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Across and around a barrier: migration ecology of raptors in the Mediterranean basin

M. Panuccio [1, 2]

[1] University of Pavia, Dipartimento di Scienze della Terra e dell'Ambiente, Via Ferrata 9, 27100 Pavia, Italy
[2] MEDRAPTORS (Mediterranean Raptor Migration Network), Via Mario Fioretti 18, 00152, Roma, Italy

Differently from the majority of birds, raptors move mostly using soaring-gliding flight rather than powered flapping flight using thermal currents over land. For this reason most of them tend to avoid flying over water surfaces. In this study are analyzed factors influencing raptor migration strategies of four species: the honey buzzard, the short-toed snake eagle, the western marsh harrier and the black kite. Each species shows a different migration pattern when crossing the Mediterranean sea. The most important factors influencing raptors during migration are: morphology, geography, flocking behaviour, weather conditions. All these elements interact with each other in shaping the migration strategies of raptors.

1 Introduction

Migration is an event that involves a huge number of birds moving from one habitat to another. Among birds breeding in the Paleartic area many long-distance migrants are found. Some species travel thousands of kilometres twice a year. The repeated journeys between breeding and wintering areas involve a considerable effort associated with high mortality risks. Since the selective forces acting on migrating birds are considerable, birds have developed a range of adaptations and strategies to cope with their journeys. "*These include not only morphological features for efficient locomotion and storage of energy but also behavioural adjustments*" [1] in order to overcome barriers and adverse weather conditions. Since migration is only a fraction of the life of a bird, morphological adaptations for migration should be integrated with other features allowing the bird to exploit resources all year long, in order to reproduce successfully.
Most birds move using powered flapping flight which also allows long non-stop flights and wide water crossings [2,3]. By contrast, Accipitriformes raptors are species that move using largely passive flight. They use soaring gliding flight in particular, exploiting thermal updraughts and ridge lifts; these kinds of currents occur on land and obviously not over water. This particular flight strategy is mostly due to the morphology of these species; the energy expenditure in powered flapping flight increases rapidly with the increase of body mass, while soaring gliding flight is convenient since it only requires the application of a small percentage of the basal metabolic rate [4,5,6]. Moreover, heavier species glide faster than smaller ones, allowing large raptors to reach a high cross-country speed, comparable with the highest speed of flapping migrants [7,8]. Finally Kerlinger [9] suggests that raptors with higher aspect ratios (aspect ratio = (Wing Span)^2 / Wing Area)) are better adapted to powered flight than species showing a lower aspect ratio (relatively short vs. relatively long wings). In this context it is readily understandable that large raptors fly mostly over land and avoid flying over large bodies of water where they cannot use soaring-gliding flight. Seas and large lakes act as ecological barriers for most land birds since they do not offer birds the possibility to land or feed, and because weather conditions are likely to change suddenly.

For soaring-gliding birds the disproportionate increase in energy consumption adds to the threats inherent to flying over water surfaces [10].
The aim of this research was to investigate which factors affect the migration strategies of European raptors in relation to the ecological barrier represented by the Mediterranean Sea. Morphological, ecological, geographical and meteorological elements shape the paths of migrating raptors moving through or around this water barrier. In particular, four species are subjects of this research (Fig.1): the short-toed snake eagle (*Circaetus gallicus*), the honey buzzard (*Pernis apivorus*), the black kite (*Milvus migrans*) and the western marsh harrier (*Circus aeruginosus*). The study of bird migration can help us achieve a more solid basis that will allow us to protect and conserve these species and their habitats as well as increase our knowledge of the dynamics of evolution.

Fig. 1 The studied species: 1) short-toed snake eagle, 2) black kite, 3) western marsh harrier, 4) honey buzzard.

