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IN FOCUS

Sea crossing as a major determinant for the evolution of migratory strategies in soaring birds

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Abstract

In Focus: Santos, C. D., Silva, J. P., Muñoz, A.-R., Onrubia, A., & Wikelski, M. (2020). The gateway to Africa: What determines sea crossing performance of a migratory soaring bird at the strait of Gibraltar? *Journal of Animal Ecology*, *89*, 1317–1328. Migrating birds undertake long journeys which pose several challenges. Water bodies are the most demanding ecological barriers for soaring birds, due to the increase in energy consumption and mortality risk. Through high-resolution GPS, Santos et al. (2020), analysed how the flight performance of 73 black kites crossing the Strait of Gibraltar was affected by external (e.g. weather conditions) and internal factors (individual experience). Kites waited for weaker crosswinds to start the crossing to minimize energy consumption, drift and altitude loss. Moreover, adults were quicker and lost less altitude than juveniles. These processes are likely to occur in all soaring species and have consequences also at a much wider spatial scale. In the Mediterranean region, species- and population-specific migration strategies appear to be influenced by interactions between species' morphology and the distribution of the land masses they traverse.

KEYWORDS

carry-over effects, detour, ecological barriers, flight style, migration, mortality risk, sea crossing, thermals

During long-distance migration, animals face challenges that are very different from those they experience during most of the annual cycle. Any living organism is not a flawless machine able to cope perfectly with all the pressures to which is subjected during its life cycle, but rather a compromise between very contrasting requirements. This is even truer for migratory birds, whose flight characteristics may be very advantageous during most of the year, in the breeding or wintering grounds, but very unfavourable during short but risky stages of the annual cycle, for example during migration. Klaassen et al. (2014) shown that more than half of the annual mortality in three raptor species occurs during migration.

Research on migratory birds, and especially raptors, has traditionally been focused in areas where birds congregate in order to minimize the length of water crossings where thermal uplift is weak or absent (Bernis, 1980; Rudebeck, 1950). Such bias towards these areas occurred, at least in the early stages, not because ornithologists aimed to investigate the behaviour in those specific conditions (but see Kerlinger, 1985), but rather because huge concentrations of species and individuals make the work more reliable.

The advent of satellite telemetry devices has allowed us to depict with fine detail the whereabouts of a bird anywhere between its nest and its wintering area, even when those are extremely far apart. Due to logistic and financial constraints, such studies normally deal with low sample sizes (but see Sergio et al., 2014), and are focused on very wide geographical areas, at the expense of analyses at a finer scale. Within this scenario the research published by Santos, Silva, Muñoz, Onrubia, and Wikelski (2020) is of striking novelty: they choose a well-known hot-spot for migratory raptors, the Strait of Gibraltar, and analysed the relationships between topography, weather conditions, internal factors and flight behaviour during a small portion of the migratory journey, all with unprecedented detail. Taking advantage of the opportunity to capture a significant number of black kites

Milvus migrans, a medium sized, facultative soaring, long-distance migratory raptor, they tagged 73 individuals with GPS accelerometers just before their 14-km jump towards Africa.

Water crossings are perhaps the most demanding stage along the migratory pathways of soaring birds, as can be seen from occasional mass mortality events (1,300+ individuals on a beach in Israel in April 1980; Zu-Aretz & Leshem, 1983). The conditions experienced during sea crossings may also have deleterious effects on subsequent breeding success, as happens with other barriers like the Sahara desert (Strandberg, Klaassen, Hake, & Alerstam, 2010).

Santos et al. (2020) succeeded in describing each sea cross attempt in terms of duration, length and tortuosity, flight altitude and speed, flight style, and whether the crossing was successful or not. Then, they evaluated whether these parameters were influenced by external factors like weather conditions (wind and solar radiation), time of day, starting altitude, as well as by internal ones (age and sex).

