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Converging migration routes of Eurasian hobbies *Falco subbuteo* crossing the African equatorial rain forest

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Autumn migration of adult Eurasian hobbies *Falco subbuteo* from Europe to southern Africa was recorded by satellite telemetry and observed routes were compared with randomly simulated routes. Two non-random features of observed routes were revealed: (i) shifts to more westerly longitudes than straight paths to destinations and (ii) strong route convergence towards a restricted area close to the equator (1° S, 15° E). The birds migrated south or southwest to approximately 10° N, where they changed to south-easterly courses. The maximal spread between routes at 10° N (2134 km) rapidly decreased to a minimum (67 km) close to the equator. We found a striking relationship between the route convergence and the distribution of continuous rainforest, suggesting that hobbies minimize flight distance across the forest, concentrating in a corridor where habitat may be more suitable for travelling and foraging. With rainforest forming a possible ecological barrier, many migrants may cross the equator either at 15° E, similar to the hobbies, or at 30–40° E, east of the rainforest where large-scale migration is well documented. Much remains to be understood about the role of the rainforest for the evolution and future of the trans-equatorial Palaearctic-African bird migration systems.

Keywords: bird migration; Eurasian hobby *Falco subbuteo*; equatorial rainforest; route convergence; ecological barrier

1. INTRODUCTION

Birds migrating independently from a common departure area are expected to diverge gradually in their migration routes with increasing distance from the departure point as a consequence of variation between flight steps in the orientation around the mean migratory direction (Mouritsen & Mouritsen 2000; cf. also Rabøl 1978, Mouritsen 1998, Alerstam 2000). Converging routes thus require special explanation and there are two main factors that may cause route convergence: topographical guidance and navigation to delimited goal areas.

It is well known that many land birds, especially those using thermal soaring migration, concentrate at migration hotspots (e.g. Gibraltar, the Bosporus and Panama) to minimize sea crossings (Kerlinger 1989; Fuller *et al.* 1998; Bildstein 2006). These concentrations presumably arise mainly by way of topographical guidance where the birds avoid flying across coastlines and the sea, although one cannot exclude that in some cases there is also an element of true navigation (homing not based on topographical guidance) towards these convergence sites. In an analogous way, coastline topography serves to guide migratory seabirds, avoiding flight over land, to concentrated passages at promontories or through narrow straits along the migratory flyways.

Navigation towards population-specific goal areas has been suggested for long-distance migrants with strongly delimited winter ranges (Thorup & Rabøl 2001). Such route convergence may not only apply towards winter goal areas but also towards narrowly defined stopover areas, as suggested by Fransson *et al.* (2005) for trans-Saharan passerine migrants with population-specific stopover areas in the eastern Mediterranean region (cf. also Alerstam 2006). Fransson *et al.* (2005) drew attention to the possibility of the birds using the geomagnetic field for navigation to these stopover goal areas.

On an individual basis, convergence of routes from repeated journeys by the same individual has been documented among ospreys *Pandion haliaetus*, towards intermediary goal areas along the migration route as well as nesting and winter sites (Alerstam *et al.* 2006). However, among the ospreys; route convergence did not seem to occur between individuals (Thorup *et al.* 2003).

We used satellite-based radio telemetry to investigate the long-distance migration of Eurasian hobbies *Falco subbuteo* between Sweden in northern Europe and Africa south of the equator. This small falcon did not show any tendencies to concentrate at narrow sea crossings when passing the Baltic and Mediterranean Seas. Also, field observations have shown that migrating adult hobbies do not concentrate at the narrow Baltic Sea passage at Falsterbo, unlike many other species of migratory raptors (Kjellén 1997). Quite unexpectedly, the routes of the four

