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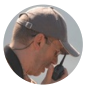

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Age-related timing of Short-toed Snake Eagle *Circaetus gallicus* migration along detoured and direct flyways

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ABSTRACT

Capsule: Juvenile Short-toed Snake Eagles *Circaetus gallicus* hatching in the peripheral populations of Greece and Italy have limited opportunities for social learning of migration routes compared to those hatched elsewhere.

Aims: To test the prediction that there would be a higher degree of migration synchrony between adult and juvenile Short-toed Snake Eagles originating from peripheral populations and using an extremely detoured flyway, when compared to other populations using a direct overland flyway.

Methods: We use linear regression models to compare seasonal changes in the age distribution of migrating Short-toed Snake Eagles counted at two migration watch-sites in Italy (Arenzano) and Georgia (Batumi), along a detoured and a direct flyway, respectively.

Results: Juveniles migrated a few days later than adults at both sites and the age ratios recorded at these two sites was similar. The daily proportion of juveniles increased along a similar slope during the migration season, thus showing a similar degree of synchrony between the age classes on both flyways.

Conclusions: Contrary to our hypothesis, juvenile and adult migration is not more synchronized in peripheral populations using a detoured flyway compared to a core population using a direct migration flyway. Our results suggest that juveniles do not learn detours to complete trans-Mediterranean migration from their parents, but from other elders.

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Social learning may improve the survival chances of young migrating birds substantially. Nevertheless, many bird species show age-dependent migration strategies which differ in terms of timing and route choice. Age-dependent migration strategies often occur *in tandem* with morphological differences and differences in the timing of other crucial annual events such as moult and breeding (Cristol *et al.* 1999, Newton 2008, Zenzal & Moore 2016). Age differences in the timing of migration are most clearly distinct among long-distance migrants. Among passerines, first-year birds migrate earlier than adults if the latter moult on the breeding grounds, while the opposite occurs in species in which adults suspend or postpone moult until they reach their wintering grounds (Schifferli 1965, Payevski 1994, 1998, Woodrey & Chandler 1997, Woodrey & Moore 1997, Jakubas & Wojczulanis-Jakubas 2010). In such species, juvenile birds move alone or in flocks made up entirely of juveniles, and largely rely on innate compass orientation to move along a north–south axis.

Conversely, in other types of migrating birds, timing and routes of migration, and other stages of the annual cycle of adults and juveniles may overlap. For example, in some populations of shorebirds adults tend to leave the breeding areas earlier than juveniles, but they also stop and moult at staging sites along the way, such that adults and juveniles arrive in the wintering areas at about the same date (Baccetti *et al.* 1999 cited by Newton 2008). Moreover, Dunlins *Calidris alpina* and Eurasian Spoonbills *Platalea leucorodia* regularly migrate in mixed-age flocks, while juvenile geese, cranes and swans migrate with their parents (Newton 2008, Henningsson & Karlsson 2009, Lok 2013). In such cases, inexperienced juveniles gain social information on navigation routes and strategic stopover sites.

Overall, it seems that adults are more likely to synchronize their autumn migration with juveniles when inherited factors do not enable young birds to survive their first migration, especially in long-lived, capital breeders (i.e. species which provision offspring

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using energy stores accumulated at an earlier time; see Jönsson 1997).

Raptors form an interesting exception to the expectation that long-lived capital breeders ought to migrate socially to improve the odds of survival for their young. Most raptors are soaring migrants which are especially prone to fatigue as they are unable to use very weak thermals and so need to fuel migratory journeys over the sea (Kerlinger 1989). Despite the fact that barrier-crossings, such as the Mediterranean along the African-Eurasian flyways, pose a major risk for juvenile raptors, most raptor species display similar age-dependent migration strategies as those found in passerines. For example, in the Eurasian Sparrowhawk *Accipiter nisus*, a short distance and partial migrant which finishes moulting at the breeding sites, juveniles migrate earlier than adults (Kjellén 1992). Conversely, among long-distance migrants which suspend moult during migration, such as the Osprey *Pandion haliaetus*, Black Kite *Milvus migrans* and European Honey Buzzard *Pernis apivorus*, adults leave before juvenile birds (Schifferli 1967, Kjellén 1992, Agostini & Logozzo 1995).

