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RESEARCH ARTICLE

From the Mediterranean Sea to Madagascar: Are there ecological barriers for the long-distance migrant Eleonora's falcon?

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Abstract We examined the connection between landscape characteristics and behaviour of a long-distance migratory raptor. Our main goal was to test whether long-distance migratory birds adjust their migration programme according to the different characteristics of the habitats crossed during the journey with special emphasis in the so-called "ecological barriers", inhospitable environments such as deserts, ice fields, seas and mountain ranges, where the opportunities to fulfil energy requirements are low or absent and environmental factors could be extremely severe. To this end, 11 Eleonora's falcons were tracked by satellite telemetry in their ca. 9000 km autumn migration route from colonies located in Western Mediterranean to their wintering grounds in Madagascar during 2007 and 2008. Our results show that Eleonora's falcons migrated during day and night-time, adjusting migration speed and daily distance in relation to the crossed region. Unlike other migrant species, Eleonora's falcons did not avoid ecological barriers by making unnecessary detours around them or converging on narrow corridors. Nocturnal migration and higher daily distances were observed when flying across the Sahara Desert and the Mozambique Channel. The circadian pattern of activity budget shows that Eleonora's falcon relies on an internal navigation mechanism that works during both day and night. Finally, our results suggest that the Sahara is an ecological barrier not only for passerines but also for raptors migrating within the Palaearctic-African flyway.

Keywords *Falco eleonorae* · Long-distance migration · Navigation · Orientation · Route convergence · Satellite tracking

Introduction

During their migratory movements between breeding and wintering ranges, birds face a variety of landscapes that can greatly affect their migration paths and schedules (Klaassen et al. 2008). Detailed understanding of the connection between landscape characteristics and behaviour of migrating birds is important in the light of current global changes. Moreover, this is particularly important in the case of long-distance migratory species for which changes in environmental conditions could affect timing of

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reproduction and migratory behaviour. In particular, “ecological barriers” have constrained the evolution of migration pathways. These are inhospitable environments such as deserts, ice fields, seas and mountain ranges, where the opportunities to fulfil energy requirements are low or absent and environmental factors could be extremely severe (e.g. extreme temperatures or adverse wind conditions; Newton 2008; Strandberg et al., in press). For example, there is a general agreement that the Sahara Desert is the major ecological barrier of the Palaearctic-African migration system, especially for small birds such as passerines (Schmaljohann et al. 2007), as Himalaya and Karakorum mountain ranges are for migratory birds in Asia (Combreau et al. 2009). Recent studies have suggested that the equatorial rainforest could be an obstacle for migrating falcons (Strandberg et al. 2009a). On the other hand, vast open ocean could be a migration corridor for landbirds, since this environment provides a wind-assisted passage relatively free of pathogens and predators (Gill et al. 2009), challenging previous hypotheses and even the physiological limits of migratory birds.

In order to overcome an ecological barrier, migrating birds can choose among different strategies. Birds can either (1) make a detour to avoid crossing the barrier; (2) concentrate along routes that involve a shorter crossing; (3) try to maximise the migration speed reducing the travelling time when flying over the barrier; and even (4) the combination of the second and third scenarios. In the first scenario, a clear significant change in migration direction when approaching the barrier would be expected, whereas, in the second scenario, converging routes rather than scattered ones would be expected. In the third case, the expected behaviour would be the achievement of higher travelling speed during the barrier crossing (eventually increasing flight speed and reducing the number of stops, e.g. flying during night; Alerstam 2009), counterbalanced by more stops when flying across more suitable regions.

To test these hypotheses, we used satellite-based telemetry to investigate the case of an extreme long-distance migratory raptor, the Eleonora’s falcon (*Falco eleonorae*), in the 9000 km migration between breeding colonies in western Mediterranean Sea and wintering areas in Madagascar. Eleonora’s falcon is one of the smallest bird species that is possible to track with satellite transmitters without exceeding 3% of bird’s body mass (Kenward 2001), and for this reason, while there are several studies on migration of large raptors, those dealing with medium and small-sized species have been absent until recently. In addition, Eleonora’s falcon crosses a huge variety of different environments such as large water bodies, deserts and dense forests that presumably could be acting as ecological barriers, and thus this species may provide interesting insights into the behavioural response of migratory birds to landscape characteristics.

Materials and methods

Study species

The Eleonora’s falcon is a cliff-nesting raptor that usually breeds on isolated small islands and feeds mainly on small birds and insects (Ferguson-Lees and Christie 2001). A unique characteristic of the species is that it adjusts its breeding season to coincide with the post-breeding autumn migration of its small passerine prey, usually in late August and early September, making it one of the latest raptor breeding seasons in the Northern Hemisphere (Walter 1979). The global population has been recently estimated between 13,000 and 14,000 breeding pairs (Dimalexis et al. 2008) after a strong decrease in population numbers in past decades, mainly due to poisoning in foraging areas, decrease of food abundance and human disturbance at colonies (Walter 1979; Dimalexis et al. 2008). Unlike bigger raptors, such as eagles and vultures that migrate by exploring thermal convection using soaring flight, the Eleonora’s falcon is characterised by higher wing aspect ratio and therefore is more adapted to flapping flight (Spaar 1997). This allows Eleonora’s falcons to migrate irrespective of large water bodies (Kerlinger 1989; Meyer et al. 2000) and therefore it is a good model to study landscape effects on avian migration patterns.