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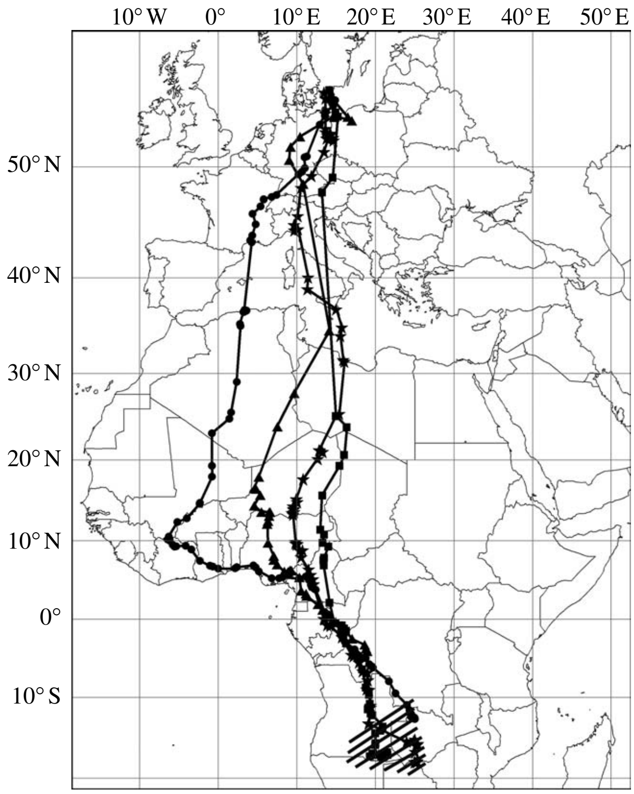

Figure 1. Autumn migration routes of four adult hobbies recorded by satellite tracking between breeding sites in southern Sweden and the winter range in southern Africa (approx. 10–18° S). The hobbies were not stationary during winter and the hatched area shows the region of winter movements (December to February) by two birds.

falcons that were recorded by satellite tracking converged strongly towards an inland area close to the equator in Africa, well north of the birds' final winter destinations in the Southern Hemisphere. In this study, we demonstrate that this convergence is highly unlikely to be a coincidence (which means that it is significantly non-random), and we evaluate and discuss the possible explanations associated with topographical guidance and goal navigation for this unexpected and extreme case of migratory route convergence.

2. MATERIAL AND METHODS

From 2005 to 2007 four adult hobbies (three females and one male) were captured at their breeding sites in southern Sweden (55.7–55.9° N, 13.4–14.2° E) and equipped with Solar PTT-100s (Microwave Telemetry Inc.), which were attached as backpacks. The transmitters weighed 9.5 g, which comprised on average 4.1 per cent of the hobbies' body mass. We could not detect any effect of the transmitters on the hobbies' hunting, feeding or brooding behaviour. Transmitters were programmed to operate on a cycle of 10 hours on and 24 hours off, and were tracked by CLS/Service Argos in Toulouse, France. Depending on satellite orbits and local conditions, we received 0–15 positions per 10-hour period. The evaluation of positions differing in accuracy was the same as described by Hake *et al.* (2001). For the autumn migration, the complete dataset comprised 786 positions, of which 32 per cent were high-quality locations (class 1–3). No spring tracks were obtained.

By interpolation between locations, we derived the longitudinal intersections for each 5° latitude between 55° N and 15° S. From these intersections we calculated, for the four tracks, the mean longitude as well as the scatter in longitude (standard deviation and range) at the different latitudes. The final position of one of the tracks was just south of 4° S and we used the intersection of latitude 4° S rather than 5° S in order to include data from all four individuals. For latitudes 10° S and 15° S, longitudinal intersections were available for three and two individuals, respectively.

Changes in longitude for each 5° latitude segment (corresponding to a north–south distance of 300 nautical miles = 556 km) were calculated and used as a basis for the simulation of randomized tracks between the initial (at 55° N) and final positions for each individual (at 4°, 10°, 15° and 15° S, respectively). The latitudinal bands of at least 556 km distance correspond to travel times of at least 2–4 days, thus reflecting independent migration segments with respect to orientation decisions depending on weather and wind. Simulations by randomly reshuffling the segments within a journey were repeated 1000 times (per track). The longitudinal scatter for the four journeys was calculated for each 5° latitude and for each simulation round, for comparison with the observed set of values for the real tracks, in order to test for non-randomness in the scatter in longitude. Standard deviation (s.d.) was used to indicate the scatter in longitudes, and virtually identical results were obtained by using total range between longitudes as an alternative measure of scatter. To test for non-randomness in mean longitude, the mean overall longitude for the four journeys across latitudes from 50° N to 10° S (i.e. averaged over the different latitudes) was calculated for each simulation round, for comparison with the corresponding overall mean longitude for the observed four journeys. Probability values for random effects were estimated from the proportion of simulations giving the same or more extreme values as observed.

