Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators

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The population decline of the Lesser Kestrel *Falco naumanni* has been the subject of studies across its Western Palaearctic breeding range, but little is known about its use of pre-migratory areas or African wintering quarters. We used geolocators to describe the temporal and spatial patterns of Portuguese Lesser Kestrel migration and wintering behaviour. Data on the complete migration were obtained from four individuals and another three provided further information. Prior to southward migration, Lesser Kestrels showed two different behaviours: northward-orientated movements to Spain and movements in the proximity of the breeding area. Autumn migration took place mostly in late September; spring departures occurred mainly in the first half of February. Wintering grounds included Senegal, Mauritania and Mali, with individuals overlapping considerably in Senegal. Movements registered within the wintering grounds suggest itinerant behaviour in relation to local flushes of prey. During spring migration, birds crossed the Sahara Desert through Mauritania, Western Sahara and Morocco before passing over the Mediterranean to reach Portugal. Autumn migration lasted 4.8 ± 1.1 days, and spring migration lasted 4.1 ± 0.3 days. The mean daily flight range varied between approximately 300 and 850 km for an entire journey of around 2500 km. Effective protection of roosting sites in both pre-migratory and wintering areas and maintaining grasshopper populations in Sahelian wintering quarters appear crucial in preserving this threatened migratory raptor across its African–Eurasian flyway. There was no evidence of any deleterious effects of fitting birds with loggers.

Keywords: geolocators, migration, pre-migratory movements, wintering range.

There is increasing conservation concern about migratory birds, many of which are classified as threatened or near-threatened. Half the migratory raptor species of the African–Eurasian flyway are globally threatened, near-threatened or declining (BirdLife International 2009). Limited knowledge of their ecology outside the breeding grounds restricts assessment of threats and solutions (Biber & Salathé 1990, Kelsey 1992). Determining the migratory schedule, route taken, stopover sites and wintering grounds is fundamental for effective conservation.

Current knowledge of avian migration patterns is largely derived from bird counts, radar observations

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and ring recovery analyses (Akesson & Hedenström 2004, Newton 2008). Satellite telemetry has revolutionized the study of bird migration (e.g. Weimerskirch *et al.* 2006, Strandberg *et al.* 2008, Qian *et al.* 2009), but inherent limitations, such as instrument size and mass, high device costs and significant tag loss (Phillips *et al.* 2004) mean that satellite tracking studies are only applied to large and medium-sized species and typically involve a small sample size (e.g. Ganusevich *et al.* 2004, Meyburg *et al.* 2004, 2005).

Miniature light-level loggers (geolocators; also known as global location sensing) have recently been developed for long-distance tracking of marine birds and mammals (Afanasyev 2004, Phillips *et al.* 2004). Their small size, low cost, long battery life and ease of attachment (for example to a leg ring) have increased the range of species whose movements can be followed remotely (Phillips *et al.* 2006, Rayner 2007, Catry *et al.* 2009a) and increased the opportunity to study individual differences (González-Solís *et al.* 2007). This technology has largely been used in seabird studies (but see Eichhorn *et al.* 2006, Stutchbury *et al.* 2009, Rodríguez *et al.* 2009).

In this study, we used geolocators to track the migratory schedule of the Lesser Kestrel *Falco naumanni*, a migratory falcon classified as globally Vulnerable (BirdLife International 2004) whose breeding range extends from the Mediterranean across southern central Asia to China and Mongolia (BirdLife International 2004). The non-breeding range is in Africa, although a few adults overwinter in Spain and southern Turkey (Cade 1982, Negro *et al.* 1991). Eastern populations, comprising those in eastern Europe, Middle East and Asia, winter mainly in eastern Africa and South Africa (Pepler & Martin 2001). Data on the numbers and distribution of western Lesser Kestrels outside the breeding range are scarce (Pilard *et al.* 2004). However, in 2007, a single roost of over 28 600 Lesser Kestrels was discovered in Senegal (LPO 2008), which may have contained 30–50% of the entire western European population, probably including birds from Portugal, Spain, France and Morocco (Pilard 2008), while Rodríguez *et al.* (2009) described the wintering ranges of three Spanish birds in West Africa, based on geolocation data. Despite this, there is no knowledge of migratory routes and little information is available on the distribution and movements of Lesser Kestrels in their wintering grounds.

