

Autumn Migration of Eleonora's Falcon *Falco eleonora* Tracked by Satellite Telemetry

Pascual López-López^{1,2,*}, Rubén Limiñana², and Vicente Urios²

¹Cavanilles Institute of Biodiversity and Evolutionary Biology, Terrestrial Vertebrates Group, University of Valencia, Polígono de la Coma s/n, 46980 Paterna, Valencia, Spain

²Estación Biológica Terra Natura CIBIO – Fundación Terra Natura, University of Alicante, Apdo, 99 E-03080, Alicante, Spain

(Accepted December 22, 2008)

Pascual López-López, Rubén Limiñana, and Vicente Urios (2009) Autumn migration of Eleonora's Falcon *Falco eleonora* tracked by satellite telemetry. *Zoological Studies* 48(4): 485-491. The migration route of Eleonora's Falcon *Falco eleonora* has largely been a mystery. To date, the most widely accepted hypothesis on Eleonora's Falcon's migration suggested a coastal route through the Mediterranean Sea eastwards, crossing the Suez Canal, and proceeding southwards through the Red Sea following the East coast of Africa to the wintering grounds in Madagascar and the Mascarene Is. This study provides the first description of autumn migration routes of 2 Eleonora's Falcons (a juvenile male and an adult male) tracked by satellite telemetry from their breeding colonies in the Western Mediterranean to their wintering grounds in southeastern Africa. Contrary to previous suggestions, Eleonora's Falcons migrated inland across the African continent and did not follow the presumed migration route across the Mediterranean Sea. We discuss the possible origin of this migratory behavior and provide data on routes, timing of migration, and scarce existing data of ringing recoveries. <http://zoolstud.sinica.edu.tw/Journals/48.4/485.pdf>

Key words: Satellite tracking, Conservation, Madagascar, Falcons, STAT.

“The use of satellite tracking has made one of the mankind's age-old dreams come true: travelling the earth on the back of migratory birds, at least indirectly, using miniature transmitter technology” (Berthold 2001). Migration is one of the critical stages of the biological cycle of avian species, with a strong influence on the life history of migratory birds (Newton 1998, Alerstam et al. 2003). We are now able for the first time to know the entire spatiotemporal pattern of migrants in a way unthinkable compared to that provided by traditional ringing methods. Actually, the exact timing of migration, important stopover sites and wintering grounds can be identified by combining data from traditional ringing programs and modern satellite telemetry technology. This is of utmost importance for the conservation of migratory bird species.

The migration route of Eleonora's Falcon

Falco eleonora has largely been a mystery, and several hypotheses were suggested to explain the “mysterious disappearance” of falcons during the wintering season (Vaughan 1961, Walter 1979). Eleonora's Falcon is a long-migrant species that breeds in scattered colonies over the Mediterranean region, with some small colonies located in the Atlantic Ocean in the Canary Is. and off the Moroccan coast (Walter 1979, Ferguson-Lees and Christie 2001). The European population has recently been revised substantially upwards, from around 12,000 mature individuals (BirdLife International 2004) to about 30,000 mature individuals (Papaconstantinou 2007). Global population trends have not been quantified, but the species is not believed to be approaching the thresholds for the population decline criterion of the IUCN Red List (i.e., declining more than 30% in 10 yr or 3 generations). For these reasons, the

*To whom correspondence and reprint requests should be addressed. Tel: 34-96-3543660. Fax: 34-96-3543670. E-mail: Pascual.Lopez@uv.es; lopez.pascual@gmail.com

species is currently evaluated as being of “Least Concern” globally (BirdLife International 2008). It breeds in late summer, coinciding with the peak of autumn passerine migration which is the main trophic resource for the species (Walter 1979). It also feeds on large insects which are captured in flight (Ferguson-Lees and Christie 2001). Up to now, ringing has provided unique data on its wintering grounds, which range from Madagascar to the Mascarene Is. (Walter 1979, Ferguson-Lees and Christie 2001). However, detailed knowledge of the migration routes of the species is still lacking. To date, the most accepted hypothesis on Eleonora’s Falcon’s migration suggests a coastal route through the Mediterranean Sea eastwards, crossing the Suez Canal and proceeding southwards through the Red Sea following the east coast of Africa to the wintering grounds in Madagascar and the Mascarene Is. (Stresemann 1954, Walter 1979).

