



The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons

Ugo Mellone, Pascual López-López, Rubén Limiñana, Gvido Piasevoli and Vicente Urios

U. Mellone (ugomellone@libero.it), P. López-López, R. Limiñana and V. Urios, Vertebrates Zoology Research Group, CIBIO Research Inst., Univ. of Alicante, ES-03690 San Vicente del Raspeig, Alicante, Spain. – G. Piasevoli, Public Inst. for the Protected Natural Values Management in the County of Split and Dalmatia, Prilaz braće Kaliterna 10, HR-21000 Split, Croatia.

Internal factors such as experience (e.g. age) and motivation for breeding, and external ones such as environmental conditions (e.g. meteorology and landscape characteristics) can promote differences in migratory behaviour and routes among seasons, regions and populations. Using satellite telemetry we investigated whether such differences occur and which factors promote them among migrating Eleonora's falcons breeding in the Mediterranean area (Spain and Croatia) and wintering in Madagascar. We found that during autumn migration no age differences occur when crossing the Sahara desert, but in the remaining African regions, juveniles were more prone than adults to fly at a slower and more tortuous rate, as well as exhibiting longer stop-overs, particularly in the Sahel region. Such differences might be promoted by a lower foraging and pre-migratory fattening efficiency in juveniles. During spring, routes were significantly more eastern than during autumn, resulting in a loop migration occurring in all studied populations. This could be accounted by seasonal variation in the distribution of trophic resources. Our results show that Eleonora's falcons integrate spatially seasonal changing resources on a continental scale throughout their annual cycle, changing their movement patterns in response to internal (age) and external (habitat) factors. This loop migration pattern may prove to be widespread among other Palearctic trans-continental migratory bird species.

Bird migration routes and behaviour during migratory journeys can vary enormously within the same species and even within populations, according to factors such as experience (age), environmental conditions (meteorology and landscape characteristics), motivation (breeding condition) and period of the year (seasons) (Kokko 1999, Alerstam 2006, 2011, Newton 2008, Mellone et al. 2012a). Landscape can vary strikingly within and among the journeys, since during the same journey birds need to cross both unfavourable regions, e.g. ecological barriers when fuelling is not possible, and regions where conditions are more favourable, making stop-overs for refuelling possible (Klaassen et al. 2008, López-López et al. 2010). In addition, conditions in the same region can vary among seasons due to rainfall seasonality and the consequent availability of trophic resources (Klaassen et al. 2010). Due to their morphology, pure soaring migrants are expected to store enough fat in order to accomplish their migratory journeys without foraging (Smith et al. 1986, Hake et al. 2003, Panuccio et al. 2006). By contrast, raptors using powered flight need to replenish their energy stores during the journey, since it seems to be more advantageous to fly lighter and forage en route than increase drag by carrying fuel reserves (Alerstam and Hedenström 1998). Therefore, the flight speed, the

geometry of migration routes and the amount of time allocated to fuel deposition are the result of the interactions among internal (experience, motivation) and external (landscape, weather conditions) factors. Overall, these factors, taken together, will ultimately shape migratory loops with seasonal differences in migration routes within the same age class (Newton 2008, Alerstam 2011).

The Eleonora's falcon *Falco eleonorae* is a long-distance migratory raptor, which breeds colonially and almost exclusively on islands in the Mediterranean Sea, with almost the entire population wintering in Madagascar (Walter 1979). To travel between the breeding colonies and wintering areas, twice each year Eleonora's falcons perform a trans-equatorial journey of ca 10 000 km, encountering a huge variety of environments and climatic conditions, with juveniles migrating independently of adults (Gschweng et al. 2008, López-López et al. 2009, 2010, Kassara et al. 2012). Therefore, its migration system provides an excellent model to study the effects of both internal and external determinants on migration behaviour. Our aim was to investigate whether there are differences in migratory routes among age classes, regions and periods of the year and to identify which are the most important factors promoting them. Moreover, for the first time, we report data for birds

belonging to the Croatian population, located in the northernmost part of the breeding range for the species (Walter 1979) and roughly half-way between the well-studied populations of Sardinia and Greece (Gschweng et al. 2008, Kassara et al. 2012).

Methods

Fieldwork

Between 2007 and 2010, we equipped 16 Eleonora's falcons (eight adults and eight juveniles) on the Balearic and Columbretes islands (Spain) with 9.5 g Argos satellite transmitters together with two adults on Svetac island (Croatia) in 2009. In the Spanish colonies, adults were captured using dho-gaza nets and a stuffed eagle owl *Bubo bubo* as a decoy, while nestlings were tagged at nests a few days before fledging. Croatian adults were trapped close to their nests using mist-nets. The transmitters were attached to birds using a teflon harness backpack.