The Lesser Kestrel is one of the most gregarious of the *Falco* species during breeding, wintering and prior to autumn migration (Olea *et al.* 2004, Minias *et al.* 2009). Pre-migratory movements are thought to exploit temporarily superabundant food resources to improve body condition before migration (Olea 2001, Ursúa & Tella 2001). These areas have been suggested to be regular pre-migratory areas with ecological and conservation importance for Lesser Kestrel populations (Olea *et al.* 2004). However, little is published on pre-migratory movements, with all studies focusing on juvenile dispersal, based on ring recoveries (Bustamante & Negro 1994, Olea 2001).

The aim of this study was to describe the complete annual migratory track and schedule of adult Lesser Kestrels breeding in Portugal. We analyse the temporal and spatial patterns of Lesser Kestrel migration, including pre-migratory movements, arrival and departure dates, routes taken, location of wintering areas and movements on wintering grounds, using recently developed geolocation techniques. Although increasing conservation efforts in the European breeding grounds of the Lesser Kestrel have proved effective (Pomarol 1996, Catry *et al.* 2009b), these efforts may be compromised if there are negative impacts in the pre-migratory areas and African wintering quarters. Information on the species' migration and winter ecology is necessary to identify threat priorities for conservation outside the breeding areas.

METHODS

Logger deployment

Nineteen Mk14 geolocators, built by the British Antarctic Survey (Afanasyev 2004), were attached to eight male and 11 female adult Lesser Kestrels from 28 March to 7 April 2008 in three different colonies at the Castro Verde Special Protection Area, southern Portugal. This area harbours almost 80% (about 430 breeding pairs) of the Portuguese Lesser Kestrel population and the colonies are mainly located in old rural buildings and artificial nesting structures (Catry *et al.* 2009b). Each 1.5-g geolocator was attached with a single cable tie to a PVC colour ring (total weight 2.3 g) and placed around the bird's tarsus. Tracked individuals weighed 127–188 g, thus the attachment represented less than 2% of the body mass. All individuals were captured in nest-cavities at night prior to

egg-laying. Lesser Kestrels are highly philopatric but move between nests within colonies (Serrano *et al.* 2001). To increase the recapture probability, we selected colonies with high recapture rates. A high proportion of these populations were marked, enabling selection of birds with a known breeding history. The loggers were attached to birds aged 1–5 years at deployment; 11 were recovered in the next breeding season. For calibration, a daylight logger was placed during the entire study period close to the colonies.

Analysis of light data

Light data from retrieved loggers were analysed using TRANSEDIT software (British Antarctic Survey 2008) to check the integrity on light curves and to fit sunset and sunrise times (10 was used as the light threshold value). Longitude, derived from the absolute time of local noon/midnight relative to Greenwich Mean Time, and latitude, derived from day length, was estimated using BIRDTRACK software (British Antarctic Survey 2008), providing two locations per day. Using known positions obtained from the deployed and calibration loggers during the breeding and winter periods, respectively, the sun elevation angle was set to −4.0°. Locations derived from curves with obvious shading events around sunset and sunrise were identified and excluded. In addition, we discarded locations obtained around the equinoxes (± 21 days), when day and night length are similar, so preventing the estimation of latitude (Wilson *et al.* 1992, Hill 1994). Mean accuracy was first assessed from variation during the breeding season, when birds remain close to the colony, allowing assessment of the influence of their behaviour. Mean accuracy was estimated to be 224 ± 15 km ($n = 128$ positions). From the calibration logger during the winter period (16 October–31 January) error was calculated as 283 ± 13 km ($n = 152$ positions). In both cases, longitude is more accurate than latitude, particularly during the winter period (longitude 127 ± 7 km vs. latitude 171 ± 16 km during the breeding period, and 60 ± 4 km vs. 273 ± 13 km during winter).