In recent decades, satellite telemetry has enabled detailed tracking of bird movements, particularly migration (e.g., Berthold et al. 1995, Fuller et al. 1995, Meyburg et al. 1995 1998, Judas et al. 2006, Limiñana et al. 2007 2008; see also Guan and Higuchi 2000 for a review), allowing the accurate mapping of migratory routes and identification of wintering grounds. For the first time we are able to know where birds are during the entire annual cycle. In reality, adequate protection of wintering grounds and stopover sites plays a key role in the maintenance of populations of migratory species (Newton 1998). However, to date, the number of species that can be tracked is limited by the transmitter weight, which should not exceed the 3% of the body mass of the tracked individual (Kenward 2001). Yet, the on-going miniaturization of platform transmitter terminals (PTTs) is increasing the range of species that can be tracked, making possible the tracking of medium-sized long-migrant species such as Eleonora’s Falcon.

Herein, we provide the first description of the autumn migration routes of 2 Eleonora’s Falcons (a juvenile male and an adult male) tracked by satellite telemetry from their colonies in the Western Mediterranean. Falcons were tracked from their breeding grounds in the Balearic Is. in Spain to their wintering grounds in Madagascar. Data on migration routes and timing are provided.

MATERIALS AND METHODS

The 2 Eleonora’s Falcons tracked in this study were captured in the Balearic Is. in autumn 2007. One adult was trapped in Cabo Formentor (Mallorca, Spain) on 17 Sept. 2007 using dhogaza nets and a stuffed Eagle Owl (*Bubo bubo*) as a decoy (Bub 1991). One chick was trapped in the nest in Tagomago I. (Ibiza, Spain) on 14 Sept. 2007. Both birds were weighed, measured, and ringed. Birds were also sexed by molecular methods (Fridolfsson and Ellegren 1999).

A Microwave Telemetry’s (Columbia, MD, USA) 9.5 g solar-powered PTT-100 PTT was affixed to the back of each bird using a Teflon harness (Kenward 2001, Limiñana et al. 2007). For the first 3 mo of operation, the PTTs were programmed on a duty cycle of 8 h on/ 15 h off; for subsequent months, the duty cycle consisted of 12 h on/ 58 h off. Data on 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 respective nominal accuracies of < 150, 150-350, 350-1000, and > 1000 m (Argos 1996). Also, to avoid biases associated with the non-independence of the data due to temporal autocorrelations, positions obtained < 1 h after the previous one were excluded from the analyses (Limiñana et al. 2007). All data were retrieved and managed using the Satellite Tracking and Analysis Tool (STAT, Coyne and Godley 2005).

Eleonora’s Falcons start migration just after finishing the breeding period (Walter 1979). Each bird was trapped and fitted with a transmitter just 1 mo before beginning migration. The onset of migration was estimated as the middle day between the last location of Eleonora’s Falcon in Spain and the first location in Africa, and the end of migration was the middle date between the date of the first location in Madagascar and the previous one. The duration of migration, distance covered, average distance covered in a day, average and maximum distances covered in 1 h (considering only locations obtained with < 4 h of difference), and average bearing during migration were calculated with data from only during the migration period. The average bearing and its standard deviation were calculated with circular statistics of the “Circular” package for R 2.2.1. (<http://cran.r-project.org>) (Fisher 1995).

RESULTS

We received a total of 188 locations of the adult falcon, 97 of which corresponded to good quality LCs (3, 2, 1, and 0), and 320 locations of the juvenile, 219 of which were of good quality.

The 2 Eleonora's Falcons tracked in this study and sexed as males completed the migration from their breeding colonies in the Balearic Is., in the western Mediterranean Sea, and arrived in Madagascar, in southeastern Africa. Falcons left the Balearic Is. in late Oct. and arrived in Madagascar in early Dec. (Table 1). The onset of migration differed by only 1 d for the juvenile and adult, whereas the end of migration differed by 10 d, with the adult arriving earlier than the juvenile (Table 1).