It should be noted that this type of analysis will help to reveal non-randomness only in the route pattern between the start and end positions of the journeys, because these two positions will be invariant and equal to the real positions for all simulations. The total distance of migration will be very similar for the simulated and real routes (with only a slight variation caused by differences in longitudinal distances at different latitudes).

To control for possible bias in longitudinal scatter caused by non-randomness in mean longitude (§3), we also ran separate simulations for two main parts of the journeys, 55° N–10° N and 10° N–15° S.

3. RESULTS

The adult hobbies initiated autumn migration through Europe in a south–southwesterly direction (figure 1; for timing, duration and distance of migration see table 1). Three individuals crossed the Mediterranean Sea from Italy or Sicily to Libya, while one bird flew via France to Algeria. Track directions were more to the south during the water crossing and changed to south–southwest during the crossing of the Sahara Desert. In the savannah zone of tropical West Africa, a course shift to the southeast occurred, leading the tracks into the remnants of equatorial rainforest which were crossed from Nigeria/Cameroon to Democratic Republic of Congo. The bird that travelled along the most westerly track changed

Table 1. Timing, duration and distance of autumn migration of four adult hobbies tracked during 2005–2007 between breeding sites in Sweden and winter areas in Africa south of the equator. (Median dates for departure from breeding areas, equator crossing and arrival to winter areas, mean number of migration days and mean distance are given for all birds. Duration = total number of days from departure to arrival. Travel = number of days with movement more than 50 km. Distance = total distance travelled based on maximally one position per transmitting cycle. Numbers in italics represent incomplete migration periods—these are not included in the mean values.)

sex	departure breeding area	equator crossing	arrival winter area	duration (days)	travel (days)	distance (km)
female 1	9 Sept 2005	31 Oct	9 Nov	62	43	11 226
female 2[a]	4 Sept 2006	24 Oct	—	*54*	*37*	*7987*
female 3	8 Sept 2006	22 Oct	5 Nov	59	38	8540
male	7 Sept 2007	22 Oct	6 Nov	61	37	9139
all birds	7 Sept	23 Oct	6 Nov	61	39	9223

[a]Stopped transmitting during active migration 27 October at 4.2° S, 19.0° E.

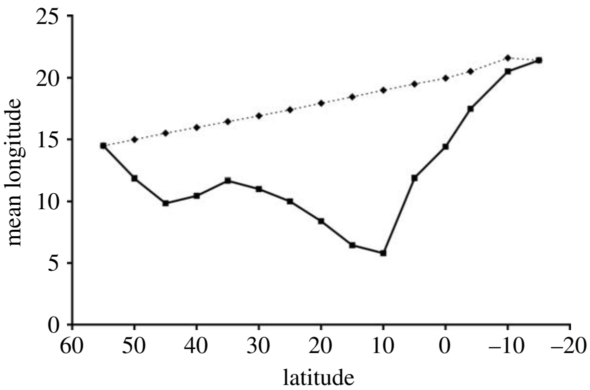

Figure 2. Comparison between mean longitude at 5° latitude intervals for observed routes of four hobbies (cf. figure 1) and for sets of simulated routes with randomized segments within each journey (means for 1000 simulations of each set of four tracks). Simulated values are connected by dotted lines. Observed mean longitudes deviate significantly from simulated means showing non-random route shift towards westerly longitudes.

