

Figure 5. Box plot of Lesser Kestrel autumn and spring migration duration. Data from Rodríguez *et al.* (2009) and Catry *et al.* (2011) come from Lesser Kestrels tracked with geolocators, whereas our study was carried out with satellite transmitters. Error bars represent 95% confidence intervals of the mean.

Portugal (sd = 2.2, n = 4; Catry *et al.* 2011). However, for spring migration, whereas Catry *et al.* (2011) reported a mean duration of 4.1 days for Portuguese Lesser Kestrels (sd = 0.7, n = 7), the duration recorded for southwestern Spanish birds was 24.3 days (sd = 10, n = 3; Rodríguez *et al.* 2009), which is more in line with our results (24.5 days, sd = 10.5, n = 4; Fig. 5). Lesser Kestrel autumn migration overlaps with the equinoxes, thus preventing the estimation of latitude using geolocators. Therefore, both previous studies (Rodríguez *et al.* 2009, Catry *et al.* 2011) estimated the departure and arrival dates relying only upon longitude data, which may have caused consistent errors, especially in autumn. It seems unlikely that the overall shorter duration obtained with geolocators compared with satellite transmitters (both in autumn and in spring) was due to different migration strategies among populations, as there were also large differences in spring migration duration between the nearby populations of southern Portugal and southwestern Spain, both tracked with geolocators. Moreover, there were more differences in autumn migration onset than in spring migration onset among populations (see also below; Rodríguez *et al.* 2009, Catry *et al.* 2011), which again may be due to the overlap of this period with the autumn equinox. Therefore, we suggest that geolocator data should be treated with more caution when estimating migration onset and end using only longitude data when the longitudinal range is not as wide as that in the route between the Iberian Peninsula and western Africa.

Lesser Kestrels tracked in this study showed different migration strategies in autumn and spring. In autumn, all tracked birds crossed the

Mediterranean on a broad front, crossing directly from the southeastern coast of Spain to northern Africa, with no birds crossing to Africa through the Gibraltar Strait area, and thus flying around 180 km over water, a common strategy in species that use powered flapping flight during migration (Kerlinger 1989). In spring, however, birds crossed to the Iberian Peninsula through the Strait of Gibraltar, due perhaps to the more westerly individual migration tracks in spring compared with those followed in autumn (Fig. 1). This clockwise loop-migration has also been observed in other raptor species migrating between Europe and western Africa, such as Marsh Harrier *Circus aeruginosus* (Strandberg *et al.* 2008), Montagu's Harrier *C. pygargus* (Limiñana *et al.* 2012) and Egyptian Vulture *Neophron pernocpterus* (García-Ripollés *et al.* 2010) and may be due to differences in dominant winds between seasons (Klaassen *et al.* 2010). These westerly spring tracks have also been described for Portuguese Lesser Kestrels (Catry *et al.* 2011). Both in autumn and in spring, Lesser Kestrels appeared to avoid the borders between Mali, Mauritania and Algeria, where sandstorms are common, making it a very hazardous area for migratory birds (Strandberg *et al.* 2010). Great individual variability in migration onset was observed in both autumn and spring, which resulted also in a great variability in migration end (Table 1). Dates of migration onset are in agreement with previous studies on migration timing of Lesser Kestrels breeding in the Iberian Peninsula, although more variability among study sites was found in autumn than in spring (Román *et al.* 2008, Rodríguez *et al.* 2009, Catry *et al.* 2011). This may be due to pressure for an early arrival to nesting areas to ensure a good breeding site (Kokko 1999), which forces the birds to begin the migration at roughly the same time.

