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ORIGINAL PAPER

Weather conditions promote route flexibility during open ocean crossing in a long-distance migratory raptor

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Abstract Weather conditions are paramount in shaping birds' migratory routes, promoting the evolution of behavioural plasticity and allowing for adaptive decisions on when to depart or stop during migration. Here, we describe and analyze the influence of weather conditions in shaping the sea-crossing stage of the pre-breeding journey made by a long-distance migratory bird, the Eleonora's falcon (*Falco eleonorae*), tracked by satellite telemetry from the wintering grounds in the Southern Hemisphere to the breeding sites in the Northern Hemisphere. As far as we know, the data presented here are the first report of repeated oceanic journeys of the same individuals in consecutive years. Our results show inter-annual variability in the routes followed by Eleonora's falcons when crossing the Strait of Mozambique, between Madagascar and eastern continental Africa. Interestingly, our observations illustrate that individuals show high behavioural plasticity and are able to change their migration route from one year to another in response to weather conditions, thus minimising the risk of long ocean crossing by selecting winds blowing towards Africa for departure and changing the routes to avoid low pressure areas en route. Our results suggest that weather conditions can really act as obstacles during migration, and thus, besides ecological barriers, the migratory behaviour of birds could also be shaped by "meteorological barriers". We briefly discuss orientation mechanisms used for navigation. Since environmental conditions during migration could cause carry-over effects, we consider that forecasting how global changes of weather patterns will shape the behaviour of migratory birds is of the utmost importance.

Keywords Argos · Eleonora's falcon · Migration · Satellite tracking · Wind · Vorticity

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Introduction

Weather conditions are paramount in shaping birds' migratory routes (Richardson 1978; Elkins 1988; Liechti 2006; Hedenström 2010). The severe fitness cost of long-distance migration has promoted the evolution of behavioural plasticity allowing for adaptive decisions on when to depart or stop in relation to local weather conditions (Alerstam 1981; and see, e.g. Saino et al. 2010). This generates a strong selective pressure for the selection of optimal wind conditions for departure and travelling, which are particularly important when birds have to face large ecological barriers (Delingat et al. 2008; Navedo et al. 2010; Saino et al. 2010), inhospitable environments such as deserts, seas and mountain ranges, where the opportunities to fulfil energy requirements are low or absent and environmental factors could be extremely severe, increasing mortality risks (Kerlinger 1989; Newton 2008; Strandberg et al. 2009; López-López et al. 2010). For example, it has been shown that Western honey buzzards (*Pernis apivorus*) change their pathways when crossing the Mediterranean sea according to prevailing winds (Agostini et al. 2005; 2007), and that the departure of Bar-tailed godwits (*Limosa lapponica*) from Alaska when crossing the Pacific ocean in a 11,000 km non-stop flight was associated with tailwinds (Gill et al. 2009). Nevertheless, data on the impact of harsh weather conditions on migration routes are scarce. It is well known that water crossings lead to increased mortality risk (Kerlinger 1989) and could even result in episodes of massive mortality [e.g. more than 1,300 raptors were found dead along a beach of the Mediterranean coast of Israel during April 1980, as reported by Zu-Aretz and Leshem (1983)]. However, this type of risk has been somewhat under-estimated in the migration literature (Liechti 2006).

Here, we describe the sea-crossing stage of the journey made by a long-distance migratory bird, the Eleonora's falcon (*Falco eleonorae*), in its pre-breeding migration from the wintering grounds in the Southern Hemisphere to the breeding sites in the Northern Hemisphere. In particular, we analyse the influence of weather conditions in shaping the oceanic route between Madagascar and continental Africa. We focus only on this part of the journey since raptors cannot stop when migrating over water, and hence weather conditions are expected to act more selectively here than when migrating over land. To our knowledge, these are the first data ever reported concerning repeated oceanic journeys by the same individuals in consecutive years. Hence, they provide an excellent benchmark to study behavioural plasticity on an individual basis in response to changing weather conditions across an ecological barrier.