Data selection

In the analyses we included only those birds completing at least the crossing of the Sahara desert, totalling 26 migration tracks (Table 1). In some cases, we did not obtain the entire migration as far as Madagascar either because of transmitter's failure or the death of the bird. Moreover, one juvenile (no. 34700) did not reach Madagascar, spending the winter between Kenya and Tanzania. Transmitters were programmed according to three different duty cycles (d.c.) as follows: 1) d.c. 1 (12 h on/18 h off), used for Spanish birds during autumn migration; 2) d.c. 2 (10 h on/48 h off) for Croatian birds during both migrations; and 3) d.c. 3 (12 h on/58 h off) for Spanish birds during spring migration, with one exception (Table 1). Each Argos data is accorded to a location class (l.c.) according to its spatial accuracy (Argos 2011). In order to plot the routes and identify the onset and ending of migrations, we considered all data collected excluding those with l.c. Z, retaining only a maximum of one location per hour (the highest quality one), and using data with l.c. 0, A and B only when in agreement

with normal rates of speed and direction (Strandberg et al. 2009). During autumn migration, we considered as adult all individuals that were at least one year old and thus with prior migration experience. In five cases we obtained repeated journeys from the same individuals (i.e. six autumn routes of three individuals and four spring ones of two individuals; Table 1). Migration tracks belonging to the same individual in the same season but in different years were treated as independent cases, since migrating raptors show high inter-year route flexibility regardless of the individual (Alerstam et al. 2006, García-Ripollés et al. 2010, Klaassen et al. 2011, Mellone et al. 2011, 2012a, Vardanis et al. 2011, Limiñana et al. 2012a, b). The migration tracks were plotted on maps and overlapped with the NDVI (normalized difference vegetation index), a measure of the vegetation's 'greenness' (Fig. 1, 2, 5) that has been suggested to be an adequate surrogate of trophic resources abundance (Pettorelli et al. 2005), including grasshoppers (Trierweiler et al. 2013), that are likely to be an easy prey for Eleonora's falcons on migration.

Age and regional differences during autumn migration

We selected a sub-set of locations only for birds programmed with d.c. 1 (Spanish birds during autumn), retaining only one location per day as close as possible to midnight, in this way building segments lasting ca 24 h (daily segments). Then, we used these points to calculate straightness, daily distance and regional migration speed. Three regions (i.e. Sahara, Sahel, Equatorial Africa; Fig. 1) were identified following the same latitudinal criteria used in López-López et al. (2010), although segments south of the Sahel were pooled in a single category (Equatorial Africa). A preliminary visual inspection of the migratory tracks, including those already published by other authors (Gschweng et al. 2008, Kassara et al. 2012), revealed that Eleonora's falcons, unlike the lesser kestrel *Falco naumanni* (Limiñana et al. 2012a) do not usually perform true stop-overs, using discrete staging areas for many days. In contrast, Eleonora's falcons slow down migration speed showing less directed movements, probably in response to the distribution of their insect prey. The above-mentioned

Table 1. Attributes of the birds used in the analyses.

Tag ID	Colony	Age	Sex	Tracking years		Duty cycle	
				autumn	spring	autumn	spring
34469	Balearic	adult	male	2007		1	
34471	Balearic	juvenile	male	2007		1	
80396	Columbretes	subadult	female	2008		1	
80399	Balearic	adult	female	2008, 2009	2009, 2010	1	3
80400	Balearic	adult	male	2008	2009	1	3
80402	Columbretes	adult	female	2008, 2009	2009, 2010	1	3
34700	Columbretes	juvenile	female	2010	2011	1	3
92528	Columbretes	juvenile	female	2010		1	
92529	Columbretes	subadult	male	2010		1	
92530	Columbretes	juvenile	male	2010		1	
92531	Columbretes	juvenile	male	2010		1	
92532	Columbretes	juvenile	male	2010	2011	1	1
96573	Svetac	adult	female	2009, 2010	2010	2	2
96574	Svetac	adult	female	2009	2010	2	2