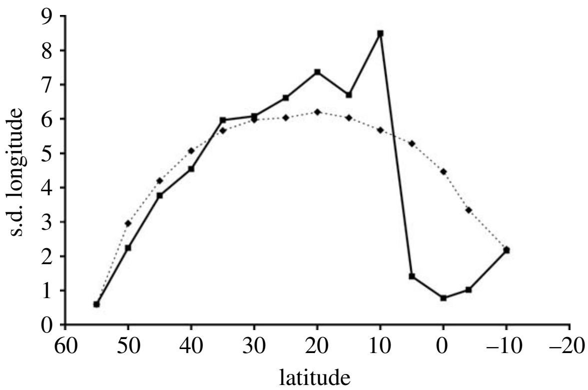

Figure 3. Comparison between scatter of longitudes (s.d. = standard deviation) at 5° latitude intervals for observed routes of four hobbies (cf. figure 1) and for sets of simulated routes with randomized segments within each journey (s.d. for 1000 simulations of each set of four tracks). Simulated values are connected by dotted lines. Observed s.d. is significantly smaller than simulated s.d. at 5° N–5° S showing non-random route convergence.

course at 10° N in northern Ivory Coast, far north of the Atlantic coast. From there it made a 2800 km flight before it reached the equatorial area (cf. figure 1).

These observed routes were significantly non-random with respect to both the pattern of overall mean longitude (figure 2) and the scatter of longitudes at different latitudes along the routes (figure 3).

The mean longitude change, first westwards from 14.4° E at latitude 55° N to 5.8° E at latitude 10° N, and then eastwards to 21.4° E at latitude 15° S (figure 2), reflects the initial south–southwesterly travel courses, which shifted to an orientation in the southeasterly quadrant at approximately 10° N (figure 1). The westward deviation from an average straight track towards the destination is extremely unlikely to arise by chance; the observed overall mean longitude (11.5° E) differed significantly ($p<0.001$) from the average of the overall mean longitudes for the 1000 rounds of the simulated tracks (18.0° E).

The routes of the four individuals diverged in agreement with random variation between segments during the first part of the journey (figure 3; $p>0.1$ for all latitude intervals 55–10° N). Maximum scatter in longitude between the four tracks was recorded at latitude 10° N where s.d. and range reached 8.5° and 19.5°, respectively (corresponding to distances of 930 and 2134 km, respectively). Further south the routes converged very rapidly to a longitudinal s.d. and range of only 0.78° and 1.9°, respectively, at the equator (figure 3). The observed s.d. at latitudes 5° N–5° S was significantly smaller than expected with random combination of segments (figure 3; $p<0.01$ at one latitude interval and $p<0.05$ at two latitude intervals). On a finer resolution (1° latitudes) the minimum s.d. and range were 0.35° and 0.6°, respectively (corresponding to distances of 39 and 67 km, respectively) at latitude 1° S (where the mean longitude was 15.5° E).

The randomization procedure did not take into account the significant westerly detour in the observed routes of the hobbies and will thus overestimate the longitudinal variation, especially at 10° N, where the hobbies reach their most western locations. This could result in spurious significant convergence patterns. To check for such a possible effect we repeated the analysis, but now separately for the first (50° N–10° N, mainly southwestern directions) and the second (10° N–10° S, mainly southeastern directions) halves of the journey. During the first part of the journey the scatter increased in an apparently random fashion, hence no convergence could be detected. The analysis restricted to latitudes