Animal tagging, PTT programming and study area

The 11 Eleonora’s falcons tracked in this study were captured in the Balearic Islands in autumn 2007 and 2008, and in the Columbretes Islands in autumn 2008 (Table 1), both in Spain. Birds were trapped using

Table 1 Signal transmission data and histories of 11 Eleonora's falcons fitted with satellite transmitters (PTTs) in their autumn migration from Western Mediterranean colonies to Madagascar during 2007 and 2008

ID#	Sex	Age	Weight	Tagging date	Tagging site	Migration onset	Migration duration	Migration end	Distance (km)	Distance/ day (km/d)	End of transmission	Country
34469	Male	Adult	335	17/09/2007	Balearic Is.	26/10/2007	38	03/12/2007	8332	219	10/01/2008	Madagascar
34471	Male	Juvenile	400	14/09/2007	Balearic Is.	27/10/2007	47	13/12/2007	9015	192	05/04/2008	Madagascar
39715	Male	Juvenile	400	14/09/2007	Balearic Is.	–	–	–	–	–	24/10/2007	Spain
80396	Female	Subadult	354	25/08/2008	Columbretes Is.	30/09/2008	45	15/11/2008	9224	205	19/10/2009	Madagascar
80397	Female	Adult	468	26/08/2008	Columbretes Is.	21/10/2008	–	–	–	–	06/11/2008	Algeria
80398	Female	Subadult	344	27/08/2008	Columbretes Is.	–	–	–	–	–	01/09/2008	Spain
80399	Female	Adult	425	13/09/2008	Balearic Is.	20/10/2008	20	10/11/2008	8991	450	–	–
80400	Male	Adult	337	13/09/2008	Balearic Is.	21/10/2008	26	17/11/2008	8874	341	30/04/2009	Algeria
80401	Female	Juvenile	488	22/09/2008	Columbretes Is.	22/10/2008	–	–	–	–	02/11/2008	Lybia
80402	Female	Adult	453	22/09/2008	Columbretes Is.	20/10/2008	27	17/11/2008	9199	341	–	–
80403	Male	Juvenile	466	24/09/2008	Columbretes Is.	23/10/2008	–	–	–	–	02/01/2009	Niger

dho-gaza nets and a stuffed Eagle Owl (*Bubo bubo*) as a decoy (Bub 1991). All birds were weighed, measured, ringed and sexed using molecular methods. Birds were equipped with Microwave Telemetry's 9.5 g solar-powered PTT-100 platform transmitter terminals (PTTs) affixed to their backs using a Teflon harness (Kenward 2001; Limiñana et al. 2007, 2008). PTTs were programmed with a duty cycle of 8 h on/15 h off for the first 3 months of operation, and for subsequent months, the duty cycle consisted of 12 h on/58 h off as described in López-López et al. (2009). Locations were collected using the Argos system, and only locations assigned to location classes (LCs) 3, 2, 1 and 0 were used for the analyses. These LCs are a measure of reliability provided by Argos and they have nominal accuracies of <150, 150–350, 350–1000 and >1000 m, respectively (Argos 1996). Lower accuracy LCs (A, B) were used only when in agreement with normal travel rates (speed and direction; Strandberg et al. 2009b). Locations belonging to class Z were not used. Also, to avoid biases associated with temporal auto-correlation, positions obtained less than 1 h after the previous one were excluded from the analyses (Limiñana et al. 2007, 2008). When more than one location was available within a given hour, we used the one of highest quality. All data were retrieved and managed using the Satellite Tracking and Analysis Tool (Coyne and Godley 2005) and are publicly available at MoveBank (http://www.movebank.org/).

Timing of migration

The onset of migration was estimated to be the middle day between the last location of Eleonora's falcons in Spain and the first location in Africa, given that the birds do not perform any pre-migratory movement and depart directly to Africa from the breeding areas (López-López et al. 2009). Similarly, the date of the end of the migration was estimated as the first location of Eleonora's falcons in Madagascar.