The 2 birds followed different routes to arrive to Madagascar (Fig. 1). The adult bird visited a total of 10 countries whereas the juvenile crossed a total of 14. Interestingly, both birds exhibited a kind of an "inverted S-shaped" migratory route. The birds crossed the Sahara Desert towards the southeast until Libya and then made an abrupt change of direction from southeasterly to the southwest until reaching Nigeria (juvenile) and Chad (adult), curiously at the same latitude (approximately 23-25°N). Afterwards, migration routes turned again to a southeasterly direction (at 8-10°N) but were separated by up to 1600 km. The 2 routes converged in southern Tanzania and northern Mozambique, in southeastern Africa. Both birds arrived in Madagascar by crossing the Mozambique Channel which means they had to fly over 600 km of open sea (Fig. 1). Mean bearing values were predominantly oriented southerly-southeasterly (Table 1).

Overall, the adult bird flew a more-direct route

covering greater distances in a day (219 vs. 192 km/d of the juvenile), which resulted in an earlier arrival at the wintering area. Both birds showed maximum speeds in the late stages of migration, when arriving at their wintering grounds. However, there were differences in the hour of the day at which these maximum speeds were attained; maximum speed for the adult bird was recorded in the afternoon, while that for the juvenile bird was recorded at night. The migration duration was 47 d for the juvenile and 38 d for the adult, during which time the birds covered about 9000 km. Also, there were differences between the 2 birds in the hour of the day at which most of the movements during migration were recorded, with juvenile movements recorded at nighttime (Fig. 2A) and adult movements recorded mostly during the daytime (Fig. 2B). However, as PTTs were functioning in a duty-cycle, an unequal frequency of Argos satellite locations did not allow confirming whether juvenile also migrated during the daytime.

At least 4 different stopover sites were identified. The average time at a stopover site was 4.8 ± 2.2 d. The adult bird made its 1st stopover of 3 d (on 24-26 Nov. 2007) at Livingstone Mountains close to Malawi Lake (Tanzania), and a 2nd one of 4 d (from 28 Nov. to 1 Dec. 2007) in inner southern Tanzania. Two stopover sites were also identified for the juvenile: one of 8 d (on 9 to 16 Nov. 2007) at the border between Nigeria and Cameroon in West Africa, and another one of 4 d (from 2 to 5 Dec. 2007) in a mountain area close to the borderline between Tanzania and Burundi.

The end of signal reception occurred on 10 Jan. 2008 (adult) and on 5 Apr. 2008 (juvenile) when birds were still in the wintering area in Madagascar. Causes of cessation of signal reception remain unknown and might have been

Table 1. Autumn migration parameters of 2 Eleonora's Falcons tracked by satellite telemetry

Name	PTT-ID	Age	Sex	Weight (g)	Migration onset	Migration duration (days)	Migration end
Tagomago	34471	Juvenile	♂	400	27 Oct. 2007	47	13 Dec. 2007
Formentor	34469	Adult	♂	335	26 Oct. 2007	38	03 Dec. 2007

Name	Distance from tagging site to wintering ground (km)	Distance/d during migration (km/d)	Mean \pm S.D. distance/h during migration (km/h) (maximum in parenthesis)	Mean \pm S.D. bearing (degrees)
Tagomago	9014.64	191.80	16.47 \pm 23.83 (138.08)	140.84 \pm 45.85
Formentor	8332.12	219.27	19.16 \pm 29.19 (188.89)	145.75 \pm 36.46