Statistical procedures

The main pre-migratory and wintering areas were identified by determining each individual's kernel distribution. These maps were based on the projected (UTM 28N) and twice-smoothed positions (i.e. by calculating, for each position, its average with the positions immediately after and before, and repeating this procedure twice; Phillips *et al.* 2004). Lesser Kestrel autumn migration (and part of spring migration for some birds) coincides with the equinoxes, which prevent the determination of the precise routes. Therefore, we estimated the departure and arrival dates associated with migration movements from longitude data (Rodríguez *et al.* 2009, Stutchbury *et al.* 2009). We identified the beginning of each migratory journey by the clear shift in longitude values, followed by a unidirectional and sharp variation in longitude (of approximately two degrees of longitude per day). Similarly, arrival dates were considered as the day at which longitude values stabilized. The correlation between days and longitude values was always high and significant during migration ($|r|$ always higher than 0.87; P always lower than 0.01), contrasting with the much lower correlation values during the days immediately before and after migration ($|r|$ always lower than 0.5). Distances between wintering and breeding areas were computed with unprojected but smoothed data (great-circle distances), assuming the mean position during the winter period. Given the low accuracy of the estimated locations, we used a conservative approach when calculating migratory distances and speeds by assuming an error of 273 km in latitude and 60 km in longitude values (see above) and by presenting minimum and maximum estimates for these parameters. All analyses were performed using software R 2.6.1 (R Development Core Team 2007), and the relevant packages PROJ4 (Urbanek 2007) and ADEHABITAT (Calenge 2006). Final maps were produced using ARCVIEW 3.2 (ESRI 1999). All means are given with standard errors.

RESULTS

Logger retrieval and device effects

Of the initial 19 loggers deployed in 2008, 11 were retrieved during 2009. From these, three had entered a 'sleep mode' at different stages after deployment and stopped recording data prior to spring migration. Nonetheless, for one female (6776) it was possible to obtain information on its pre-migratory behaviour. From the remaining seven, four had onboard clock errors (i.e. large clock drifts, resulting in large errors in locations

registered during the first months of tracking); however, for three of the four, it was possible to collect data related to migratory schedules, which were based solely on clear shifts in longitude data (Table 1). Device problems among retrieved loggers were largely due to physical damage caused by the birds themselves, a problem that has been reported for some terrestrial species, including Lesser Kestrels (Rodríguez *et al.* 2009). Finally, four loggers (all deployed on females) provided data for the entire migration and wintering period (71% of valid locations on average; minimum 58%; maximum 78%), allowing the analysis of main migratory movements and wintering areas (Table 1). There was no significant difference in mean body mass between birds with and without loggers when recaptured before the start of the incubation period (163 ± 19.3 g, $n = 9$ and 154 ± 15.0 g, $n = 106$, respectively, $t_{113} = -1.56$, $P = 0.121$). After deployment, two females in 2008 and two in 2009 were recaptured during colony monitoring: all successfully produced fledglings ($n = 5, 4, 3$ and 1). One female with a logger was the first to lay and had the largest clutch (six eggs) of any within the colony.

Pre-migratory movements from the breeding area

Two Lesser Kestrels made northward movements from their breeding area prior to autumn migration. One female (6773) moved over 700 km from 19 July to northeast Spain, while the other (6776) left the breeding area in the first days of August, moving north to Spain (Fig. 1). Two other birds made shorter movements but because of insufficient accuracy of achieved locations we could not determine whether the tracked individuals stayed in Portugal or moved to areas near the border (perhaps to the largest known pre-migratory roosting site in the Spanish Extremadura, less than 150 km northeast of Castro Verde).

Autumn migration

Autumn migration started in September, with most birds departing in the second half of the month (mean = 23 September ± 3.34 days), and lasted 4.8 ± 1.1 days ($n = 4$, Table 1). The average speed was approximately 600 km/day, covering a mean distance of 2500 km between breeding and wintering grounds (Table 1). Tracked Lesser Kestrels reached the wintering areas from 17 September to 2 October (mean = 26 September ± 3.35 days, $n = 4$, Table 1). It was impossible to identify the route taken because the large errors in latitude during the equinox obliged us to discard location data from this period (see Methods).