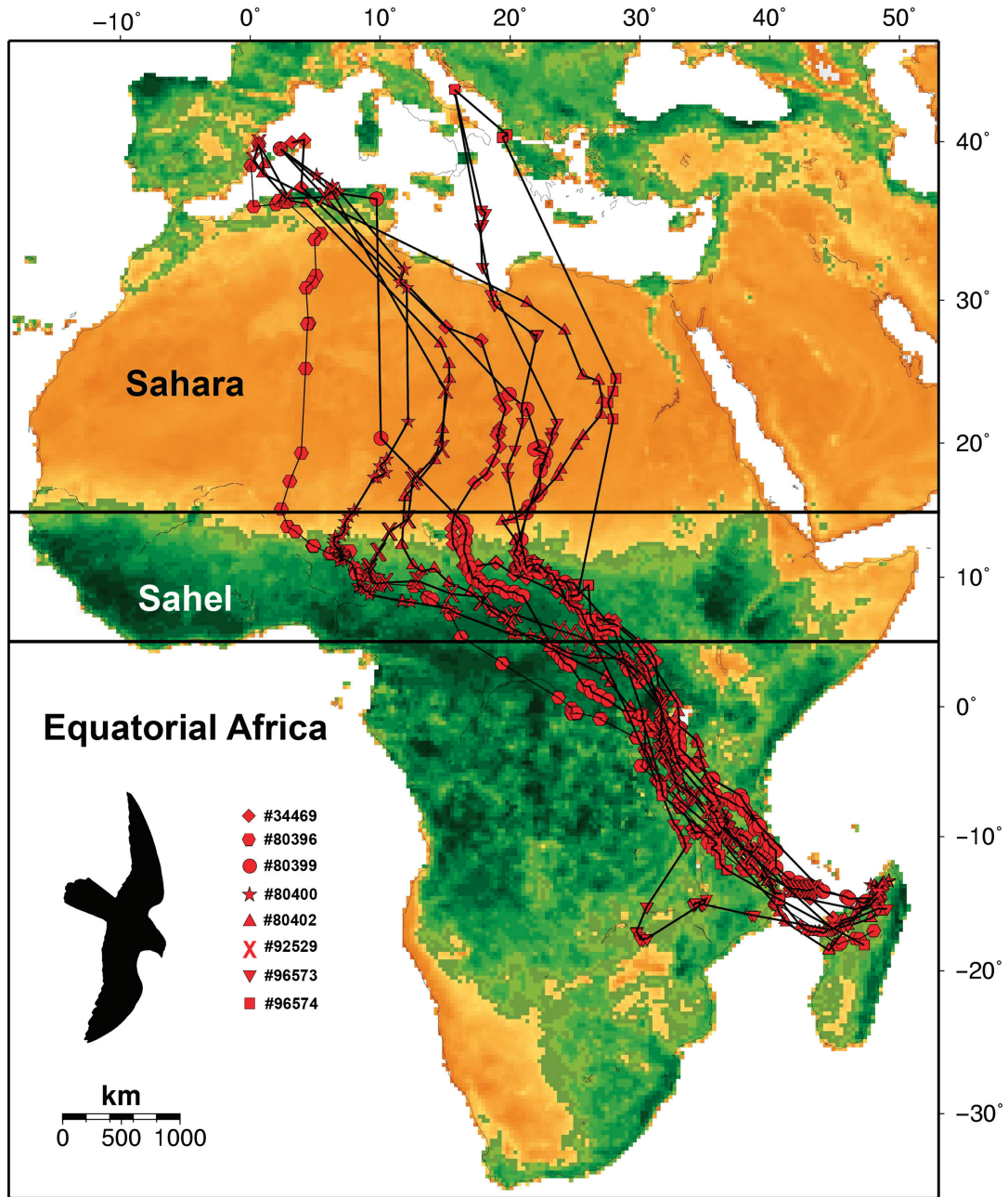


Figure 1. Eleven autumn migration tracks of eight adults Eleonora's falcons. Routes belonging to the same individual in different years maintain the same symbol. The background represents the normalized difference vegetation index (NDVI) for November 2009 (legend in Fig. 4).

authors reported that Eleonora's falcons performed long stop-overs but did not specify how they identified these. Therefore, in order to quantify the occurrence of this behaviour, half-way between a stop-over and a fly-and-forage strategy (Strandberg and Alerstam 2007), we adopted a multiple approach as follows.

We calculated the straightness of the migration tracks by dividing the distance between the tagging site and the final point of migration by the distance obtained summing up all daily segments, only for birds that accomplished the whole journey reaching the wintering grounds. We also calculated partial straightness for each region that was completely crossed. Straightness can vary between zero and

one. Values close to zero indicate tortuous paths, while straight paths have values close to one (Benhamou 2004).

Regional migration speed was obtained by dividing the straight distance (between the first and the last point of a region traversed) by the time elapsed (measured in number of days), e.g. for the Sahara the distance between the breeding colony and the first location in the Sahel, and so on. In order to identify 'short-distance days', indicative of stop-over/fly-and-forage behaviour (Klaassen et al. 2010, Limiñana et al. 2012a), we selected all days with daily distance (the distance between two points) lower than 50 km (regardless the flight direction), and also days < 100 km, but only if the direction showed a northern

component (reversed with respect to the general direction), i.e. in the semi-circle sector from 270° to 90°. The above mentioned thresholds were chosen rather conservatively, since an Eleonora's falcon can cover these distances in less than a couple of hours (Rosén et al. 1999), and then use the rest of the day for foraging. Nevertheless, this method allows the comparison of the spatial distribution of these short-distance days between age classes. Segments in Madagascar were excluded because they were all belonging to one juvenile individual that wandered before settling in the wintering area.

The effect of internal (age) and external (region) effects upon the three above mentioned variables (straightness, regional speed, short-distance days), were tested by means of three general linear mixed models (GLMM) in which age, region and their interaction were fixed factors and track ID represented a random factor. Non-significant terms were removed stepwise from the models according to their p-value within the model, starting from the interactions, until we obtained models that retained only significant variables. The straightness model included only two regions since there was not enough data of juveniles in Equatorial Africa. Finally, age differences concerning these three variables were also evaluated by means of Mann–Whitney two-tailed tests within each region. Regional variations in short-distance days within the same age class were analysed using the Kruskal–Wallis test. All analyses were carried out using SPSS 15.0.

Stop-over behaviour during spring migration

Data from birds migrating during spring was available at different time intervals, according to the duty cycle of the transmitters (Table 1). In order to calculate daily distance while avoiding any loss of available information, one location per duty cycle was selected and then the distance resulting from these segments was divided by the number of days in between. Segments resulting in a speed lower than 50 km day⁻¹ were considered as indicators of stop-over or fly-and-forage behaviour.

Seasonal differences in migration routes

For each track we determined at which longitudes the latitudes 30°N, 20°N, 10°N, 0° and 10°S were crossed. Then, we evaluated whether there were differences in longitude between seasons at each latitude by means of Mann–Whitney two-tailed tests. We calculated 'average' routes for each season as the sum of segments defined by the average longitudes where the different latitudes were crossed. We used these routes to calculate the overall detour ratio for each season, i.e. how much routes were longer than the straight loxodrome line connecting breeding sites with wintering grounds (as in Klaassen et al. 2010). Juvenile birds during autumn migration were excluded from these analyses in order to avoid any bias, since it has already been shown that they migrate significantly further west than adults (Gschweng et al. 2008). We also excluded Croatian birds since the low sample size did not allow for the carrying out of a separate analysis. We therefore used eight tracks for autumn migration

(belonging to six adults) and seven tracks for spring (belonging to three adults and two immatures).