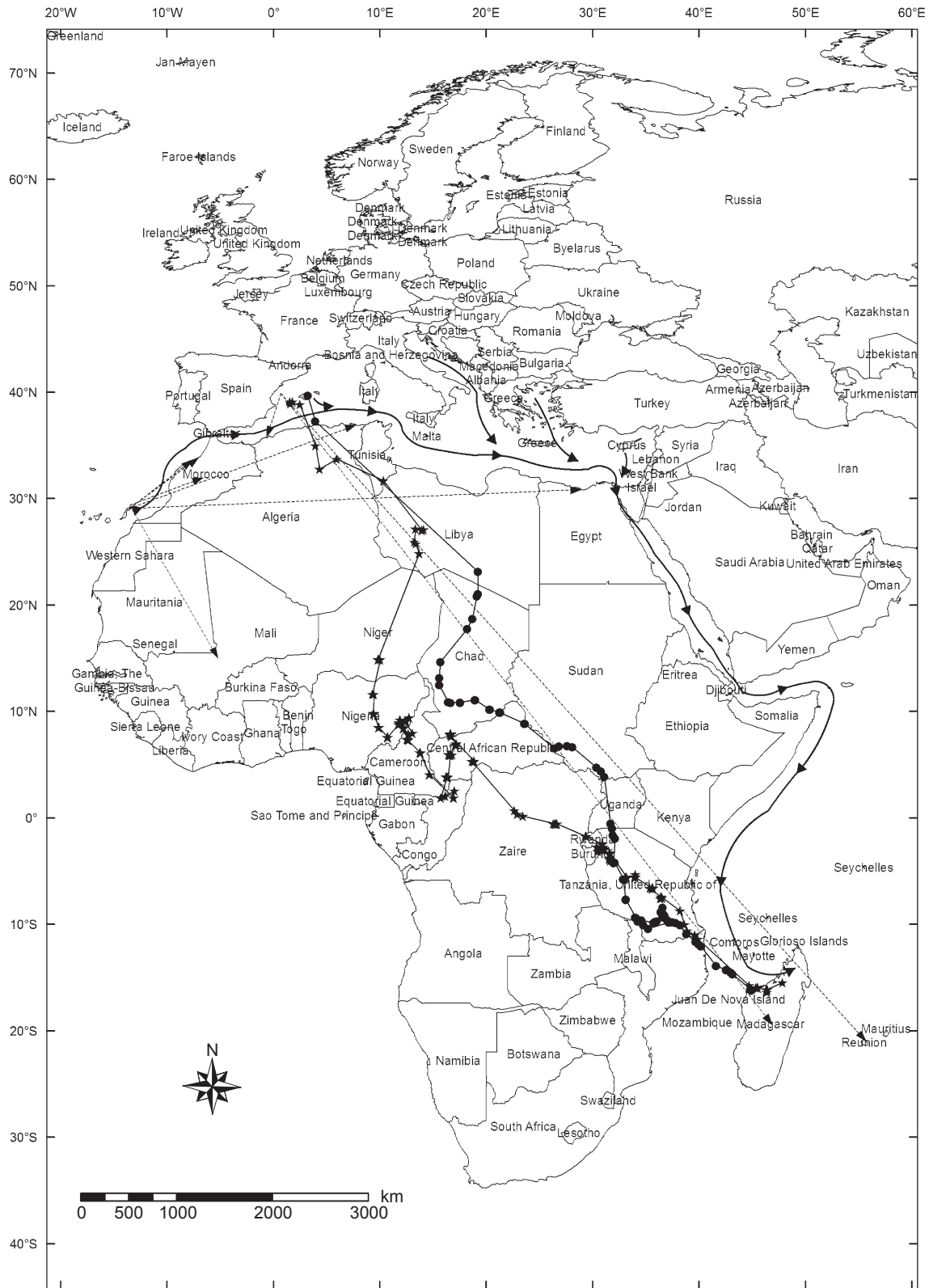


Fig. 1. Migration routes of 2 Eleonora's Falcons tracked by satellite telemetry. The adult route (PTT-ID 34469) is shown by the solid line with dots, and the juvenile route (PTT-ID 34471) is shown by the solid line with stars. The migration route proposed by Walter (1979) is shown as a solid line following the Mediterranean Sea and East coast of Africa. Marking and ringing recoveries are shown by dashed arrows.

due to a fault in the PTTs, loss of the equipment or even the death of the birds. For this reason no data on spring migration are available.

DISCUSSION

This study provides the first description of the timing autumn migration routes of Eleonora's Falcon breeding in the western Mediterranean

to their wintering grounds in southeastern Africa. Detailed knowledge on migratory routes and wintering areas for this species was previously lacking. Given the enormous interest by the ornithological community in the migration route followed by Eleonora's Falcon, the raw data and maps were made publicly available at the website of the Seaturtle Organisation (www.seaturtle.org/tracking) from the start of the project in 2007.