Wintering period

Data from eight of 11 retrieved geolocators indicate that all eight birds did migrate (three devices entered sleep mode prior to migration) and probably wintered in western Africa, spending part of the winter period in Senegal (Table 1). The wintering period for the four tracked birds with usable data for the entire period lasted for 136 ± 3.32 days (Table 1). Two birds spent part of the winter in Mauritania (and one might have moved to Mali) but individual core areas of activity (25, 50, 75 and 95% kernels) overlapped considerably in Senegal (Fig. 2). Minimum and maximum latitudes of wintering areas (95% kernels) ranged between 10.6°N and 18.7°N, where the habitat is dominated mainly by tropical grasslands, savannas and shrublands. Gradual movements to both the west and east were detected during the wintering period, as shown by the variation in longitude values (Fig. 3). Female 6773 migrated to the border of Mauritania and Mali, where it stayed until 25 October, then moving to Senegal for a month (from 26 October to 21 November), and returned to the Mauritania/Mali area until spring migration (Figs 2 and 3). The limits of its core areas were more than 800 km apart. Two other birds (6772 and 6774) showed relatively large areas of movement, whereas female 6781 apparently stayed in the same area from November until the beginning of spring migration (Fig. 3).
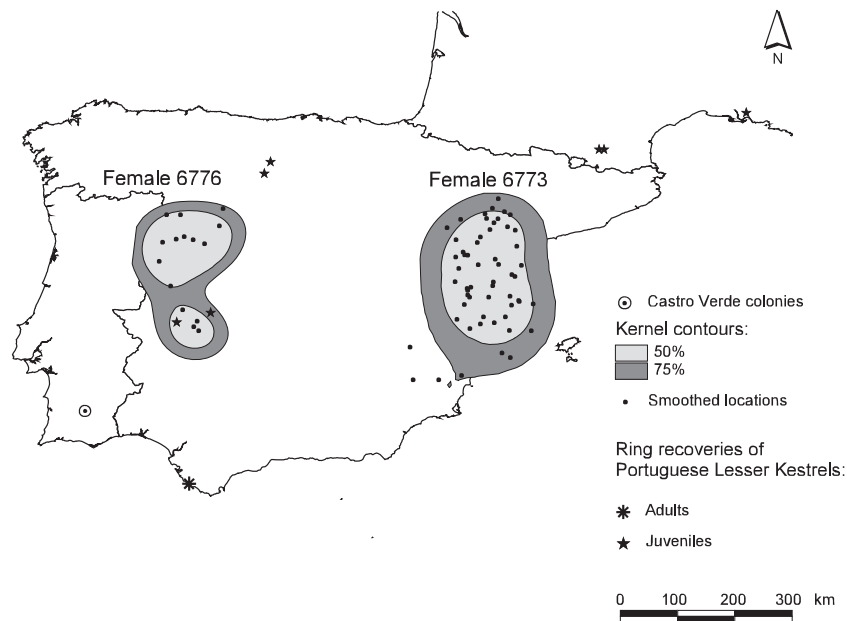
Spring migration

Spring departure from the wintering grounds occurred from 9 February to 9 March (mean = 15 February ± 3.94 days, $n = 7$; Table 1). All individuals crossed the Sahara Desert through Mauritania, Western Sahara and Morocco before passing over the Mediterranean to reach the Portuguese breeding grounds (Fig. 2). Female 6773 took a slightly different route and may have crossed the Strait of Gibraltar (Fig. 2). On average, spring migration took 4.1 ± 0.3 days ($n = 7$) with distance travelled averaging 650 km/day ($n = 4$, Table 1). Arrival

Table 1. Autumn and spring migration of the Lesser Kestrel recorded by global location sensing loggers. Age (at recapture) is presented in years. The migration date estimates were based on longitudinal data (see Methods). Distances and speed estimates assumed a mean error of 273 km in latitude and 60 km in longitude (minimum and maximum estimates are presented in parentheses). For the loggers that suffered onboard clock errors, only the most likely wintering grounds (in parentheses) and spring migration parameters are presented. Four other loggers did not provide any data on migration (see Results).

Bird logger	Sex	Age	Loggers data	Autumn migration				Distance between wintering and breeding grounds (km)	Winter period (days)	Spring migration		
				Migration period	No. of travel days	Speed (km/day)	Wintering ground			Migration period	No. of travel days	Speed (km/day)
6766	M	4	Onboard clock errors: partial data available	–	–	–	[Senegal]	–	–	09–13 Mar	5	–
6771	F	3	Onboard clock errors: partial data available	–	–	–	[Senegal]	–	–	22–25 Feb	4	–
6772	F	4	Good	23–30 Sep	8	316 (282–351)	Senegal and Mauritania	2529 (2252–2807)	131	10–13 Feb	4	632 (563–702)
6773	F	5	Good	14–17 Sep	4	603 (513–671)	Senegal and Mauritania /Mali	2413 (2053–2682)	145	09–13 Feb	5	483 (411–536)
6774	F	4	Good	25–28 Sep	4	653 (582–722)	Senegal	2612 (2328–2889)	137	12–14 Feb	3	871 (776–963)
6779	F	3	Onboard clock errors: partial data available	–	–	–	[Senegal]	–	–	09–12 Feb	4	–
6781	F	6	Good	30 Sep–2 Oct	3	855 (760–945)	Senegal	2565 (2279–2836)	131	11–14 Feb	4	641 (570–709)