Annual cycle

For birds for which year-round data was available (four cases belonging to three adult birds) we calculated the percentage of each stage within the annual cycle (autumn and spring migration, wintering, pre-breeding movements and breeding).

Results

Autumn migration: age differences

During autumn migration, adult Spanish Eleonora's falcons spent on average 31.3 days reaching the wintering grounds (SD = 9.3, n = 7; Fig. 1) while the three juveniles (Fig. 2) employed 51 days on average (SD = 11.8, n = 3). Croatian Eleonora's falcons reached the wintering grounds in 28 days (SD = 10.4, n = 3; Fig. 1). The Spanish adults' average route straightness was 0.83 (SD = 0.05, n = 7), while, for the two juveniles wintering in Madagascar, the straightness values were 0.7 and 0.64, with 0.6 for the bird wintering in mainland Africa. For Spanish adults, the actual average straight distance between breeding sites and wintering areas was 7740 km (SD = 140, n = 7), while the distance travelled was 9319 km (SD = 631, n = 7). For the two juveniles wintering in Madagascar straight distances were 7744 km and 8578 km, with, respectively, 11 024 km and 13 378 km being the distances travelled. For the juvenile wintering in continental Africa the distances were 6070 km and 10 049 km.

Autumn migration: regional differences

The GLMMs revealed that straightness varied according to age ($F = 8.94$, $p = 0.006$), regional migration speed according to age ($F = 10.08$, $p = 0.008$) and region ($F = 16.96$, $p < 0.001$) and short-distance days according to all factors: age ($F = 14.62$, $p = 0.002$) region ($F = 9.4$, $p = 0.001$), and their interaction ($F = 6.43$, $p = 0.006$). Further pairwise tests showed that, as far as regional migration speed was concerned, there were no significant differences between adult and juveniles in the Sahara desert ($U = 11$, n.s., Fig. 3b), while differences were significant during the crossing of the Sahel ($U = 0$, $p = 0.003$) and in Equatorial Africa ($U = 1$, $p = 0.005$). A similar pattern occurred with straightness (Fig. 3a, 4; Sahara: $U = 15$, n.s.; Sahel: $U = 6$, $p = 0.04$; there being not enough cases for juveniles in Equatorial Africa). Short-distance days were equally distributed among adults and juveniles in the Sahara desert (Fig. 3c; $U = 24$, n.s.; mean_{adults}: 0.75, SD = 1.5, n = 8; mean_{juveniles}: 0.22, SD = 0.5, n = 6), but we observed a significant imbalance towards juveniles in the Sahel ($U = 3$, $p = 0.01$; mean_{adults}: 1.5, SD = 1.1, n = 8; mean_{juveniles}: 6.4, SD = 3.3, n = 5) and Equatorial Africa ($U = 4.5$, $p = 0.02$; mean_{adults}: 0.75, SD = 1.2, n = 8; mean_{juveniles}: 4.8, SD = 4.4, n = 5). Within adults, short-distance days were evenly distributed among regions ($K = 2.9$, n.s.), while among juveniles they were more