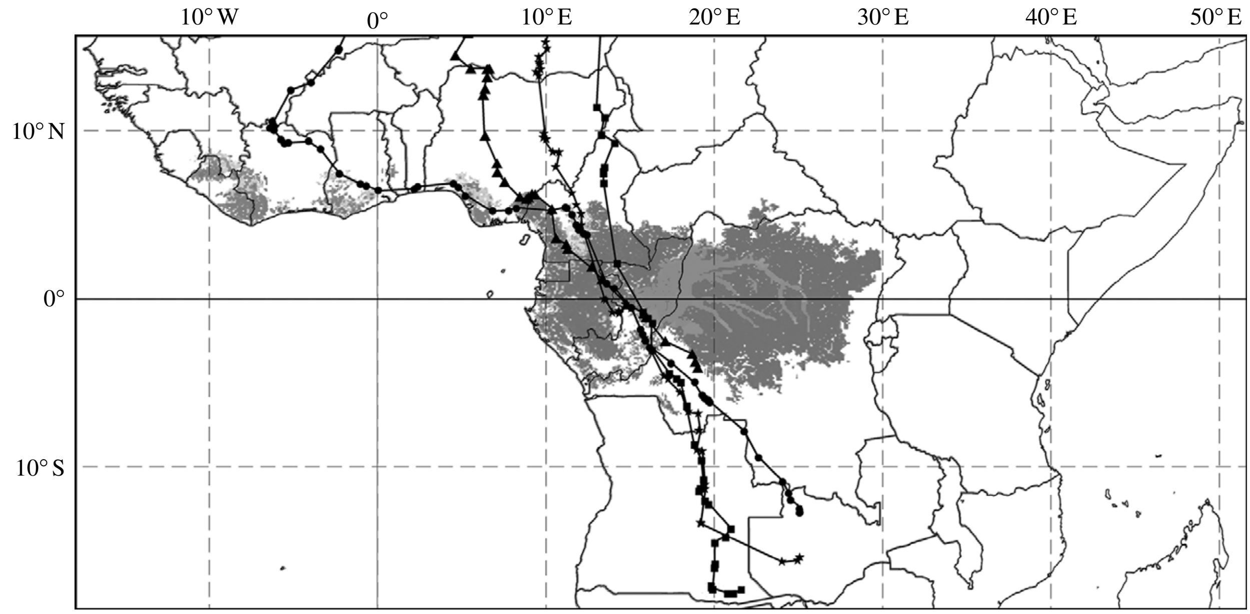

Figure 4. Migration routes of hobbies in relation to the distribution of evergreen rainforest in equatorial Africa. Forest indicated by grey areas: dark grey, intact forest; medium grey, wet forest enclosing the Congo River system; light grey, degraded areas with forest patches. The distribution of larger areas of continuous tropical rainforest was drawn with the aid of the 'Global distribution of current forests by UNEP World Conservation Monitoring Centre' (www.unep-wcmc.org/forest/global-map.htm).

10° N–10° S showed that the s.d. at 5° N was significantly smaller ($p<0.05$) than expected from random variation, confirming that the hobbies converged in the final part of their migrations. No further significant deviations from randomness in longitudinal scatter could be detected.

Even if observed tracks show significant non-random patterns with respect to both mean longitude and longitudinal scatter, caution is needed as only four individuals form the basis of our analyses.

4. DISCUSSION

(a) *Possible explanations for route convergence*

The hobby routes showed two distinctly non-random features: (i) a general shift to more westerly longitudes in comparison with a straight average path towards the destinations, and (ii) a strong constriction towards a small area in Congo close to the equator.

The westward shift of the routes was most pronounced over the Sahara desert (at least for three of the four individuals) and this may be related to the dominating easterly winds in this zone (Erni *et al.* 2005). The birds may have been drifted by the easterly crosswinds and/or have evolved a preferred orientation west of south to make some profit from the wind (or avoid wind costs; further details given in Strandberg *et al.* in preparation). The routes had a westerly inclination already in Europe (at least for three of the four individuals), which is unlikely to be caused by winds (dominantly from the west in Europe). A possible association with the avoidance of long crossings over the Alps or the Mediterranean Sea seems not to be well supported by the actual tracks. One of the hobbies definitely crossed the Alps and such crossings were also probable for two of the other birds. Furthermore, the hobbies did not hesitate to cross water bodies, as shown by the bird migrating along the westernmost route, which flew a distance of 740 km directly over the open sea from southern France to Algeria, a flight that lasted approximately 27 hours (including a day and the succeeding night). Meyer *et al.* (2000, 2003) also reported frequent sea crossings by smaller falcons at the Spanish south coast during radar studies in both autumn and spring. Their dataset included common kestrel *Falco tinnunculus*, Eurasian hobby and lesser kestrel *Falco naumanni*. Furthermore, amur falcons *Falco amurensis*, migrating from northeastern Asia to winter in South Africa, are supposed to make water crossing of up to 2000 km over the Indian Ocean (Moreau 1972; Chapman 1999; Bildstein 2006).

