PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2008) **275**, 2887–2896
doi:10.1098/rspb.2008.0575
Published online 2 September 2008

All across Africa: highly individual migration routes of Eleonora's falcon

Marion Gschweng[1,*], Elisabeth K. V. Kalko[1,2], Ulrich Querner[3], Wolfgang Fiedler[3] and Peter Berthold[3]

[1]*Institute of Experimental Biology, University of Ulm, 89069 Ulm, Germany*
[2]*Smithsonian Tropical Research Institute, Balboa, Republic of Panama*
[3]*Max Planck Institute for Ornithology, 78315 Radolfzell, Germany*

Eleonora's falcon (*Falco eleonorae*) is a rare raptor species that delays its breeding period until late summer to feed its young with passerines at the peak of autumn migration. Since the 1950s, this slender winged falcon has been believed to migrate along a historical route via the Red Sea to its main wintering area in Madagascar. In our study, we used satellite telemetry to investigate the real migration route of Eleonora's falcons and found that the species displayed a highly individual migration pattern. Furthermore, juvenile falcons migrated via West Africa to Madagascar and two juveniles could be tracked during spring migration and to their summering areas in East and West Africa. As juveniles migrated independently of adults, we discuss inherited navigation strategies forming part of a complex navigation system. We propose the idea of an orientation mechanism that naive falcons could apply during their long-distance migration towards their faraway wintering area located in the open ocean.

Keywords: individual migration pattern; inherited navigation strategies; long-distance migration; navigation system; orientation mechanisms; wintering and summering of Eleonora's Falcon

1. INTRODUCTION

Eleonora's falcon (*Falco eleonorae*) is a highly specialized bird of prey with a peculiar breeding biology. It mainly breeds on the cliffs of small islands in the Mediterranean and Macronesia in large colonies of up to 630 breeding pairs (Morocco). Together with the smaller sooty falcon (*Falco concolor*), it is the only raptor species that delays its breeding period until late summer and feeds its young with migrating passerines during the peak of autumn migration (Walter 1979*b*). The nestlings fledge within 35–37 days after hatching (Vaughan 1961; Walter 1979*b*) and at the age of only 10 weeks they start their enormous journey of several thousand kilometres to their wintering grounds in Madagascar, where 70 per cent of the world population is estimated to overwinter (Walter 1979*b*).

Since the 1950s, Eleonora's falcons have been thought to follow a species-specific migration route, taking them down the entire Mediterranean towards Suez (Stresemann 1954), down the Red Sea coast, around the Horn of Africa and along the East African coast, before arriving in Madagascar (figure 1, dotted line). The idea of this historical route was supported by two observations made in Tanzania and Somalia (Stresemann 1954; Turner 1978), where flocks of several hundred individuals were observed. The recovery of a single-ringed bird in Mali, which was ringed on Lanzarote, Canaries, however, has fuelled speculation that the species may also migrate via the African continent (Delgado & Quilis 1990) and Ristow & Wink (1992) hypothesized that Eleonora's falcon could migrate inland 'as any other raptor does'.

The species is well studied at its breeding sites (Dimalexis *et al.* 2008), but there is an enormous lack of data on migration routes and wintering areas (Ristow, in International Species Action Plan Eleonora's Falcon 1999), as only few observations of the species have been made outside its breeding grounds (Vaughan 1961; Ristow & Wink 1992), and published data from the wintering grounds are scarce (Rand 1936; Milon *et al.* 1973; Benson *et al.* 1976; Walter 1979*b*; Meyburg & Langrand 1985; Zefania 2001). The few available data beyond its breeding and wintering grounds were observations in the Mediterranean region including inland Tunisia, inland Morocco (see review in Ristow & Wink 1992) and Northern Egypt (T. Coles 2004, personal communication) and only one single observation of an individual on Mount Cameroon (Hivekovics & Palatitz 1998).

It is so far unknown where non-reproductive individuals stay over until they reach fertility, which occurs at the age of 3 years in males and 3–4 years in females (Ristow *et al.* 1989). As non-reproductive Eleonora's falcons are not tied to their birthplaces, they do not return to their breeding sites during the first and second summer of their lives (Walter 1979*b*). Based on their banding efforts, Terrasse (1963) and Ristow (1975) provided some answers to the whereabouts of the non-reproductive falcons, but the ringing recoveries have been so far restricted to the Mediterranean region and Madagascar.

In our study, we found that juvenile Eleonora's falcons travel without the guidance of adult falcons. Thus, the question arises as to how inexperienced falcons can navigate to their distant wintering area. Larger bird species mainly migrate in flocks during daytime and juveniles are guided by adults along traditional routes

*Author for correspondence (marion.gschweng@uni-ulm.de).

Received 29 April 2008
Accepted 5 August 2008

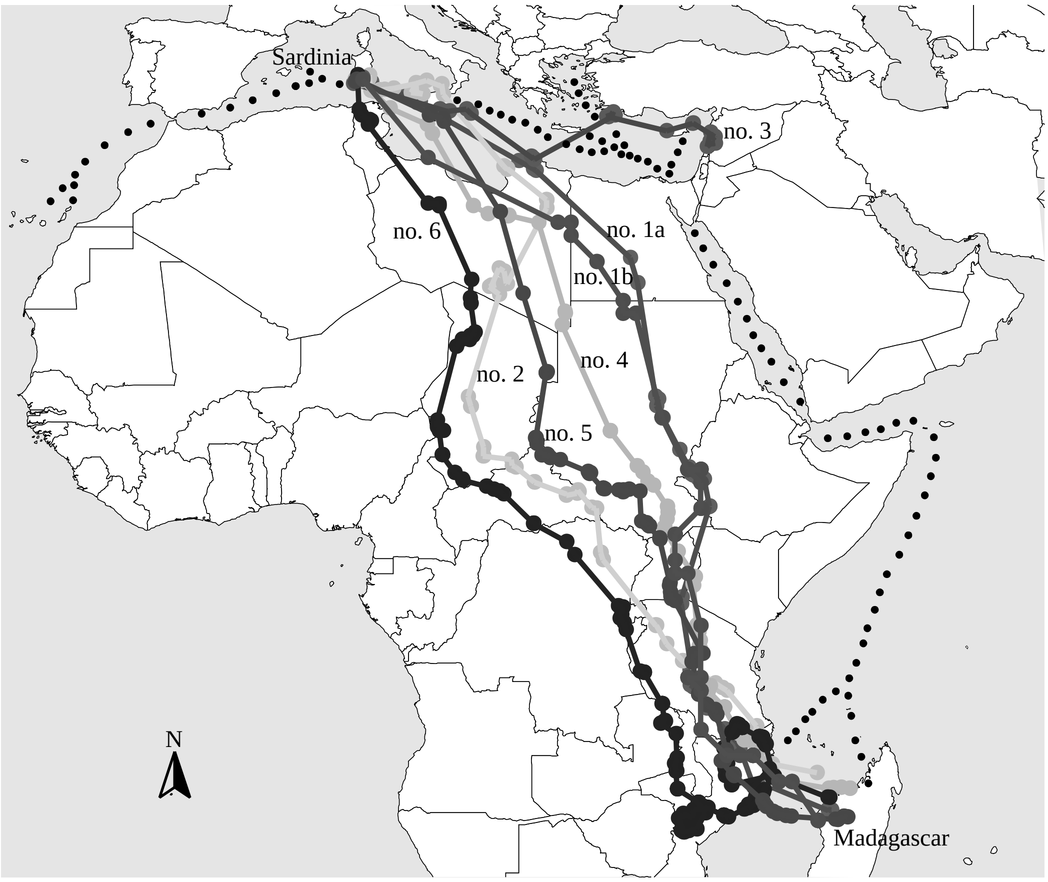

Figure 1. Autumn migration of six adult Eleonora's falcons and historical route (dotted line) modified after Walter (1979*b*).

