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Extremely detoured migration in an inexperienced bird: interplay of transport costs and social interactions

Ugo Mellone, Rubén Limiñana, Egidio Mallia and Vicente Urios

U. Mellone (ugomellone@libero.it), R. Limiñana and V. Urios, Estación Biológica Terra Natura, Inst. Universitario de Investigación CIBIO, Univ. of Alicante, Apdo. 99, ES-03080 Alicante, Spain. Present address of RL: Inst. de Investigación en Recursos Cinegéticos, (IREC) CSIC–UCLM–JCCM, Ronda de Toledo, s/n, ES–13005 Ciudad Real, Spain. – E. Mallia, Parco Gallipoli Cognato Piccole Dolomiti Lucane, Località Palazzo, IT–75011 Accettura (MT), Italy.

We tagged two juvenile short-toed eagles in southern Italian peninsula with GPS satellite transmitters. According to previous visual observations, two different migratory routes for Italian short-toed eagles to reach Africa in autumn have been proposed: via Sicily and via Gibraltar. These routes include different over-water distances to cross the Mediterranean Sea, and thus different proportions of flight modes (soaring–gliding vs flapping–gliding) with resulting different transport costs. Considering different scenarios of energy cost of transport, with flapping-gliding flight over water being more costly than flying over land using soaring–gliding flight, we predicted a maximum optimal detour of 1218 km. Both individuals reached Africa using the longest, detoured, route, avoiding the longest water crossing. To achieve this they began migrating northwards, keeping for ca 700 km a direction opposite to that followed by any other migrating bird from the Northern hemisphere in autumn. The comparison of optimal detour predictions with observed migratory tracks suggests that this migratory strategy prioritizes not only energy minimization, but also safety, given the mortality risk associated with the sea crossing. Finally, it is unlike that these inexperienced individuals followed such a complex route relying only on endogenous information and we therefore suggest, also on the basis of field observations, that social interactions (adult guidance) allow these individuals to learn the detoured route.

In order to successfully accomplish their migratory journey, naive juvenile birds can rely either on endogenous information, like the clock-and-compass strategy, a genetically defined orientation programme based on a succession of vectors with directions and lengths defined by a circannual clock, or upon exogenous cues, as the guidance by conspecific adults (Gwinner and Wiltschko 1980, Åkesson and Hedenström 2007, Newton 2008). The selective pressure to fine-tune the migratory flight direction with high accuracy is expected to be higher in soaring birds, which concentrate where sea-crossings are narrower, in order to minimize mortality risks, as well as energy consumption associated with flapping flight (Kerlinger 1989).

The short-toed eagle *Circaetus gallicus* is a long-distance, large, migratory raptor with low-aspect ratio wing morphology and, hence, less adapted to flapping flight and more prone to use soaring flight (Kerlinger 1989). The species breeds in Europe and has its wintering grounds in tropical Africa (Ferguson-Lees and Christie 2001). The migratory strategies of the Italian population of this species are rather puzzling (Agostini et al. 2002, 2009) and have never been studied through satellite telemetry. The aim of this study was to investigate the migratory routes of inexperienced short-toed eagles during their first autumn migration and the influence of transport cost in shaping these routes. To do that, we tagged two juvenile short-toed eagles from one of the southernmost breeding areas of the Italian peninsula with satellite transmitters. We chose to tag the juveniles in this area since two migratory routes for this region have been hypothesized (Agostini et al. 2009), in contrast to other European populations of the species (like Spain or France), which can only migrate to their wintering grounds in sub-Saharan Africa crossing the Strait of Gibraltar. Analysing the causes underlying these two possible routes may provide important insights into orientation mechanisms and energetic constraints during migration in this species.

Theoretical predictions

According to visual observations, it has been hypothesized that short-toed eagles breeding in peninsular Italy use two different flyways during autumn migration, with the most important one (involving roughly 1000 individuals, Panuccio et al. 2011) following the Italian peninsula towards France, and where mainly adults are observed (Agostini et al. 2002, 2004). Instead, the second one is less conspicuous (roughly 200 individuals), crosses the central Mediterranean via the island of Marettimo (Fig. 1), and is