2 Study Area

2.1 The Central Mediterranean

The shortest sea crossing available to raptors to reach Europe from Africa and vice versa in this area is the Channel of Sicily, between the Tunisian Peninsula of Cap Bon and western Sicily (Fig. 2). Since even at its narrowest point the sea crossing still exceeds one hundred kilometres, broad-winged raptors are rarely observed migrating in this area; the most common species are honey buzzards, marsh harriers, black kites and Montagu's harriers (*Circus pyargus*). All these species are capable of undertaking long powered flights over the sea [11, 12,13,14]. In both spring and autumn, raptors carry out 'island hopping' migration, using the islands of Marettimo, Pantelleria, Malta (to name but the most important) as stop-over sites where they can roost and exploit thermal currents to limit the use of powered flight. The highest concentration of migrating raptors in the area is between Sicily and southern continental Italy, namely over the Strait of Messina and along the Calabrian Apennines. In spring in particular, tens of thousands of raptors concentrate on the first site where they can be seen on both sides of the Strait while in the autumn raptors migrate along the mountain chains of southern continental Italy where their migration can be observed thanks to the narrowness of the peninsula, just a few dozen kilometres wide.

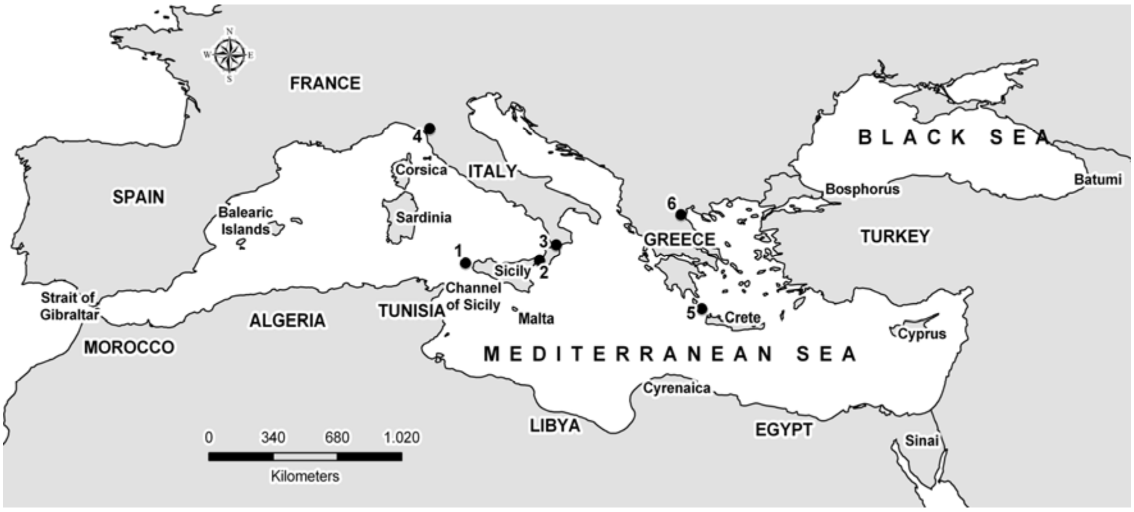

Fig. 2 The study area. The black dots indicate the fieldwork sites: 1) Marettimo island; 2) Strait of Messina; 3) Calabrian Apennines; 4) Apuan Alps; 5) Antikhitira island; 6) Mount Olympus.

2.2 The Eastern Mediterranean

At the southernmost point of the Balkans Peninsula, south of the Peloponnesus (Greece), are found some small islands as well as the huge island of Crete (Fig. 2). Crossing the Mediterranean in this area involves flying over the sea for about 300 km, which implies a long powered flight that only few species of raptors attempt. Unlike the central Mediterranean area where raptor migration has been studied since the late 1980s, information concerning flyways used by migrating raptors in the Eastern Mediterranean remains patchy. On the island of Antikythira (30 km northwest of Crete) the Hellenic Ornithological Society has an observatory with a ringing station. Its preliminary observations have led me and my colleagues to initiate fieldwork in Greece. The findings at the watchpoint on Mount Olympus were more complicated; indeed I went there on the basis of a mere hypothesis and some Google Earth images. Nonetheless the research has yielded good results, in particular thanks to observations of hundreds of eagles moving in a direction contrary to usual (northwards in autumn and southwards in spring).

