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Individual variation in orientation promotes a 3000-km latitudinal change in wintering grounds in a long-distance migratory raptor

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Migrating juvenile birds rely on endogenous information in choosing the direction in which to fly, but such input may be overridden by social interactions with experienced individuals. We tagged seven juvenile Short-toed Eagles *Circaetus gallicus* with GPS transmitters in southern Italy. This trans-Saharan migrant flies mainly by soaring and is therefore not well adapted to performing long water crossings. Five of the seven tagged juveniles used the longer but apparently safer route towards the Strait of Gibraltar, and two migrated along a southerly trajectory and subsequently spent the winter in Sicily, apparently forced to do so by the 150-km-wide Sicily Channel. One of these individuals took the longer route the following autumn. These results, combined with long-term (15 years) visual field observations involving thousands of individuals, suggest that inexperienced Short-toed Eagles may learn their migratory routes from experienced adults, whereas some of them migrate south in response to an innate orientation instinct. Transport costs, inherited information and geography apparently interact, forcing some Short-toed Eagles to winter 3000 km to the north of the majority of their conspecifics.

Keywords: flocking, migration, navigation, raptors, Short-toed Eagle, social interactions.

The behaviour of migrating birds can be subject to great intraspecific variation, depending upon population, age or experience, and sex (Newton 2008, Thorup *et al.* 2010, Panuccio *et al.* 2013). Differences in orientation are determined by the geographical origin of the individuals, leading to the development of migratory divides (Bobek *et al.* 2008), and by their experience, which is mainly shaped by age. Generally adult individuals have navigational capabilities that allow them to reach their goal precisely, even when using complex routes that involve changes of course and correcting for displacements (Holland 2014). However, juveniles rely mainly on a clock-and-compass strategy, as they have inherited information that tells them in which direction to fly and for how long, thanks to an endogenous circannual clock that is under direct genetic control (Berthold 2001). This age-related difference has also been confirmed by continent-wide displacements, with adults being able to adjust their heading and juveniles continuing to migrate in their original direction (Thorup *et al.* 2007).

In soaring species, such as broad-winged raptors and storks, there are many social diurnal migrants (Newton 2008). This behaviour probably evolved to facilitate the location of thermal currents and the learning of optimal routes by inexperienced individuals through conspecific guidance, in response to the mortality risk and high energy consumption associated with orientation mistakes (Kerlinger 1989, Maransky and Bildstein 2001, Agostini 2004, Chernetsov *et al.* 2004). Any incorrect decision could lead birds to fly over water surfaces such as seas and oceans, where thermal currents are absent (thus forcing them to perform flapping flight; Kerlinger 1989). Water bodies also provide no landing possibilities for raptors in adverse weather conditions, eventually causing

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high mortality rates (Zu-Aretz & Leshem 1983). In a recent study, Oppel *et al.* (2015) suggested that the lack of information transfer between adults and juveniles in a declining population of a soaring migrant raptor may increase the use of a suboptimal route by inexperienced juveniles, leading eventually to their death. The Short-toed Eagle *Circaetus gallicus* is a long-distance migratory raptor that breeds mainly in Europe and spends the winter mainly in tropical Africa (Ferguson-Lees & Christie 2001). Pairs raise a maximum of one juvenile per year. Like other long-lived species, it exhibits delayed sexual maturity and at least during their first 3 years of life Short-toed Eagles do not occupy a breeding territory (Mellone *et al.* 2011b). Given the high energy consumption of flapping flight, the species is adapted to use soaring flight (Kerlinger 1989, Agostini *et al.* 2015); it thus avoids long sea crossings and migrates mainly in loose, mixed-age flocks of two to four individuals (Panuccio *et al.* 2012). Previous studies based on visual observations showed that most Short-toed Eagles breeding in southern Italy migrate through the Strait of Gibraltar (Agostini *et al.* 2002, Agostini & Mellone 2008, Panuccio *et al.* 2012, 2015). Interestingly, however, observations carried out in Marettimo Island, between Sicily and Tunisia, also showed the existence of another migratory pathway, comprising almost exclusively juveniles (Agostini *et al.* 2009).