Materials and methods

Study species

The Eleonora's falcon is a cliff-nesting raptor that breeds mainly on small Mediterranean islands in late August and early September, adjusting its breeding season to coincide with the post-breeding migration of small passerines, its main prey during reproduction (Walter 1979). This long-distance migratory species winters in Madagascar and travels more than 18,000 km every year for breeding and wintering (Ferguson-Lees and Christie 2001). On the basis of satellite tracking data, migration routes have been recently discovered (Gschweng et al. 2008; López-López et al. 2009). The Eleonora's falcon has narrow wings and therefore is characterised by high aspect ratio (calculated as the quotient between wingspan and wing area; Kerlinger 1989), being adapted to flapping flight instead of soaring. Hence, it can migrate irrespective of large water bodies, and is more flexible than soaring species in changing route, providing a good model to study the influence of weather conditions on avian migration.

Animal tagging

We captured and tagged 11 Eleonora's falcons in the breeding colonies located in Balearic and Columbretes Islands (Spain) in autumn 2007 and 2008. Birds were trapped using dho-gaza nets and a stuffed Eagle Owl (*Bubo bubo*) as a decoy. All birds were equipped with Microwave Telemetry's 9.5 g solar-powered PTT-100 platform transmitter terminals, accounting for less than 3% of their body mass and affixed to their backs using a Teflon harness (Kenward 2001). Locations were collected using the Argos system (Argos 2008). Detailed data on animal histories, tagging methods and data retrieval are available in López-López et al. (2010). Hours are given according to local time. Wind data were downloaded from the NCEP/ NCAR Reanalysis project (http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.pressure.html). The reanalysis data were created using various assimilated observations/ measurements and atmospheric models, and this dataset includes a temporal coverage of observation four times per day with a spatial resolution of 2.5° x 2.5° from 1948 until the present (Kalnay et al. 1996).

Data analyses

On the basis of satellite telemetry data, we calculated the position of each bird at any given hour when wind data were available (every 6 hours) by interpolating locations and using as a reference the speed of each bird when migrating over the ocean. This speed was calculated by dividing the distance between the first and the last location recorded over the sea by the elapsed time. Speed data during the sea crossing was obtained for all birds but one (bird #80400); thus, for this bird, we used the lowest speed value recorded for the other birds (60 km/h) for the estimation of interpolated locations along the routes. At these interpolated locations, we collected U (West-East component) and V (South-North component) wind vectors at 850 mb, corresponding approximately to 1,300 m altitude above sea level, from which we inferred wind direction and wind speed. It has been shown by means of radar tracking that the chosen value of 850 mb roughly corresponds to the average value of a falcon's altitude when migrating over sea (Meyer et al. 2000). The data of the NCEP/ NCAR Reanalysis project have been used widely to analyse wind influence on Argos-satellite-tracked birds (Shamoun-Baranes et al. 2003; Thorup et al. 2003; Klaassen et al. 2010). Wind directions were analysed using circular statistics (Batschelet 1981).

We compared 2009 vs 2010 average wind direction measurements during the ocean crossing by means of the Watson–Williams test for two samples (Zar 1984). To this end, we pooled the data of all individuals within each year (three in 2009 and two in 2010).

In addition, we inspected maps of relative vorticity (downloaded from the CIMSS Tropical Cyclone website at: http://tropic.ssec.wisc.edu/archive/) at the same pressure level (850 mb) of wind data, which are available for every 3 h. Vorticity is a measure of the spin of an air mass such as a low- or high-pressure weather system (Batchelor 2000). In the Southern Hemisphere, cyclonic rotation is associated with negative vorticity, thus coinciding with troughs of low pressure areas associated with cyclones or storms, which are unfavourable conditions for migrating birds (Richardson 1978).