3 Methods and their limits

"*The human eye is one of the best tools for studying migration*" [15]
This research present and discuss data collected almost by visual observation. For this reason it shall be considered as research made on the visible migration of raptors. Since raptors mostly fly during daylight and migrate at lower altitudes compared to other birds (i.e. waders), this method is useful [2,9]. In all cases, this method requires carrying out field observations from one or more watchpoints at the same time over the whole study period. At each watchpoint one or more observers, aided by binoculars and telescopes, scans the sky and the horizon to detect migrating raptors [16]. The recorded data will vary depending on the site. But this data has usually included the number of individuals, date and time, age and sex, as well as various information concerning their migratory behaviour (i.e. altitude, flight direction). I was careful not to take for granted the behaviour of raptors in the study sites and decided not necessarily to take a census of migrants [17,18]. Since it is recognised that weather conditions strongly

affect the migration of birds, I also investigated whether they influenced observations or had led to errors in data collection. Among the limitations posed by visual observations methods, it must be pointed out that individuals flying at over 7-800 meters could pass undetected; indeed this is not rare, especially on sunny days with strong thermal activity [9]. The migration front that can be covered from one single watchpoint usually does not exceed four to five kilometres. Moreover, direct observations do not make it possible to follow the movements of raptors beyond a few kilometres. In the last decades two further methods have become commonly used, namely radar and satellite telemetry. The former allows the collection of high quality data concerning flight altitude, speed and direction of migrants passing in the radar range [19,20]. With a satellite transmitter it is possible to follow a single individual for several years, mapping its movements in ways that were unthinkable a few years ago. In addition, a wide range of different data are also collected, such as flight altitude and speed throughout the journey as well as data on habitat use, home range size and many others [21, 22, 23]. The quality of transmitters has been improved over the years and now allows the collection of more accurate and more abundant data. In spite of all these technologies, visual observation remains a widespread and irreplaceable practice, allowing the collection of a huge sample of data that provides reliable information on the timing of migrations as well as numbers reflecting population trends [24, 25, 18]. Visual observations were also chosen because, in comparison with other methods, they have a lower impact on budgets. This was a significant factor given that this research had limited financial support and was largely self-funded. Finally, direct observations permit the implementation of communication activities involving a large number of people in monitoring activities, and constitute therefore a good approach for popularising knowledge of wildlife and evolutionary biology and, in the final instance, protecting migrating raptors [26].

Nonetheless, visual observation was not the only method used in the study. I also analyzed ring recoveries of western marsh harriers ringed during the breeding season in Europe and recovered during winter both in Europe and in Africa. In addition, I created a model to explain the distribution of short-toed snake eagles in Italy using published and unpublished data on their nest localization.

Finally, in order to provide hypotheses to explain different behaviours in raptors I used the software created by Professor Colin Pennycuick. This software allows the calculation of energy consumption rates in the two different types of flight, namely powered flapping flight and soaring-gliding flight. For this calculation, the body mass (Kg), wing span (m) and wing area (m^2) of a bird model are required. This software calculates an estimate of energy rates in Watt assuming an absence of wind. Additional details as well as theoretical support are provided in Pennycuinck [6]. This method was largely used in its previous versions as well [7, 4, 27].