To evaluate the results of visual observations in a wider context, we tagged juvenile Short-toed Eagles from southern Italy with satellite transmitters to follow them during their first autumn migration, until they were established in their wintering grounds. In a previous study (Mellone *et al.* 2011a) we presented data from two individuals, both of which followed the western route to Gibraltar. These results, together with the visual observations, suggested that inexperienced Short-toed Eagles breeding in southern Italy and Greece may learn the safest routes during their first migration, in order to avoid long and risky sea crossings (Agostini *et al.* 2002, Agostini & Mellone 2008, Mellone *et al.* 2011a, Panuccio *et al.* 2012, 2015). In this paper, we present data for five additional satellite-tracked juveniles, which included birds that followed the more direct southerly route. Our results suggest that the more direct southern route is suboptimal and likely to be less safe, as juveniles taking it did not make it to Africa, and also that the longer western route can be learned, as one of the individuals that took the Sicily route used the western route in the following year. We discuss these differences in intraspecific migratory strategies and why they coexist within the same population.

METHODS

Seven juvenile Short-toed Eagles were caught at their nests in the region of Basilicata (southern Italy) during 2010 (two individuals), 2011 (three individuals) and 2013 (two individuals). We worked on four territories, and therefore in three cases we tagged two juveniles from the same territory, but in different years. The territories were separated by *c.* 100 km. When nestlings were 55–60 days old, they 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 (Mellone *et al.* 2011a,b). Satellite transmitters were programmed to record one GPS position every 1 or 2 h (nominal location error: 18 m; Argos 2008) and to transmit the collected data to satellites every 3 days. We examine their autumn migration from the natal area towards their wintering grounds, in particular, on their first autumn migration. Departure dates were considered as the first displacement of more than 5 km from the nest, without visiting it again.

When the transmitters stopped working or when they started to send stationary data, then the possible causes of death were verified in the field.

RESULTS

During their first migration, the seven juvenile Short-toed Eagles exhibited two alternative patterns: five individuals chose the longer western route, migrating northward for *c.* 700 km and then crossing France *en route* to the Strait of Gibraltar, to finally reach the usual sub-Saharan wintering grounds (Fig. 1). All these birds began to migrate in September (days: 10, 15, 20, 20, 27). The other two birds (#57007 and #79938) started to migrate on 2 October and 18 September, respectively. Despite showing some periods of northward movement, these individuals finally migrated southwards (Fig. 2a). After crossing the Strait of Messina, they showed complex movements for around 1 month, constantly following the southern coast of Sicily and even reaching the island of Marettimo (30 km west of Sicily). Subsequently,