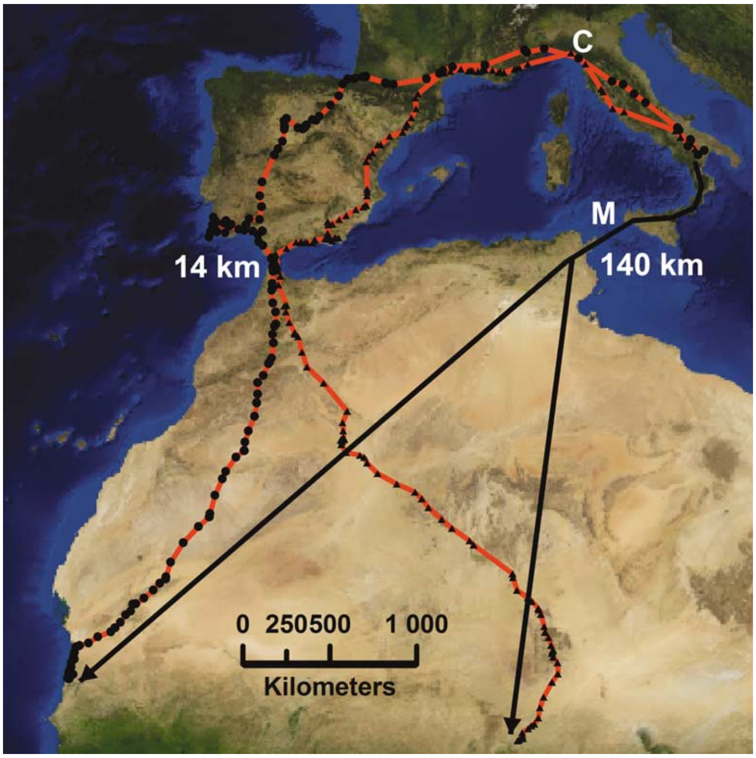

Figure 1. Autumn migratory routes of two juvenile short-toed eagles born in southern Italy and tracked by satellite telemetry (Biagio: circles; Nic: triangles). The tracks interpolations of the GPS locations (see Methods). Black tracks: direct, hypothetic, routes across the Sicily Channel. The over-water distances (km) of the two possible sites to cross the Mediterranean Sea (Gibraltar: 14 km; Sicily: 140 km) are indicated. 'C' (Capriglia) and 'M' Marettimo are the watchsites were the field observations mentioned in the discussion have been carried out.

used almost exclusively by juvenile birds (Agostini et al. 2009). In order to reach tropical Africa, the first flyway would involve a very large detour compared to the second one. Detours are optimal when the costs of transport across the direct (shorter) route are higher than those that involve the detoured (longer) route (Alerstam 2001). For example, soaring birds may choose a detoured flyway when the direct route crosses ecological barriers, e.g. water bodies where soaring flight is impossible and hence, birds have to rely upon the more energy-demanding flapping flight to cross the barrier (Alerstam 2001). Therefore, the higher the difference in energy consumption between the two flight modes (soaring–gliding vs flapping–gliding), the longer the extra distance expected to be covered across non-barrier areas in order to avoid the barrier. Assuming different values of the ratio between the energy cost of transport during flapping flight and the energy cost of transport during soaring flight, it is possible to predict different scenarios of optimal detours, i.e. different values of maximum extra distances expected according to a strategy of energy minimization (Alerstam 2001). Kerlinger (1989) predicted that generally, in large raptors, flapping flight would represent an energy consumption three to six times higher than soaring flight, while Panuccio et al. (2011), using the procedure described by Pennycuick (2008), calculated that for the short-toed eagle this value is 8.7 times higher. In order to estimate the extra distance (D) up to which the detour would remain energetically economical, we fitted these values of increased energy consumption of flapping flight, as well as the barrier distance (Y_b) that short-toed eagles migrating from our study area must cross when following a direct route (140 km between Sicily and Tunisia, Fig. 1), in the Eq. (11) of Alerstam (2001)

$$D/Y_b = (C_1/C_2) - 1$$

where C_1 is the transport cost across the barrier (flapping flight; ranging from 3 to 8.7, see above) and C_2 is the transport cost across non-barrier areas (soaring flight; considered as 1). Solving the equation in the scenario with the lowest difference of transport cost ($C_1 = 3$), the expected extra distance would be 280 km, while for $C_1 = 6$ it would be 700 km, and when the increase in transport costs is much higher (8.7) the extra distance up to which the detour would remain economical is 1218 km. We compared these distance values with those observed for the short-toed eagles tracked by satellite telemetry, given that knowing the exact birthplace and wintering site allows to calculate the exact extra distance covered in the detour, in contrast with the direct route.