Results

Overall, we obtained five spring ocean tracks belonging to three adult individuals (Fig. 1). In 2009, the three individuals migrated directly from Madagascar to Somalia, flying non-stop for about 1,500 km. The maximum longitudinal distance among tracks was 195 km. Birds started the sea crossing in a 14-h time window as follows: the first female (transmitter #80399) started migration at 1251 hours on 11 April, followed by the second female (transmitter #80400), which started migration at 1935 hours on 11 April; and finally, the male (transmitter #80402), which started migration at 0250 hours on 12 April. Flight speeds during sea crossing were 60 km/h (during 10.4 h; bird #80399) and 63.1 km/h (during 2.2 h; bird #80402).

In 2010, two of the three individuals tracked the previous year (since bird #80400 stopped transmission on 30 April 2009 when it was in Algeria) migrated towards Tanzania for about 1,200 km, keeping a much more westward course than that recorded in 2009. Eleonora's falcons departed from Madagascar at 0230 hours on 13 April (transmitter #80399), and at 0435 hours on 14 April (transmitter #80402). The maximum longitudinal distance recorded between tracks during sea crossing was 78 km, and two locations belonging to different individuals were recorded almost 26 h apart each other in a narrow funnel of just 22 km. Flight speeds during sea crossing were 60.5 km/h (during 6.7 h; #80399) and 72.6 km/h (during 7.1 h; #80402). Bird #80402 is still transmitting on September 2010 while the transmitter #80399 stopped working in Egypt on 27 April 2010.

Wind directions during the whole ocean crossing differed between consecutive years, being more westward and concentrated during 2010 than 2009 (wind $direction_{2009}$=36.3°, SD=74.3°; wind $direction_{2010}$= 94.5°, SD=1.9°; Watson–Williams test for two samples; $W_{15,7}=0.1568$, $P<0.05$). Wind direction recorded at the onset of migration were strongly westward-directed in both years (mean 94.1°, SD=2.2°, $N=5$). Wind speed during oceanic crossing averaged 35 km/h for the two years (SD=48.9, $N=22$).

The vorticity patterns at the onset of migration of the first bird beginning the oceanic crossing each year are shown in Fig. 1. Interestingly, two troughs of low pressure corresponding to negative values of relative vorticity were located in the northern Mozambique Channel just between Madagascar and Africa in 2009, forcing birds to fly northwards and acting as a barrier for a more direct route towards Tanzania (Fig. 1a). In contrast, in 2010 the onset of migration coincided just when the Mozambique Channel was free of troughs of low pressure, allowing birds to reach the African coast in a shorter route from northern Madagascar to the coast of Tanzania (Fig. 1b).

Discussion

Satellite telemetry allows us to gain new insights into avian migration ecology, especially regarding relevant topics such as birds' response to environmental conditions as well as orientation during migration (Thorup et al. 2003; Gill et al. 2009; Hedenström 2010). Bird migration shows a high degree of plasticity at both individual and evolutionary levels (Alerstam et al. 2006; Pulido and Berthold 2010). As far as we know, the data presented here are the first report of repeated oceanic journeys of the same individuals in consecutive years. Our results show inter-annual variability in the routes followed by Eleonora's falcons when crossing the Strait of Mozambique between Madagascar and eastern continental Africa. Interestingly, individuals showed high route flexibility between years, migrating independently from each other following narrow funnels, and changing route according to weather conditions. In both years, birds started sea crossing in a short time window of 1–2 days, and data gathered during this stage suggest that they did not migrate in the same group. Recorded flight speeds suggest tailwind assistance, since the values of flight speed recorded for this species by radar tracking were only 44 km/h (Rosén et al. 1999). In both years, wind conditions at migration onset were always favourable to cross en route for Africa, thus suggesting a fine-tuned selection for the best departure time in order to minimize energy expenditure during open ocean crossing. However, wind assistance en route differed between years, being lower in 2009 than 2010. In 2009 birds used a longer flyway and were forced to fly directly towards Somalia instead of landing on Africa in advance through a shorter pathway, in contrast to what they did in 2010, probably in order to avoid the low