4 Results and Discussion

4.1 The role of morphology and energy consumption rates

As mentioned above morphology plays a role of paramount importance in determining raptor flyways and behaviour. Among Accipitriformes, different species show different rates of energy consumption as well as different skills in the exploitation of thermal currents. This heterogeneity, due to species-specific and sex-specific differences in morphology, leads to different migration strategies. Just to cite two opposite cases, harriers (*Circus* spp.) largely use powered flapping flight [11] and migrate on a broad front over open sea, while lesser-spotted eagles (*Aquila pomarina*) concentrate at the Bosporus and Suez Straits to avoid having to fly over four different stretches of sea in the course of their migration: the Black Sea, the Marmara Sea, the Mediterranean Sea and the Gulf of Suez [28, 29]. Other species exist that exhibit an intermediate behaviour. In the case of short-toed snake eagles the consumption of energy during powered flapping flight is 8.7 times the energy used during soaring-gliding flight [30]. This result may explain why short-toed snake eagles breeding in central-southern Greece do not cross the Mediterranean sea, preferring to migrate across the Bosporus both in autumn and spring. Similarly short-toed snake eagles breeding in Italy use a circuitous flyway, crossing the Mediterranean at the Strait of Gibraltar. The role of morphology in relation to energy consumption could also explain differences in the migration of juvenile honey buzzards and western marsh harriers in the Eastern Mediterranean. The honey buzzards travel south-southwest during autumn migration and are strongly attracted by geographical features such as peninsulas and islands, in an attempt to reduce as much as possible their flight over sea. By contrast, western marsh harriers are less attracted by land masses, flying along approximately parallel flyways that appear to have a northeast-southwest orientation [31]. These differences are explained by the different rates of energy consumption during powered flapping flight which in juvenile honey buzzards is almost twice that of western marsh harriers. In this case weight is probably the element that leads to a higher energy consumption. Indeed a comparison of the aspect ratio shows that it is quite similar for both species (7.28 vs. 7.16) while the body mass is heavier in juvenile honey buzzards compared to western marsh harriers [32].

4.2 Geography

Since Accipitriformes tend to move mostly over land, the distribution of land masses clearly affects their migration strategies. We have seen before that populations of short-toed snake eagles breeding on peninsulas (Italy and southern Balkans) facing wide stretches of water make long detours to avoid crossing the sea. In relation to this species and geography, the results of the model explaining its distribution in Italy clearly shows that short-toed snake eagles are distributed mostly at higher latitudes, assuming similar ecological conditions, since their colonization process reflects their migratory route and vice versa. In the case of adult individuals, geography plays a role in the sense that the distribution of ecological barriers interacts with the ability of raptors to succeed in determining the routes passing through or avoiding barriers. Natural selection should favour individuals choosing what constitutes the best migration strategy in their specific case. This could mean choosing a conservative strategy to reduce mortality risks, as in the case of short-toed snake eagle, or minimising migration times as much as possible as in the case of western marsh harriers. Moreover since migration is age-dependent in several species, juveniles exhibit different flight strategies when compared with adults [33, 34, 12]. In the case of short-toed snake eagles, a fraction of juveniles migrates without following the adults and attempts to cross the Mediterranean. In doing so they are attracted by islands, like the islands of Marettimo and Antikythira where, in October, flocks of dozens of eagles reluctant to initiate the water-crossing can be observed [35, 36]. Similarly, on the same islands, dozens of other juvenile raptors are regularly observed passing through later in the season in comparison with adults.

4.3 Wintering ecology

In winter, unlike during the breeding season, raptors manifest an increased mobility which sometimes leads to a true nomadic behaviour [26]. For instance European black kites overwintering in the Sahel move daily and cover every winter a distance of 7000 km over their vast wintering areas [37]. Conversely, some species of raptors are far less nomadic during winter and exhibit considerable inter-year site fidelity, such as in the case of American kestrels (*Falco sparverius*) and ospreys (*Pandion haliaetus*) [26]. Many long-distance Palaearctic migrants spend the winter in Africa south of the Sahara. This is a vast area, extending over 20 million km² and comprising many different habitats from deserts to humid forests. Several species of European raptors overwinter in the belts of the Sahel and Sudan steppe habitats, while other species, such as the European honey buzzard, spend the winter in the wet forests of Western Africa [33, 38]. However not all species of migrating raptors overwinter in the tropics: many species spend the winter on the European side of the Mediterranean basin. In the case of common buzzards (*Buteo buteo*), only few individuals were observed crossing the Channel of Sicily, just as few individuals were observed wintering in Tunisia [39, 40]. The same behaviour has been reported for other species such as the red kite (*Milvus milvus*), showing that some species choose shorter distance migration [41]. In this case, the costs associated with the journey to Africa and overcoming the barriers that the Mediterranean Sea and the Sahara Desert represent, clearly exceed the benefits they could receive. By contrast, for a species with a highly specialized diet such as the short-toed snake eagle, spending the winter in Europe would not be possible. Nonetheless, some individuals of this species are regularly observed in winter in southern Sicily [42].