Although the overall migration duration was longer in spring than in autumn, Lesser Kestrels took less time in spring (as travelling days) to cover roughly the same migration distance, as most of the migration days in spring were spent in stopovers (Fig. 1). This resulted in a longer distance travelled per day (Table 1). In contrast, flight speed was not significantly different between seasons, and hence the higher mean daily distance covered in spring is the result of the higher number of travelling spells during the night. Alerstam (2009) suggested that nocturnal and diurnal migration are combined to minimize the time spent to cross an ecological barrier, in our case the Sahara desert. The seasonal differences that we found in this respect, with birds more likely to fly during night in spring, could reflect a strategy of time minimization to ensure a good breeding site (Kokko 1999). Also, if wind directions are less favourable during spring (Shamoun-Baranes *et al.* 2003), it is possible that Lesser Kestrels spent more hours travelling at night to take advantage of the weaker winds and lower air turbulence that is experienced during spring. This could explain the observation that flight speeds in spring were slightly higher at night (Fig. 3). However, birds crossing the Sahara undertook stopovers of up to 26 days. It could be that Lesser Kestrels crossed the desert quickly to reach a good stopover site in northern Africa, but it is unlikely that intraspecific competition takes place during this stage of the life cycle, as the species forages in large groups during stopovers and pre-migration (Olea *et al.* 2004, Premuda *et al.* 2004). Lesser Kestrels could have taken advantage of these stopovers to replenish their energy stores before breeding, as given the lower latitude, birds might have found better feeding resources in Morocco than they could have found in Spain at the same date.

Analysis of the time budget gives a rather different picture to other long-distance migrating falcons with similar morphological characteristics such as Hobby *Falco subbuteo* (Strandberg *et al.* 2009b) and Eleonora's Falcon *F. eleonorae* (López-López *et al.* 2010). These two species almost never stop during the day when migrating across an ecological barrier like the Sahara, and Eleonora's Falcon migrated consistently at night. Instead, Lesser Kestrels interrupted migration during the day more frequently than those species, and migrated at night to a much lesser extent than Eleonora's Falcon, even during spring, when nocturnal migration was more frequent. This pattern of activity resulted in a lower daily distance in autumn (292 km/day; Table 1) compared with the two previous species during the same season in the desert (approximately 400 km/day; Strandberg *et al.* 2009b, López-López *et al.* 2010), being more similar to the typical autumn daily distance of soaring migrants observed wintering in the Sahel (around 200–250 km/day), such as Short-toed Eagle *Circaetus gallicus* (Pavón *et al.* 2010), Egyptian Vulture (García-Ripollés *et al.* 2010), Marsh Harrier (Strandberg *et al.* 2008) and Montagu's Harrier (Limiñana *et al.* 2007, 2012). Therefore, besides morphological characteristics, probably the overall migration distance is one of the main determinants of the daily flight range, as Eleonora's Falcon and Hobby, being trans-equatorial migrants, might be more time-selected (see also Alerstam 2003, Strandberg *et al.* 2009a, Klaassen *et al.* 2012). On the other hand, Lesser Kestrels can cover greater daily distances than soaring migrants because they are able to fly also during the night; for example, #51903 performed long flights (probably non-stop) of 1626 km in autumn and 1240 km in spring in approximately 2 days (in both cases), which supposed travelling rates of 852 and 629 km/day in autumn and spring, respectively.

During winter, all tracked Lesser Kestrels settled within a small latitudinal belt, approximately 2800 km from their breeding areas. However, individual wintering areas were distributed over a wider range of longitudes and no overlap between them was observed, individuals breeding in the same colony being separated by nearly 1200 km during the winter. This distribution may reflect, at least partially, the distribution of locusts during this season (Mullié 2009, Catry *et al.* 2011), as the species feeds almost exclusively on locusts and grasshoppers during the winter (Ferguson-Lees & Christie 2001). This source of food is very important for several trans-Saharan migratory species during the winter in the Sahel, as well as for other resident species (Mullié 2009). Only two of the tracked birds eventually settled in Senegal, one of the most important countries for wintering Lesser Kestrels from western Europe (Rodríguez *et al.* 2009, Catry *et al.* 2011); this may indicate that high densities of wintering Lesser Kestrels may also be found in other Sahelian regions. During winter, only two of the birds moved over large areas among several staging sites (#51900 and #51903; see also Catry *et al.* 2011). The overall wintering area identified for Lesser Kestrels is also used by other trans-Saharan migratory raptors such as Short-toed Eagle (Pavón *et al.* 2010, Mellone *et al.* 2011a), Egyptian Vulture (García-Ripollés *et al.* 2010), Montagu's Harrier (Limiñana *et al.* 2011) and Marsh Harrier (Strandberg *et al.* 2008). Consequently, the Sahel is of great importance for the conservation of many European raptors and also for many other birds (Zwarts *et al.* 2009). Current land-use changes in the Sahel may represent a threat for several trans-Saharan migratory species (Sanderson *et al.* 2006, Newton 2008, Zwarts *et al.* 2009). For example, agricultural intensification implies an increased pesticide use to control locusts and grasshoppers, which has a negative effect on predator species feeding on these insects (Keith & Bruggers 1998, Sánchez-Zapata *et al.* 2007).

