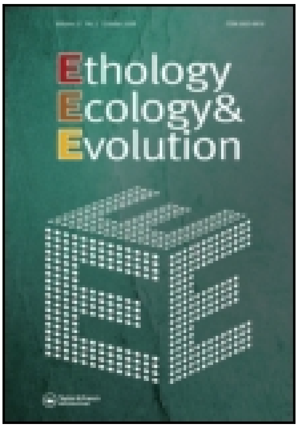

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Ecological barriers promote risk minimisation and social learning in migrating short-toed snake eagles

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Ecological barriers promote risk minimisation and social learning in migrating short-toed snake eagles

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The short-toed snake eagle (*Circaetus gallicus*) uses mostly soaring flight over land during migration to avoid long sea crossings. In particular, birds breeding in central Italy cross the Mediterranean Sea at the Strait of Gibraltar, using a route through northwestern Italy during both autumn and spring migration. Birds breeding in Greece, such as those breeding in Italy, are expected to use the same strategy passing through northeastern Greece and avoiding the longer sea crossing between southern Greece and Libya. In order to verify this hypothesis, contemporaneous observations were made at two watchsites, in northwestern Italy (Apuane Alps) and northeastern Greece (Mount Olympus), during autumn 2009 and spring 2010. During autumn migration 376 birds were seen migrating at Mount Olympus, nearly all heading NNE. Most birds were seen migrating in flocks, and at least 23 flocks contained both adults and juveniles. Over the Apuane Alps a total of 1042 short-toed snake eagles, all migrating NNW, was counted. At this watchsite the proportion of juveniles was lower than that reported at Mount Olympus. During spring migration, 606 birds were seen at Mount Olympus, 602 heading south. At the Apuane Alps 1307 birds were counted, all heading SSE. The orientation behaviour of short-toed snake eagles confirms that those breeding in Greece, like those breeding in central Italy, use a circuitous route during both spring and autumn. In particular those breeding in Greece are expected to cross the sea at the Dardanelles and/or at the Bosphorus. In addition, the higher proportion of juveniles reported at Mount Olympus during autumn migration would suggest that social learning could have been much favoured by natural selection in the case of birds breeding in Greece rather than in Italy, highlighting a relationship between the length of the barrier and the tendency of juveniles to follow the adults.

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INTRODUCTION

During migration, birds can organise their travels according to alternative criteria, namely time, energy expenditure or safety (ALERSTAM & LINDSTRÖM 1990). In particular, strategies that minimise energy consumption and mortality risk evolved in broad-winged species, such as eagles, vultures and storks (KERLINGER 1989; NEWTON 2008; BILDSTEIN et al. 2009). In these species, long powered flapping flights over water require the expenditure of huge amounts of extra cost (PENNYCUICK 1972, 1975) and increase mortality risk (e.g. more than 1300 raptors were found dead along a beach of the Mediterranean coast of Israel during April 1980 as reported by ZU-ARETZ & LESHEM 1983). For these reasons, the routes of broad-winged raptors are constrained by the geographical distribution of land-masses, leading to detours that often involve complex changes of course in order to concentrate at straits where sea-crossings are narrower (KERLINGER 1989; ZALLES & BILDSTEIN 2000; ALERSTAM 2001; BILDSTEIN 2006). In some species these migration pathways can even involve movements that are opposite to the main migration direction, thus leading to the so-called "circuitous migration" (AGOSTINI et al. 2002a; YAMAGUCHI et al. 2008). Flocking behaviour, and in particular mixed-age flocks, are of paramount importance in these species, since inexperienced juveniles cannot know the safest route during their first migration (MARANSKY & BILDSTEIN 2001; AGOSTINI 2004; CHERNETSOV et al. 2004) and, hence, the selective pressure to migrate together with the adults should be higher than in species more adapted to flapping flight.

The short-toed snake eagle (*Circaetus gallicus*) is a summer resident in Europe, wintering in tropical Africa (FERGUSON-LEES & CHRISTIE 2001). In Greece a breeding population of 350–500 pairs has been estimated with a wide distribution over the whole mainland (HANDRINOS & AKRIOTIS 1997; BIRDLIFE INTERNATIONAL 2004). There is lack of information concerning migration pathways used by birds belonging to populations breeding in the Balkans. This species mostly uses soaring flight over land during migration, avoiding the crossing of water surfaces and concentrating at the Strait of Gibraltar and at the Bosphorus (MEYBURG et al. 1998; KIRWAN et al. 2008; PAVÓN et al. 2010). As suggested by AGOSTINI & MELLONE (2008) "the benefits associated with the low cost of thermal soaring flight, compared to flapping flight over water, are probably great for these birds during both spring and autumn migrations, as this species has a low aspect ratio and is thus less well adapted to flapping flight than some other raptors". As a result, short-toed snake eagles breeding in the Italian Peninsula follow a circuitous route rather than directly crossing the central Mediterranean, entering and departing Europe via the Strait of Gibraltar, and travelling through northwest Italy, France and Spain (AGOSTINI et al. 2002a, 2002b; PREMUDA 2004). In particular, hundreds of short-toed snake eagles, mostly adults, are observed annually migrating northwards during autumn and southwards during spring along the Tyrrhenian coast, exploiting thermal currents and updrafts on the western slopes of the Apuane Alps (PREMUDA et al. 2010). Since the water surface separating the Greek mainland from African coasts is approximately 2–3 times longer than the Channel of Sicily (Fig. 1), it is expected that short-toed snake eagles breeding in central and southern continental Greece, like those breeding in the Italian Peninsula, avoid that long sea crossing