Random tracks simulations

In order to test whether the observed migration routes converged towards predetermined targets, e.g. areas where a strong route convergence would be unlike to arise by chance, and thus significantly different from a direct migration route, we generated random tracks using observed migration parameters. This analysis followed the Strandberg et al. (2009a) rationale. To this end, we calculated the longitudinal intersections of the observed paths for each 5° latitude interval between 35°N and 15°S and calculated the mean longitude as well as the scatter in longitude (standard deviation and range) at the different latitudes. Then, the changes in longitude for each 5° longitude segments were calculated and used to generate random tracks by reshuffling these segments between the initial and the end locations at 35°N and 15°S, respectively. After each round of reshuffling the longitude at each of the latitudes (11 different latitudes in our case) for each individual was obtained. Then we calculated the longitude mean and scatter in the same way that we did for observed tracks and this procedure was repeated 1,000 times per individual. To test for non-randomness in mean longitude, the mean overall longitude and scatter for the simulated journeys was calculated for each simulation round and compared with the corresponding overall mean longitude and scatter for the observed tracks, following Strandberg et al. (2009a). Probability values for random effects were estimated from the proportion of simulations giving the same or more extreme values than those observed (see Strandberg et al. 2009a for further details on the method). To avoid possible bias in longitudinal scatter caused by non-randomness in mean longitude and in order to detect convergences in only a single part of the migration route, simulations were also generated by dividing the journey in a single interval between 35°N and 15°S (the case explained above), two intervals, between 35°N–10°N and 10°N–15°S, and three intervals, between 35°N–15°N, 15°N–0° and 0°–15°S.

Migration speed and barriers

To analyze if there were differences in flight speed, daily distance and time budget when crossing different habitat types, the migration routes were divided into five different regions namely Sahara, Sahel, equatorial region, SE Africa plains and Mozambique Channel (Fig. 1). Regions were defined as bands of latitudinal range as follows: (1) Sahara (from 35°N to 15°N), (2) Sahel (from 15°N to 5°N), (3) equatorial region (from 5°N to 3°S), (4) SE Africa plains (from 3°S until the start of sea crossing) and (5) the Mozambique Channel.

We used successive telemetry locations to divide the real migration paths into segments and only segments between 1 and 4 h long were used for the analysis. We calculated flight speeds for each segment and following Strandberg et al. (2009b) we considered only segments with speed >5 km/h belonging to active migration (travelling), while for the others we assumed that the bird was not migrating (stationary segments). Raw data (i.e. flight speeds calculated from the real telemetry locations) showed high variation both between and within individuals in relation to regions, and therefore did not fit the canonical assumptions of standard statistical tests such as Generalized Linear Models (e.g. variance homogeneity, normal distribution of residuals). To overcome this, we performed Monte Carlo simulation analysis on individual birds (Rubinstein and Kroese 2007). To test for differences in migration speed among regions, the average speed per region was calculated with the observed data (average *observed* speed per region). Then, migration speeds were reshuffled within each individual and 999 simulation rounds were performed for each individual. After that, average migration speed per region was calculated for each simulation round (average *simulated* speed per region) and was compared with the observed average migration speed. Finally *P*-values were estimated as the proportion of simulations giving the same or more extreme values as observed. The null hypothesis assumed that there were no differences between observed and simulated speeds. Because the alternative hypothesis was non-directional a two tailed probability distribution was used. The threshold of significance was set at $\alpha = 0.05$.

Daily distance across the different regions was calculated for each bird, dividing the distance between the first and last locations in each region by the elapsed hours, and then multiplying by 24 h. The number of daily travelling hours were also estimated by dividing the mean speed of migration on travelling days (km/24 h; based on locations between different days) by mean short-interval speeds (km/h; including only segments >5 km/h; Strandberg et al. 2009b).

Circadian patterns of migration

To analyze migratory behaviour in relation to the time of day we used only intervals shorter than 4 h (Limiñana et al. 2007; Strandberg et al. 2009b), with