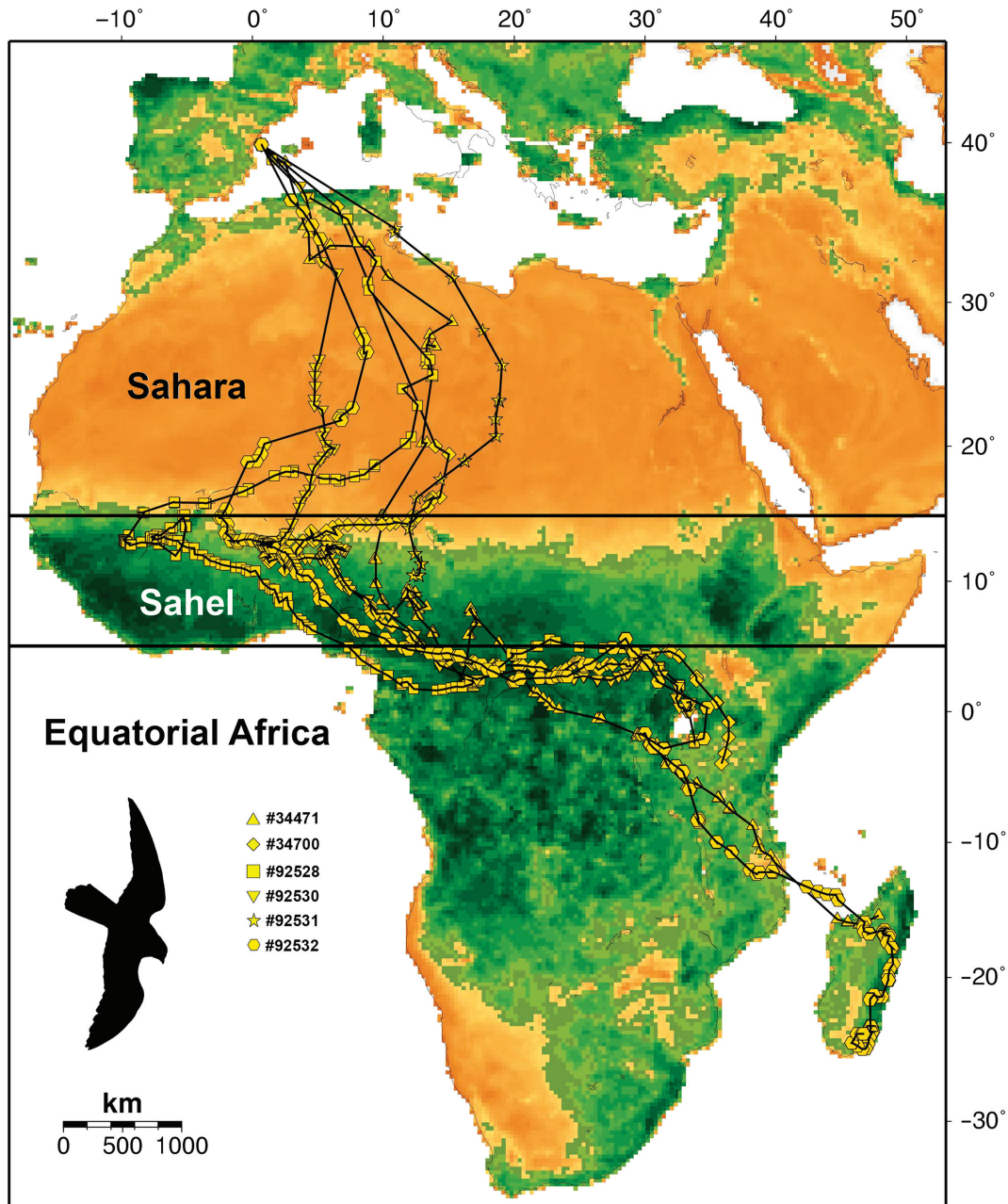


Figure 2. The autumn migration tracks of six juveniles Eleonora's falcons. The background represents the NDVI for November 2009 (legend in Fig. 4).

frequent in the Sahel ($K = 11.2$, $p = 0.004$). In the Sahel, stop-over segments mainly occurred in Mali, Burkina Faso and Nigeria, around 12° – 13° of latitude (Fig. 4).

Finally, as far as repeated journeys by the same individual were concerned, we found neither route nor stop-over site fidelity during autumn ($n = 3$ adults), with the same individual flying in the Sahara desert on a route up to 1200 km from that followed the previous year (Fig. 1, 4).

Stop-overs during spring migration

During spring migration, adult Spanish Eleonora's falcons spent 27.6 days on average to reach the breeding grounds ($SD = 7.4$, $n = 5$) while the immature no. 92532 spent

62 days (Fig. 5). Out of five tracks for Spanish adults, we found an average of 3.2 ($SD = 3.7$, range = 0–9) short-distance days (all during April) in Ethiopia/Somalia, with one bird also stopping for six days in Cameroon. Among the two Spanish immatures, bird no. 34700 stopped for 27 days in Ethiopia/Somalia and nine in Chad, while bird no. 92532 stopped for 13 days in Ethiopia/Somalia, two in Chad and seven in Northern Algeria. In the two spring journeys of Croatian adults, we found seven short distance days in bird no. 96573 and five in bird no. 96574, all of them in Ethiopia during April.

Repeated spring journeys were available for two Spanish adults, with very different routes between years, especially when crossing the Sahara desert. For example,

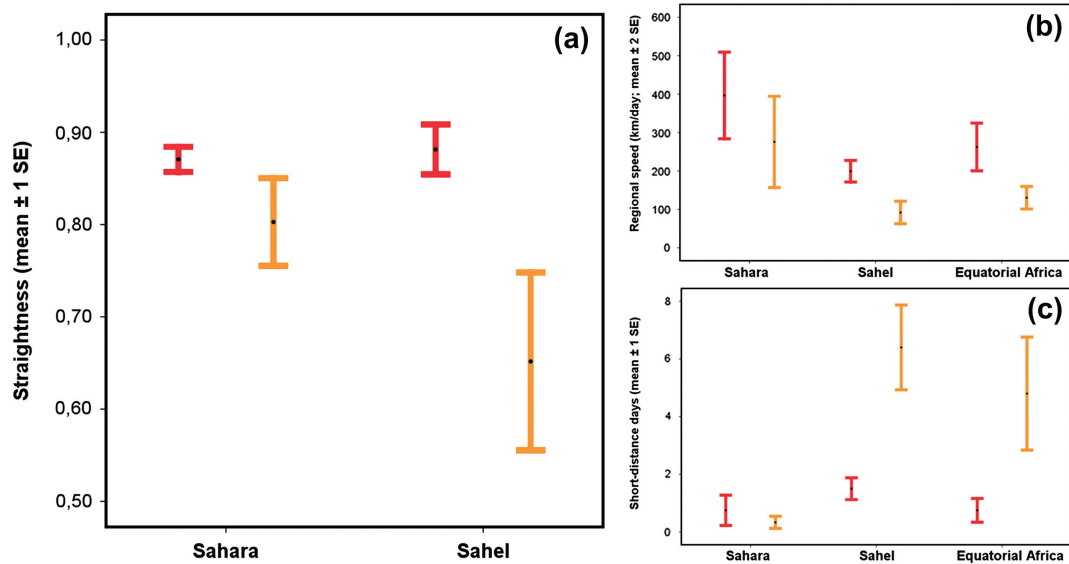


Figure 3. Regional variation in straightness (a), migration speed (b) and number of short-distance days (c) of adults (red) and juveniles (yellow) Eleonora's falcons during autumn migration.

adult no. 80399 used two stop-over areas in Ethiopia only ca 200 km apart in 2009 and 2010, and then crossed the Sahara on tracks separated by up to ca 2800 km.