Juvenile birds of species such as European Honey Buzzards, therefore, migrate over a broad front, often including long sea-crossings which presumably substantially reduce their chances of survival (Agostini & Logozzo 1995, Agostini *et al.* 1999, 2002b, 2004b, Schmid 2000, Hake *et al.* 2003). Visual observations at several sites in southern Italy have shown that some medium-sized soaring raptors do regularly cross the central Mediterranean in mixed-age flocks. For example, first-year Black Kites which migrate early learn the shortest route over the sea (using an island-hopping strategy from Italy via western Sicily to Tunisia) by following relatively late adults (Agostini *et al.* 2004a, Panuccio *et al.* 2014). The same phenomenon is occasionally observed among European Honey Buzzards migrating in the same area (Agostini *et al.* 1999, 2004c, Agostini 2004). However, most juveniles probably migrate too late to follow adults and are likely to end up travelling longer distances over the sea. Moreover, the early departure of adult birds from the breeding grounds prevents juveniles from directly acquiring benefits from migrating with adults, such as the higher efficiency of thermal detection by flocks compared to individual migrants (Kerlinger 1989, Leshem & Bahat 1999, Maransky & Bildstein 2001, van Loon *et al.* 2011).

The risk of drowning during sea-crossings is greater for larger and heavy species of soaring raptors such as eagles and vultures (Bildstein et al. 2009, Oppel *et al.* 2015). Moreover, juvenile migrants which originate from small and peripheral populations probably have most trouble finding guidance from elders, as demonstrated by the high degree of mortality among juvenile Egyptian Vultures *Neophron percnopterus* which attempt to cross the Mediterranean directly as they leave from declining breeding populations in the Balkan peninsula (Oppel *et al.* 2015). It seems logical that in such cases natural selection should lead to a larger overlap of adult and juvenile migration periods to facilitate social learning of strategic migration routes. This hypothesis has previously been suggested for the Short-toed Snake Eagle *Circaetus gallicus* migration system (Panuccio *et al.* 2012). However, to our knowledge, so far no study has rigorously tested for differences in age-dependent migration timing of a single species across multiple flyways.

The aim of this study, therefore, was to test whether social learning for barrier avoidance has caused differences in the synchrony of adult and juvenile migrants of the same species along two distinct flyways. Our focal species is the Short-toed Snake Eagle, one of the heaviest soaring long-distance migrants, which breeds in Europe and winters in tropical Africa, south of the Sahara desert (Ferguson-Lee & Christie 2001). The European population is divided into several subpopulations and juveniles originating from peripheral populations have been observed in mixed-age flocks engaging in extremely detoured routes which are not used by other species (Agostini *et al.* 2002, Panuccio *et al.* 2012, Mellone *et al.* 2011, 2016). In particular, unlike Black Kites and European Honey Buzzards (see also Lucia *et al.* 2011), Short-toed Snake Eagles breeding in Italy and Greece follow long, extremely detoured routes rather than directly crossing the Mediterranean Sea, compensating for the drift effect of crosswinds *en route* (Panuccio *et al.* 2013) and concentrating where water crossings are narrower, at the Strait of Gibraltar (Italian population) and the Bosphorus (Greek population). These flyways probably retrace the colonization process (Agostini & Mellone 2008, Panuccio *et al.* 2015) and could be explained by the high cost of powered flight for this species over large water bodies (Agostini *et al.* 2015).

As in other raptors, however, substantial numbers of juvenile birds fail to learn the safe overland detours by following older birds and end up travelling south, probably relying on an innate compass direction (Agostini *et al.* 2004a, 2009, Lucia *et al.* 2011, Panuccio *et al.* 2011, Mellone *et al.* 2016). Juveniles originating from peripheral populations in Italy and Greece are likely to perish while crossing the sea if they fail to learn strategic detours from elders. In contrast, juveniles from other populations do not need to engage in extreme detours to find safe, overland migration routes, and are assumed to have a higher chance of survival in the absence of adult guidance. This is the case, for example, for eagles originating from western Russia and migrating along the eastern Black Sea coast. Consequently, we expect stronger selection for overlapping migration timing of juvenile and adult eagles that use an extremely detoured flyway out of peripheral populations in Italy and Greece, compared to eagles using the direct Black Sea flyway out of Russia (Figure 1).