(e.g. white storks *Ciconia ciconia*), but in Eleonora's falcon, such guidance can be excluded.

Detailed studies of orientation and navigation have established that birds determine compass directions by means of the geomagnetic field, the stellar sky or the Sun (Wallraff 2005; Wiltschko & Wiltschko 2005). Using their compasses, birds follow genetically encoded directions that lead them to their wintering areas (Alerstam & Lindström 1990; Berthold 1996, 2001; Helbig 2003). An innate time and direction programme called vector navigation, which has been experimentally tested for a number of bird species (Gwinner & Wiltschko 1978; Schmidt-Koenig & Keeton 1978; Helbig *et al.* 1989; Able 1993; Able & Able 1996), is likely to guide birds from their birth places to their wintering areas. With this inherited programme, juvenile birds can navigate over long distances without the guidance of experienced adults.

If migration routes were determined by an inherited programme that defines time and direction, one would expect species-specific routes in the form of narrow corridors. This is indeed the case in different bird species such as white storks (Berthold 2001; Chernetsov *et al.* 2004), lesser spotted eagles (*Aquila pomarina*; Meyburg & Meyburg 1999) and other species (Thorup & Rabol 2001), where all individuals of one species migrate on narrow corridors into their wintering grounds and subsequently disperse widely.

The real migration route of Eleonora's falcon is not yet known and Madagascar as the main wintering area has not yet been confirmed. Furthermore, the whereabouts of immature falcons in their first 2 years are still unknown. In order to clarify these questions, we tagged 13 falcons with satellite transmitters and collected data beyond the breeding sites from 2003 until 2006. As Eleonora's falcons revealed an unexpected and surprisingly individual migration pattern, we discuss inherited navigation strategies as well as additional orientation mechanisms by comparing adult falcons with juvenile, hence naive falcons.

2. MATERIAL AND METHODS

(a) *Study area, animals and tagging*

We tagged 13 falcons from two colonies on Sardinia, Italy (table 1). One colony on the Isola di Toro comprised approximately 60–70 breeding pairs and the other colony on the Isola di San Pietro consisted of approximately 120 breeding pairs. In 2003, three adult and two juvenile falcons were fitted with 18 g solar-powered satellite transmitters (PTTs 100 series, Microwave Telemetry, Inc.). In 2004, we tagged another three adult and two juvenile falcons with the same transmitters. In 2005, three juvenile falcons were additionally fitted with newly developed, lighter 12 g solar-PTTs. The weights of the birds and tags are summarized in table 1.

The whole process of capturing, weighing, ringing and fitting of the transmitters took 30–45 min. The adult birds were captured at their nest sites and nestlings were taken out of their nests and carried away from the nest site to avoid disturbing the remaining nestlings. During the fitting of transmitters in daytime, the birds were carried into the shade. To calm the birds, we covered their eyes with a woollen tissue cap. After treatment, fledglings were returned to their nests and the adult falcons were released close to their nest sites.

PTTs were attached as backpacks using a harness with neck and body loops (Kenward 2001; Steenhof *et al.* 2006). The transmitters had two anterior and two posterior wire loops through which 25 in. of Teflon ribbon was fixed with

Table 1. Life cycles and signal transmission data of 13 transmitters applied to Eleanora's falcons.

falcon platform number	capture/ nest site	body mass (g)/ transmitter weight (g)/ % of body mass	start of transmission/ end of signals	departure date/ start of migration	duration of signal transmission (d)
adult female **1**: 40532	Toro Island	370/18/4.8	12 Aug 2003–30 Nov 2004	27 Oct 2003	476
adult female **2**: 40535	Toro Island	370/18/4.8	15 Aug 2003–21 Nov 2003	25 Oct 2003 (9 Oct to Sicily)	98
adult female **3**: 40537	Toro Island	360/18/5.0	17 Aug 2003–23 Jan 2004	20 Oct 2003	94
adult female **4**: 49886	Toro Island	450/18/4.0	28 Aug 2004–31 Mar 2005	23 Oct 2004	215
adult female **5**: 49887	Toro Island	440/18/4.0	28 Aug 2004–07 Jul 2005	22 Oct 2004	313
adult female **6**: 49890	San Pietro	470/18/3.8	25 Aug 2004–21 Apr 2005	29 Oct 2004	266
juvenile **a**: 40534	Toro Island	440/18/4.0	22 Sep 2003–26 Nov 2003	28 Oct–31 Oct 2003	65
juvenile **b**: 40536	Toro Island	435/18/4.1	22 Sep 2003–20 Feb 2004	21 Oct 2004	151
juvenile **c**: 49885	San Pietro	440/18/4.0	19 Sep 2004–15 Dec 2004	26 Oct or 27 Oct 2004	87
juvenile **d**: 49888	San Pietro	440/18/4.0	18 Sep 2004–04 Nov 2005	25 Oct 2004	413
juvenile female **e**: 59889	San Pietro	490/12/2.4	02 Oct 2005–08 Jan 2006	31 Oct 2005	93
juvenile male **f**: 49891	Toro Island	440/12/2.7	13 Aug 2005–19 Jan 2006	26 Oct or 27 Oct 2005	302
juvenile male **g**: 49897	Toro Island	450/12/2.6	13 Aug 2005–15 Aug 2006	31 Oct 2005	337

an additional aluminium tag below the insertion of the antenna. The overall weight of the harness was approximately 2 g, depending on the length of the Teflon ribbon needed to fix the transmitter.

(b) *Transmitter data*

Satellite data were received through the ARGOS satellite-based positioning system, processed with Excel and displayed via ArcView GIS v. 3.2a (ESRI GIS and Mapping Software, USA), and Animal Movements Extension to ArcView GIS v. 1.1 (Hooge & Eichenlaub 1997). Transmitters attached in 2003 and 2005 were programmed with duty cycles of 10/48 hours (10 hours switched on, 48 hours switched off), and in 2004 with duty cycles of 6/16 hours with a programmed inactivation of the tag after 1 year.

To display migration routes, only location classes (LCs) 3, 2, 1 and 0 were used. LCs of inferior and poor quality (LC A, B and Z) were excluded. The deviations indicated by ARGOS for class LC 3 (best quality) are 150 m, LC 2 up to 350 m, LC 1 up to 1 km and LC 0>1 km. Unless stated otherwise, transmitter data are given in coordinated universal time. Where important data points were missing, we used also LCs of lesser quality (LC A) and added the LC after the latitude/longitude, e.g. 49.89 N/8.98 E (LC A).

The duration of the signal transmission for each transmitter varied substantially. The shortest signal transmission was 65 days and the longest 15 months (table 1).

(c) *Statistical analyses*

To test for differences in the migration routes between adult and juvenile falcons, we included all individuals that could be tracked from the breeding quarters (Sardinia) to the wintering area (Madagascar, Comoros, and Democratic Republic of the Congo (DRC)). The second autumn migration of individual no. 1 (figure 1, route b) was excluded from the analyses.

We connected confirmed locations of LCs 3, 2, 1 and 0 by creating polylines for each individual (ArcView GIS v. 3.2a and animal movements extension) and determined longitudinal values of flight lines at selected lines of latitude (30°, 20°, 10°, 0°, −10°). Limited precision was accepted between latitudes due to the different qualities of LCs (accuracy between <150 m (LC 3) and >1 km (LC 0)) and the assumed course of the flight paths between the satellite fixes.