Our results show that in long-distance migratory birds, individuals from the same breeding population could be widely spaced during the wintering season, but this has been little studied to date (Limiñana *et al.* 2011). This may have several conservation implications, as efforts in the breeding areas could be inefficient if there is no information on possible threats during winter. Similarly, knowing the whole winter range is very important, as different conservation problems can arise in different areas (Zwarts *et al.* 2009). Also, knowing this wintering distribution is important in view of the ongoing changes in the distribution of migratory birds that may occur due to climate change (Godet *et al.* 2011). Evaluating the location and land-use changes of stopovers is also important for conservation of migratory birds (Sheehy *et al.* 2011). Furthermore, as we have found here, there may be different migration strategies in spring and autumn. These seasonal differences in migration could also carry different mortality rates (e.g. Strandberg *et al.* 2010), as birds could be exposed to different risks in different passage areas (e.g. sandstorms) or the different routes could represent different energy consumption rates, which ultimately affects survival. Therefore, it is necessary to take into account all these factors in optimal conservation planning for long-distance migratory birds. New studies to link breeding, wintering and migration ecology of these species, as well as those to analyse carry-over effects, are very important to gain a general picture of the conservation problems of these species.

Studies including more than one complete migration cycle in the Lesser Kestrel would be important to analyse in terms of inter-year variations or consistency in migration routes and timing (Mellone *et al.* 2011b). It would also be interesting to conduct migration studies with other populations within the wide breeding range of the species, such as the Asian population, which is thought to winter in southern Africa (Rodríguez *et al.* 2011). This would allow a comparison of migratory behaviour under two different migration distances (roughly 3000 vs. 8000 km) and to obtain a more complete view on the migration ecology and conservation priorities of this species across its whole range.

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REFERENCES

Alberdi, M. 2006. *Actuaciones del plan de acción para la conservación de las aves de las estepas cerealistas de la Comunidad Valenciana 2006*. Informe inédito. Equipo de Seguimiento de Fauna – VAERSA. Valencia: Consellería de Territorio y Vivienda.

Alerstam, T. 2003. Bird migration speed. In Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*: 253–267. Berlin: Springer-Verlag.

Alerstam, T. 2009. Flight by night or day? Optimal daily timing of bird migration. *J. Theor. Biol.* **258**: 530–536.

Argos 2011. *Argos User's Manual*. Toulouse: CLS/Service Argos.

BirdLife International 2011. Species factsheet: *Falco naumanni*. http://www.birdlife.org (accessed 1 August 2011).

Catry, I., Dias, M.P., Catry, T., Afanasyev, V., Fox, J., Franco, M.A. & Sutherland, W.J. 2011. Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. *Ibis* **153**: 154–164.

Coyne, M.S. & Godley, B.J. 2005. Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar. Ecol. Prog. Ser.* **301**: 1–7.

Ferguson-Lees, J. & Christie, D.A. 2001 *Raptors of the World*. London: Helm.

García-Ripollés, C., López-López, P. & Urios, V. 2010. First description of migration and wintering of adult Egyptian Vultures *Neophron percnopterus* tracked by GPS satellite telemetry. *Bird Study* **57**: 261–265.

Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proc. Royal Soc. B.* **276**: 447–457.

Godet, L., Jaffré, M. & Devictor, V. 2011. Waders in winter: long-term changes of migratory bird assemblages facing climate change. *Biol. Lett.* **7**: 714–717.

Hooge, P.N. & Eichenlaub, B.. 1997. *Animal Movement Extension to Arcview*. Anchorage: Alaska Science Centre-Biological Science Office, U.S. Geological Survey.

Íñigo, A. & Barov, B. 2010. *Action Plan for the Lesser Kestrel Falco naumanni in the European Union*. Madrid: SEO/BirdLife and BirdLife International for the European Commission.