Recent developments in satellite transmitters,

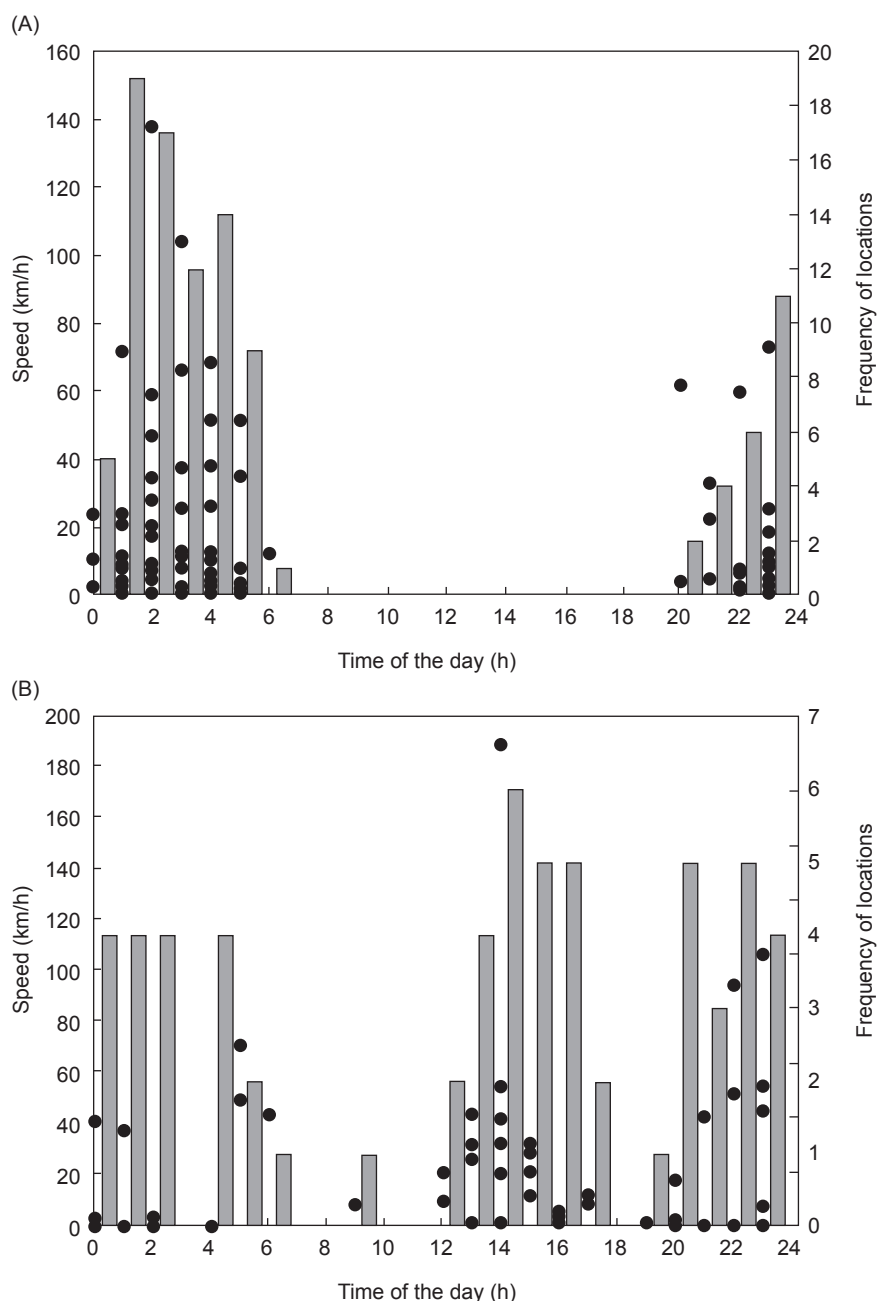


Fig. 2. Migration speed (dots) and frequency of locations (bars) of 2 Eleonora's Falcons tracked by satellite telemetry according to the hour of the day. (A) Juvenile (PTT-ID 34471); (B) adult (PTT-ID 34469).

which are now lighter than 10 g, have enabled us to study the migratory behavior of medium-sized birds, such as Eleonora's Falcon. The standard protocol (Kenward 2001) recommends fitting transmitters which are < 3% of an animal's body mass for migratory birds to avoid hurting animals or to prevent disturbances that could alter the animal's normal behavior. In our case, the total weight of the complete tracking equipment (including the transmitter and harness) did not exceed 3% of the birds' body mass.

The 2 tagged birds (1 adult male and 1 juvenile male) left the breeding areas at the same time, in late Oct. However, the birds traveled different migratory routes and showed differences in daily distances covered during migration and hence, they had different dates of arrival at the wintering grounds, with the adult arriving earlier than the juvenile. More interestingly, the similar "inverted S-shape" of the migration route that both birds performed is remarkable, resulting in parallel changes in migration direction at similar latitudes but different longitudes (Fig. 1). Likely explanations for this curious phenomenon vary from differences in main wind directions according to latitude, changes in prey availability as birds entered the Sahelian area, or even genetic inheritance, making birds change direction in some kind of inherited endogenous program, so-called "vector navigation" (Berthold 2001). As only 2 birds were tracked in this study, no definitive conclusions can be drawn.