We used the 'repeated-measures general linear model' (SPSS v. 13.0 2004) to test for differences of longitudes at the selected lines of latitude between the adult and juvenile falcons. Longitudinal values were calculated for each individual and chronologically sorted along the migration route. Latitudes were treated as the within-subject factor (repeated measures for each individual), while the two age groups (adult and juvenile) were treated as the between-subject factor. In our dataset sphericity could be assumed and we therefore used the univariate approach to test the within-subject effects.

3. RESULTS

(a) *Autumn migration*

The adult falcons departed between 20 and 29 October, while the juveniles started migration between 21 and 31 October (table 1). In one case, a female adult falcon (figure 1, no. 6) and her chick (figure 2, juvenile c) were fitted with transmitters in the same breeding season. While the chick left the breeding site between 26 and 27 October, its mother left 2–3 days later on 29 October.

All the adult falcons crossed the Mediterranean by heading south/east-southeast. Five out of the six adults deviated only slightly from this course throughout the whole journey (figure 1). Only one female changed its course and migrated east for 4 days (figure 1, no. 3). After a zigzag course via the Mediterranean, the bird arrived at the Lebanon coast on 29 October where signal transmission ended (table 1). As the route of this individual substantially deviated from the course of all other adult falcons, we exclude it from further analyses. The complete migration of the adults ($n=5$) from Sardinia to Madagascar took an average of 22.4 days (s.d. $=\pm 3.44$, $n=6$), considering six spring migration tracks (female no. 1 with two spring migration tracks (a, b)).

Contrary to the adults, the juvenile falcons took different routes and first departed in a south/southeasterly direction. They kept this course for 4.9 days (s.d. $=\pm 1.57$, $n=7$) and

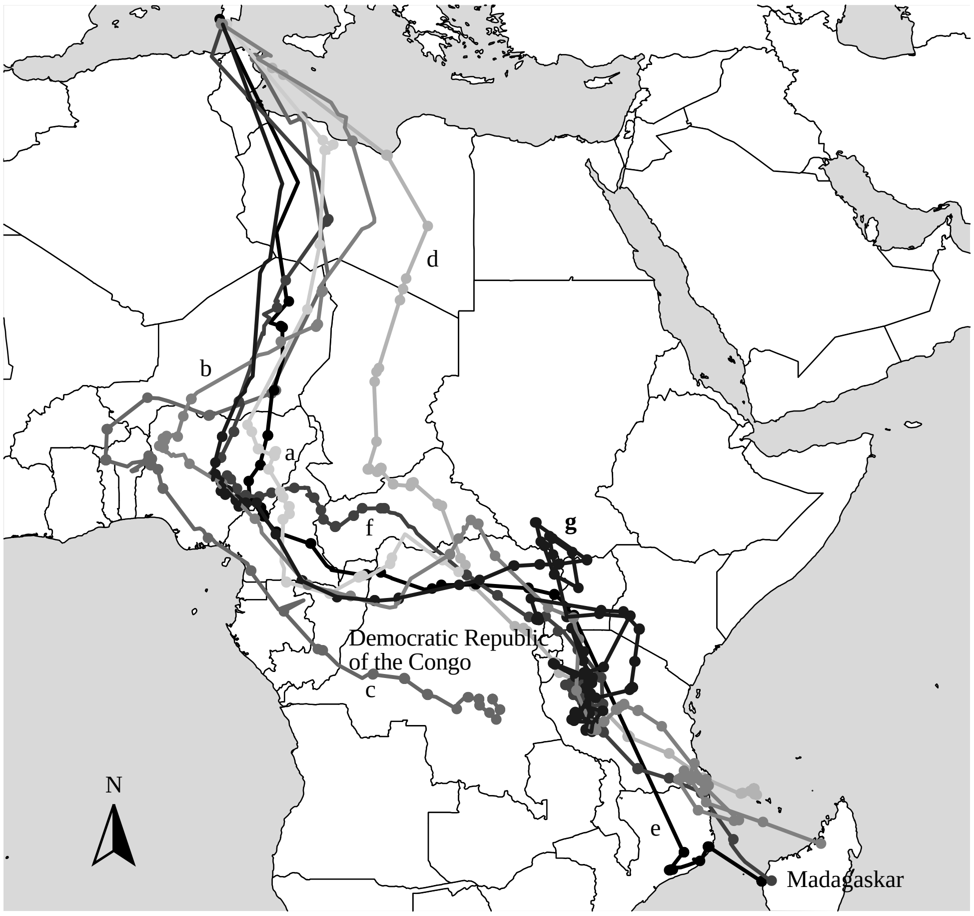

Figure 2. Autumn migration of seven juvenile Eleonora's falcons with stopover in West Africa.

then changed their primary direction slightly to the south/southwest for an average of 3.9 days (s.d. $= \pm 1.34$, $n=7$). After a mean stopover of 13.6 days (s.d. $= \pm 1.39$, $n=7$) in West Africa (Niger, Nigeria, Cameroon, Ivory Coast, Benin, Togo and Burkina Faso), they displayed a 'Zugknick' (an abrupt change of course) and then headed further east/southeast throughout the remaining route via the African continent (figure 2).

The juvenile falcons took much longer than the adults to reach their wintering area. Five out of the seven tagged individuals migrated for an average of 64.4 days (s.d. $= \pm 23.6$, $n=5$). The journeys of two juveniles which ended in the northern and southern DRC are not considered. To our knowledge the autumn migration of these two juveniles was not completed at the time when signal transmission ended. They are therefore excluded from further analyses.

The displayed migration patterns of the adults and juveniles differed substantially between the two age groups (figure 3). Results of the statistical spatial analyses showed that longitudinal positions of all 10 birds (5 juveniles and 5 adults) changed significantly during the migration (repeated-measures general linear model: latitude: $F_{4,32}=89.38$, $p<0.001$). Furthermore, the factor age group had a significant effect on the latitudinal course of the migration routes (latitude $\times$ age group: $F_{4,32}=8.56$, $p<0.001$). The analysis of the between-subject effects further supported the strong age effect on the migration pattern (ANOVA: $F_{1,8}=8.89$, $p=0.018$).

Summarizing the adult and juvenile autumn migration, the adult and juvenile falcons revealed different spatial migration patterns with the juveniles following a more western course than the adults. The temporal patterns differed as well as with the juveniles that took three times longer than the adults and included a substantial stop over of approximately two weeks in West Africa.

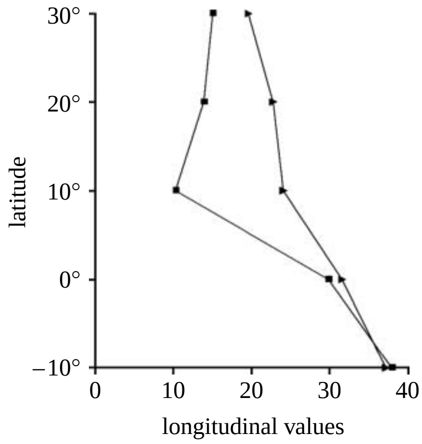

Figure 3. Mean longitudinal values of the migration route of juvenile ($n=5$) and adult ($n=5$) Eleonora's falcons along latitudes. Each symbol represents the mean of five values from one age group (squares, juveniles; triangles, adults).