Keith, J.O. & Bruggers, R.L. 1998. Review of hazards to raptors from pest control in Sahelian Africa. *J. Raptor Res.* **32**: 151–158.

Kerlinger, P. 1989. *Flight Strategies of Migrating Hawks*. Chicago: University of Chicago Press.

Klaassen, R.H.G., Strandberg, R., Hake, M., Olofsson, P., Tøttrup, A.P. & Alerstam, T. 2010. Loop migration in adult Marsh Harriers *Circus aeruginosus* as revealed by satellite telemetry. *J. Avian Biol.* **41**: 200–207.

Klaassen, R.H.G., Ens, B.J., Shamoun-Baranes, J., Exo, K.-M. & Bairlein, F. 2012. Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*. *Behav. Ecol* **23**: 58–68.

Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**: 940–950.

Limiñana, R., Soutullo, A. & Urios, V. 2007. Autumn migration of Montagu's Harriers *Circus pygargus* tracked by satellite telemetry. *J. Ornithol.* **148**: 517–523.

Limiñana, R., Soutullo, A., López-López, P. & Urios, V. 2008. Pre-migratory movements of adult Montagu's Harriers *Circus pygargus*. *Ardea* **96**: 81–96.

Limiñana, R., Soutullo, A., Arroyo, B. & Urios, V. 2011. Protected areas do not fulfil the wintering habitat needs of the trans-Saharan migratory Montagu's Harrier. *Biol. Conserv*. doi: 10.1016/j.biocon.2011.10.009.

Limiñana, R., Soutullo, A., Urios, V. & Reig-Ferrer, A. 2012. Migration and wintering areas of adult Montagu's Harriers (*Circus pygargus*) breeding in Spain. *J. Ornithol* **153**: 85–93.

López-López, P., Limiñana, R. & Urios, V. 2009. Autumn migration of Eleonora's Falcon *Falco eleonorae* tracked by satellite telemetry. *Zool. Stud.* **48**: 485–491.

López-López, P., Limiñana, R., Mellone, U. & Urios, V. 2010. From the Mediterranean Sea to Madagascar: are there ecological barriers for the long-distance migrant Eleonora's Falcon? *Landscape Ecol.* **25**: 803–813.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. & Norris, D.R. 2007. Optimal conservation of migratory species. *PLoS One* **2**: e751.

Mellone, U., Limiñana, R., Mallia, E. & Urios, V. 2011a. Extremely detoured migration in an inexperienced bird: interplay of transport costs and social interactions. *J. Avian Biol.* **42**: 468–472. doi: 10.1111/j.1600-0587.2011.05454.x.

Mellone, U., López-López, P., Limiñana, R. & Urios, V. 2011b. Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor. *Int. J. Biometeorol.* **55**: 463–468.

Mellone, U., López-López, P., Limiñana, R. & Urios, V. 2011c. Wintering habitats of Eleonora's Falcons *Falco eleonorae* in Madagascar. *Bird Study*. doi:10.1080/00063657.2011.632401.

Mihoub, J.-B., Gimenez, O., Pilard, P. & Sarrazin, F. 2010. Challenging conservation of migratory species: Sahelian rainfalls drive first-year survival of the vulnerable Lesser Kestrel *Falco naumanni*. *Biol. Conserv.* **143**: 839–847.

Mullié, W.C. 2009. Birds, locust and grasshoppers. In Zwarts, L., Bijlsma, R.G., Van der Kamp, J. & Wymenga, E. (eds) *Living on the Edge: Wetlands and Birds in a Changing Sahel*: 202–223. Zeist: KNNV Publishing.

Negro, J.J. 1997. *Falco naumanni* Lesser Kestrel. *Birds of Western Palearctic. Update* **1**: 49–56.

Newton, I. 2008. *The Migration Ecology of Birds*. London: Academic Press.

Olea, P.P., Vera, R., de Frutos, A. & Robles, H. 2004. Pre-migratory communal roosts of the Lesser Kestrel in the boreal summer. *J. Raptor Res.* **38**: 278–282.