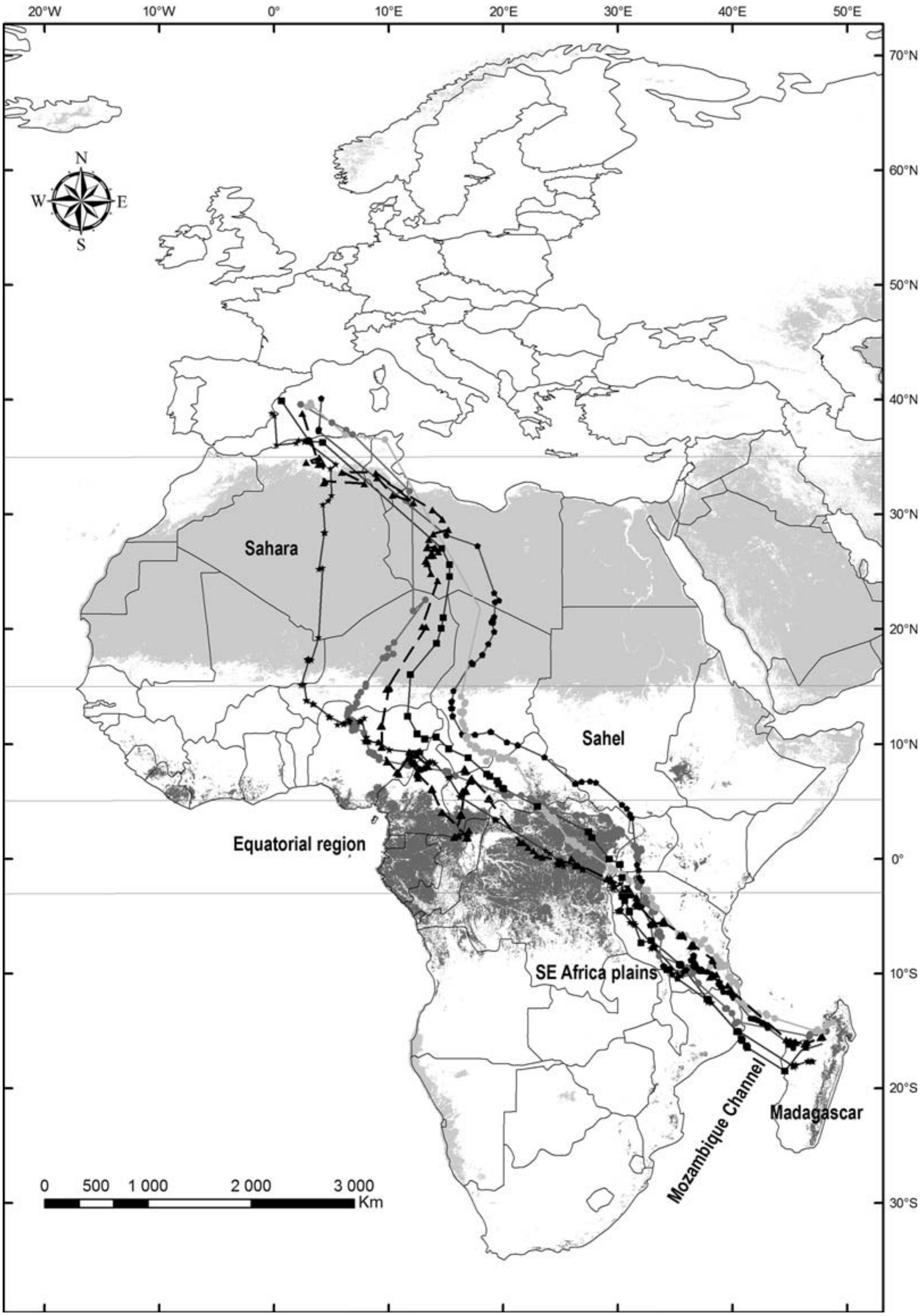

Fig. 1 Autumn migration routes of six Eleonora's falcons (*Falco eleonorae*) tracked by satellite telemetry from their breeding colonies in the Western Mediterranean to Madagascar during 2007 and 2008. Route of adult birds shown with *solid line* and the juvenile with *dashed line*. Desert and equatorial rainforest regions are highlighted in two shades of *grey* (adapted from Olson et al. 2001). The main geographic regions used for analyses are shown (see text for details)

each interval assigned to an hour according to local time at the end of the segment. Local time was calculated by correcting GMT times according to each time zone. Nocturnal segments were those for which at least half the time length occurred after sunset or before sunrise. The exact time of sunrise and sunset for every location was obtained from the website http://aa.usno.navy.mil. Segments were considered either "travelling" or "stationary" according to the same criteria mentioned before (stationary if migration speed was <5 km/h) (Strandberg et al. 2009b). Differences in travel rates among regions were tested by means of contingency tables.

Results

After trapping and marking 11 Eleonora's falcons, we obtained six complete autumn migration routes from the Western Mediterranean breeding colonies to wintering areas in Madagascar, corresponding to four adults, one subadult (second calendar year) and one juvenile (Fig. 1). Detailed migration parameters, bird histories and signal transmission data are shown in Table 1. The comparison of the observed routes with randomly simulated ones did not show significant differences that would suggest convergence towards goal areas or travelling along narrow corridors (Fig. 2). Similar results were obtained when excluding the juvenile from analyses and when dividing the journey in two or three intervals (all tests non-significant, Table 2).

Daily distances differed among regions (Kruskal–Wallis test: $H_{4,30} = 16.18$, $P = 0.003$), with the highest value observed in the Mozambique Channel and the lowest in the Sahel (Fig. 3). The comparison of observed speeds with expected speeds among different regions showed a high variation within individuals, with results being significant in 11 cases (Table 3). Observed speeds were lower than expected in the Sahel (four cases) and in the equatorial region (two cases), while higher speeds were observed in the Sahara and in the Mozambique Channel, respectively. The average number of daily travelling hours was 11.3 ± 4.6 h (range: 5–24), with higher values in the Mozambique Channel (24 h) and the Sahara (12.7 ± 6.6 h), and the lowest in the Sahel region (9.2 ± 3.2 h).

Birds migrated during both day and night and within all regions (Fig. 4), although during night-time there were differences in the number of travelling segments among regions (Fig. 5; $\chi^2 = 29.67$, d.f. = 3, $P < 0.001$). The nocturnal travel rate was higher in Sahara than in the Sahel ($\chi^2 = 24.1$, d.f. = 1, $P < 0.001$). However, no differences occurred among the equatorial region and SE Africa plains ($\chi^2 = 2.01$, d.f. = 1, n.s.). During day-time, no differences occurred among the four regions ($\chi^2 = 3.4$, d.f. = 3, n.s.) but interestingly, of the six Saharan segments, none was a stationary one.