Figure 1. Pre-migratory movements and kernel activity ranges (encompassing 50 and 75% of the locations) of two Lesser Kestrel females prior to autumn migration. Recovery sites of ringed Portuguese Lesser Kestrels (and recovered elsewhere in July, August and September of the same year) are shown.

dates at the breeding grounds were from 12 February to 13 March (mean = 18 February ± 4.06 days, *n* = 7; Table 1). Female 6773 arrived on 13 February and laid the first egg more than 2 months later, on 21 April.

DISCUSSION

Logger retrieval, device effects and data quality

Eleven of 19 tagged birds (58%) were recaptured and the geolocators retrieved. Relatively high return rates, non-significant differences in individual body condition among birds with and without devices and successful breeding for the few monitored tagged birds suggest minimal impact of logger deployment, as also shown by Rodríguez *et al.* (2009). Mean geolocator accuracy (224 ± 15 and 282 ± 13 km during the breeding and wintering periods, respectively) was lower than seabird tracking results (e.g. 186 ± 114 km, Phillips *et al.* 2004; 202 ± 171 km, Shaffer *et al.* 2005) due to high light interference in terrestrial habitats (from shadowing effects, for example). However, our conclusions are mainly based on large-scale movement patterns, typically based solely on longitude data (as

the within-winter or the spring migratory movements), resulting in reduced errors. We therefore believe that the magnitude of the geolocation error does not alter any of our main findings.