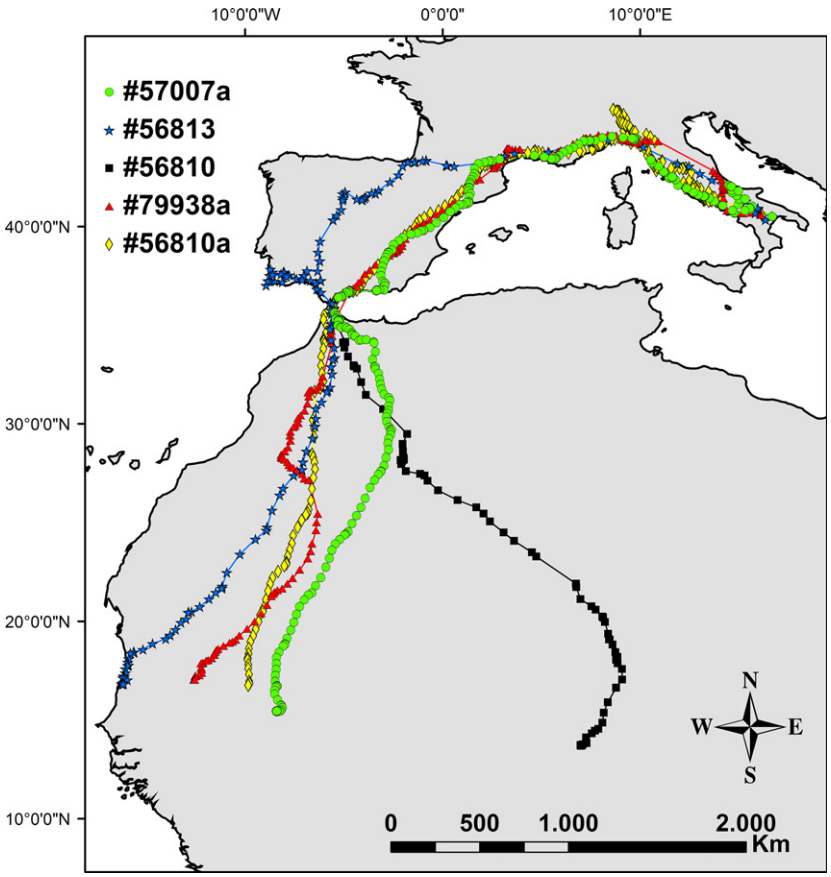

Figure 1. Five migration tracks of juvenile Short-toed Eagles using the western route and wintering in tropical Africa.

they returned to Sicily several times during October: bird #57007 travelled back and forth between Sicily and Marettimo twice, and #79938 did so three times (Fig. 2b). Both birds finally spent the winter in Sicily, 3000 km north of the other individuals south of the Sahara.

As to the birds coming from the same territory (three territories, six migrations), there were two cases in which the two juveniles used the western route, whereas the routes for the other territory alternated between years (#79938 towards Sicily in 2011 and #79938a towards the Strait of Gibraltar in 2013).

During the summer of the following year, both birds that used the southern route during the first year wandered between Sicily and southern Italy. In the second half of September, bird #79938 was killed while moving southward in Sicily, and bird #57007 began the migration using the western route, and was killed in southern Spain in the beginning of October (Fig. 3). Of birds that used the western route, we only identified mortality for #56810, which had been killed in Nigeria during its first winter. None of the tracked birds died of natural causes during migration.

DISCUSSION

There is a growing body of literature showing the importance of social interactions and learning for navigation, both through empirical observations (Agostini 2004, Chernetsov *et al.* 2004, Mueller *et al.* 2013, Pettit *et al.* 2013) and with theoretical models (Couzin *et al.* 2005, Bode *et al.* 2012, Flack *et al.* 2015).

Here we confirm previous results (Agostini *et al.* 2002, Mellone *et al.* 2011a,b, Panuccio *et al.* 2012, Premuda *et al.* 2015) that the majority of Short-toed Eagles born in southern Italy use a detoured strategy to reach Africa, following the longer but apparently safer route towards the Strait of Gibraltar. However, two juveniles