Study areas and methods

Migrating Short-toed Snake Eagles were observed at watchpoints in Italy and Georgia. The Italian watchpoint was in the Ligurian Apennines (northwest Italy), at the northernmost point of the mid-western Mediterranean basin, near Arenzano (44°25′23″N 8°40′53″E; Figure 1). Here, the ridge of the Apennines, after running parallel to the coast, reaches its closest proximity to the sea as well as the minimum transverse width for the entire Italian peninsula. The observation post was on the closest culmination to the sea (2 km inland) at 500 m above sea level. Watchpoints in Georgia were located northeast of Batumi, in a geographical bottleneck of a few kilometres width between the Black Sea to the west and the cloud-covered Pontic Mountains to the east (Verhelst *et al.* 2011, Vansteelant *et al.* 2014; Figure 1). Two count stations were chosen on an approximate east–west transect, 2 and 6 km east of the coast (41°41′05″N 41°43′51″E and 41°41′08″ 41°46′43″E) at 338 and 424 m above sea level. Previous surveys at Batumi showed that the peak autumn migration of Short-toed Snake Eagles occurred during the second half of September, whereas it occurred one week earlier at Arenzano (median dates 20 September versus 27 September; Verhelst *et al.* 2011, Baghino *et al.* 2012). For this reason, data concerning the age of migrants were extracted for the main migration period which lasted 22 days from 8 to 29 September at Arenzano (in four seasons, 2009–12) and from 16 September to 7 October at Batumi (in five seasons 2010–14). Characters used in separating age were those given by Forsman (1999). Birds were classified as either juveniles (migrating for the first time) or adults (experienced individuals migrating for at least the second time). Observations were made using binoculars and telescopes and were interrupted only during rain.

The data were analysed using a generalized linear model (GLM) with Poisson-distributed errors, using the daily proportion of juveniles (number of juveniles/ number of birds of known age) as a dependent variable, and the Julian calendar date and site (Arenzano or Batumi) as covariates. We verified the fit of the model by applying a Shapiro–Wilk test on model residuals. We tested the significance of the two covariates in explaining variation of the dependent variable using an ANCOVA on the model. Afterwards we compared the coefficient of the slopes (daily proportion of juveniles ~ Julian date) of the two sites using a z test to verify whether the difference between the two slopes was significant.

Results

At Arenzano and Batumi, mean (± se) annual totals of Short-toed Snake Eagles recorded on migration were

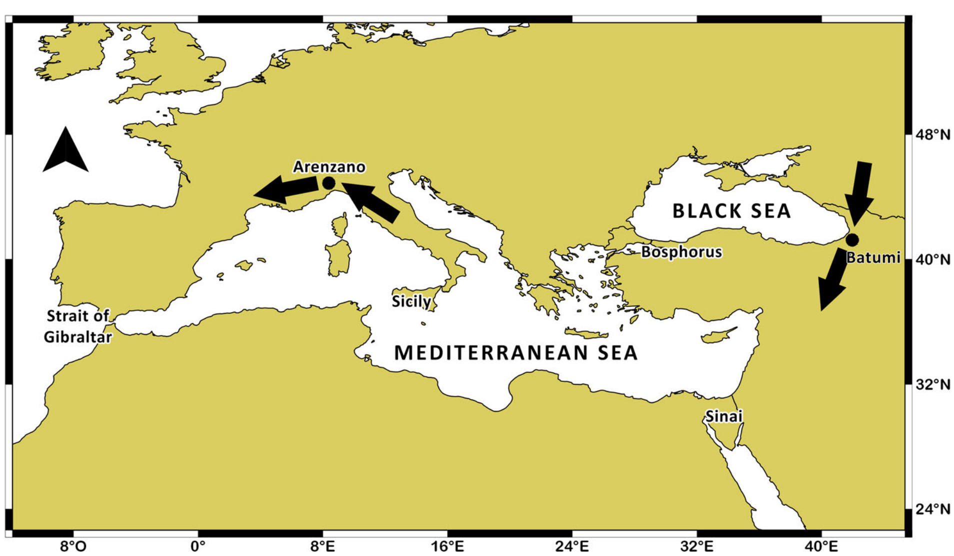

Figure 1. Location of the study areas in northwest Italy (Arenzano) and Georgia (Batumi).