Age, wind conditions and starting altitude emerged as the main factors affecting the sea crossing performance. First of all, generally black kites wait several days for strong westward winds to subside. Crosswinds increased the risk of drifting away from the shortest route over water, losing altitude, and imposed a more frequent use of flapping flight, which means more energy consumption. Flapping effort was affected also by the altitude reached by the kites at the starting point: the higher the kites were when beginning their crossing, the lower was their energy consumption during the flight. Starting altitude was also the only variable affecting the probability of aborting the sea crossing, with higher starting altitudes being more likely to be rewarded with a successful crossing. Juvenile inexperienced migrants exhibited worse performance than individuals with previous crossing experience: they reached lower altitude over the sea surface and took significantly more time, with no significant difference in terms of distance. Black kites migrate in mixed age flocks (Panuccio, Agostini, Mellone, & Bogliani, 2014), but during the crossing adults are more efficient than juveniles. Juveniles may keep visual contact with them and with the closest point of the African coast, using a similar over water route, but covering it more slowly.

The processes highlighted in Santos et al. (2020) research take place in a small geographical area, but depict one of the main selective agents among those that shaped the migratory flyways of soaring birds. Species that minimize flight distances over water have to fine tune their travels from the onset of migration, in order to reach the intermediate goal areas where the sea crossings are shorter (Vansteelant, Shamoun-Baranes, van Manen, van Diermen, & Bouten, 2017; Vidal-Mateo et al., 2016).

The migration strategies involved in crossing the Mediterranean sea vary across species and populations. The black kites entering Africa from the Strait of Gibraltar mainly originate from the Central-Western Europe breeding areas. All soaring bird species breeding in those regions follow the same route, including more than 300,000 individuals (Martín, Onrubia, De la Cruz, & Ferrer, 2016). On the other hand, black kites breeding in the Italian peninsula have to cross the Sicily channel, which entails 150–200 km of overwater flight, a ten-fold wider sea surface. Interestingly, they do not avoid this obstacle but try to minimize risk and energy consumption through an island-hopping strategy (Panuccio et al., 2014).

The complex geography of the Central Mediterranean region seems to have favoured the emergence of a range of sea crossing strategies, and the external influences on sea crossings demonstrated by Santos et al. (2020) may also interact with wing morphology to produce different trade-offs among species (Figure 1).