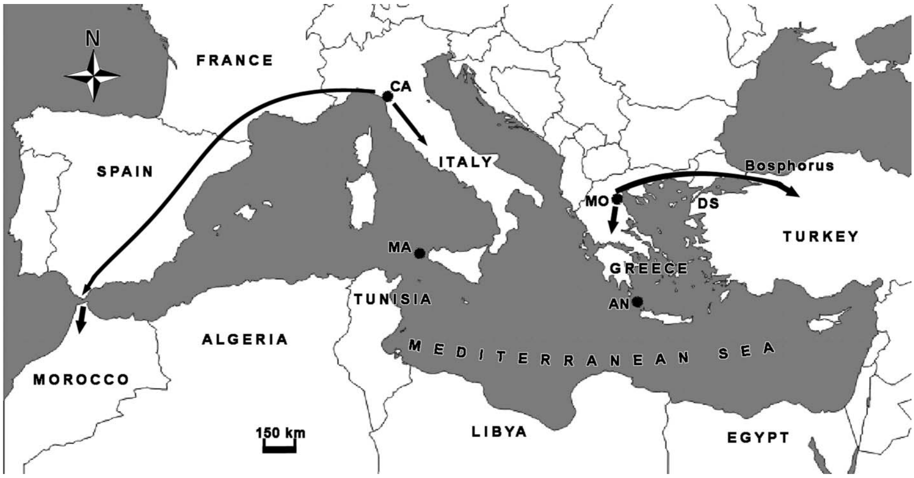

Fig. 1. — The study area (CA: Capriglia, Apuane Alps; MO: Mount Olympus; MA: Marettimo; AN: Antikythira; DS: Dardanelles).

using a circuitous route, perhaps concentrating at the Dardanelles' Strait and/or at the Bosphorus. The aim of this study was to verify this hypothesis through systematic observations on the slopes of Mount Olympus (northeast Greece) during both autumn and spring, focusing on orientation and flocking behaviour of birds belonging to different age classes. Data recorded at the site were compared with those recorded in the same periods at the Apuane Alps (Capriglia), along the western slope of central Italy.

STUDY AREA AND METHODS

The mountain chain in this area of north-eastern Greece has geographic characteristics similar to the Apuane Alps, being parallel and very close to the coast (approx. 7 km) and forcing migrants to concentrate on a narrow corridor. Observations were made between 9 September and 1 October 2009 and between 6–26 March 2010, the peak of the autumn and spring migration of the short-toed snake eagle in the Mediterranean basin (Agostini et al. 2002b; Baghino et al. 2009), using a post located along the eastern slopes of the mountain chain (approx. 40°01′N, 22°29′E).

At the Apuane Alps observations were made between 12–27 September 2009 and 6–26 March 2010. The observation post was located at an altitude of about 400 m (approx. 43°58′N, 10°14′E).

Age classes were determined according to Forsman (1999) and Clark (1999). The overall number of adults, immatures and juveniles was estimated according to the proportions recorded in the sample of aged individuals (Kjellén 1992; Agostini et al. 2002b). Observations were made aided by telescopes and binoculars.

In order to provide theoretical information concerning energy consumption of short-toed snake eagles during powered and gliding flight, assuming no wind, we used a published flight performance program based on flight mechanics (Pennycuick 2008). Body mass, wing span and wing area included in the analysis were calculated following methods by Pennycuick (2008) using data provided by G. Cattaneo & M. Campora (wingspan 1.74 m; wing area 0.43 m^2; mass 1.6 kg, unpub. data).

RESULTS

Autumn migration

At Mount Olympus, we counted a total of 376 short-toed snake eagles peaking on 19 September, when the passage of 107 individuals was reported. Most migrants were seen heading towards NNE and only 9 (2%) birds, 7 of which were migrating alone, disappeared heading SSW. It was possible to determine the age of 127 (34%) birds. Most birds were adults (78 individuals, 61%), while 47 (37%) were juveniles and only 2 (2%) were immatures. Among birds heading SSW 6 were aged; of them 5 were juveniles and 1 immature. We estimated the passage of 231 adults, 139 juveniles and 6 immatures. The short-toed snake eagle showed a strong tendency to migrate in flocks, with only 64 (17%) of all individuals observed migrating alone. On average, groups consisted of 3.4 ± 0.2 (SE) birds, and 47% of flocks ($n = 92$) contained two birds. We recorded at least 23 flocks containing both adults and juveniles.