Methods

Animal tagging

On the 23 July 2010, two juvenile short-toed eagles were caught at their respective nests in the region of Basilicata (southern Italy). Nestlings were 55–60 d old, almost completely grown but not yet fledging. Birds were measured and ringed, and a Microwave Telemetry 45-g solar/GPS PTT-100 transmitter was affixed to their back using a tubular Teflon ribbon harness (García-Ripollés et al. 2010, Pavón et al. 2010). A blood sample was obtained from the brachial vein and conserved in ethanol for sex determination. The entire procedure took less than one hour for each bird. Satellite transmitters were programmed to record one GPS position every two hours (nominal location error: <18 m; Argos 2008) and to transmit the collected data to satellites every three days.

Data analysis

In order to compare the two possible abovementioned routes hypothesized for the Italian population of short-toed eagles (Agostini et al. 2009), we measured using Google Earth the minimum distances from the natal site to their wintering area (identified by satellite telemetry), for both individuals and for the two different possibilities to reach Africa: 1) the Sicily Channel (over-water distance: ca 140 km), and 2) the Strait of Gibraltar (over-water distance: ca 14 km; Fig. 1). In both cases, the distances were measured for hypothetic straight routes that minimized the water crossing, thus always over land (except for the two above mentioned sea-crossings).

Results

Both eagles departed to Africa roughly at the same time. 'Nic' (tag no. 56810, female) left the natal area the 15 September 2010, and 'Biagio' (tag no. 56813, male) the 20 September 2010. They headed northwards (bearing 310°) for ca 700 km, thus taking a direction opposite to that usually followed by migrating birds of any other species in the Northern hemisphere during autumn migration. Afterwards, they changed course abruptly, crossing France and then changed course again, heading towards the Strait of Gibraltar, from where they crossed the Mediterranean Sea to Africa the 11 October 2010 (Nic) the 19 October 2010 (Biagio). They arrived to their wintering grounds at Sahel the 30 October 2010 (Nic) and the 2 November 2010 (Biagio), located in Niger and Mauritania, respectively (Fig. 1). Therefore, comparing the two different possible scenarios (reaching Africa through the Sicily Channel or through the Strait of Gibraltar), both short-toed eagles used the longest, indirect, route.

The minimum possible distances calculated between nest site and first location in the wintering grounds if birds had travelled across the Sicily Channel would have been 3361 km and 4228 km for Nic and Biagio, respectively. According the actual routes, those crossing the Mediterranean Sea through the Strait of Gibraltar, these distances are 5084 km for Nic and 4726 km for Biagio. Hence, they performed detours that extended the overall migration distance (extra distances) by 1723 km (51.3%, Nic) and 498 km (11.8%, Biagio).

Discussion

Orientation in naive migrants

Both juvenile short-toed eagles reached their wintering grounds performing a circuitous migration that involved a long northward movement during the first step of the journey, confirming one of the previous hypothesis based on field observations (Agostini et al. 2002). Both individuals crossed the Mediterranean Sea at the Strait of Gibraltar, thus following the longest route of the two hypothesized for this species migrating from Italy in autumn (Agostini et al. 2009).

Two alternative hypotheses can explain how these inexperienced birds followed such a complex detoured route: 1) juvenile short-toed eagles may have followed an inherited program, like the clock-and-compass strategy (Mouritsen 2003), flying northwards for 700 km and then turning to the west and then south-west, crossing the Mediterranean Sea only when there was no other possible alternative (i.e. at the Strait of Gibraltar), or 2) they may have followed experienced adult birds that have used the detoured route before, and hence learning from them (Maransky and Bildstein 2001, Agostini 2004, Chernetsov et al. 2004, Newton 2008).