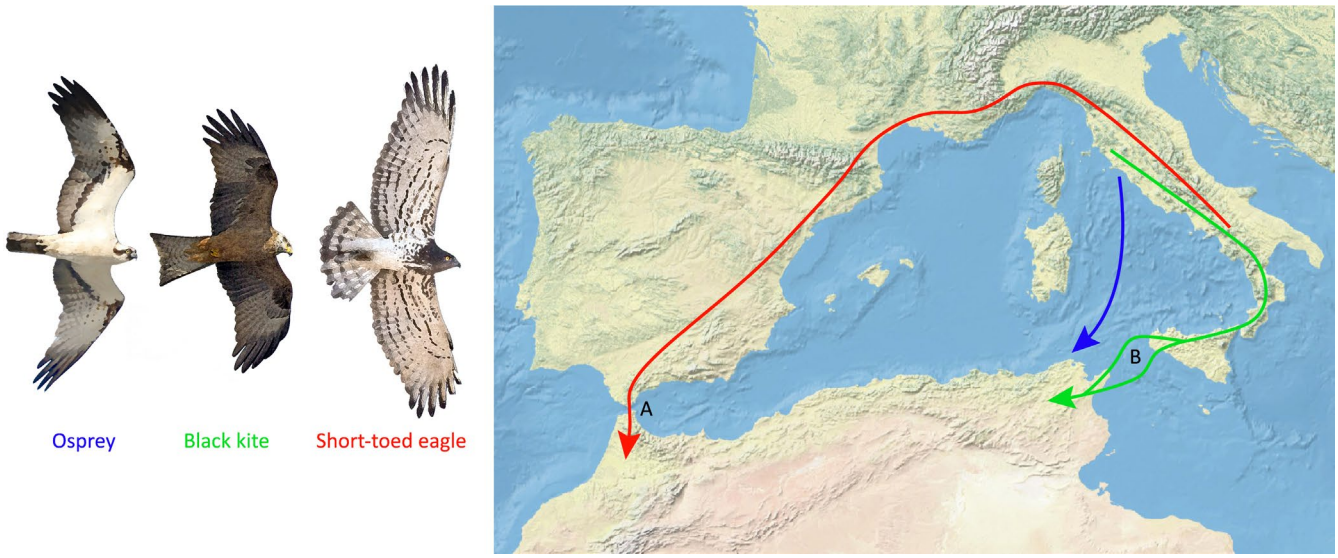

FIGURE 1 Schematized post-breeding migration routes of the populations of three raptor species breeding in peninsular Italy, during the crossing of the Mediterranean sea. Ospreys (blue track) have narrow, long wings that make them more suited to powered flight and less risk-sensitive during sea crossings. Black kites (green track) have an intermediate morphology and minimize the sea crossing through an island-hopping strategy. Short-toed eagles (red track) have wings with a low aspect ratio, pushing them to perform a long detour and minimize as much as they can the powered flight over the sea. 'A': Strait of Gibraltar (minimum crossing = 14 km); 'B': Sicily Channel (150+ km). Adapted from Duriez et al. (2018), Mellone, Lucia, Mallìa, and Urios (2016) and Panuccio et al. (2014)

The black kite shows intermediate flight behaviour between obligate soaring species and those that are able to endure flapping flight for longer stretches (see also Spaar, 1997). The short-toed eagle *Circaetus gallicus* is a trans-Saharan migrant with a low aspect ratio wing morphology, which entails extremely high transport costs during flapping flight. As a consequence, individuals breeding in the Italian peninsula avoid the crossing of the Sicily channel by embarking on a long detour through France and Spain that may increase the overall migration distance up to 50%, but reduce the water crossing length by 90% (Mellone, Liminana, Mallia, & Urios, 2011; Mellone et al., 2016; Panuccio, Agostini, & Premuda, 2012). On the opposite side of this behavioural spectrum, there are raptors with higher aspect ratio wing morphology, which systematically cross hundreds of kilometres over water, such as the marsh harrier *Circus aeruginosus* (Agostini & Panuccio, 2010) and the osprey *Pandion haliaetus*. Recently, the latter species has been the subject of a research that analysed its flight behaviour during the crossing of the Mediterranean sea: ospreys, followed through GPS/accelerometers, were able to gain altitude taking advantage of thermals developing over the sea (Duriez, Peron, Gremillet, Sforzi, & Monti, 2018). Even if the atmospheric convection was much weaker than over land, with the aid of some flapping effort ospreys were able to take advantage of a weak uplift to reach altitudes up to 900 m above the sea surface.

This comparison among the three species highlights how the response to a major obstacle like the sea crossing is species-specific and depends mainly upon wing morphology (Agostini, Panuccio, & Pasquaretta, 2015). Such differences in motion capacity have profound effects also on the colonization patterns of these raptors: while the osprey is virtually cosmopolitan, the short-toed eagle is absent from large Mediterranean islands, perhaps because its colonization pathways are much more constrained by the distribution of land masses (Panuccio, Lucia, Agostini, Ottonello, & Bogliani, 2015).

In order to follow the migratory pathways that avoid risky sea-crossings, the juveniles of some species, such as the above mentioned short-toed eagle, need to migrate together with adults, learning the safer routes by means of social interactions (reviewed by Berdahl et al., 2018). Such behaviour may be disrupted when a population experiences a strong decrease, the density becomes lower, and therefore the meeting of an adult 'guide' becomes less likely to occur. A similar process has been described in the Egyptian vultures *Neophron percnopterus* of the Balkan Peninsula. Oppel et al. (2015) found that the only factor affecting the mortality of migrating juveniles was their natal origin: those coming from the area with a lower probability of encountering an adult were forced to follow a simple southerly route dictated by innate vector navigation, which involved a wide sea crossing (300+ km). Sadly, nine out of ten birds died during the attempt. This selective mortality rate may trigger a positive feedback loop with quick demographic consequences, as it accelerates the population decline.

The predicted shifts in global wind patterns (Weimerskirch, Louzao, de Grissac, & Delord, 2012) may also increase costs and mortality associated with sea crossings. Therefore, expanding the framework proposed by Santos et al. (2020), will be key to forecasting the far-reaching impacts of ongoing environmental change. Since early arrival on breeding grounds can increase the chances of successful breeding (Sergio et al., 2014), future research should be carried out during the pre-breeding migration, possibly with longer lasting transmitters. Such approach would allow the links between sea crossing behaviour, arrival time and subsequent breeding output to be assessed: during spring motivational asymmetries should be stronger among different age classes, with adults being less wind selective than during the post-breeding journey, and non-breeding immatures showing a more conservative strategy.

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