4.4 Flocking behaviour, orientation and information transmission

Flocking can be observed in several species of migrating birds, a phenomenon implying the existence of a social function for this behaviour [9, 38]. Among Accipitriformes, flocking behaviour varies in accordance with behavioural ecology and dependence on soaring-gliding flight. The black kite is a species that often breeds in colonies which, almost always, leave together at the end of the reproductive season. For this reason, their tendency to remain together during the autumn migration is particularly evident [43, 44, 45]. It is well-known that soaring raptors are more efficient at thermal localization when they travel in flocks rather than alone [9]. Anyone who has spent some time watching migrating raptors will have had the opportunity to observe individuals diverting their course in order to join a flock of soaring raptors. Moreover a flock of migrants is more likely to encounter random thermal currents than an individual on its own. This occurs because larger flocks sample wider areas [9]. Since this mechanism is more evident in species strictly using soaring gliding flight, it is not surprising that huge flocks are observed in some species but only small flocks in other species that also use powered flapping flight during migration. In Mexico, supersized flocks of hawks exceeding fifty thousand individuals are regularly observed [26]. I have personally observed flocks of hundreds of lesser-spotted eagles on the Bosporus (up to one thousand) and flocks of 2-3000 steppe buzzards in Batumi (Georgia). By contrast, flocks of western marsh harriers or Montagu's harriers rarely exceed a few dozens of individuals, such as in the Messina Strait where I observed flocks of hundreds of honey buzzards and very small flocks of harriers [46]. When raptors approach the point where water crossing begins, their tendency to remain in flocks become stronger. This is because raptors often hesitate before undertaking a crossing and the larger the flock, the greater the chance that an individual will begin crossing and that the others will follow [9]. This behaviour can easily be verified by comparing the migration of the same species in the same geographical area over land and over water. As in the case of migrating black kites passing through southern Italy in autumn, as they migrate over the Apennines they are usually observed moving in flocks of dozens of individuals while on two islands of the Sicilian Channel concentrations of up to one thousand kites are regularly reported [43, 44, 47].

In the species studied, if we consider adult (experienced) individuals, only the western marsh harrier follows (mostly) its innate axis of migration (NE-SW). In the other species studied, adults use flyways that only partly reflect their innate axis. Adult individuals display true navigation and orientation abilities, modifying their direction of migration and changing their migratory behaviour in relation to weather conditions and ecological barriers [33, 34]. Flocking behaviour allows the transmission of information between experienced and inexperienced individuals. In the short-toed snake eagles this is particularly evident since, as mentioned before, they make a long detour. The high degree of synchronism in the migration period of juveniles and adults belonging to the Greek population allows the formation of mixed-age flocks (Fig. 3).

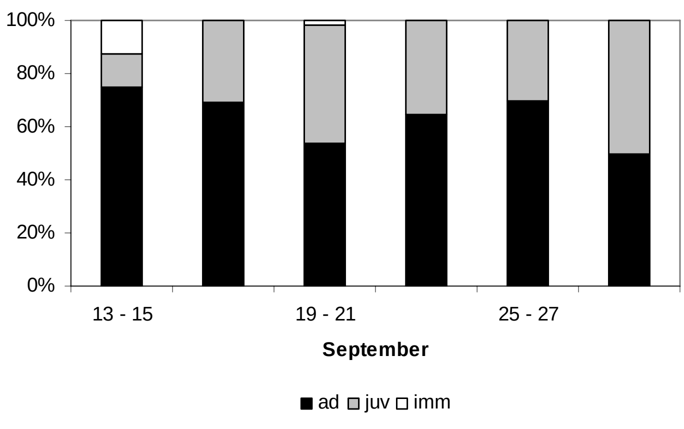

Fig. 3 Percentage of juvenile, adult and immature short-toed snake eagles observed migrating at Mount Olympus (Greece) between 13 and 30 September 2009.

