

Two different migration strategies in response to an ecological barrier: Western Marsh Harriers and juvenile European Honey Buzzards crossing the central-eastern Mediterranean in autumn

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During their migratory journey en route to Africa, European birds face a barrier: the Mediterranean Sea. Differently from the majority of birds, Accipitriformes use mostly soaring-gliding flight rather than powered flight. For this reason many species of raptors tend to avoid the water-crossing by following land masses. Different degrees in dependence on soaring flight are shown by different species of raptors. In this paper, we compare the migration of Western Marsh Harriers and juvenile European Honey Buzzards by the means of simultaneous observations at two sites: Mount Olympus (northern Greece) and the island of Antikythira (southern Greece). Differences in migration timing, water-crossing behaviour, sex and age classes (in the case of Western Marsh Harriers), show that these species use different migration strategies when crossing the Mediterranean region in autumn. Western Marsh Harriers migrate through parallel flyways, while juvenile European Honey Buzzards migrate island hopping being attracted by landmarks and following leading lines of land masses. A simulation process demonstrated marked differences in the energy consumption rates between the two species, highlighting that the powered flapping flight is particularly more disadvantageous for the European Honey Buzzard rather than for the Western Marsh Harrier. In this case, the morphological features of the studied species could explain the existence of two different migration strategies.

Key words: migration, Mediterranean Sea, *Circus aeruginosus*, *Pernis apivorus*, water-crossing behavior.

INTRODUCTION

Flight styles of birds have been evolved under strong selective forces, reflecting interactions between birds, biotic and abiotic factors. Among birds, migrants are expected to show morphological characters that minimize the cost of flight for efficient migration (Alerstam, 1990; Åkesson & Hedenström, 2007). In contrast to most of birds that mainly use powered flapping flight, large raptors use mostly soaring-gliding flight that allows them to minimize flight energetic cost and to maximize speed (Kerlinger, 1989; Spaar

& Bruderer, 1997a). Actually, the migration speed of large raptors that use thermal soaring and gliding is comparable to the highest speeds recorded for powered flapping flight in smaller birds (Åkesson & Hedenström, 2007).

Among migrating raptors, different skills in the exploitation of thermal currents have been reported, with large body species gliding faster and having higher abilities in soaring-gliding flight compared to species with smaller body mass (Spaar, 1997). The energy consumption during powered flight increases disproportionately with the increasing of body mass (Pennycuik, 2008). Soaring raptors tend to avoid the crossing of water surfaces where they cannot use ther-

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mal currents and where the mortality risks increase with the length of the crossing (Zu-Aretz & Leshem, 1983). Kerlinger (1989) suggested that the aspect ratio $((\text{Wing Span})^2 / (\text{Wing Area}))$ is of a critical importance in order to explain the water crossing tendency of migrating raptors. Aspect ratio is a dimensionless measure that is used to compare the shape of the wings of birds: in general species with longer and narrower wings are better adapted to use powered flapping flight (Kerlinger, 1989). When crossing water barriers, flight behaviour of raptors varies among species linked to morphologic traits such as the shape and area of their wings.

The most common raptor species crossing the Mediterranean Sea are the Western Marsh Harrier (*Circus aeruginosus*) and the European Honey Buzzard (*Pernis apivorus*; Finlayson, 1992; Rebassa, 1995; Zalles & Bildstein, 2000; Agostini *et al.*, 2002, 2003; Sammut & Bonavia, 2004; Panuccio *et al.*, 2005a; Kirwan *et al.*, 2008; Agostini & Panuccio, 2010). These two species show different water crossing patterns. Studies on crossing behaviour made by using satellite telemetry, radar, direct observations and band recovery data suggest that during autumn migration, Western Marsh Harriers undertake long water crossings heading toward SSW-SW by crossing the Mediterranean Sea mostly during the last 20 days of September (for a review see Agostini & Panuccio, 2010). During the same period, there is a temporal overlap with the migration of juvenile European Honey Buzzards; still, this species seems to be more reluctant than harriers in using powered flight (Kerlinger, 1989). As a result, juvenile European Honey Buzzards tend to follow leading lines and change their migratory direction following landmarks (i.e. coasts, promontories and islands). This behaviour was reported between Central Italy and the island of Malta where, differently from Western Marsh Harriers, hundreds of European Honey Buzzards, after starting the sea crossing at the Circeo Promontory, deviate eastward following the Italian peninsula and passing 2-3 days after over the island of Malta (Agostini *et al.*, 2002, 2004). Up to now, there is not sufficient information available on the migration of raptors along the Central-Eastern Mediterranean flyway (Lucia *et al.*, 2011). In previous studies, the aspect ratio was considered as a “key” factor to explain different migration strategies of species in order to overcome sea barriers (Kerlinger, 1989, Panuccio & Agostini, 2010). Still, previous comparative studies on the water-crossing tendency of

Western Marsh Harriers and European Honey Buzzards have been limited to a few selected sites.