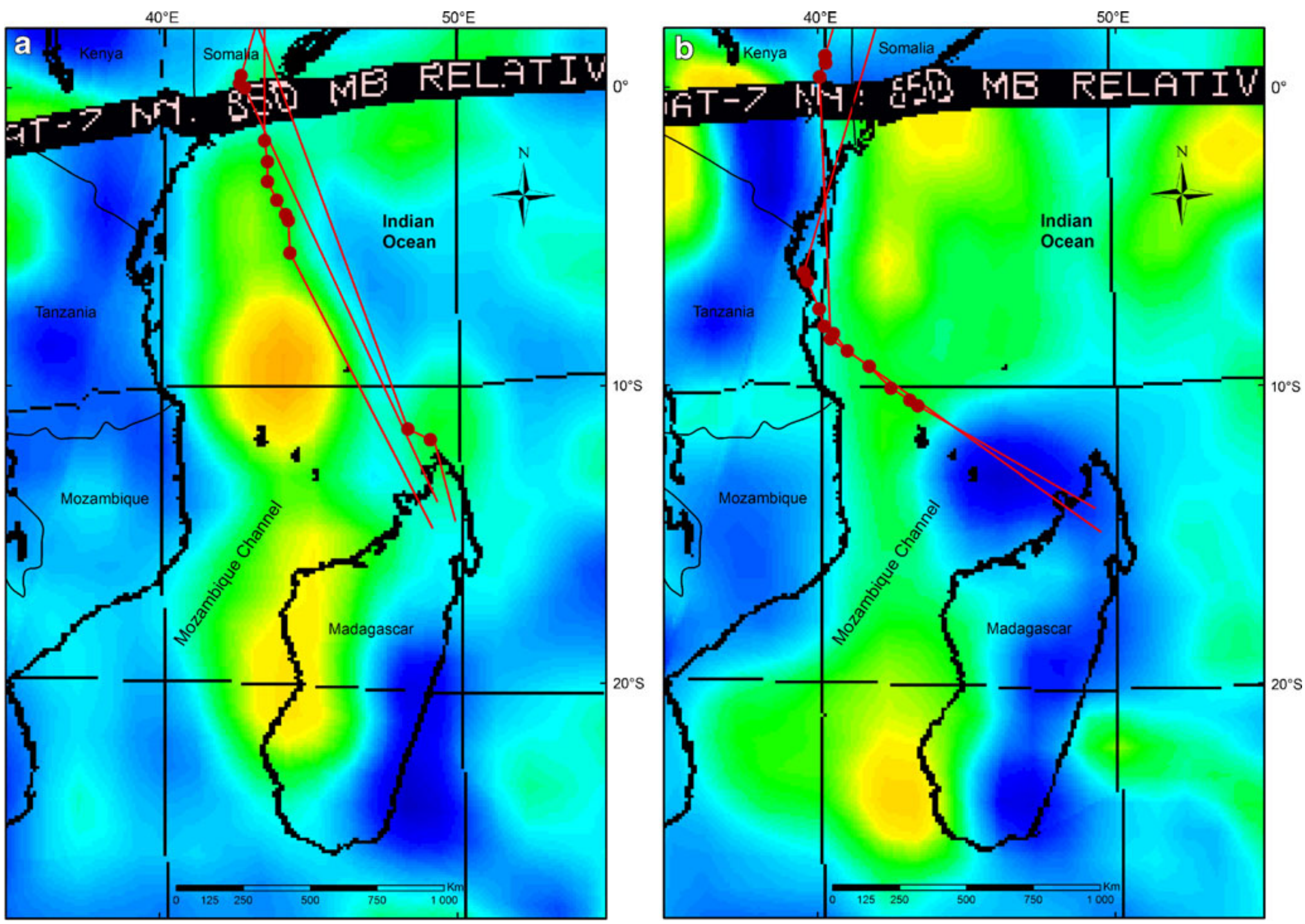

Fig. 1 Vorticity patterns at the onset of migration of the first Eleonora's falcon (*Falco eleonorae*) tracked by satellite telemetry in **a** 2009 and **b** 2010. *Red solid lines* Individual tracks, *red dots* satellite telemetry locations. Negative vorticity areas (*yellow*) coincide with troughs of low pressure, whereas positive vorticity areas (*blue*) correspond to areas of stable meteorological conditions (see Materials and methods for details of data sources)