(b) *Crossing the Mozambique Channel*

All of the tagged falcons that reached the East coast of Africa crossed the Mozambique Channel. Four of the six adult falcons crossed in a period between 15 November and 2 December. One female (figure 1, no. 6) delayed its crossing for more than three months and did not cross

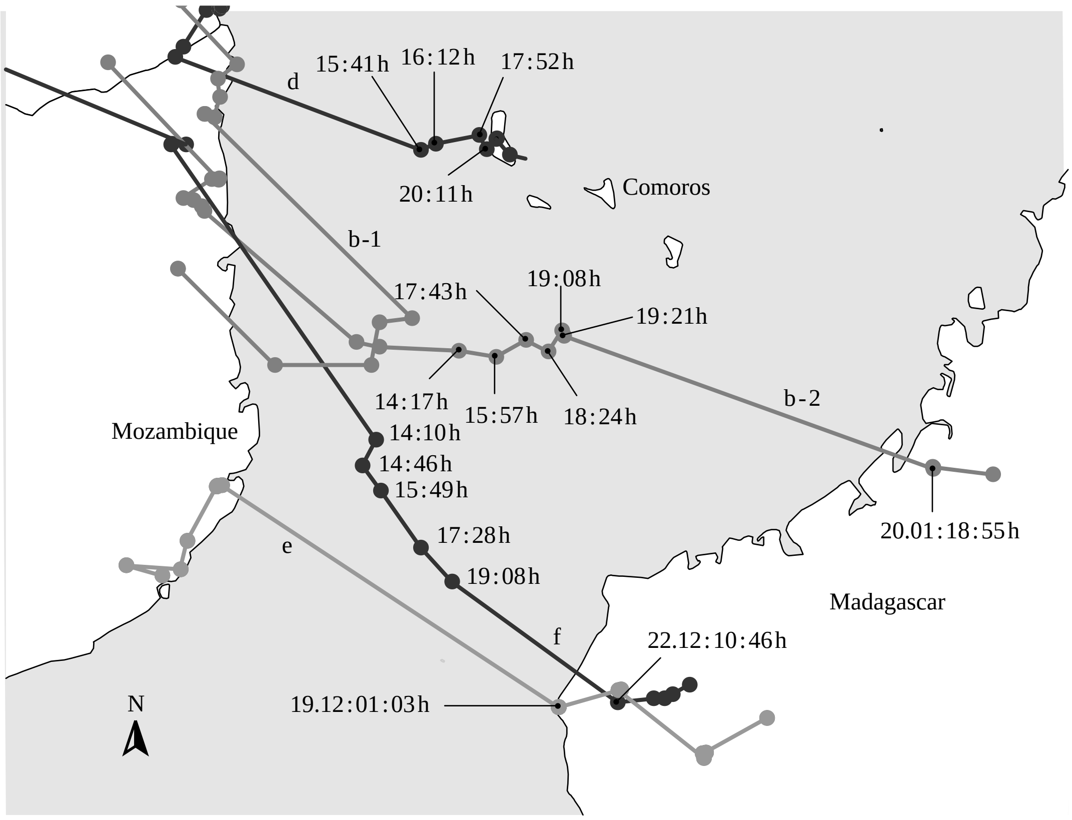

Figure 4. Detailed crossing of the Mozambique Channel of four juvenile Eleonora's falcons.

until 3 March. Thus, five out of the six tagged adult falcons crossed to Madagascar, although one individual did this in a different cycle of the wintering period. The four juvenile falcons that successfully arrived at the East coast started their crossing about two weeks later than the adults between 2 and 20 December.

To support our subsequent discussion on the navigational strategies of naive Eleonora's falcons, the detailed timing of the crossing of the Mozambique Channel for juveniles is given here: one juvenile started its crossing during the night of 19 December but turned around over the open ocean after more than two hours of flight (figure 4, b-1). We relocated the bird on mainland Mozambique on the night of 21 December. One month later, on the afternoon of 19 January, it attempted to cross a second time and successfully arrived at the West coast of Madagascar, where it could be located on 20 January, 18.55 local time. This second crossing started during daytime (figure 4, b-2) and the juvenile could be tracked over open ocean until 19.21 local time on 19 January in the middle of the Mozambique Channel. On the evening of the 20 January, we received signals from mainland Madagascar again. Early on 2 December, another juvenile started at the most northerly point of all the individuals (figure 4, d) and landed on the Comoros in the evening of 3 December. It mainly migrated during daytime, whereas the landing on the Comoros was after sunset at 20.11, local time. We located two more juveniles on Madagascar (figure 4, e, f) on 19 and 22 December but were unable to track the exact timing of their crossing.

(c) *Wintering areas*

Wintering areas of juvenile falcons were not as consistent as that of adult falcons. Besides one adult female, all the adults wintered for at least part of the wintering period in Madagascar. Of seven juvenile falcons, only three arrived in Madagascar, one juvenile landed on the Comoros and one juvenile that was tracked in 2005 overwintered in the eastern DRC.

Summarizing the data, the adult falcons reached Madagascar by mid-November, whereas the juvenile birds arrived one month later between December and January. Of the 13 falcons, 9 crossed the Mozambique Channel, 1 chose a different wintering area, 1 migrated to the Lebanon where we lost the signals, and for the 2 remaining individuals (juveniles) we lost signals in the DRC before their autumn migration was completed.

All the tagged falcons landed in a narrow strip of land at the west coast of Madagascar between 18.0° S/44.0° E and 15.1° S/47.8° E. In Madagascar, the restricted wintering grounds were located on the central high plateau and the northern part of the island. Madagascar as the main wintering area as well as the DRC as a new wintering area will be described in a separate publication on Eleonora's falcons.

(d) *Spring migration of adults*

The spring migration of the two adult females differed substantially in time spent on migration, the route taken and the distance covered back to their breeding sites. One adult female (figure 5, no. 1) took 89 days and covered 17 000 km—more than twice the distance and five times the duration of its autumn migration. It stayed in Madagascar until 19 April and migrated back over the Mozambique Channel covering 1300 km over water. It landed on Pemba Island (Tanzania) on 21 April. During 2 days, it migrated to the southern highlands of Ethiopia, where it stayed for 7 days. The falcon then proceeded in northwestern direction and arrived in Chad on 7 May. From 8 May, the bird flew on to Niger, Nigeria and