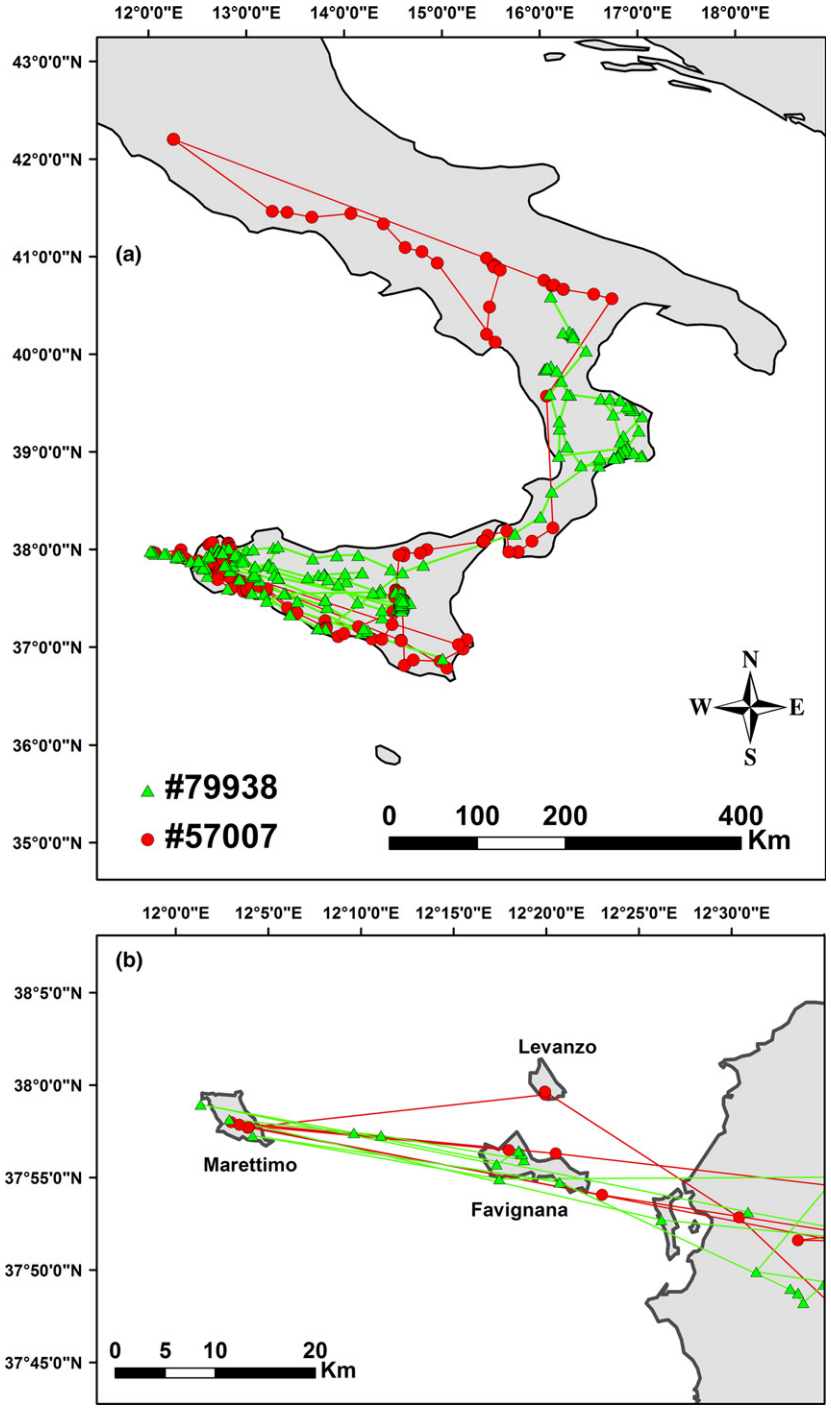

Figure 2. (a) Two migration tracks of juvenile Short-toed Eagles using the southward route and wintering in Sicily. Inset (b) shows their route between Sicily and the island of Marettimo.

migrated southwards and were consequently forced to spend the winter in Sicily, presumably because they were unable to cross an ecological barrier, the Sicily Channel (which is at least 150 km wide). Their migratory restlessness appears to have led them to attempt the crossing via the island of Marettimo several times, but ultimately they stopped doing so and spent the winter

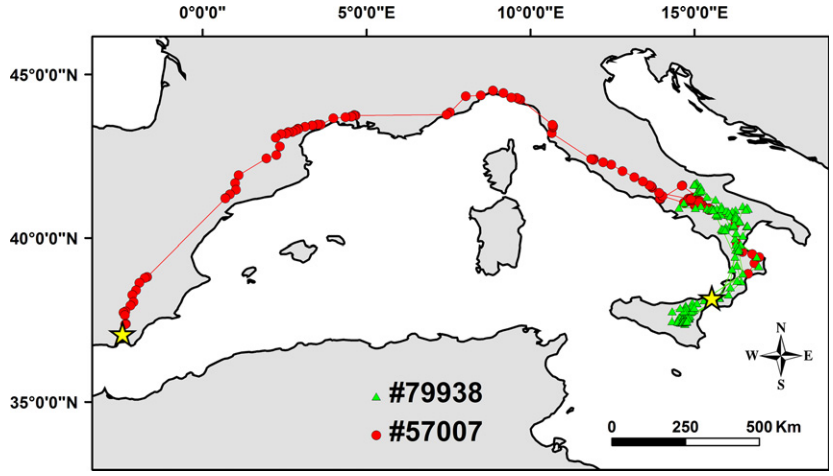

Figure 3. Movements of two Short-toed Eagles that wintered in Sicily in their first year recorded in summer/autumn of their second year. Stars indicate location of their deaths.

in Sicily. During the following year, one of these two individuals migrated westwards towards Spain, showing that the learning process can occur not only in juvenile eagles, but more generally in inexperienced ones.