The most challenging result to explain is the strong route convergence close to the equator. After being separated by more than 2000 km at 10° N the different hobbies converged to a very restricted area at or just south of the equator (mean position approx. 0.7° S, 15.4° E) where all tracks passed within 70 km from each other (note that the tracks were from different individuals and recorded during three different years). Further south the routes diverged again to become separated by 200–400 km in longitudinal distance. Are there any special characteristics to make the focal area of the route convergence a crucial target area in hobby migration?

(i) *Height and ground level*

The focal area is situated in the Congo Republic at heights 400–1000 m above sea level. This is part of the wide-ranging plateau between the coastal lowlands of Gabon (300 km or more to the west) and the Congo River basin (150 km or more to the east). Hence, the focal area is surrounded by areas of the same altitude (lowest parts more than 300 m above sea level) and there are no protruding mountains or other striking height features to suggest a special target area for migrating birds.

(ii) *Coastal guiding*

The Atlantic coast is 700 km west of the focal area, which rules out coastal guidance as an immediate explanation for the route convergence at this site. Three of the hobbies passed Cameroon without contact with the African coast at all. However, the individual migrating furthest to the west was guided some distance eastwards along the south coast of West Africa. This bird had changed to a south-easterly direction well before reaching and following the Atlantic coast from Ghana to Nigeria (travelling approx. 30–80 km inland from the coastline and never closer than 28 km from the coast). Further east in Nigeria this bird left contact with the coast to approach the focal area over a distance of more than 1000 km without coastal contact or guidance.

(iii) *Lowland rainforest*

A closer inspection of the routes in relation to the distribution of continuous lowland rainforest (figure 4) suggested that the hobbies concentrated their routes in order to minimize the crossing of such forest areas. The focal area is dominated by farmland, degraded woodland and moist savannah that reaches from the south into the block of evergreen forest similar to a peninsula as far north as the equator (figure 4; see Moreau 1972 about vegetation as well as rainfall zones). By migrating via the focal area the hobbies can reduce the travel distance across continuous rainforest by half, to approximately 450–600 km. This indicates that the rainforest represents an ecological barrier for the migrating falcons. The rainforest might be a barrier in terms of unsuitable conditions for foraging both below and above the forest canopy, also owing to unfavourable weather conditions (i.e. long periods of daily rainfall) associated with this type of habitat.

By minimizing distance across closed rainforest, the hobbies may follow a corridor with partly more open habitat, possibly providing better conditions for soaring and for hunting prey (e.g. barn swallow *Hirundo rustica*; see below). Also, the degraded areas in southern Cameroon and naturally non-forested areas in northern Congo might have some leading line effects on the migrating birds, mediating the hobbies south through semi-open habitat. It should, however, be noted that the hobbies anyway have to cross a considerable distance over the rainforest before they reach less forested areas (see figure 4).

(iv) *Geomagnetic field and other navigation cues*

The hobbies may have located the focal area by response to the distribution of continuous rainforest and other habitats, but also with the aid of geomagnetic or other 'map' cues. The geomagnetic field intensity and inclination angle form a grid in West and Central Africa that may be theoretically useful for navigation based on magnetic cues, but there are no geomagnetic features that make the focal area (with magnetic coordinates of field intensity 33 μT and inclination 30° S) stand out from other areas in this region (information about the International Geomagnetic Reference Field was obtained from http://geomag.usgs.gov).

Nor can we suggest any particularly striking cues of infrasound or odours to be associated with the focal area (except perhaps odours from this 'habitat peninsula' of farmland with special vegetation/burning, etc.). This is not to say that the hobbies do not reach the focal area by true navigation, only that the location of the focal area fails to provide any immediate clues to possible navigation cues in addition to the guiding effect of forest distribution and habitats (figure 4). We think that the routes suggest the existence of long-distance goal navigation south of 10° N, a latitude that corresponds approximately with the geomagnetic equator.

5. CONCLUSION

It is well known that 'those parts of Africa which are predominantly under evergreen forest are of comparatively little importance as wintering areas for the migrants' (Moreau 1972, p. 60). Moreau (1966, 1972) pointed out that no species of migrant lives in these forests exclusively and only a handful of species occur regularly, e.g. barn swallow, common swift *Apus apus* and wood sandpiper *Tringa glareola*. The northern migrants exploit almost exclusively seasonal and ephemeral resources in more open woodland, savannah and steppe (habitats with rainy seasons) as a basis for their winter existence in Africa (Moreau 1972).