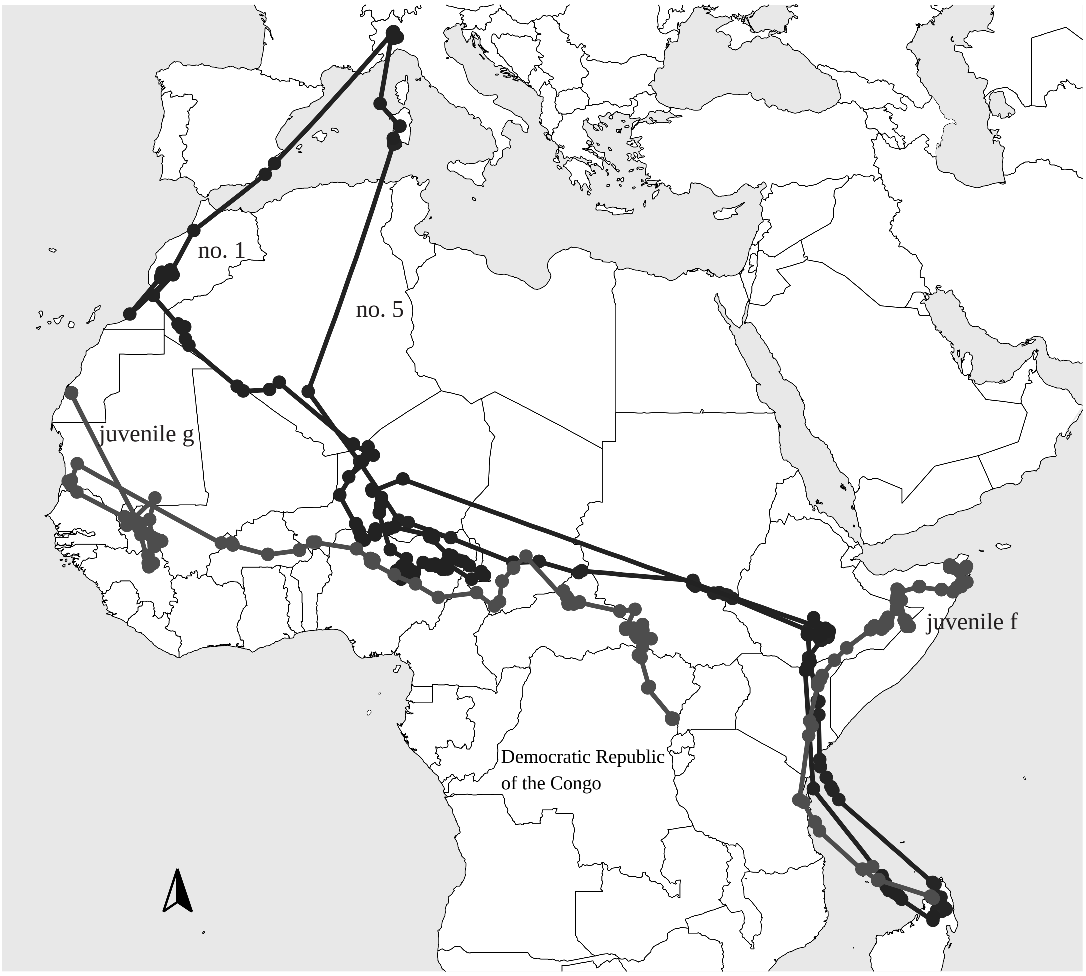

Figure 5. Spring migration of two adult females (nos 1 and 5) and of two juveniles (f and g), including their summering at the Horn of Africa and in West Africa, respectively.

Cameroon and remained in West Africa for a prolonged stopover covering 29 days. After this, it headed further northwest to the Moroccan coast and migrated towards the Mediterranean. It arrived on the Italian mainland on 10 July 2004 (LC A) and stayed there for nearly two months, until proceeding to its breeding ground on Sardinia (figure 5). On 13 September 2004, approximately two months after the start of the egg-laying period, the falcon arrived late at its breeding site on San Pietro Island, Sardinia.

A second female (figure 5, no. 5) could be tracked for 10.5 months, including one autumn and one spring migration. It left Madagascar on the 23 April and took a route back to its breeding site via Kenya, Ethiopia, Sudan, the Chad, Nigeria, Niger and Algeria and arrived back on Sardinia on the 22 May, approximately two months before the egg-laying period would start (first eggs on Sardinia around 20 July; M. Gschweng 2003, personal observations; Medda 2003). After its transmitter switched off on 7 July 2005 (table 1), the falcon was observed to be in good condition in its breeding area close to a nest site two months later (M. Gschweng *et al.* 2005, personal observations). Its complete spring migration lasted 29 days, during which the bird travelled 8500 km, covering nearly the same distance as during its autumn migration.

Comparing the two females, the distance flown during autumn migration was nearly the same for both the adult falcons (no. 1, 8700 km; no. 5, 8600 km), whereas for spring migration, the first female (no. 1) covered less than half the distance of the second female (no. 5). What is noticeable is the same stopover area of both the falcons in Ethiopia as well as the loop over West Africa (Cameroon, Nigeria and Niger) during their spring migration (figure 5).

(e) *Spring migration to summer areas of juvenile falcons*

For the first time, it was possible to locate the summering area of two non-reproductive Eleonora's falcons outside their breeding area. One juvenile (figure 5, f) started from its wintering area in northern Madagascar on 7 May 2006 and crossed the Mozambique Channel similar to an adult female 2 years before (figure 5, no. 1). It migrated via the Comoros and was located on Mafia Island, Tanzania on 9 May. It flew further north and reached eastern Ethiopia on 14 May, where it stayed for 7 days. On 22 May, it proceeded north to the northern tip of the Horn of Africa and stayed in the region for one month until 19 June 2006, when signal transmission ended.

A second juvenile (g) took a completely different course. It started from its wintering area in the DRC on 11 April 2006 and migrated northwest for 12 days. A change to a western course took the falcon via Sudan, the Central African Republic, Chad, Cameroon, Nigeria, Niger, Burkina Faso, Mali and Mauritania. It arrived at the west coast of Mauritania on 29 June. It spent the summer in the region of Mauritania, Senegal, Mali and Morocco until 16 August 2006, when we lost signals.

This juvenile could be tracked for 98 days during its spring migration and in its summer area in West Africa (figure 5).

Data for spring migration of the adults and juveniles cannot be compared, as the adults migrated back to their breeding sites on Sardinia, Italy, whereas the juveniles migrated to two completely different summer sites.

4. DISCUSSION

(a) *Autumn migration*

We conclude from our data that Eleonora's falcons do not take a species-specific route as it has been depicted in the historical route proposed by Stresemann (1954). Contrary to this, they displayed an enormous variability of routes and the juveniles migrated independently of the adults.

Apart from one adult female that flew to the Lebanon (figure 1, no. 3), five of the six adult falcons took a direct route to Madagascar. We can confidently rule out that the zigzag course of the adult female that landed in the Lebanon may have been caused by disorientation due to the satellite transmitter, as only negligible magnetic disturbances to the geomagnetic field produced by the transmitter are produced by solar powered PTTs (measured for a 30 g transmitter; Mouritsen *et al.* 2003). However, disorientation due to sickness of the bird cannot be ruled out.

After crossing the Mediterranean and the Sahara, the juveniles made a substantial stopover in West Africa. It is probable that the juveniles used this stopover to refuel, as it coincides with high insect abundance in the month after peak rainfall (Cumming & Bernard 1997), which is for the chosen sites, in September (Hijmans *et al.* 2005). Mt Cameroon is ranked among the 25 most important forested areas for birds in Africa (Collar & Stuart 1985) and lies within two Endemic Bird Areas (Olson *et al.* 2001). The routes of the juveniles merged at the Cameroon mountain chain and a Hungarian Team of ornithologists (Hivekovics & Palatitz 1998) observed one individual of Eleonora's falcon at this site during a census. It is therefore necessary to conduct future surveys in order to check the regular appearance of juvenile Eleonora's falcons.

As all of the tracked juvenile falcons migrated via West Africa, it is likely that genetic disposition led the falcons via a path that might have developed a long time ago. Interestingly, a similar migration pattern was found for one individual of the Eurasian hobby (*Falco subbuteo*) tracked by satellite telemetry in 2005 (Strandberg *et al.* 2006). This individual migrated via West Africa (stopover at northwest Ivory Coast in mid-October) and abruptly changed its course to an eastern direction. The similarity in migration behaviour might reflect in part the phylogenetically close relationship between the two sister species, Eleonora's falcon and Eurasian hobbies (Wink & Ristow 2000; Ristow *et al.* 2004).

As shown in our analysis, migration routes of the juvenile Eleonora's falcons differed substantially from the routes taken by the adult falcons. Thus, we derive from our data that the juveniles migrated independently of the adult falcons. As a consequence, they cannot learn distinct landmarks on their first autumn migration in contrast to other bird species as white storks (Chernetsov *et al.* 2004). We therefore conclude from our results that the juvenile navigation strategies applied to reach the wintering area in Madagascar must rely on inherited information.