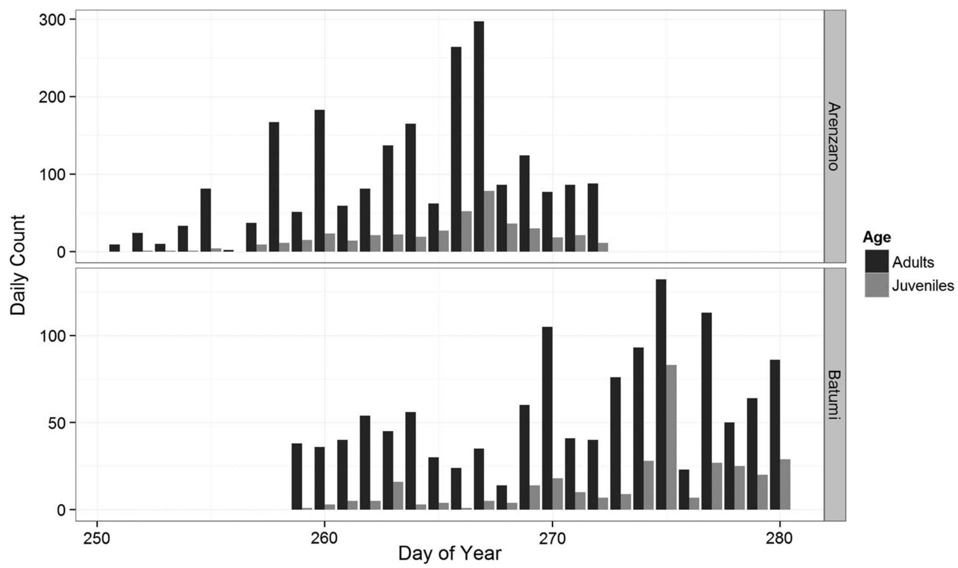

Figure 2. Daily number of juvenile and adult Short-toed Snake Eagles observed at Arenzano (8–29 September 2009–12) and at Batumi (16 September–7 October 2010–14).

1197.0 ± 138.3 and 1321.4 ± 98.1, respectively. At Arenzano, a total of 3808 eagles were seen migrating in 955 flocks with a mean (± se) of 3.9 ± 0.2 individuals per flock. At Batumi, observers were unable to record separate flocks, mostly because the largest numbers of eagles were seen on days of intensive migration during which tens of thousands of migrants of ten or more species passed over in uninterrupted streams. However, it was clear that single-species flocks of Short-toed Snake Eagles occurred only rarely at Batumi, since more than 79% of all records were of solitary birds. Among those birds where age was determined (Arenzano, $n = 2537$; Batumi, $n = 1579$), a total of 414 (16.3%) and 324 (20.5%) were juvenile, respectively. Thus, a slightly but significantly higher proportion of juveniles was reported along the direct flyway at Batumi ($\chi^2 = 11.4$, df = 1, $P < 0.01$). The migration timing of eagles was on average 8 days earlier for adults and 9 days earlier for juveniles at Arenzano (median dates: adults = 22 September; juveniles = 23 September) than at Batumi (median dates: adults = 30 September; juveniles = 2 October; Figure 2). Adults migrated on average 1 day earlier than juveniles at Arenzano and 2 days earlier at Batumi. The GLM shows that both, *date* and *site* are significant terms in explaining the daily variation of the proportion of juveniles (Table 1). In particular *date* was the most important term, with a positive parameter estimate indicating that the proportion of juveniles increased over the migratory season. *Site* was a less significant term, with a lower number of days with high proportions of juveniles at Batumi than in Arenzano. The residuals of the model were approximately normally distributed ($P = 0.06$) suggesting a good fit. Finally, the two slopes were similar ($z = 0.37$; $P > 0.9$; Figure 3) indicating that the proportion of juveniles increases at a similar daily rate throughout the migration season at each site.

Table 1. Summary of the GLM explaining the variation in the daily proportion of juvenile Short-toed Snake Eagles migrating over Batumi and Arenzano.

Explanatory terms	*F*	*P*	estimate ± se
Date	15.4	0.0003	0.008 ± 0.002
Site	5.7	0.02	−0.06 ± 0.03 (Batumi)

Discussion

Our results are not consistent with the hypothesis that natural selection promoted a larger overlap in the migration periods of juvenile and older birds in a population using a detoured flyway. In addition, the fact that the proportion of juvenile birds increases significantly throughout the season at both sites suggests that juvenile Short-toed Snake Eagles do not learn detours from their parents, but from other elders.