We made simultaneous observations at two sites of Central-Eastern Mediterranean and we analyzed the differences in timing, age and sex classes as well as the variation of number of raptors observed in relation to wind direction during the water-crossing. The basic objective of this study was to investigate potential differences in water crossing tendency of Western Marsh Harriers and European Honey Buzzards along a route for which there is a lack of information. We made an attempt to test whether the two migratory patterns previously observed in central Mediterranean are also observed in the study area. We further provided a discussion on the alternative hypotheses which are likely to explain the observed migration strategies. In order to test the role of the morphologic differences between the two species, we used a computer simulation process that provides information on energy consumption rates of the two species during both powered flapping and soaring gliding flight.

MATERIALS AND METHODS

Study area and data collection

Observations were made simultaneously at the island of Antikythira (Southern Greece) and at Mount Olympus (Northern Greece) from 9th September to 1st October 2009, when a temporal overlap of the migration of Western Marsh Harriers and juvenile European Honey Buzzards occurs (Agostini *et al.*, 2002, 2003, 2004). A total of 207 hours of fieldwork was undertaken at each site. Observations were performed from 9:00 (solar time) until dusk, by using binoculars and telescopes.

Antikythira is a small island (20 km²; max. altitude 378 m), oriented in a NW-SE direction, located 32 km SE of the island of Kythira, 59 km S of the Peloponnesus Peninsula and 33 km NW of Crete which in turn is located approximately 280 km NE of the Cyrenaica Peninsula (Libya; Fig. 1). At this site, observations were made from a watchpoint (35° 51' 48" N; 23° 17' 50" E) located in the northern side of the island at an approximate elevation of 220 m above the sea level. This site is known to be an important bottle-neck for the autumn migration of raptors (Lucia *et al.*, 2011).

In northern Greece, a watchpoint (40° 01' 50" N; 22° 29' 40" E) was used on the eastern slope of the Olympus mountain (2917 m) located at an approximate elevation of 900 m above the sea level. The dis-