Seasonal differences and annual cycle

There were no significant differences between spring and autumn migration tracks during the crossing of the Sahara desert (30°N: $U = 17$, n.s.; 20°N: $U = 21$, n.s.). In contrast, in the remaining three intervals the differences were significant (10°N and 0°: $U = 0$, $p = 0.001$; 10°S: $U = 2$, $p = 0.005$),

with spring routes lying further to the east than autumn ones (Fig. 1, 5, 6). These 'average' autumn migration routes were 7% longer than an ideal straight route, while spring ones were 5% longer. The low sample size did not allow carrying out this analysis with Croatian birds, but looking at migration tracks obtained (Fig. 1, 5), the same loop migration pattern clearly was observed.

Autumn and spring migration accounted for 7% and 9% of the annual cycle, while wintering, pre-breeding movements and breeding accounted for 41%, 18% and 25% respectively ($n = 4$).

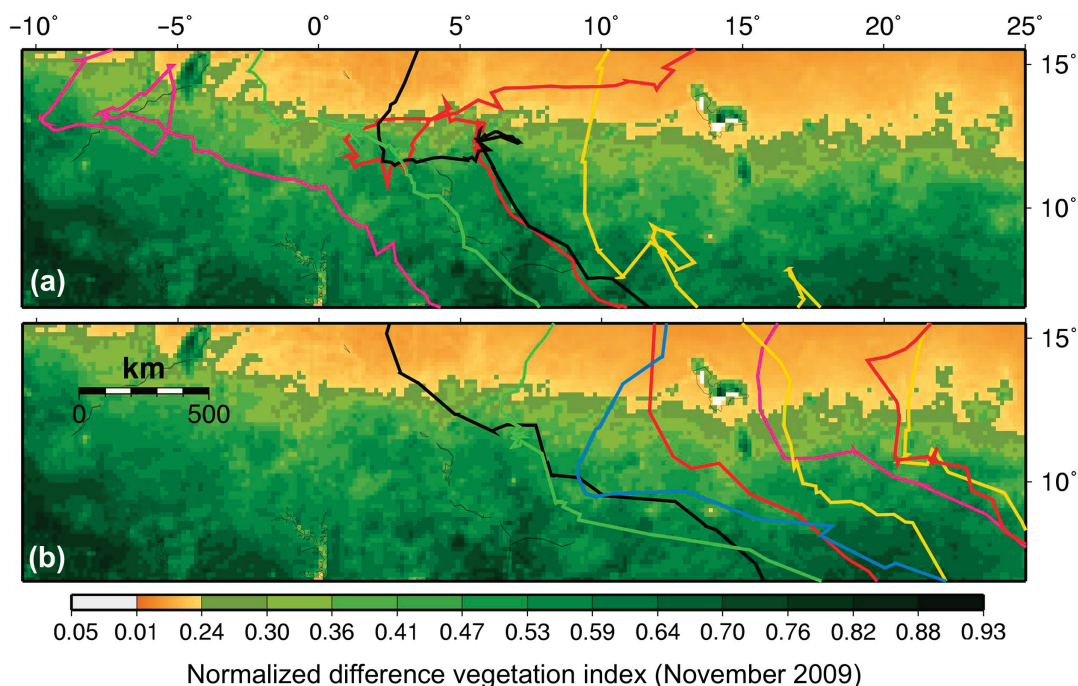


Figure 4. Tracks of juveniles (a) and adults (b) Spanish Eleonora's falcons crossing the Sahel. The same colour indicates different routes in different years from the same adult individual. The background represents the NDVI for November 2009 (see legend).