Pre-migratory movements from the breeding area

Ring recoveries show juvenile northward movements prior to southward migration (Fig. 1; Bustamante & Negro 1994, Olea 2001), probably to areas where orthopteran abundance peaks later, thus enhancing juvenile survival and improving body condition before migration (Olea 2001, Ursúa & Tella 2001). Nevertheless, adult pre-migratory movements have rarely been recorded (Fig. 1; Riols & Pilard 2007) and previous studies suggest that they disperse less than juveniles or remain near their breeding colonies until migration (Bustamante & Negro 1994, Olea *et al.* 2004). We observed two different behaviours in our tracked adult individuals: two birds clearly made pre-migratory movements, possibly gathering in known post-nuptial roosts in northwestern and northeastern Spanish provinces of Léon, Arágon and Navarra (Ursúa & Tella 2001, Olea *et al.* 2004), whereas another two made local movements.
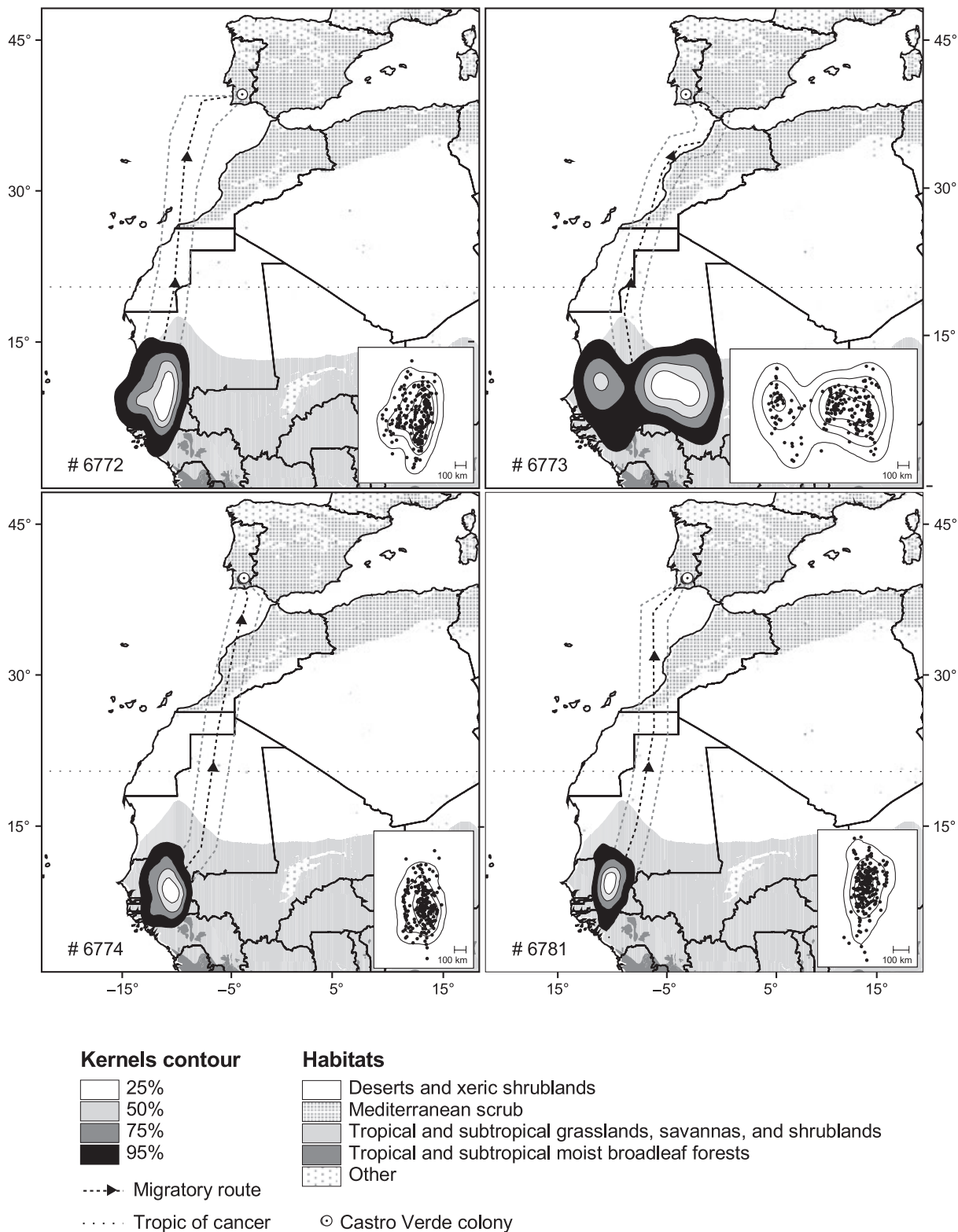
Figure 2. Individual core areas (25, 50, 75 and 95% kernel contours) of Lesser Kestrel activity during the wintering period (21 October to 31 January) and spring migratory routes to breeding areas in Castro Verde, Portugal. Grey dashed lines along the migratory trajectory represent the confidence intervals assuming a 124-km error in longitudes (see Methods). Locations in which the kernels were based are plotted in the lower part of each panel.
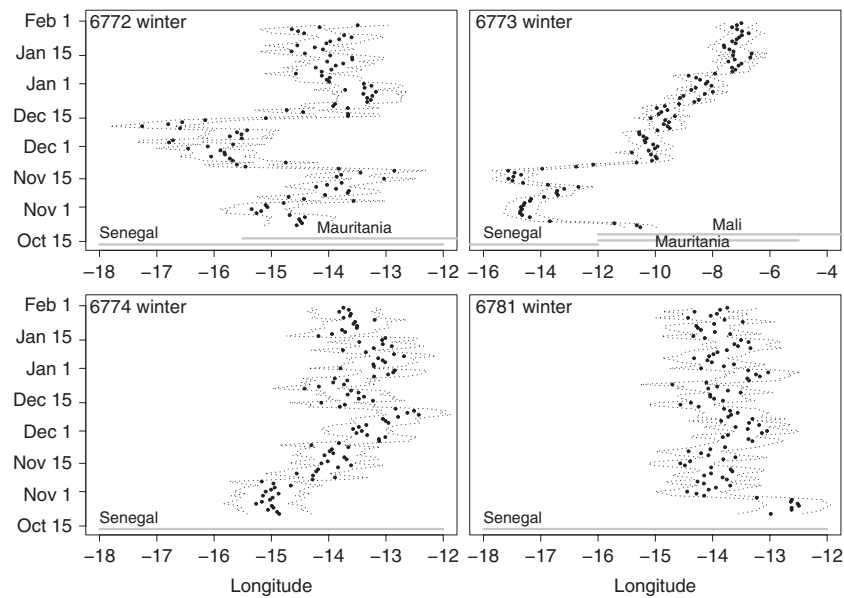
Figure 3. Winter behaviour of tracked Lesser Kestrels in western Africa. Longitude variation reveals different patterns of movement among four females. Each point corresponds to the average longitude of the date (two locations per day). Dashed lines represent the estimated error for the longitude (60 km, or 0.56°, see Methods), assuming a mean latitude of 15°N.