In this species, juvenile birds are independent soon after a long nestling period (Ferguson-Lee & Christie 2001) and the lapse between fledging and departure is about 40 days (Bakaloudis *et al.* 2005). A study in Greece showed that adult Short-toed Snake Eagles left their nesting areas mostly during the third week of September (Bakaloudis *et al.* 2005). Our surveys showed that, even at the end of the core migration period, adults outnumbered juveniles at both study

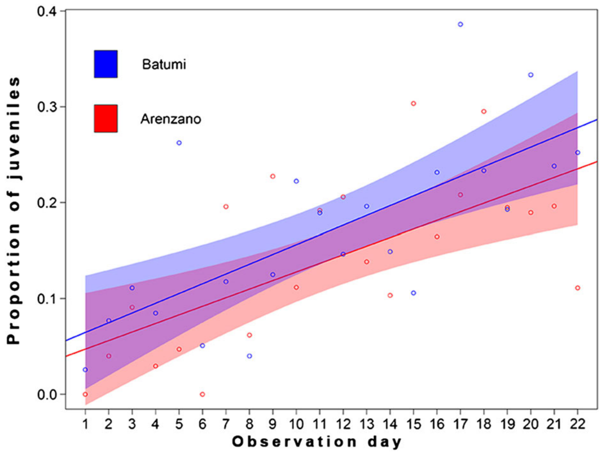

Figure 3. Proportion of juvenile Short-toed Snake Eagles recorded at Arenzano and Batumi during the observation periods (22 days at each site).

sites. The daily proportion of juveniles reported at Arenzano did not exceed 35%, consistent with previous studies at this site (Agostini *et al.* 2002a, Baghino *et al.* 2012). The proportion of juveniles reported at Batumi was significantly but only marginally higher, never exceeding 40%. Consequently, while juveniles tend to start their first migration a few days later than their parents, the number of juveniles that are able to learn detours by following other elders seems to be substantial at both sites.

Among five juveniles that were satellite-tracked from their natal sites in southern Italy and that used the detoured pathway, four began their migration well within the adult migration period, on 10, 15 and 20 (two birds) September and only one on 27 September (Mellone *et al.* 2016). Two others, tracked from the same area and beginning their migration on 18 September and 2 October, did not use the detoured route, and finally spent the winter in Sicily, about 3000 km north of birds using the detoured route (Mellone *et al.* 2016). These findings strongly suggest that juveniles are more prone to benefit from social learning if they migrate sufficiently early, even if they originate from peripheral populations. As suggested by Mellone *et al.* (2016), the small sample size of tracked birds cannot exclude the effect of casual events. However, long-term field studies also show that juveniles typically arrive on Mediterranean islands and peninsulas late in the season (mostly in October), occasionally forming large flocks when facing a water barrier (e.g. 70 birds seen together in western Sicily on 12 October 2004; Agostini *et al.* 2009, Lucia *et al.* 2011, Panuccio *et al.* 2011).

Although substantial numbers of juvenile Short-toed Snake Eagles migrate early enough to learn safe routes around the Mediterranean (Premuda *et al.* 2015), at least dozens of juveniles belonging to populations breeding in peninsular Italy and Greece fail to connect with elder conspecifics along the way and fail to learn the detoured flyway in their first year. It is interesting to note, however, that one of two satellite-tracked juveniles that migrated to Sicily in its hatching year did use the detoured route into sub-Saharan Africa during the following year, showing that the learning process can still take place later in life.

Two satellite-tracked juveniles left their natal areas in southeast Spain on 4 and 17 September heading southwest and crossed the Strait of Gibraltar three and four days later, respectively (Pavón *et al.* 2010). The fact that these birds travelled to Gibraltar in a near straight line suggests they probably also followed elder conspecifics shortly upon departure. Juveniles migrating without elders displayed an innate aversion to flight over water, even when approaching relatively short stretches of sea (Agostini *et al.* 2016b). Thus, the relatively high numbers of juveniles that are able to locate geographical bottlenecks (such as at Batumi) flying in small flocks or solitarily, often on days of intense migration with other soaring species, suggests that these birds can migrate along direct flyways both by following elders of other soaring species and by avoiding sea barriers. Indeed, the eastern Black Sea shore is not oriented perpendicular to the main travel direction of Short-toed Snake Eagles (both adults and juveniles) coming from Russia, which may arrive directly from the north, or otherwise by having tracked the Black Sea coast northwest to southeast. Similarly, birds originating from Spain can locate Gibraltar relatively easily by tracking the coast until they have no other option than to cross the sea.