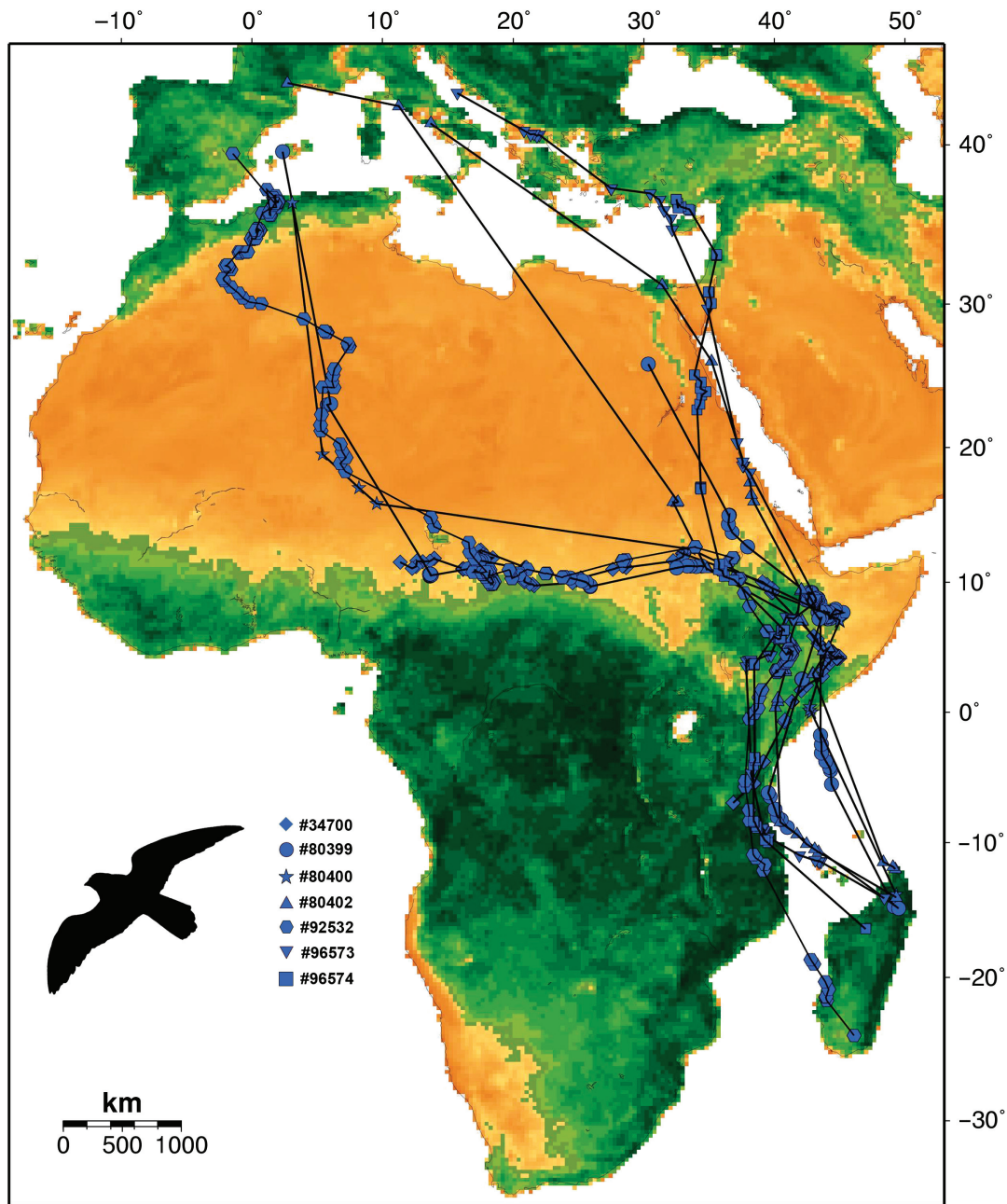


Figure 5. Nine spring migration tracks of seven Eleonora's falcons. The background represents the NDVI for April 2010 (legend in Fig. 4).

Discussion

Age and regional differences during autumn migration

The results of the analyses concerning straightness, regional migration speed and stop-over days all share the same age-related pattern with no differences during the Sahara crossing and significant differences in the remaining two regions, with the juveniles showing more tortuous routes, slower speeds and more stop-over days than adults, especially in the Sahel. The Sahara desert is an ecological barrier where foraging is barely possible and rapidly changing

weather conditions can even result in the birds' deaths (Strandberg et al. 2010). Therefore, Eleonora's falcons try to cross this region as fast as possible regardless their age class and the observed variability in travel rates is perhaps largely dependent on weather conditions. By contrast, the regions that follow and the Sahel in particular, host benign habitats where an insectivorous bird such as the Eleonora's falcon can find large amounts of food in the right season (Zwarts et al. 2009). Why then, is there such a difference in migration performance between adults and juveniles? Juveniles stopped as soon as the habitat became suitable for foraging, just south of the edge of the Sahara (Fig. 4). The same pattern was also observed for juveniles from

Sardinia and Greece, stopping in the same regions and landscape type (*Acacia savannah*) for approximately two weeks (Gschweng et al. 2008, Kassara et al. 2012). This difference between age classes might be explained by differences in fuel accumulation before starting migration due to differences in hunting skills. Similar age-dependent patterns have also been observed in other species of raptors (Restani 2000, Ueta and Higuchi 2002, Strandberg and Alerstam 2007). Irrespective of age, the Sahel belt is known to be an important stop-over area for many trans-equatorial migrants, some even stopping for several weeks (Pearson and Lack 1992, Tøttrup et al. 2011) to exploit the favourable foraging conditions occurring after the end of the summer rains. Therefore, it is possible to argue that, the Sahel in particular, is a vast, rather 'diffuse' stop-over area, where juveniles Eleonora's falcons use a fly-and-forage strategy. Such differences ultimately trigger the overall age differences in migration duration, with juveniles needing in some cases twice the time of adults to accomplish the entire journey.