Our tracking results are consistent with a pattern already shown by long-term field studies carried out in the last 15 years (Agostini *et al.* 2009). Observations during these field studies have highlighted that the endogenous programme of inexperienced juveniles can be overridden by social interactions with adult birds, leading to juveniles migrating on the longer, western route. Indeed, thousands of individuals migrating in mixed age flocks have been observed from the watchsites of Capriglia and Arenzano (NW Italy) during the last 15 years following the western route, with juveniles always in flocks with adults (average: 1459 per year, 78% adults; Agostini *et al.* 2002, Panuccio *et al.* 2012, Premuda *et al.* 2015). These observations suggest that the five Short-toed Eagles that initially migrated northwards before heading south through the Strait of Gibraltar were probably following experienced adults. Also the results obtained from the two birds migrating via the Sicilian route are consistent with field observations that also show a larger number of individuals taking this route. The migratory flow of inexperienced Short-toed Eagles through southern Italy, although less heavy than the one following the western route (Premuda *et al.* 2015), is quite conspicuous especially on the island of Marettimo, where every October, 150–200 individuals, mainly juveniles (79%; Agostini *et al.* 2009, Panuccio *et al.* 2011), are observed, exhibiting the same indecisive behaviour shown by our satellite tracks (Fig. 2b). Therefore, combining both these visual observations and the satellite data presented in this study, it can be argued that every year a small proportion of juvenile Short-toed Eagles (perhaps around 20% of the juveniles raised in the Italian peninsula; Premuda *et al.* 2015) follow an inherited migration direction, heading to the south without learning the western route from adults, and attempt to cross the Sicily Channel.

This raises the question of why such a bimodal pattern of orientation occurs, and why these individuals are not able to learn the 'safe' western route and instead follow the route that would involve a long and risky sea crossing. Perhaps meeting an experienced individual depends upon random circumstances, and the probability might be higher for juveniles belonging to core territories within the breeding population rather than peripheral ones (Oppel *et al.* 2015). In our case, it does not seem that this could be the explanation, because the territories from which the birds heading to the south originated are not the most peripheral. We even had one case of juveniles born in the same territory in different years and using different routes.

Meeting an adult should be easier at the beginning of the migration period rather than at the end. Unfortunately, our sample size does not allow for testing whether the earlier departing juveniles

are more prone to following the detoured route, which could result from 'lucky' individuals fledging earlier and developing better flight capabilities, thanks to innate abilities and/or to a higher quality territory. Among southward migrating Eagles, #57007 did indeed begin migration quite late, but #79938 began even earlier than some northward migrating individuals. Perhaps meeting an experienced adult to follow is more probable in the earlier period (10–20 September is the most important period for adult migration; Agostini *et al.* 2002, Panuccio *et al.* 2012, Premuda *et al.* 2015), but is finally a casual event based on random circumstances.

Short-toed Eagles migrating southwards through Italy spend the winter in Sicily, completely outside their traditional wintering grounds in Africa (Ferguson-Lees & Christie 2001). Considering the diet of a species that relies almost exclusively on snakes, this locality may appear suboptimal, but regular wintering records have been known for 30 years (Mascara 1985, Corso 2005), involving predominantly juveniles. In agreement with migration data, the observation of an individual feeding on a Black Rat *Rattus rattus* suggests a certain degree of flexibility with regard to food choice (S. Grenci pers. obs.).

Climate change and the availability of artificial food resources have been proposed as possible causes of the northward shift in the wintering grounds reported in many species during the last decade (Morganti 2014, Shephard *et al.* 2015) but our study shows that ecological barriers may also influence this shift, given that these barriers are unfavourable or even impossible to cross for a soaring migrant species such as the Short-toed Eagle. The combination of transport costs, inherited information and geography force these Short-toed Eagles to spend the winter 3000 km north of their conspecifics. Indeed, rising winter temperatures generated by climate change (IPCC 2014) may promote the survival of individuals wintering in Sicily, because prey availability would be enhanced by warming conditions.

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