Interestingly, satellite-tracking also suggests that juvenile eagles following the suboptimal central Mediterranean flyway were very hesitant to fly long distances over open water (Mellone *et al.* 2016). Two eagles that wintered in Sicily made highly complex movements for about a month, travelling between Sicilian mainland and Marettimo two and three times each, before settling for the winter. This strongly suggests juvenile eagles only engage in sea-crossings when they can see another landmass further south. Juveniles rarely reach islands as isolated as Malta, located about 90 km south of Sicily (Del Hoyo *et al.* 1994, Coleiro 1999). Due to the aversion for flying over water, and given the lack of adaptation towards high synchrony between adult and juvenile eagles, birds that end up in the central Mediterranean flyway may have a much higher chance of survival than we assumed at the start of this research. By arresting migration, instead of pursuing a dangerous trans-Mediterranean flight to Africa, birds can survive their first northern winter in the Mediterranean region, until they learn the more suitable detoured flyway later in life (Mellone *et al.* 2016). It is unclear, however, why juveniles of other, even more risk-sensitive species such as Egyptian Vultures, do not adopt a similar strategy when they face a crossing of the Mediterranean (Oppel *et al.* 2015). We, therefore, strongly encourage comparative research into sea-crossing decisions of soaring migrants in relation to weather conditions, visibility of land, and between different flyways.

Another explanation for the lack of adaptation towards higher synchronicity of adult and juvenile migrants in peripheral populations is the notion that timing of both age groups is too constrained by other factors. Juveniles seem to initiate autumn migration as soon as they have reached sufficient body condition to do so, and they are probably unable to migrate any earlier than they do. However, the main reason for why so many juveniles are left to fend for themselves is probably because their parents are unwilling or unable to delay their autumn migration for other, selfish reasons. Perhaps the likelihood that a juvenile is able to follow other unrelated 'elders' offsets the need for parents to delay migration in order to guide their young, even in relatively small, peripheral and patchy populations. The fact that in many capital breeding species adults with failed broods return to Africa earlier than successful breeders emphasizes that adults in general prefer to return to their breeding grounds as early as possible (Kjellen *et al.* 2001, Kölzsch *et al.* 2016). By leaving Europe as early as possible they can potentially compete successfully for superior habitat on the wintering grounds, complete their moult and prepare for the following migration and breeding season. Probably adults simply increase their life-long fitness most effectively by increasing their own chances of survival, rather than the survival chances of individual offspring.

Regardless of which factors constrain adaptation towards synchronized migration of adult and juvenile migrants, the fact that Short-toed Snake Eagles are apparently able to survive along multiple flyways can make the species more resilient in face of global environmental changes (Gilroy *et al.* 2016). Indeed, flyway-specific threats that lead to high mortality (Hewson *et al.* 2016) may be compensated by higher survival among that part of the population that uses another, safer flyway. A similar diversity of migration strategies exists in populations of other raptors, such as the European Honey Buzzard, that uses different routes across the Mediterranean between years and seasons and depending on wind conditions (Agostini & Logozzo 1995, Agostini *et al.* 2016a). As such, migratory diversity increases resilience of migrant bird populations, thereby countering population declines, but may also increase resilience of individual birds. For example, an individual that ran into adverse conditions along their usual route may be able to learn an alternative route very quickly by following other individuals, such that social learning greatly increases the resilience of individual birds to cope with environmental change or extreme events. Considering that the wintering range of Short-toed Snake Eagles may shift northward due to climate change (Huntley *et al.* 2007), the southward route into the Italian peninsula and onto Mediterranean islands may even become more advantageous than travelling all the way to sub-Saharan Africa, potentially relaxing the need for juveniles to migrate synchronously with adults during the first autumn migration and causing a divergence of age-dependent migration strategies. By sustaining monitoring of raptor migration at Arenzano, Batumi and other locations in the future, we hope to keep our finger on the pulse of these migration systems.

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