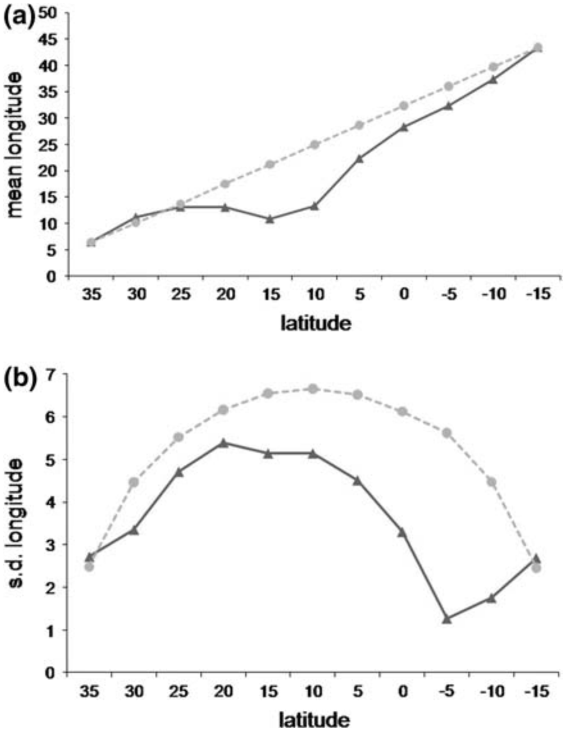

Fig. 2 Comparison between **a** mean longitude and **b** scatter of longitudes (measured as standard deviation), for the six observed routes of Eleonora's falcons (connected by a *solid line with triangles*) and 1,000 simulated random tracks (*dashed line with circles*). Values were calculated at 5° latitude intervals

Discussion

Our results show that Eleonora's falcons tracked from Western Mediterranean islands migrate during day and night-time, travelling through inland Africa until reaching the wintering areas in Madagascar. Similar inland routes have been reported for Eleonora's falcons tracked from other Mediterranean colonies

Table 2 Comparison between observed migration parameters (mean longitude and scatter in longitude measured as standard deviation) and a set of 1,000 simulated random tracks per animal

	Latitudinal range	Individuals	Mean longitude observed	Mean longitude simulated	Mean s.d. longitude observed	Mean s.d. longitude simulated	Number of random simulations	*P*-value longitude	*P*-value s.d. longitude
1 interval	35°N 15°S	All	21.049	24.896	12.445	12.285	6000	0.818	0.560
	35°N 15°S	Adults	22.551	25.896	11.931	12.046	4000	0.786	0.649
2 intervals	35°N 10°N	All	11.313	9.856	2.618	2.580	6000	0.360	0.717
	10°N 15°S	All	29.497	28.356	10.745	11.250	6000	0.362	0.667
	35°N 10°N	Adults	13.173	11.523	2.982	2.793	4000	0.333	0.542
	10°N 15°S	Adults	30.718	29.631	10.041	10.734	4000	0.457	0.551
3 intervals	35°N 15°N	All	10.911	8.618	2.712	1.747	6000	0.279	0.557
	15°N 0°	All	18.691	19.548	8.073	7.505	6000	0.609	0.333
	0° 15°S	All	35.337	35.847	6.523	6.503	6000	0.557	0.500
	35°N 15°N	Adults	12.751	10.423	3.127	2.086	4000	0.256	0.415
	15°N 0°	Adults	20.776	21.636	8.017	7.384	4000	0.705	0.250
	0° 15°S	Adults	36.126	37.108	6.068	5.921	4000	0.750	0.333

To analyze for convergence in the migratory route, comparisons were made between the migration route as one single interval, and by dividing into two and three latitudinal intervals. Comparisons were also made including all individuals together (juvenile, subadults and adults) or only adults

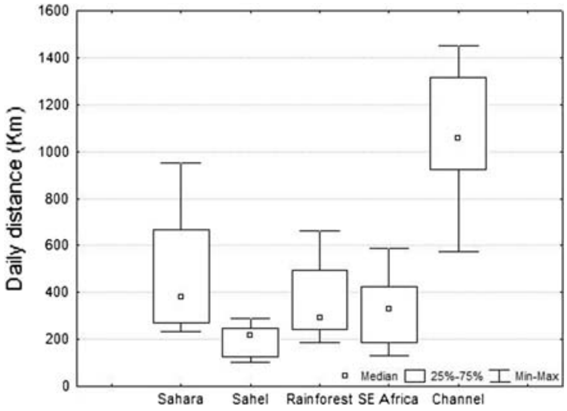

Fig. 3 Daily distance covered across the five main regions during autumn migration of six Eleonora's falcons tracked by satellite telemetry. Median, 25 and 75% percentiles and maximum and minimum data are shown