pressure area between Madagascar and Africa (Fig. 1a). Alternatively, they would have crossed the area with the highest vorticity, where weather changes can be sudden and less predictable, with stronger winds and hazardous weather such as rain and storms, which are especially dangerous during the crossing of ecological barriers (Strandberg et al. 2009). Consequently, our observations illustrate that Eleonora's falcons show high behavioural plasticity and are able to change migration route from one year to another in response to weather conditions, thus minimising the risk of long ocean crossing by selecting winds blowing towards Africa for departure and avoiding low pressure areas en route. A literature review showed that there is only one paper analysing the sea crossing behaviour of a satellite-tracked bird facing extreme weather. This paper showed how a Peregrine falcon (*Falco peregrinus*), after having selected tailwind conditions to cross the Gulf of Mexico, met a hurricane during the crossing, retreated from it, being forced to go back to the mainland and, after having waited the hurricane to pass, completed the sea crossing successfully in a second attempt (McGrady et al. 2006).

In a review of worldwide patterns of raptor migration, Bildstein (2006) stated that "truly oceanic migration remains an exceptional form of raptor migration". Indeed, the 1,500 km journey observed in 2009 is, to our knowledge, one of the longest successful non-stop open water journeys ever reported for a raptor. Some species, such as the Merlin (*Falco colombarius*), have shown to be able to perform successfully an overwater flight of about 1,000 km from Iceland to Great Britain (Bildstein 2006), and a juvenile Oriental honey buzzard (*Pernis ptilorhyncus*) was tracked from Japan to China (Higuchi et al. 2005). Other raptors, such as the Amur falcon (*Falco amurensis*), are thought to take an even longer overwater route, from India to East Africa (Bildstein 2006).

Remote tracking systems such as satellite telemetry or geolocators allow researchers to unravel the migratory routes of birds (Felicísimo et al. 2008; Gschweng et al.

2008; López-López et al. 2009; Stutchbury et al. 2009). In addition, they provide great insights into a bird's capabilities of selecting optimal weather conditions, and serve to suggest what orientation systems might be used to accomplish their journeys. In our case, the fact that all falcons migrated during both night- and day-time (see also López-López et al. 2010), navigating across oceanic landscapes without any conspicuous target, suggest that neither their navigation skills nor their ability to compensate for wind displacement can rely on any system that simply involves landmark cues. Thus, the true orientation mechanism that Eleonora's falcons use remains unknown. Direction cues obtained from celestial objects and their related skylight polarization pattern, combined with some time-keeping mechanisms, the Earth's magnetic field or even the use of olfactory cues or sea waves as a reference are the most likely candidates (Alerstam and Petterson 1976; Akesson and Hedenstrom 2007).

We have shown that weather conditions can really act as obstacles during migration, and thus, besides ecological barriers (Newton 2008; e.g. Strandberg et al. 2009, López-López et al. 2010), the migratory behaviour of birds could also be shaped by "meteorological barriers". Since environmental conditions during migration could cause carry-over effects (Strandberg et al. 2009), forecasting how global changes of weather patterns will shape the behaviour of migratory birds is of the utmost importance. In the near future, high-resolution detailed tracks will hopefully allow us to unravel finer-scale route deviations and to study more thoroughly orientation mechanisms, as well as bird's behavioural response to changes in local conditions in a changing world (Robinson et al. 2009).

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