The percentage of juveniles migrating together with adults is higher in observations made in Greece compared with the ones recorded in Italy. Similarly, observations in southern Greece have indicated a lower number of juvenile short-toed snake eagles migrating later than adults, while across the Channel of Sicily the number of young observed is larger. In addition, on the basis of data collected for a single year in Greece (far more data is available for Italy), I ventured the hypothesis that the different proportion of juveniles observed in Greece and in Italy might reflect the different length of the crossing between Europe and Africa; indeed the distance between Greece and Libya is more than twice that of Italy and Tunisia. This hypothesis is formulated on the assumption that the width of the water barrier acts as a strong selective force. Moreover, I suggest that a relationship exists between the size of the barrier and the tendency of juveniles to follow adults as a result of a higher mortality of short-toed snake eagles attempting to cross the Mediterranean between southern Greece and Libya rather than across the Channel of Sicily [30].

4.5 Migration and weather conditions

Weather conditions strongly affect bird migration; this is easily understandable. For instance a strong head wind makes a flight more difficult since birds move in a medium that is itself in motion, namely air. The direction and speed travel of a flying bird is the sum of the wind vector and the bird's own flight vector relative to the surrounding air [2]. This means that, to cover the same distance, a bird requires more energy in a strong headwind than when wind is absent [6]. Another easily understandable example is provided by heavy rain. Most birds are compelled to land during such weather conditions. However every case has its exceptions and I was surprised to observe hundreds of steppe buzzards (*Buteo buteo vulpinus*) migrating under heavy rainfall in Batumi (Georgia) in October 2011. Among the findings of this research I would like to underline that both adult honey buzzards and short-toed snake eagles are able to compensate the effects of crosswinds to avoid a drift effect and in both cases I recorded this behaviour when raptors migrate close to the coast [48]. This concurs with a recent study made by satellite tracking revealing that migrating raptors tend to compensate the effect of lateral winds close to a natural barrier, in all probability to avoid the risk of being blown off over the sea or desert [49]. A previous study investigating the effect of crosswinds on raptors of different ages during migration showed that juveniles are more likely to be drifted by winds while adults compensate the drift effect [21]. However, recent visual observations at some raptor migration watchsites seem to suggest that juveniles are able to compensate the drift effect when migrating close to landmarks or leading lines. For instance, counts made on the island of Antikythira did not show significant differences in numbers of juvenile honey buzzards recorded during lateral winds and other wind directions (headwinds and tailwinds) [32]. Moreover, when focusing on the effect of prevailing winds during peak passages at the site (headwinds and tailwinds), juveniles were observed mostly with headwinds, while on days with strong tailwind components very few raptors were recorded (Fig. 4). This result is likely to have been caused by the fact that juvenile honey buzzards let themselves be carried away during tailwind, travelling toward Crete and bypassing the island altogether. Tailwinds offer them in fact a less energetically costly flight over the sea.

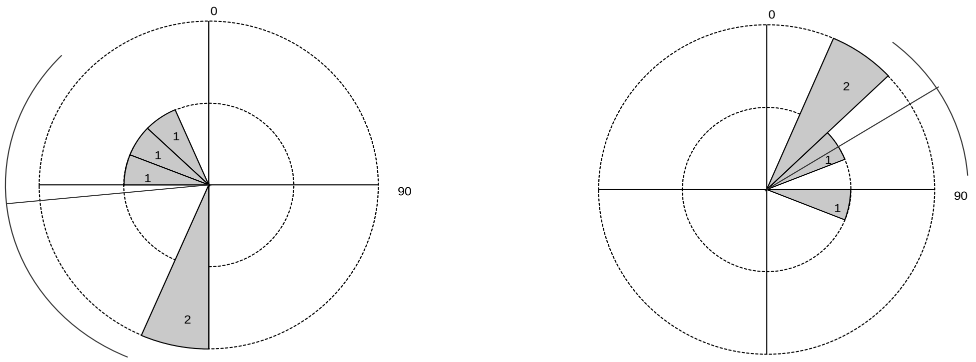

Fig. 4 Prevailing wind directions during peak days (left) and days with no passage (right) of juvenile honey buzzards over the island of Antikythira (autumn 2009).