Seasonal differences

When comparing autumn vs. spring migration routes, two main differences arose: 1) unlike the long non-stop flights (> 1200 km) observed in spring, during autumn Eleonora's falcons try to minimize the flight distance over the Mozambique Channel, crossing where it is narrowest (ca 600–800 km; Fig. 1) and then heading northeast in Madagascar, since the main wintering grounds are located in the northern part of the island (Gschweng et al. 2012, Mellone et al. 2012b); 2) around ca 5° S, during spring, Eleonora's falcons shift their course eastwards, heading towards Ethiopia and Somalia (Fig. 5, 6). Such differences provide the shape for a loop migration pattern that seems to be consistent and widespread between different years, individuals and population of Eleonora's falcons. In fact, in addition to our Spanish and Croatian birds, birds belonging to the Sardinian and Greek populations also exhibited the same pattern (Gschweng et al. 2008, Kassara et al. 2012). Loop migrations can arise either as a result of wind, habitat or motivational differences between seasons (Klaassen et al. 2010, Alerstam 2011, Agostini et al. 2012, Limiñana et al. 2012b, 2013). Prevailing wind patterns might explain why Eleonora's falcons seek to minimize the water crossing during autumn migration but not in spring, when winds are more supportive (Kemp et al. 2010, Mellone et al. 2011). However, wind drift cannot be invoked to explain why Eleonora's falcons show such an eastward directional shift towards Ethiopia during spring instead of going to their breeding areas retracing their autumn itinerary, or simply heading northwest because winds are mainly easterlies during both seasons (Kemp et al. 2010). A similar change of course was reported for individually tracked Red-backed shrikes (*Lanius collurio*; Tøttrup et al. 2011), and explained in the light of more suitable habitat. Thus, if winds are not the reason, an alternative explanation might be habitat suitability: after the long non-stop flight over the ocean and before the crossing of another ecological barrier such as the Sahara desert Eleonora's falcons need to replenish their energy stores. The observed eastward shift also coincides with the region where the majority of spring short-distance

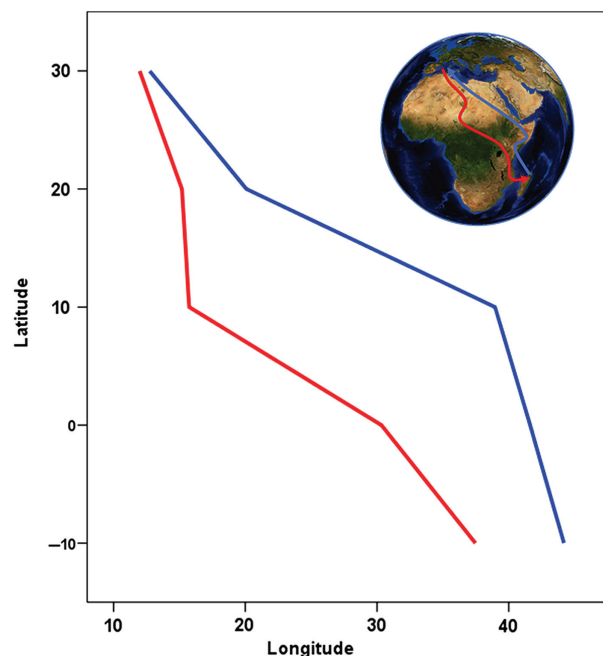


Figure 6. Mean longitude plotted against latitude (at intervals of 10°) of the migratory tracks of adult Eleonora's falcons during autumn (red) and during spring (blue). The inset shows a schematic representation of the same tracks.

days occurred (i.e. Ethiopia). This region experiences rain peaks precisely during spring (the 'belg' season, Glantz 1987; see also Pearson and Lack 1992), that might boost insect abundance (Janzen and Schoener 1968, Trierweiler et al. 2013). The high inter-year variation in rainfall patterns (Glantz 1987), as well as individual conditions, could explain the spatial and temporal variation in the occurrence of such stop-over areas (see also Tøttrup et al. 2012). According to Pearson and Lack (1992), the loop migration that many Palearctic migrants seem to perform in this area may be explained by climatic patterns, since in April Ethiopia and Somalia are green, while much of the Sahelian belt is very dry, with the opposite occurring in early autumn (compare the northern limit of the Sahelian green belt in Fig. 1 and 2 vs Fig. 5).

Conclusions

Are Eleonora's falcons time or energy minimizers? Despite the spring routes being slightly shorter than the autumn ones, adults performed longer stop-overs in spring than in autumn, resulting in a longer time spent during spring migration (9% vs 7% of the annual cycle), suggesting a lack of urgency in reaching the breeding areas. In fact, Eleonora's falcons do not immediately occupy their breeding colonies after spring arrival, but, instead, spend up to two months in pre-breeding areas that may be far away from the colonies (18% of the annual cycle; Mellone et al. 2013), delaying their reproduction until mid-summer, unlike other Palearctic migratory birds (Walter 1979, Mellone et al. 2012c).

The fact that the two immatures also deviated eastwards to Somalia and Ethiopia during spring migration suggests that this orientation shift might also be endogenously

controlled, e.g. the temporal and spatial components of the loop migration strategy have been ‘fixed’ in Eleonora’s falcons’ innate circannual program (Thorup et al. 2010; Fig. 6). Eleonora’s falcons spatially integrate seasonal changing resources on a continental scale throughout their annual cycle, changing their movement patterns in response to internal (age) and external factors (habitat). Some regions crossed by Eleonora’s falcons during migration can be used as foraging areas and their selection as such is highly dependent upon the season, promoting a loop migration. Future research using GPS devices, with higher spatial and temporal resolution, will provide new insight into how Eleonora’s falcons mix pure migrational behaviour with the fly-and-forage and stop-overs strategies, and will eventually help to identify priority areas for their conservation.

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