At the Apuane Alps we reported the passage of 1042 short-toed snake eagles peaking on 23 September, when the passage of 222 individuals was reported. Migrants were seen heading towards NNW and none was seen heading south. It was possible to determine the age of 506 (49%) birds. Most birds were adults (394 individuals, 78%), while 75 (15%) were juveniles and 37 (7%) immatures. We estimated the passage of 809 adults, 156 juveniles and 77 immatures. At this site, 767 (74%) individuals were observed in flocks. On average, groups consisted of 3.2 ± 0.1 (SE) birds, and 48% of flocks ($n = 242$) contained two birds. We recorded at least 51 flocks containing both adults and juveniles.

Lastly, comparing the two study areas within the same period (12–27 September), the proportion of juveniles was lower at Apuane Alps rather than on Mount Olympus (15% vs 39%; contingency table: $\chi^2 = 23.2$, df = 2, $P < 0.01$).

Spring migration

At Mount Olympus we counted 606 birds; of them 602 were seen heading SSW and only 4 heading NNE. The peak passage occurred on 24 March, when 264 birds were counted. A total of 173 (29%) individuals were aged, 169 adults (98%) and 4 (2%) immatures. We estimated the passage of 592 adults and 14 immatures. As in autumn, most of the short-toed snake eagles (503; 83%) migrated in flocks composed of 2.8 ± 0.2 (SE) birds, and 43% of flocks ($n = 134$) contained two birds.

At the Apuane Alps we counted 1307 birds, all seen heading SSE. The peak passage occurred on 18 March, when a total of 443 birds were counted. A total of 706 (54%) individuals were aged, 696 adults (99%) and 10 (1%) immatures. We estimated the passage of 1289 adults and 18 immatures. A total of 1027 (79%) short-toed snake eagles migrated in flocks composed of 3.9 ± 0.2 (SE) birds, and 40% of flocks ($n = 263$) contained 2 birds.

Computer simulation concerning energy consumption during gliding and powered flight shows that short-toed snake eagles require 8.7 times the energy used for soaring-gliding flight for the powered flight (see Pennycuick 2008).

DISCUSSION

Our results confirm the hypothesis that birds breeding in central and southern Greece use a circuitous route during both spring and autumn migration and probably cross the Mediterranean Sea at the Dardanelles' Strait and/or at the Bosphorus. At both sites and seasons short-toed snake eagles showed a conservative migration strategy, avoiding the crossing of large stretches of water. This was already known just for Italy (Agostini et al. 2002a) but it is a new finding for Greece. Thus, these migration patterns are the result of a migration strategy performed by individuals breeding in peninsulas facing wide bodies of water. Our field observations agree with the theoretical model: in fact the huge increase of energy consumption during powered flight means that a 400 km crossing across the Mediterranean using flapping flight is equivalent to a soaring-gliding flight of approximately 3500 km over land around the barrier. In this picture, social learning plays an important role in the evolution of this migration strategy since, during their first migration, inexperienced birds migrating alone would tend to move southwards along an innate direction of migration (Kerlinger 1989). Probably the higher survival rate of juveniles migrating together with adults rather than alone favoured high synchronicity of departure times from the breeding grounds in populations of Italy and Greece. The flocking behavior is the "tool" allowing for information transmission between birds belonging to different age classes (Couzin et al. 2005). In addition, the higher proportion of juveniles recorded in Greece rather than in Italy during autumn migration, if compared with the breeding success of the Greek and Italian populations of this species (Ferguson-Lees & Christie 2001; Bakaloudis et al. 2005), suggests that nearly all juveniles belonging to the Greek population use the circuitous route, learning this flyway by following the adults. Conversely, as expected, five juveniles that did not migrate in mixed-age flocks at Mount Olympus were seen heading southwards along the innate direction of migration. Perhaps the length of the sea crossing, longer between southern Greece and Libya rather than between western Sicily and Tunisia, would negatively affect the survival of juveniles in Greece more than in Italy. As a result, the overlap of migration periods of birds belonging to different age classes could have been much favoured by natural selection in the case of birds breeding in Greece rather than in Italy. This assumption would agree with recent autumn surveys made at the islands of Antikythira (located 33 km NW of Crete) and Marettimo (approximately 30 km off western Sicily; Fig. 1). While, at the first site, Lucia et al. (2011) reported the passage of a few dozen juvenile short-toed snake eagles moving southwards late in the season, during the first half of October, in the same period higher numbers of juveniles (at least 150–200 birds) were reported undertaking the crossing of the Channel of Sicily (approximately 150 km wide) via Marettimo, between western Sicily and Tunisia (Agostini et al. 2004b, 2009). Social learning concerning migration routes has been suggested to occur in other species of birds such as the black kite (*Milvus migrans*; Agostini et al. 2004a), the white stork (*Ciconia ciconia*; Chernetsov et al. 2004) and, occasionally, the European honey buzzard (*Pernis apivorus*; Agostini et al. 1999; Agostini 2004).

In conclusion, like short-toed snake eagles breeding in central Italy, birds breeding in central-southern Greece use the route that probably reflects the colonisation process during both migrations: a further example of how colonisation history, ecological barriers, and morphological characteristics of migrants probably interact in shaping migratory routes and migration strategies of birds belonging to different age classes.

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