(b) *Orientation of naive Eleonora's falcons*

Different theories are discussed as to how naive migrants reach their wintering areas (Alerstam 2006). In the case of Eleonora's falcon, it is likely that vector navigation forms the basis of its orientation system. This is supported by the fact that all the juvenile falcons changed their flight path after a certain time to a certain direction. However, the tracked falcons did not fly in a narrow corridor but displayed an extremely individual migration pattern. If the birds were to navigate exclusively via vector navigation, it would lead to a well-defined migration corridor to their wintering area (Berthold 1996). As this was not the case with Eleonora's falcon, we assume that they must additionally rely on other navigation mechanisms.

As is known from other studies (Mouritsen 1998; Wiltschko & Wiltschko 2005; Alerstam 2006), birds use the Earth's magnetic field as a compass, whereas total intensity and/or inclination provide information on position. Hand-raised birds of a population of pied flycatchers (*Ficedula hypoleuca*) changed migratory direction in an altered magnetic field when they experienced the (artificial) magnetic field of northern Africa (Beck & Wiltschko 1988). Apparently, certain magnetic conditions served as a 'signpost' and initiated the second leg of migration of this species (Wiltschko & Wiltschko 2005). Assuming that juvenile Eleonora's falcons did experience a magnetic signpost in West Africa as well as at the East coast of Mozambique, this could explain their abrupt change of course. They would then apply and combine different vectors, leading them to their next goal (e.g. flying for 48 hours to the east).

Although differential changes in geomagnetic parameters are much more critical along an east–west gradient than along a north–south gradient (Alerstam 2006; Alerstam *et al.* 2006), Chernetsov *et al.* (2008) have shown in displacement experiments with reed warblers (*Acrocephalus palustris*) that they are capable of compensating for displacement along an east–west gradient. However, contrary to our naive falcons on their autumn migration, these warblers were on spring migration, thus having probably learned to navigate via map-based elements in combination with celestial cues and were no longer naive migrants at the time of the study. In a study with naive pied flycatchers, the birds investigated did not compensate for displacements during autumn migration (Mouritsen & Larsen 1998). It is very unlikely that juvenile Eleonora's falcons should be capable of navigating along an east–west gradient with the help of the Earth's magnetic field, especially when crossing the Straits of Mozambique. Without a very precise additional mechanism for navigation, even the smallest deviations from their course (e.g. by wind drift) would make the falcons miss their goal area and fly out into the open ocean. Contrary to this, all our tagged naive birds that successfully arrived in Mozambique crossed to Madagascar and one bird crossed to the Comoros after having started to cross the Channel.

From our results, we conclude that in addition to vector navigation and map-based elements, a further mechanism must come into play permitting reliable and safe navigation across the Mozambique Channel. Vision could be one of these mechanisms. However, this would imply that naive birds must navigate during daytime at least during the second part of their crossing to successfully locate Madagascar. Contrary to this, three out of four falcons (figure 4, d, e, f) landed on Madagascar in the night (between 20.00 and 01.00). Mouritsen *et al.* (2004) described the ability of enhanced night vision in night-migratory songbirds, but whether this holds true for at least 200 km of navigation over open ocean is debatable. If not exclusively by vector navigation in combination with the magnetic field of the Earth, how was it possible for the naive birds to locate the islands in the open ocean?

The naive birds focused on two different areas along their pathways: before the Cameroon Mountain Chain and before Lake Victoria. Given the fact that naive birds do not possess an inherited map of landscape topography, it remains unclear how juveniles navigate along such topographical features. One possibility of a mechanism that has only rarely been examined is the capability of sensing infrasound. Infrasound created by coasts or mountain chains has been proposed as part of a navigational map for pigeons and migratory birds (Kreithen 1978; Quine & Kreithen 1981; Hagstrum 2000). Thus, naive birds that were equipped with this capability could use prominent landscape topography (e.g. the Cameroon Highlands or the Kilimanjaro region) for orientation. As a consequence, this would lead to an early channelling from this extremely broad front in the juveniles' migration routes. Additionally, the naive migrants could compensate for wind drift and avoid deviation of the inherited course, especially while navigating over open ocean.

After focusing on one target area, for example, the coast of Mozambique, the optimal position for take-off to Madagascar might be found by determining the shortest distance for the crossing of the Mozambique Channel. This appears best displayed by one juvenile falcon (figure 4, e) that landed near the central coast of Mozambique and slowly moved north along the coastline for a period of 3 days until it located the shortest distance to cross over.

As the crossing of the Mozambique Channel represents an additional physiological and navigational challenge for naive falcons, the birds should ideally search for the best position for take-off from the Mozambique coast in order to take the shortest crossing. This seems to have been realized by one juvenile that slowly moved north along the Mozambique coastline until it departed to Madagascar at the shortest possible distance. One juvenile, however, took off much further north and turned around over open ocean (figure 4, b-1). Perhaps this individual experienced navigational difficulties, as it migrated during night time and orientation by vision was strongly reduced or impossible. If the use of infrasound played a role in the navigation system of the juvenile, the bird would have been capable of navigating by night. On the other hand, adverse wind conditions may have forced the bird to turn around as shown by a study of Meyer *et al.* (2000) where raptors (e.g. black kite, *Milvus migrans*; honey buzzard, *Pernis apivorus*) did not cross open water during strong headwinds.

We conclude from our data that Eleonora's falcon relies on a basal navigation system that is constantly recalled but additionally uses a second navigation system with additional mechanisms that are employed only as and when required.

(c) *Wintering*

Despite this high variation of autumn migration routes, both the adults and juveniles converged on one narrow wintering area within Madagascar, which confirms the extrapolation of Walter, who expects 70 per cent of the world population of Eleonora's falcon to overwinter in Madagascar (Walter 1979*b*). As every tracked falcon that reached the East African coast made at least one attempt to cross the Mozambique Channel, we postulate that an even higher percentage of the world population winters in Madagascar. This hypothesis is supported by the fact that the crossing of the Mozambique Channel forms a part of the inherited migration pattern, which the naive Eleonora's falcons display.

So far, there are no other known wintering areas for Eleonora's falcons on African mainland, although observations of flocks of up to 300 individuals in Tanzania (Turner 1978), and in 'British Somaliland', together with hobbies have been reported between the months of April and May (Archer & Godman 1937). However, the observations in Somalia took place during the spring migration period and therefore provide no evidence for the assumption that these falcons stayed in this region over winter. Turner (1978) concluded for Tanzania that Eleonora's falcon is an uncommon winter visitor, mainly confined to the central high plateau with extreme records of 20 November and 14 April. These observations perfectly fit our satellite data, as our tracked falcons were migrating through Tanzania from 7 November until 24 November during their autumn migration. The adult falcons left Madagascar at the end of April (20 and 22 April), which also coincides with the observations in Tanzania around 14 April (Turner 1978). An observation of an immature Eleonora's falcon at the Bazaruto archipelago in Mozambique in January 1996 (Koehler & Koehler 1996) could indicate that the species stays over in some regions where there is high food abundance as did the adult female that stayed in Mozambique for three months (December to March). To conclude, Madagascar and the surrounding islands, including Reunion (M. Salamolard 2005, personal communication) and Comoros (Louette *et al.* 2004), as well as probable stopover sites during migration such as Mozambique and its offshore islands, remain the only currently known wintering areas for adult Eleonora's falcons.

(d) *Spring migration of adults*

The spring migration of two adult females displayed even more individuality than the autumn migration of all the tracked adult falcons (figure 5). One female (no. 1) made one stop over in Ethiopia for 7 days and another substantial stop over in West Africa for 29 days, possibly due to a higher insect abundance during this season. It is unlikely that the bird chose these sites owing to wintering passerines, as the diet of Eleonora's falcons outside their breeding grounds mainly consists of insects such as locusts, dragonflies, beetles and termites (Walter 1979*b*; Ristow *et al.* 1983). In a study in which 23 stomach contents of this species collected in Madagascar were examined, only one contained a small bird and 21 contained mainly locusts and other insect matter (Rand 1936). Furthermore, during a five-month period in which they were studied in Madagascar (M. Gschweng 2004, unpublished data), none of the Eleonora's falcons observed ever tried to catch a bird, which further supports this assumption. The second female made a stopover of 7 days in Ethiopia, too. This fact probably identifies the highlands of Ethiopia as well as West Africa as important stopover sites for the spring migration of Eleonora's falcon.