either in Sardinia (Gschweng et al. 2008) or Greece (http://www.ornithologiki.gr/life/falcoel/en/program/satellite_map.php; unpubl. data). The Eleonora's falcons tracked in this study migrated through the Sahara Desert, the Sahelian region and the equatorial rainforest without making any detour to avoid those regions, until finally converging in SE Africa (Tanzania and Mozambique) just before crossing the Mozambique Channel. Despite individual variation, our analysis did not discover the existence of narrow migration corridors through ecological barriers (e.g. the Sahara Desert or the equatorial rainforest; Berthold 2001; Strandberg et al. 2009a). In fact, the only apparent convergence occurred in the final part of the route, which leads to the shortest route between mainland Africa and Madagascar.

Our results are different than those obtained by Strandberg et al. (2009a) for the Eurasian hobby (*Falco subbuteo*) using the same random tracks simulation analysis, despite the close taxonomic relationship between the two species and their similar food habits (Ferguson-Lees and Christie 2001). In their migration from Northern Europe to Southern Africa, Eurasian hobbies converged in a narrow corridor after crossing the equatorial rainforest, suggesting that the rainforest acts as an ecological barrier for migratory birds, perhaps related to reduced feeding opportunities at this habitat (Strandberg et al. 2009a). Commenting on the results of satellite tracking of Eleonora's falcons breeding in Sardinia, the same authors hypothesized that this could also happen for Eleonora's falcons because the adults partially avoided the rainforest, migrating along the eastern border, and juveniles changed their direction abruptly after beginning the crossing of the rainforest (Gschweng et al. 2008). However, in our study, four of six adults crossed the equatorial rainforest, and

Table 3 Comparison between observed migration speeds (in km/h) with randomly simulated expected speeds after 999 reshufflings for the five main regions crossed by satellite tracked Eleonora's falcons

Tag ID	Region	Average speed observed	Average speed simulated	*P*-value
34469	Sahara	46.5	34.5	0.210
	Sahel	10.2	34.0	**0.000**
	Equatorial rainforest	42.6	33.7	0.244
	SE Africa plains	14.6	34.1	**0.000**
	Mozambique Channel	31.8	34.0	0.858
34471	Sahara	30.1	28.0	0.750
	Sahel	5.0	28.6	**0.000**
	Equatorial rainforest	16.4	27.7	**0.000**
	SE Africa plains	16.8	27.8	0.072
	Mozambique Channel	62.1	28.7	0.176
80396	Sahara	27.0	18.8	0.352
	Sahel	8.6	18.5	0.304
	Equatorial rainforest	13.6	18.8	0.652
	SE Africa plains	9.1	18.6	0.094
	Mozambique Channel	x	x	x
80399	Sahara	x	x	x
	Sahel	22.1	35.7	**0.000**
	Equatorial rainforest	35.9	35.8	0.968
	SE Africa plains	32.6	35.7	0.478
	Mozambique Channel	62.0	35.8	**0.000**
80400	**Sahara**	41.4	25.6	**0.022**
	Sahel	18.5	25.4	**0.000**
	Equatorial rainforest	16.5	25.5	**0.006**
	SE Africa plains	38.0	25.6	**0.018**
	Mozambique Channel	x	x	x
80402	Sahara	71.4	38.0	0.172
	Sahel	37.1	37.7	0.952
	Equatorial rainforest	24.6	39.0	0.762
	SE Africa plains	8.7	38.9	**0.000**
	Mozambique Channel	60.8	38.8	0.052

Significant results ($P < 0.05$) are highlighted in bold

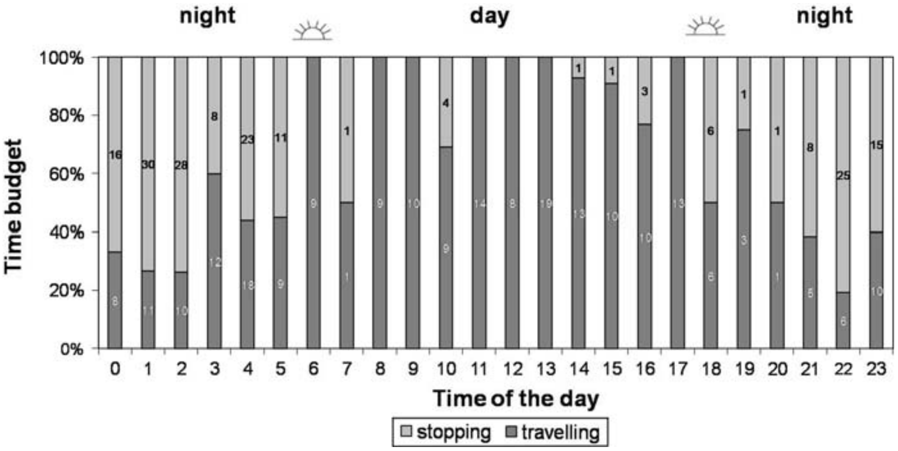

Fig. 4 Time budget of migratory Eleonora's falcons in relation to hour of the day. Segments were divided as travelling (if migration speed exceeded 5 km/h) or stationary (migration speed <5 km/h). Data on all regions are pooled. The number of segments is indicated on the *bars*