According to previous both empirical and theoretical studies (Thorup et al. 2010, Panuccio et al. 2011), the second hypothesis is the most parsimonious one and therefore, the most likely to have occurred. The first hypothesis would imply very complex genetic rules, as for example to avoid any water crossing longer than 20 km, as well as travelling in order to always keep water on the left, which is a very complex genetic rule in itself to easily occur (Thorup et al. 2010). In this sense, it should be noted (Fig. 1) that birds migrated inland the Italian peninsula, without following the coast, and that they experienced the first sea crossing only at the Strait of Gibraltar. The first hypothesis can be dismissed also in the light of field observations that showed that some juveniles short-toed eagles born in Italy may be following a more simple inherited genetic program, but this results in a completely different migratory route in respect to the detoured one: at the island of Marettimo, between Sicily and Tunisia (along the hypothesized direct route; Fig. 1), roughly 200 short-toed eagles, mostly juveniles (79%), are observed each year in October (Agostini et al. 2009). The geographical location of this island (south-west in respect to the Italian breeding grounds), the late period (two weeks later than the migration peak of adults) and the age proportion (mostly inexperienced juveniles, while in northern Italy juveniles are usually <20%; Panuccio et al. 2011) suggest that these individuals start migrating too late in order to learn the detoured migration from adults and hence, they follow an inherited south-west direction, which is indeed the most commonly observed in the majority of bird species migrating between Europe and Africa (Newton 2008).

Instead, the second hypothesis seems to be more reliable and it is in agreement with field observations concerning this species and carried out within the same flyway of our individuals. Roughly 1000 short-toed eagles (mostly adults, including probably the whole breeding population of peninsular Italy; Agostini and Mellone 2008) are observed every year migrating northwards in mixed-age flocks (juveniles: 14–21%; Agostini et al. 2002, 2004, Panuccio et al. 2011) during the second half of September over the watchsite of Capriglia, in northern Italy (near the end of the first step of the autumn journey of tracked birds; Fig. 1), and then westwards at the watchsite of Arenzano (Fig. 1; Agostini et al. 2002, 2004, Panuccio et al. 2011). Probably, the inexperienced eagles tracked in this study followed one or more experienced adult birds, at least during the first step of the journey. Confirming previously published data, also in 2010, during the period including the days of passage of the two satellite-tracked individuals, a total of 1389 individuals, including both adult and juvenile birds, have been observed migrating northwards at Capriglia (Premuda 2010). Thus, our results can probably be applied to a much higher proportion of juvenile individuals. According to the second hypothesis, social interactions may have played an important role in shaping their migratory strategy (Maransky and Bildstein 2001), allowing these inexperienced birds to learn from adult conspecifics the conservative route through the Strait of Gibraltar. Theoretical predictions suggest that, within a flock of birds, information can be transferred even when group members do not know which individuals have the correct information, and a very small proportion of informed individuals may be sufficient to achieve great accuracy (Couzin et al. 2005).

Evolution and energetic constraints of the circuitous route

Visual observations suggest that this circuitous route is also used during spring migration, with short-toed eagles breeding in Italy returning to Europe through Strait of Gibraltar and then crossing Spain and France (Panuccio et al. 2011). This is one of the largest detours performed by any bird species during migrations (Alerstam 2001, Bildstein 2006, Yamaguchi et al. 2008). Nonetheless, this circuitous route implies a sea-crossing of only 14 km, instead of that of 140 km that would imply following the alternative shorter route, thus reducing the energetic costs and risks associated with long sea crossings (Kerlinger 1989). The species favours the route that implies the shorter flight distance over water even if the total distance travelled is larger. While one individual (Biagio) fits well in the scenario of moderate increase in cost of transport during flapping–gliding flight, since the extra distance of 498 km is within the interval 280–700 km obtained according to the values given by Kerlinger (1989), the other individual (Nic) overcame even the less conservative prediction (1723 km observed extra distance vs a maximum predicted one of 1218 km). Probably, besides energetic constraints, the higher safety of flying over land may force short-toed eagles to choose the circuitous route even when the extra distance increases beyond an economical threshold, since a long powered flapping-flight over the sea might increase also mortality risks (Zu-Aretz and Leshem 1983). Furthermore, differences observed in energetic cost estimations are especially due to the different location of wintering grounds, since both birds used the same route to avoid the Mediterranean Sea, diverging consistently only after the arrival in Northern Africa. Wind drift while crossing the Sahara desert could have also play a role in determining the final wintering areas of these tracked birds (Klaassen et al. 2010).

During migration, birds can choose to arrange their travels according to time, energy expenditure and safety (Alerstam and Lindström 1990). Here, we have shown that the migratory strategy of the short-toed eagle prioritizes not only energy consumption, but also risk minimization, even if this leads to a longest route and a delayed arrival at the wintering grounds. This strategy has evolved in response to its morphology and to the distribution of land masses, and consequently of ecological barriers (Henningsson and Alerstam 2005).

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