(e) *Summer sites of juveniles*

Neither of the tracked juvenile falcons returned to their birthplaces on Sardinia, Italy, but stayed in Africa over the summer. This coincides with the lack of information on observations from second calendar year falcons at the breeding sites (Ristow 1975; Medda 2003).

The two tracked juvenile falcons (f, g) took a completely different route each and chose a different area in which to spend the summer. Unfortunately, our satellite data were not sufficient to clarify whether they stayed until the end of the breeding season and whether the falcons returned to their wintering area in the following autumn. Walter (1979*a*) summarizes the ringing recoveries of immature and subadult falcons ringed in Paximada, Greece (recoveries in Spain, Greece, Corsica, and the south western Black Sea), which were between 250 and 1600 km away from their birth places. All the sites were located north (northeast to northwest) of these. Ristow & Wink (1992) provided data of 29 recoveries from 3500 nestlings ringed off Crete, Greece, with the southernmost recovery being a 1-year-old falcon found in Algeria at the Mediterranean coast. Only one summer record comes from Mauritania at 16 June 1988 (Meininger *et al.* 1990), which perfectly fits our satellite data of one juvenile that stayed over summer at the west coast of Mauritania until 29 June.

To summarize, our satellite data provide new insights into the migration routes of Eleonora's falcons and the whereabouts of non-breeding individuals. It opens up new perspectives with regard to navigational strategies and fuels speculation on the evolutionary mechanisms that shaped the migration routes of juvenile Eleonora's falcons. The high inter- and intra-individual variability of autumn and spring migration routes, the variety of important stopover sites, the discovery of a new wintering area of a juvenile Eleonora's falcon in the DRC and the summer areas of juveniles underline the vulnerability of this species as it makes protection measurements very difficult.

All work reported herein was in accordance with ethical standards and guidelines in the care and use of experimental animals of the University of Ulm, Germany. Permission for fieldwork was granted by the Regione della Sardegia, Assessorato della Difesa dell' Ambiente, Cagliari, Sardinia; Prot. 8548 (Autorizzazione ai sensi dell' art. 6, L. R. 23/98 - Integrazione autorizzazione n° 01/2004 dell 6.08.2004 prot. N. 2730).

We thank all the volunteers who kindly assisted with the fieldwork from 2003 to 2005, especially A. Fadda who supported fieldwork and assisted in obtaining the relevant permission. D. Ristow provided useful information on the biology of Eleonora's Falcon. We also thank F. Spina for his support in carrying out the project in Sardinia. Our thanks additionally go to M. Kaatz who introduced mounting backpacks and M. Herkt who introduced the application of ArcView GIS v. 9.2. J. Fietz and S. Berger helped with statistical analyses and M. Finn corrected the English. T. Alerstam and one anonymous reviewer improved a former version of the manuscript. The Regione Della Sardegna and the Istituto Nazionale della Fauna Selvatica, Italy, kindly granted permission for fieldwork on Sardinia. This work was partly funded with grants from the Otto Wolf Foundation and the Academic Exchange Programme, Germany, to M.G.

REFERENCES

Able, K. P. 1993 Orientation cues used by migratory birds: a review of cue-conflict experiments. *Trends Ecol. Evol.* **8**, 367–371. (doi:10.1016/0169-5347(93)90221-A)

Able, K. & Able, M. A. 1996 The flexible migratory system of the savannah sparrow (*Passerculus sandwichensis*). *J. Exp. Biol.* **199**, 3–8.

Alerstam, T. 2006 Conflicting evidence about long-distance animal navigation. *Science* **313**, 791–794. (doi:10.1126/science.1129048)

Alerstam, T. & Lindström, A. 1990 Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration* (ed. E. Gwinner), pp. 331–351. Berlin, Germany: Springer.

Alerstam, T., Hake, M. & Kjellen, N. 2006 Temporal and spatial patterns of repeated migratory journeys by ospreys. *Anim. Behav.* **71**, 555–566. (doi:10.1016/j.anbehav.2005.05.016)

Archer, G. & Godman, E. M. (eds) 1937 *The birds of British Somaliland and the Gulf of Aden*. London, UK: Gurney and Jackson.

ArcView GIS 3.2a for Windows 2000 *ESRI GIS and mapping software*. Redlands, CA: ESRI.

Beck, W. & Wiltschko, W. 1988 Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas). In *Acta XIX Congr. Int. Ornithol*, vol. II, pp. 1955–1962. Ottawa, Canada: University of Ottawa Press.

Benson, C. W., Colebrook-Robjent, J. F. R. & Williams, A. 1976 Contribution a l'ornithologie de Madagascar. *L'Oiseau et R.F.O.* **46**, 118–119.

Berthold, P. (ed.) 1996 *Control of bird migration*. London, UK: Chapman and Hall.

Berthold, P. (ed.) 2001 *Bird migration. A general survey.* Oxford, UK; New York, NY: Oxford University Press.

Chernetsov, N., Berthold, P. & Querner, U. 2004 Migratory orientation of first-year white storks (*Ciconia ciconia*): inherited information and social interactions. *J. Exp. Biol.* **207**, 937–943. (doi:10.1242/jeb.00853)

Chernetsov, N., Kishkinev, D. & Mouritsen, H. 2008 A long-distance avian migrant compensates for longitudinal displacement during spring migration. *Curr. Biol.* **18**, 188–190. (doi:10.1016/j.cub.2008.01.018)

Collar, N. J. & Stuart, S. N. 1985 *Threatened birds of Africa and related islands*. The ICBP/IUCN Red Data Book.

Cumming, G. S. & Bernard, R. T. F. 1997 Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**, 309–317. (doi:10.1007/s004420050240)

Delgado, G. & Quilis, V. 1990 New data concerning the migration of Eleonora's falcon *Falco eleonorae*. *Ringing Migr.* **11**, 111–112.

Dimalexis, A. *et al.* 2008 The status of Eleonora's falcon (*Falco eleonorae*) in Greece. *J. Ornithol.* **149**, 23–30. (doi:10.1007/s10336-007-0207-4)

Gwinner, E. & Wiltschko, M. 1978 Endogenously controlled changes in migratory direction of the garden warbler, *Sylvia borin*. *J. Comp. Physiol.* **125**, 267–273. (doi:10.1007/BF00656605)

Hagstrum, J. T. 2000 Infrasound and the avian navigational map. *J. Exp. Biol.* **203**, 1103–1111.

Helbig, A. 2003 Evolution of bird migration: a phylogenetic and biogeographic perspective. In *Avian Migration* (eds P. Berthold, E. Gwinner & E. Sonnenschein), pp. 3–20. Heidelberg, Germany: Springer Verlag.

Helbig, A. J., Berthold, P. & Wiltschko, W. 1989 Migratory orientation of blackcaps (*Sylvia atricapilla*): population-specific shifts of direction during the autumn. *Ethology* **82**, 307–315.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978. (doi:10.1002/joc.1276)

Hivekovics, A. & Palatitz, P. 1998 Summary of a study by Hungarian ornithologists on Mount Cameroon. *Bull. Afr. Bird Club* **5**, 97–100.