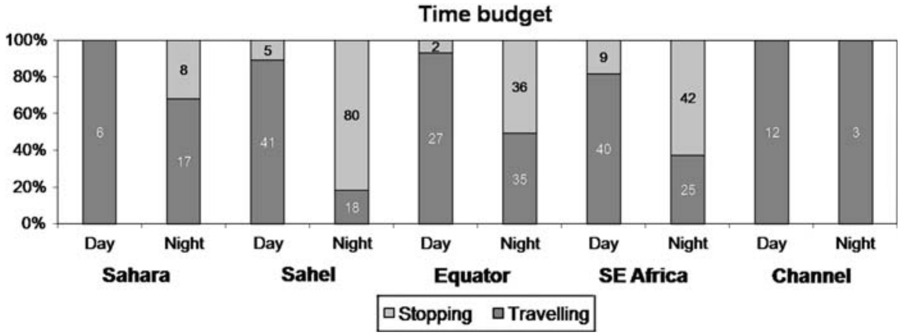

Fig. 5 Daily time budget of Eleonora's falcons in relation to the five main regions crossed during autumn migration from the Western Mediterranean to Madagascar. The number of segments is indicated on the *bars*

those that avoided the rainforest were already migrating using a more easterly route. In contrast to Eurasian hobbies that winter in open habitats (Ferguson-Lees and Christie 2001, see also the map in Strandberg et al. 2009a), Eleonora's falcons live in rainforests in Madagascar during the winter, suggesting that this environment does not represent a real barrier for the species.

Daily distance travelled varied among regions, due to changes in flight speed and time budget. Although is difficult to unravel a fixed pattern in these changes, it is interesting to note that the lowest speeds occurred in the same region, the Sahel, where the nocturnal travel rate was also lower, probably to counterbalance the extreme energetic consumption previously experienced during the crossing of the Sahara Desert. In fact, during the Sahara crossing Eleonora's falcons increased their nocturnal travel rate and did not stop during daytime. Locations over favourable habitats such as oases, or with certain topographic attributes (e.g. valleys) were not observed along the route. Taking into account that feeding opportunities are quite low in desert landscapes, the absence of stationary daylight segments suggest that the birds avoid foraging in this environment and try to spend as much time as possible in active migration in order to overcome the barrier as soon as possible. This is in agreement with our third scenario, for which birds would try to maximise the migration speed when flying over an ecological barrier (Alerstam 2009). Similar results have been reported for other raptor species whose migration have been investigated by mean of satellite telemetry, such as the osprey (*Pandion haliaetus*), honey buzzard (*Pernis apivorus*), marsh harrier (*Circus aeruginosus*) and hobby (Kjellén et al. 2001; Hake et al. 2003; Klaassen et al. 2008; Strandberg et al. 2009b, in press). These species also reached faster speeds during the Sahara crossing, exceeding the speeds recorded in other regions. The absence of differences for these species in travel rates between the equatorial region, where the main environment is the rainforest, and SE Africa, where open savannahs dominate the landscape, suggests that for these birds the rainforest does not represent an ecological barrier.

The circadian pattern of activity budget showed a consistent high rate of nocturnal migration throughout all regions. Nocturnal flights of migrating raptors have been reported mostly over water (see De Candido et al. 2006 and references therein), presumably because thermal updrafts are absent during both day and night, resulting in no differences in energy expenditure (Alerstam 2009). Regular nocturnal migration over land has been only shown for the Levant sparrowhawk (*Accipiter brevipes*) (Stark and Liechti 1993; Spaar et al. 1998) and less frequently for the Eurasian hobby (Strandberg et al. 2009b). This behaviour is more typical of other groups of migrating birds, especially passerines (Berthold 2001; Alerstam 2009). These findings suggest that these species, now including Eleonora's falcon, rely on an internal navigation mechanism that works during both day and night.

Finally, our results support the hypothesis that the Sahara is an ecological barrier not only for passerines (Berthold 2001; Schmaljohann et al. 2007) but also for raptors migrating within the Palaearctic-African flyway. The crossing of the Sahara has a profound influence on survival and fitness of migrants (Strandberg et al., in press; García-Ripollés et al., in press) and, for this reason, an increase in migratory speed during the Sahara crossing is important in order to minimize the associated risks, such as starvation, disorientation, unfavourable weather conditions and even sand storms. Given that Eleonora's falcon abruptly increase their energetic consumption during the crossing of desert landscapes, the lower travel rates observed in the Sahel region just after having crossed the Sahara desert may reflect a strategy to replenish their energy reserves in a more productive environment. Our study also shows that long-distance migratory birds adjust their migration activity according to the different landscapes crossed during the journey, but that the response differs among individuals. In the light of the rapid shift of world biomes due to global change (Williams et al. 2007), detailed understanding of the connection between landscape characteristics and behaviour of long-distance migratory birds is of utmost importance. This is especially important in the case of long-migrant species crossing such a great variety of environments as Eleonora's falcon do, for which small changes in environmental conditions could have unexpected consequences that could jeopardize timing of reproduction and even the survival of maladjusted birds (carry-over effects), given the mismatch between migration schedules and food availability (Both et al. 2006). Forecasting how global changes will shape the future behaviour of migratory birds constitutes the next challenge.