The convergence of the routes of hobbies to the narrowest crossings of the equatorial rainforest suggests that the rainforest may be avoided by the northern migrants not only for their winter stay but also during migration periods, having the effect of an ecological barrier that contributes to concentrate the birds into corridors with more suitable habitats for travelling and foraging. We think that it is unlikely that this pattern applies only to the hobby. If the pattern is more general, there may well exist a concentrated passage across the equator, at approximately 15° E, of land birds that have passed West Africa on their way to winter quarters at Southern Hemisphere latitudes in Africa. Other northern birds migrating over more easterly regions can reach southern Africa by crossing the equator east of the continuous rainforest block, in Uganda and Kenya, at 30–40° E. Indeed, a large-scale trans-equatorial migration passage by huge numbers of both passerine and non-passerine species takes place in Uganda and Kenya (Moreau 1972; Pearson & Backhurst 1976; Alerstam 1990; Newton 2008).

Interestingly, the distribution of rainforest also may have an influence on the routes of Eleonora's falcon *Falco eleonorae* migrating from the Mediterranean and Madagascar (Gschweng *et al.* 2008). Adult Eleonora's falcons did not penetrate into the rainforest belt as they followed a more northeastern route, in contrast to the juvenile birds. Just after the juvenile birds entered the rainforest they made a sudden sharp turn to the east/northeast, and continued across the northern rim of the forest belt. Only one bird travelled right across the forest, via the hobbies' focal area.

There is a concentration of ring recoveries of Fennoscandian spotted flycatchers *Muscicapa striata* immediately south of the equatorial rainforest belt in western Zaire, mainly during the spring migration period (Fransson 1986). This suggests that the flycatchers make a stopover in this region before the spring crossing of the rainforest (and also to some extent after the autumn crossing of the forest), which is thus a probable barrier for the birds. However, the recoveries are from a rather wide longitudinal interval 13–25° E (mean 20° E), indicating that the flycatchers may cross the rainforest on a broad front and not in a restricted region similar to the hobbies, although this is difficult to know without tracking data from individual birds (see also ring recoveries close to the

African equatorial rainforest, e.g. of garden warbler *Sylvia borin*, willow warbler *Phylloscopus trochilus* and red-backed shrike *Lanius collurio,* in Zink 1973–1985). For most species of long-distance migrants, ring recoveries from equatorial Africa are far too few to throw any light on the patterns and strategies associated with the birds' passage of the evergreen rainforest zone.

Very large numbers of barn swallows migrating to the Southern Hemisphere pass both to the east of the rainforest and along westerly routes across Nigeria, Cameroon and Congo (De Bont 1962). If this is a well-defined migration corridor for barn swallows, one cannot exclude that hobbies exploit this abundance of prey during their trans-equatorial passage. However, we did not find any evidence that the hobbies slowed down or made a stopover in the focal area, which would have indicated that they strongly associate with swallow roosts (Strandberg *et al.* in preparation).

Our satellite tracking results for the hobbies thus lead us to a novel perspective: that the continuous evergreen rainforest constitutes an important factor to affect the major flyways and stopover strategies by which migratory land birds travel to and from their winter quarters in southern Africa. From the distribution of this forest one may expect that there exist two main access routes to the Southern Hemisphere: (i) across the equator approximately 15° E where the rainforest crossing is clearly reduced in distance, and (ii) at 30–40° E where birds can circumvent the rainforest on its eastern side (and where populations arriving via northeast Africa can continue without being confronted with the rainforest).

To what extent this scenario applies to different species (some species such as the spotted flycatcher may be more prone towards broad front crossing; see above), if it differs between juveniles and adults (Gschweng *et al.* 2008), or between southward and northward migration, and if individual birds may change between the different flyways in different seasons, are as yet unanswered questions. It is a most fascinating and important task for the future to understand the role of the rainforest as a possible ecological barrier of continent-wide significance, in addition to the effects of desert and sea, for the evolution and future of the Palaearctic-African bird migration systems.

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