At the Strait of Messina raptors face a water-crossing that is 3 km long at its narrowest point. Honey buzzards and harriers are the most common raptors at the site and they do not fear such water-crossing given their ability to fly longer distances over water. As a matter of fact, they mostly cross the Strait with strong headwinds (Fig. 5), i.e. when weather conditions are not suitable for a longer water crossing, while with following winds raptors could choose more direct routes by flying over the open sea on the Tyrrhenian sea [46].

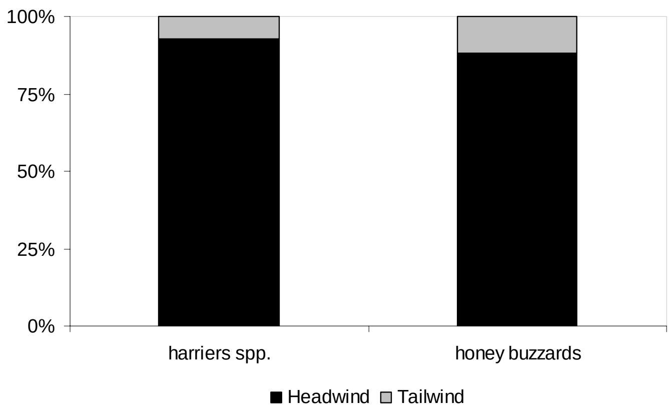

Fig. 5 Percentage of harriers and honey buzzards observed migrating across the Strait of Messina with tailwinds and headwinds (spring 2004).

4.6 Differential migration

Among migratory birds differential migration is extremely common. According to Cristol and coll. [50] differential migration occurs also when the distance covered is different for a portion of a population compared to the rest. In this research I analyze the differential migration of the western marsh harrier. It represents a good model species since it shows a wide distribution all over Europe and its various populations behave in different ways. Previous research carried out in the central Mediterranean area suggests that the imbalance between males and females observed wintering in many areas of Europe may be due to a stronger tendency in males to migrate over longer distances compared to females as a result of Bergmann's rule [51]. A recent study made in western France shows that many adult males are female-coloured [52]. However, although if this plumage pattern would be widespread in other populations of the species, this does not necessarily contrast with previous studies made in the Central Mediterranean area both during migration and winter [31]. These studies were made through visual observations and the sex of adults was defined by plumage observation. As a matter of fact, adult males outnumbered females in the sample of western marsh harriers crossing the Mediterranean sea en route to

Africa. Therefore the winter segregation hypothesis still appears reliable, at least for populations overwintering in and migrating through the central and eastern Mediterranean area. Undoubtedly further investigations would be required to establish whether or not visual sexing of western marsh harriers makes any sense. Moreover in the sample of 45 western marsh harriers ringed during the breeding season and recovered during winter, the mean migratory distance is higher for males than for females. These records seem to confirm the tendency of males to migrate further than females as it was hypothesized by visual observations research, although if this difference is not significant in the sample of ringed birds (Fig. 6).

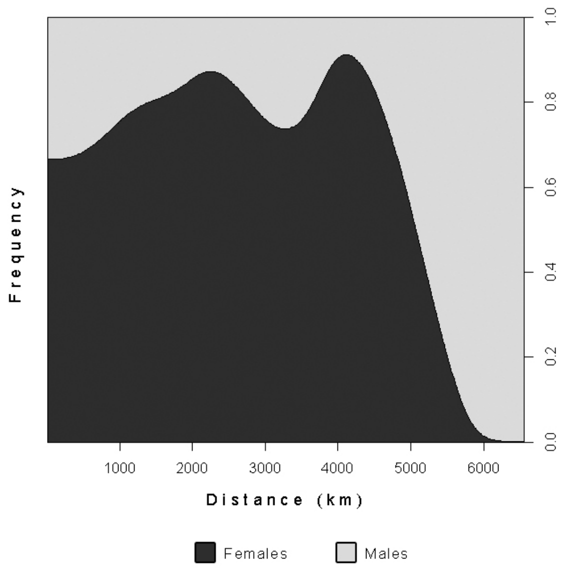

Fig. 6 Frequency of male and female western marsh harriers found in winter at different distances from their breeding grounds.

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