Autumn and spring migration: timing, routes, duration, distance and speed

Our data, based on seven tracked individuals, agree with the timing of autumn migration observed across the Strait of Gibraltar (late September; Róman *et al.* 2008), whereas spring passage took place earlier than suggested (late February and early March; Róman *et al.* 2008), with five of seven of the birds crossing the Mediterranean before 15 February. Southward and northward migratory journeys were of similar durations (4.8 ± 1.1 and 4.1 ± 0.3 days, respectively). Although the timing and duration of post-nuptial migration were similar to the results from Rodríguez *et al.* (2009) in southern Spain, spring migration and arrival at the breeding grounds differed markedly (24.3 ± 10 days, with arrivals in late March, *n* = 3). The shorter duration of spring migration found in our study is supported by the unmistakable pattern of light transition values across the day (dark and light) when birds started to visit the breeding cavities. The mean daily flight distance during migration ranged for different individuals between approximately 300 and 850 km, covering a distance of about 2500 km. Medium and large raptors tracked by satellite techniques only occasionally move more than 500 km/day

(Newton 2008). Nonetheless, among the *Falco* genus, recent data recorded from a Hobby *Falco subbuteo* revealed a non-stop flight over a distance of 740 km in 25 h (Strandberg *et al.* 2009). Observed spring migratory routes (only one bird might have crossed the Mediterranean through Gibraltar) reinforce the idea that Lesser Kestrels are capable of crossing the Mediterranean over broad fronts (Greenberg & Marra 2005).

Wintering range

After crossing the Sahara Desert, all individuals, and those of Rodríguez *et al.* (2009), spent at least part of the winter period in Senegal. Overall, Portuguese Lesser Kestrels wintered further east than Spanish ones (Rodríguez *et al.* 2009), with some birds apparently not using the area adjacent to the recently discovered large roost (28 000 individuals; LPO 2008) in western Senegal. They may have been using the smaller and less stable peripheral roosts recently discovered over 100 km further east (P. Pilard, pers. comm.). As for all migrant species (Sherry & Holmes 1996), food is probably the most important ecological factor affecting distribution and movements of Lesser Kestrels across their winter quarters. Grasshopper abundance and distribution in the Sahelian area are

driven mainly by the annual movement of the Inter-Tropical Convergence Zone, which determines the rainfall patterns and the distribution of habitats (Jones 1995). In Senegal, recent land cover changes have led to changes in the distribution pattern of grasshoppers (Mullié 2009) and might explain the present location of core areas of activity for Lesser Kestrels. Surveys showed that the newly created steppes and grasslands attracted very high numbers of acridivores, including Lesser Kestrels, dispersed over a feeding area of *c.* 3500 km^2 (Mullié 2009). The movements observed during the wintering period (within Senegal and to Mali and Mauritania) suggest some itinerancy in relation to local flushes of food, and this is considered to be the main strategy among raptor species wintering in Africa (Newton 2008). High concentrations of several raptor species (including Lesser Kestrels) in large communal roosts close to Desert Locust *Schistocerca gregaria* swarms during the outbreak of 2004 have been detected in Mauritania (Sánchez-Zapata *et al.* 2007). Among Lesser Kestrels, displacements of more than 200 km from usual roosts were identified in South Africa in response to increasing food densities (Pepler & Martin 2001).

Conservation implications

Declines of raptors in West Africa have been attributed to deforestation, agricultural intensification, overgrazing, erosion, pesticide use and illegal hunting (Thiollay 2006). It has been suggested that recent changes in land cover have resulted in increased grasshopper populations in vast Sahelian areas, so resulting in increased use of chemical insecticides (Mullié 2009). The implementation of tested biopesticides, less toxic for predator species, may be a viable alternative to the currently used broad-spectrum chemical products (LPO 2008, Mullié 2009).

The apparent fidelity of Lesser Kestrels to large roosts (Olea *et al.* 2004, LPO 2008) makes identifying and protecting these roosting sites important. Identified problems include agricultural intensification for pre-migratory sites (DEMA 2005) and human disturbance and woodcutting on the wintering grounds (LPO 2008, 2009).

This study presents new data on the migratory and wintering behaviour of Iberian Lesser Kestrels, which might be crucial for the conservation of this globally threatened species. Nonetheless, the limited number of successful tracked individuals underlines the need for further work to support the described patterns and increase the current knowledge of this species' migration.

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