Hooge, P. N. & Eichenlaub, B. 1997 *Animal movement extension* (eds U.S.G. Survey). Anchorage, AK: Alaska Science Center—Biological Science Office.

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

Koehler, P. & Koehler, U. 1996 *Annotated list of birds observed in January 1996 in the Bazaruo Archipelago, Mozambique*. Cape Town, Republic of South Africa: BirdLife South Africa.

Kreithen, M. L. 1978 Sensory mechanisms for animal orientation—can any new ones be discovered? In *Animal migration, navigation, and homing* (eds K. Schmidt-Koenig & W. T. Keeton), pp. 25–34. Berlin, Germany: Springer.

Louette, M., Meirte, D. & Jocque, R. 2004 Oiseaux. In *La faune terrestre de l'archipel des Comores. Studies in afroctropical zoology* (ed. M. Louette), p. 114. Paris, France: Tervuren MRAC.

Medda, M. 2003 Analisi del comportamento riproduttivo del falco della regina (*Falco eleonorae*) nell'Isola di San Pietro (Sardegna). Cagliari, Italy: University of Cagliari.

Meininger, P., Duiven, P., Marteijn, E. & van Spanje, T. 1990 Notable bird observations from Mauritania. *Malimbus* **12**, 19–24.

Meyburg, B.-U. & Langrand, O. 1985 Evolution, Verbreitung und Status der Greifvögel (Falconiformes) Madagaskars. In *Proc. Int. Symp. on African Vertebrates, Systematics, Phylogeny, Bonn*, pp. 193–205.

Meyburg, B.-U. & Meyburg, C. 1999 The study of raptor migration in the Old World using satellite telemetry. In *Proc. 22nd Int. Ornithol. Congr.* (eds N. J. Adams & R. H. Slotow), pp. 2992–3006. Johannesburg, Republic of South Africa: BirdLife South Africa.

Meyer, S. K., 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. *Behavior* **137**, 379–399. (doi:10.1163/156853900502132)

Milon, P., Petter, J.-J. & Randrianasolo, G. 1973 Oiseaux. In *Faune de Madagascar*, vol. 35. Tananarive, Madagascar; Paris, France: Orstom and CNRS.

Mouritsen, H. 1998 Redstarts, *Phoenicurus phoenicurus*, can orient in a true-zero magnetic field. *Anim. Behav.* **55**, 1311–1324. (doi:10.1006/anbe.1997.0696)

Mouritsen, H. & Larsen, O. N. 1998 Migrating young pied flycatchers (*Ficedula hypoleuca*) do not compensate for geographical displacements. *J. Exp. Biol.* **201**, 2927–2934.

Mouritsen, H., Huyvaert, K. P., Frost, B. J. & Anderson, D. J. 2003 Waved albatrosses can navigate with strong magnets attached to their head. *J. Exp. Biol.* **206**, 4155–4166. (doi:10.1242/jeb.00650)

Mouritsen, H., Feenders, G., Liedvogel, M., Wada, K. & Jarvis, E. D. 2004 Night-vision brain area in migratory songbirds. *Proc. Natl Acad. Sci. USA* **102**, 8339–8344. (doi:10.1073/pnas.0409575102)

Olson, D. M. *et al.* 2001 Terrestrial ecoregions of the world: a new map of life on earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938. (doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)

Quine, D. B. & Kreithen, M. L. 1981 Frequency shift discrimination: can homing pigeons locate infrasounds by Doppler shifts? *J. Comp. Physiol.* **141**, 153–155. (doi:10.1007/BF01342661)

Rand, S. L. 1936 The distribution and habits of Madagascar birds. *Bull. Am. Mus. Nat. Hist.* **72**, 143–499.

Ristow, D. 1975 Neue Ringfunde vom Eleonorenfalken (*Falco eleonorae*). *Die Vogelwarte* **28**, 150–153.

Ristow, D. & Wink, M. 1992 Distribution of non-breeding Eleonora's falcon *Falco eleonorae*. *Il Merill* **28**, 1–10.

Ristow, D., Wink, C. & Wink, M. 1983 Biologie des Eleonorenfalken (*Falco eleonorae*): die Anpassung des Jagdverhaltens an die vom Wind abhängigen Zugvogelhäufigkeiten. *Die Vogelwarte* **32**, 7–13.

Ristow, D., Scharlau, W. & Wink, M. 1989 Population structure and mortality of Eleonora's falcon *Falco eleonorae*. In *Raptors in the modern world*, pp. 321–325. Berlin, Germany: WWGBP.

Ristow, D., Witte, L. & Wink, M. 2004 Sex determination of nestlings in Eleonora's falcon *Falco eleonorae*: plumage characteristics and molecular sexing. In *Raptors worldwide* (eds R. D. Chancelor & B.-U. Meyburg), pp. 459–466. Berlin, Germany: WWWGBP.

Schmidt-Koenig, K. & Keeton, W. T. (eds) 1978 *Animal migration, navigation, and homing*. Berlin, Germany: Springer.

SPSS 2004 *SPSS base 13.0 for Windows user's guide*. Chicago, IL: SPSS, Inc.

Steenhof, K., Bates, K. K., Fuller, M. R., Kochert, M. N., McKinley, J. O. & Lukacs, P. M. 2006 Effects of radiomarking on prairie falcons: attachment failures provide insights about survival. *Wildl. Soc. Bull.* **34**, 116–126. (doi:10.2193/0091-7648(2006)34[116:EOROPF]2.0.CO;2)

Strandberg, R., Alerstam, T., Hake, M. & Olofsson, P. 2006 The journey of a female hobby across two continents: from Sweden in Northern Europe to Zambia in South Africa. In *Tracker news* (ed. Microwave Telemetry, Inc.), p. 2. Columbia, MD: Microwave Telemetry, Inc.

Stresemann, E. 1954 Zur Frage der Wanderungen des Eleonorenfalken. *Vogelwarte* **17**, 182–183.

Terrasse, J. F. 1963 A propos de deux reprises de *Falco eleonorae*. *L'oiseaux et R.F.O.* **33**, 56–60.

Thorup, K. & Rabol, J. 2001 The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. *J. Avian Biol.* **32**, 111–119. (doi:10.1034/j.1600-048X.2001.320203.x)

Turner, D. A. 1978 Eleonora's falcon wintering in Tanzania. *Scopus* **2**, 49–50.

Vaughan, R. 1961 *Falco eleonorae*. *Ibis* **103**, 114–128. (doi:10.1111/j.1474-919X.1961.tb02424.x)

Wallraff, H. G. 2005 *Avian navigation: pigeon homing as a paradigm*. Berlin, Germany; New York, NY: Springer.

Walter, H. 1979*a Breeding locations of Falco eleonorae* (ed. H. Walter), pp. 56. Los Angeles, CA: University of California.

Walter, H. (ed.) 1979*b Eleonora's falcon. Adaptations to prey and habitat in a social raptor*. Chicago, IL; London, UK: The University of Chicago Press.

Wiltschko, W. & Wiltschko, R. 2005 Magnetic orientation and magnetoreception in birds and other animals. *J. Comp. Physiol. A* **191**, 675–693. (doi:10.1007/s00359-005-0627-7)

Wink, M. & Ristow, D. 2000 Biology and molecular genetics of Eleonora's falcon *Falco eleonorae*, a colonial raptor of Mediterranean islands (24). In *Raptors at risk* (ed. WWGB/Hancock House), pp. 653–658.

Zefania, S. 2001 Observation of sooty and Eleonora's falcons in Madagascar. In *Wings over Africa, Proc. Int. Seminar on Bird Migration: Research, Conservation, Education and Flight Safety*, pp. 151–159.