Nevertheless, our results do not support the presumed migration route proposed by Stresemann (1954) and accepted by Walter (1979). By contrast, our 2 birds migrated inland across the African continent for almost 2 mo until arriving at the wintering grounds in Madagascar. This suggests a likely "inland migration route" followed by Eleonora's Falcons. This is also supported by some ringing data. According to the Spanish National Database of Migratory Species, at least 7 Eleonora's Falcons ringed in Spain were recaptured on the African continent: 2 in Argelia (on 31 Nov. 1988 and 17 June 1997), 3 in Morocco (on 17 June 1990, 1 June 1994, and 15 July 2002), 1 in Egypt (on 5 Dec. 1998), and the most inland one was recorded in Mali on 7 Mar. 1989 (published by Delgado and Quilis 1990). The latter was ringed on Alegranza I. (Lanzarote, Spain) on 12 Sept. 1986 (Fig. 1). This is a small island where Eleonora's Falcons breed in the Atlantic Ocean, more than 1000 km from the Mediterranean Sea and fuels the possibility of a straight inland migratory route

for western populations of Eleonora's Falcons (Delgado and Quilis 1990). Also 2 records were recorded in the wintering grounds, 1 on Reunion I. (on 30 Nov. 2000) and 1 in Madagascar (on 28 Jan. 2003) (Fig. 1).

Finally, how Eleonora's Falcon can orient during this long migratory travel (more than 9000 km on average in a straight line) remains unknown. It is especially fascinating that juvenile naive birds reach the same wintering grounds as their parents in southeastern Africa. Two alternative (but not mutually exclusive) hypotheses can be proposed to account for the origin of this migration route: (1) a fitness hypothesis for which migration might be constrained by energetic and survival costs, and (2) a phylogenetic hypothesis for which birds would perform such a long-distance migration as a result of their evolutionary origins.

In light of new data obtained by satellite telemetry that shows how Mediterranean Eleonora's Falcons migrate across the African continent, it is very likely that other western populations of the species (such as those located in Morocco and the Canary Is.) also use some kind of straight-line migration route from the Atlantic Ocean to the wintering grounds in southeastern Africa (Delgado and Quilis 1990). The 2 birds tracked in this study used 43 d on average to reach Madagascar, so it would be very costly in energetic and survival terms to use a migratory route of more than 12,000 km for an individual breeding in the Atlantic Ocean (as suggested by Stresmann 1954 and Walter 1979) instead of a "direct" migration route of 9000 km. The fitness hypothesis would account for this behavior, as the migration route is conservative in energetic terms. As a consequence of this shorter migratory route, birds would be expected to show a decreased mortality rate, and hence more energy could be invested in future reproduction. Another non-mutually exclusive explanation is that some inherited migration program could be transmitted from parents to descendants. This could be the result of historic and/or genetic factors reflected in the speciation of the *Falco* clade, accounting for the phylogenetic hypothesis. This group is made up of Eleonora's Falcon and its closest relatives, the Sooty Falcon *F. concolor*, the Hobby *F. subbuteo*, the Red-footed Falcon *F. vespertinus*, and the Amur Falcon *F. amurensis*, all of which come from a shared ancestry (Wink and Ristow 2000) and all share the same wintering areas in southeastern Africa (Ferguson-Lees and Christie 2001). This could account for the long-distance

behavior of these species and the fact that all of them show similar migration patterns. Although both hypotheses are not yet demonstrated, in the near future, as more satellite transmitters are fitted to Eleonora's Falcons, we hope to definitively answer this question.

Acknowledgments: The Terra Natura Foundation financed this project. We would like to thank J. de la Puente, A. Bermejo, E. Escudero (SEO-Monticola), J.L. Martínez (GOB), and M. Suárez (GOB) who helped trap the adult Eleonora's Falcon. Also, thanks are due to T. Muñoz (GOB) who helped trap the juvenile. The "Conselleria de Medi Ambient" of the "Govern Balear" kindly gave permission to fit the transmitters in the Balearic Is., and special thanks are due to J. Mayol and J. Muntaner. J. García sexed the falcons, and the blood samples were provided by Lluís Parpal of the "Centre de Recuperació de Fauna de Balears". O. Frías, from the "Oficina de Especies Migratorias" (Spanish Ministry of Environment) provided the ringing data. We thank 2 anonymous reviewers for their helpful comments on the original draft of the manuscript. P. López-López was supported by a FPU grant (reference AP2005-0874) of the Spanish Ministry of Science and Innovation. This paper complies with all current laws in Spain.