Pavón, D., Limiñana, R., Urios, V., Izquierdo, A., Yáñez, B., Ferrer, M. & De la Vega, A. 2010. Autumn migration of juvenile Short-toed Eagles *Circaetus gallicus* from South-eastern Spain. *Ardea* **98**: 113–117.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. 2004. Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.* **266**: 265–272.

Premuda, G., Mellone, U. & Cocchi, L. 2004. Osservazioni sulla modalità della migrazione primaverile dei rapaci a Capo d'Otranto [Spring raptor migration routes at Capo d'Otranto]. *Avocetta* **28**: 33–36.

Rodríguez, A., Negro, J.J., Bustamante, J., Fox, J.W. & Afanasyev, V. 2009. Geolocators map the wintering grounds of threatened Lesser Kestrels in Africa. *Divers. Distrib.* **15**: 1010–1016.

Rodríguez, A., Alcaide, M., Negro, J.J. & Pilard, P. 2011. Using major histocompatibility complex markers to assign the geographic origin of migratory birds: examples from the threatened Lesser Kestrel. *Anim. Conserv.* **14**: 306–313.

Román, J.R., Onrubia, A., Muñoz, G., Benjumea, R., Muñoz, A.R., de la Cruz, A., González, M., Cuenca, D., Barrios, L., Torralvo, C., Elorriaga, J., Zufiaur, P., Pérez, B., León, M. & Cortés, V. 2008. The migration of Lesser Kestrel *Falco naumanni* across the Strait of Gibraltar. In **LPO** (eds) *Résumés des Communications du VII Congrès Internationnal sur le Faucon Crécerellette*: 67. Almendralejo: LPO.

Romero, M. 2011. *El Cernícalo Primilla* (Falco naumanni) *en la Comunidad Valenciana*. MSc Thesis, Universidad de Valencia.

Sánchez-Zapata, J.A., Donázar, J.A., Delgado, A., Forero, M.G., Ceballos, O. & Hiraldo, F. 2007. Desert locust outbreaks in the Sahel: resource competition, predation and ecological effects of pest control. *J. Appl. Ecol.* **44**: 323–329.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & Van Bommel, F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Cons.* **131**: 93–105.

Shamoun-Baranes, J., Baharad, A., Alpert, P., Berthold, P., Yom-Tov, Y., Dvir, Y. & Leshem, Y. 2003. The effect of wind, season and latitude on the migration speed of White Storks *Ciconia ciconia*, along the eastern migration route. *J. Avian Biol.* **34**: 97–104.

Sheehy, J., Taylor, C.M. & Norris, D.R. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. *J. Ornithol.* **152**: S161–S168.

Soutullo, A., Cadahía, L., Urios, V., Ferrer, M. & Negro, J.J. 2007. Accuracy of lightweight satellite telemetry: a case study in Iberian Peninsula. *J. Wildl. Manag.* **71**: 1010–1015.

Strandberg, R., Klaassen, R.H.G., Hake, M., Olofsson, P., Thorup, K. & Alerstam, T. 2008. Complex timing of Marsh Harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. *Ardea* **96**: 159–171.

Strandberg, R., Alerstam, T., Hake, M. & Kjellen, N. 2009a. Short-distance migration of the Common Buzzard *Buteo buteo* recorded by satellite tracking. *Ibis* **151**: 200–206.

Strandberg, R., Klaassen, R.H.G., Olofsson, P. & Alerstam, T. 2009b. Daily travel schedules of adult Eurasian Hobbies *Falco subbuteo* – variability in flight hours and migration speed along the route. *Ardea* **97**: 287–295.

Strandberg, R., Klaassen, R.H.G., Hake, M. & Alerstam, T. 2010. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors *Biol. Lett.* **6**: 297–300.

Thiollay, J.M. 2006. The decline of raptors in West Africa: long-term assessment and the role of protected areas. *Ibis* **148**: 240–254.

Trierweiler, C. 2010. *Travels to feed and food to breed. The annual cycle of a migratory raptor, Montagu's Harrier, in a modern world*. PhD Thesis Dissertation, University of Groningen.

Zwarts, L., Bijlsma, R.G., van der Kamp, J. & Wymenga, E. 2009. *Living on the Edge: Wetlands and Birds in a Changing Sahel*. Zeist: KNNV Publishing.

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