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References

Alerstam T (2009) Flight by night or day? Optimal daily timing of bird migration. J Theor Biol 258:530–536. doi:10.1016/j.jtbi.2009.01.020

Argos (1996) User's manual. CLS/Service Argos, Toulouse

Berthold P (2001) Bird migration. A general survey. Oxford University Press, New York

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. Nature 44:81–83

Bub H (1991) Bird trapping and bird banding. Cornell University Press, Ithaca

Combreau O, Judas J, Lawrence M (2009) Importance of satellite tracking in Houbara Bustard conservation program in Asia. In: Proceedings of the 2009 bird fish tracking conference. Microwave Telemetry Inc., Elicott City

Coyne MS, Godley BJ (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

De Candido R, Bierregaard RO, Martell MS Jr, Bildstein KL (2006) Evidence of nocturnal migration by Osprey (*Pandion haliaetus*) in North America and Western Europe. J Raptor Res 40:156–158

Dimalexis A, Xirouchakis S, Portolou D, Latsoudis P, Karris G, Fric J, Georgiakakis P, Barboutis C, Bourdakis S, Ivovič M, Kominos T, Kakalis E (2008) The status of Eleonora's falcon (*Falco eleonorae*) in Greece. J Ornithol 149:23–30. doi:10.1007/s10336-007-0207-4

Ferguson-Lees J, Christie DA (2001) Raptors: birds of prey of the world. A & C Black Publishers, Ltd., London

García-Ripollés C, López-López P, Urios V (in press) First description of migration and wintering of adult Egyptian vultures *Neophron percnopterus* tracked by GPS satellite telemetry. Bird Study

Gill RE, Tibbitts TL, Douglas DC, Handel CM, Mulcahy DM, Gottschalck JC, Warnock N, McCaffery BJ, Battley PF, Piersma T (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc R Soc B 276:447–457

Gschweng M, Kalko EKV, Querner U, Fiedler W, Berthold P (2008) All across Africa: highly individual migration routes of Eleonora's falcon. Proc R Soc B 275:2887–2896. doi:10.1098/rspb.2008.0575

Hake M, Kjellén N, Alerstam T (2003) Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. Oikos 103:385–396

Kenward R (ed) (2001) A manual for wildlife radio tagging. Academic Press, London

Kerlinger P (1989) Flight strategies of migrating hawks. University of Chicago Press, Chicago

Kjellén N, Hake M, Alerstam T (2001) Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. J Avian Biol 32:57–67

Klaassen RHG, Strandberg R, Hake M, Alerstam T (2008) Flexibility in daily travel routines causes regional variation in bird migration speed. Behav Ecol Sociobiol 62:1427–1432

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

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

Meyer SK, Spaar R, Bruderer B (2000) To cross the sea or to follow the coast? Flight directions and behaviour of migrating raptors approaching the Mediterranean Sea in autumn. Behaviour 137:379–399. doi:10.1163/156853900502132

Newton I (2008) The migration ecology of birds. Academic Press, London, pp 699–727

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51:933–938. doi: 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Rubinstein RY, Kroese DP (2007) Simulation and the Monte Carlo method, 2nd edn. Wiley, New York

Schmaljohann H, Liechti F, Bruderer B (2007) Songbird migration across the Sahara: the non-stop hypothesis rejected!. Proc R Soc B 274:735–739

Spaar R (1997) Flight strategies of migrating raptors; a comparative study of interspecific variation in flight characteristics. Ibis 139:523–535

Spaar R, Stark H, Liechti F (1998) Migratory flight strategies of Levant sparrowhawks: time or energy minimization? Anim Behav 56:1185–1197

Stark H, Liechti F (1993) Do Levant sparrowhawks *Accipiter brevipes* also migrate at night? Ibis 135:233–236

Strandberg R, Klaassen RH, Hake M, Olofsson P, Alerstam T (2009a) Converging migration routes of Eurasian hobbies *Falco subbuteo* crossing the African equatorial rain forest. Proc R Soc B 276:727–733. doi:10.1098/rspb.2008.1202

Strandberg R, Klaassen RHG, 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 RHG, Hake M, Alerstam T (in press) How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol Lett. doi: 10.1098/rsbl.2009.0785

Walter H (ed) (1979) Eleonora's falcon. Adaptations to prey and habitat in a social raptor. The University of Chicago Press, Chicago

Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc Natl Acad Sci USA 104:5738–5742