REFERENCES

- Alerstam T, A Hedenström, S Akesson. 2003. Long-distance migration: evolution and determinants. *Oikos* **103**: 247-260.
- Argos. 1996. User's manual. Toulouse, France: CLS/Service Argos.
- Berthold P. 2001. Bird migration. A general survey. 2nd ed. New York: Oxford Univ. Press.
- Berthold P, E Nowak, U Querner. 1995. Satelliten-Telemetrie eines Zugvogels von Mitteleuropa bis in das Südafrikanische Winterquartier eine Fallstudie am Weisstorch (*Ciconia ciconia*). *J. Ornithol.* **136**: 73-76. (in German with English summary)
- BirdLife International. 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife Conservation series No. 12. Cambridge, UK: BirdLife International.
- BirdLife International. 2008. Species factsheet: *Falco eleonora*. Available at <http://www.birdlife.org> (Accessed 16 Dec. 2008).
- Bub H. 1991. Bird trapping and bird banding. Ithaca, NY: Cornell Univ. Press.
- Coyne MS, BJ Godley. 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.
- Delgado G, V Quilis. 1990. New data concerning the migration of Eleonora's Falcon *Falco eleonora*. *Ringling Migrat.* **11**: 111-112.
- Ferguson-Lees J, DA Christie. 2001. Raptors: birds of prey of the world. London: A & C Black Publishers.
- Fisher NI. 1995. Statistical analysis of circular data. Cambridge, UK: Cambridge Univ. Press.
- Fridolfsson AK, H Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116-121.
- Fuller MR, WS Seegar, PW Howey. 1995. The use of satellite telemetry systems for the study of bird migration. *Israel J. Zool.* **41**: 243-252.
- Guan HL, H Higuchi. 2000. Review on satellite tracking of migratory birds and its prospect. *Zool. Res.* **21**: 412-415.
- Judas J, O Combreau, M Lawrence, M Saleh, F Launay, G Xingy. 2006. Migration and range use of Asian Houbara Bustard *Chlamydotis macqueenii* breeding in the Gobi desert, China, revealed by satellite tracking. *Ibis* **148**: 343-351.
- Kenward RE. 2001. A manual for wildlife radio tagging. London: Academic Press.
- Limiñana R, A Soutullo, P López-López, V Urios. 2008. Pre-migratory movements of adult Montagu's Harriers *Circus pygargus*. *Ardea* **96**: 81-96.
- Limiñana R, A Soutullo, V Urios. 2007. Autumn migration of Montagu's Harriers *Circus pygargus* tracked by satellite telemetry. *J. Ornithol.* **148**: 517-523.
- Meyburg BU, X Eichaker, C Meyburg, P Paillat. 1995. Migrations of an adult Spotted Eagle tracked by satellite. *Br. Birds* **88**: 357-361.
- Meyburg BU, C Meyburg, JC Barbraud. 1998. Migration strategies of an adult Short-toed Eagle *Circaetus gallicus* tracked by satellite. *Alauda* **66**: 39-48.
- Newton I. 1998. Population limitation in birds. San Diego, CA: Academic Press.
- Papaconstantinou C. 2007. Eleonora's Falcon. Ruling the Aegean skies. Athens, Greece: Hellenic Ornithological Society.
- Stresemann E. 1954. Zur Frage der Wanderungen des Eleonorenfalken. *Vogelwarte* **17**: 182-183. (in German with English summary)
- Vaughan R. 1961. *Falco eleonora*. *Ibis* **103a**: 114-128.
- Walter H. 1979. Eleonora's Falcon. Adaptations to prey and habitat in a social raptor. Chicago, IL: Univ. of Chicago Press.
- Wink M, D Ristow. 2000. Biology and molecular genetics of Eleonora's Falcon *Falco eleonora*, a colonial raptor of Mediterranean islands. In RD Chancellor, BU Meyburg, eds. Raptors at risk. Midrand, South Africa: World Working Group of Birds of Prey.