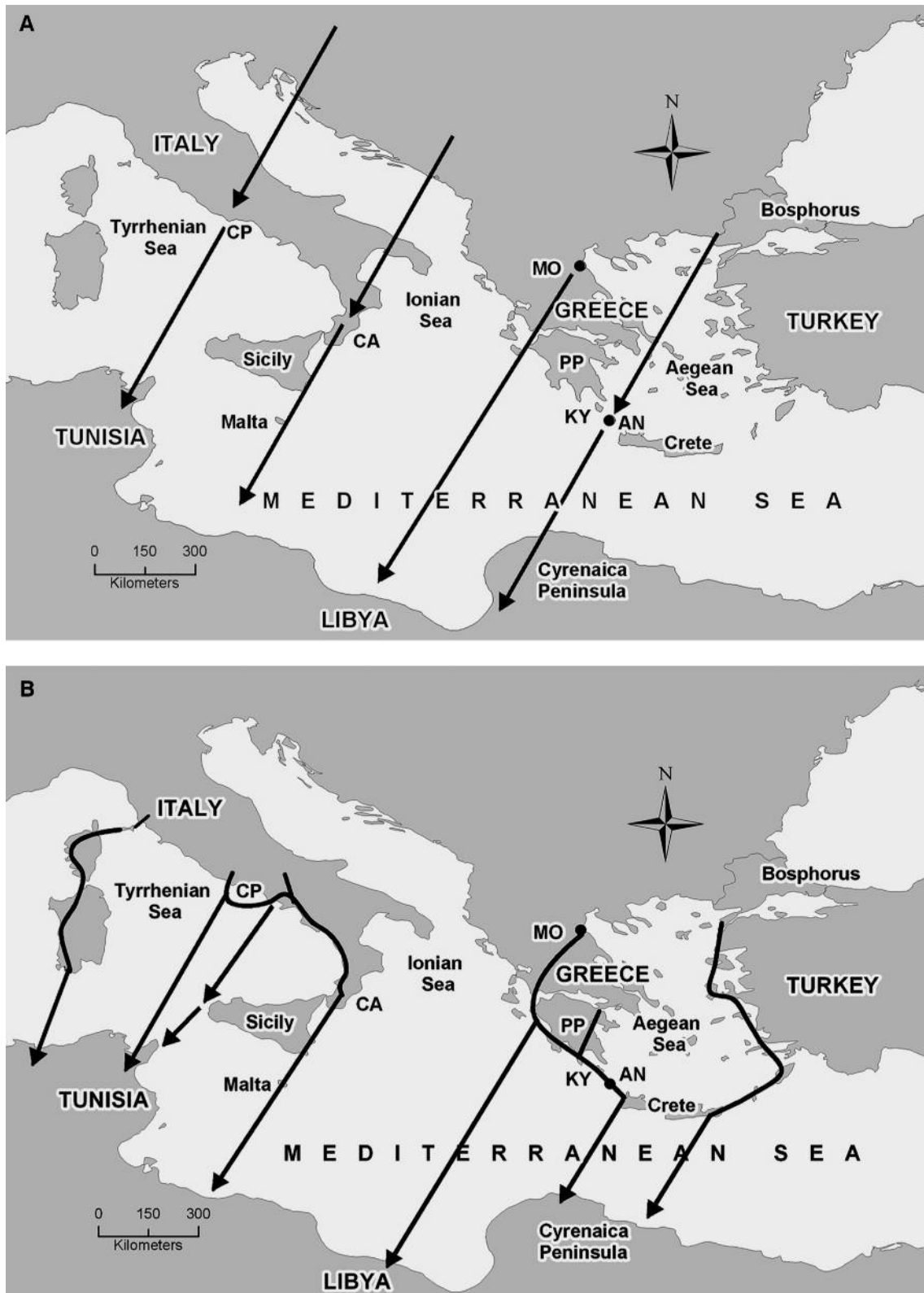


FIG. 1. The study area (MO: Mount Olympus; AN: Antikythira; KY: Kythira; PP: Peloponnesus peninsula; CP: Circeo promontory; CA: Calabrian Apennines) and the supposed flyways of Western Marsh Harriers (A) and juvenile European Honey Buzzards (B) in central and in eastern Mediterranean (Agostini *et al.*, 2003, 2004; Handrinos & Akriotis, 1997; this study).

tance between the watchpoint and the coast line of the Aegean Sea is 7.5 km. In this site migrating raptors are forced to fly in a narrow corridor between the mountain chain and the sea (Panuccio *et al.*, 2012). In case of low visibility (i.e. clouds) observations were made from a watchpoint located at a lower level.

Data analysis

We used a Pearson's correlation coefficient to investigate the temporal correlation between the migratory flows of both species, the Western Marsh Harrier and the European Honey Buzzard. Prior the analysis, a Shapiro-Wilk test was applied to test for normality assumptions. The test was performed after log-transforming the numbers of raptors observed at the two sites.

We divided the days of observations into 12 two-day periods. Raptors during migration show a cross-country speed from 31 to 43.9 km h⁻¹ (Spaar, 1997), for this reason it is deduced that they could cover the distance between Mount Olympus and the island of Antikythira in about two days. Further confirmations are provided by Western Marsh Harriers and European Honey Buzzards equipped with satellite transmitters that showed an average speed, respectively, of 204 and 176 km day⁻¹ during travelling days (Hake *et al.*, 2003; Strandberg *et al.*, 2008). For this reason data count from Mount Olympus (from 10 to 29 September) were compared with data collected two days later at Antikythira (from 12 September to 1 October).

To investigate the circadian pattern of migration, each observation day was divided into three time periods (solar time): 09:00-11:59 (morning), 12:00-14:59 (midday), and 15:00-18:00 (afternoon).

In the case of Western Marsh Harrier, at each site the total number of adult males, adult females and juveniles were derived by multiplying their proportions in the sample of identified individuals. In particular, to eliminate a bias resulting from the easier identification of the adult males, we estimated the proportion of females and juveniles by dividing unidentified individuals of the group female/juvenile between the two groups according to their proportions among the identified birds. Also in the case of European Honey Buzzards the overall number of adults and juveniles was estimated based on the proportions recorded in the sample of aged individuals (Kjellén, 1992; Forsman, 1999; Panuccio *et al.*, 2005b).

Considering that sea-crossings are crucial during migration, we investigated the potential effect of late-

ral winds on the intensity of the migratory flow of the two species at the island of Antikythira. The resulting path of a flying bird is largely influenced by wind direction. Winds, that are perpendicular to the direction in which the bird is moving, could cause a shift of the birds' path. This effect is called wind drift and many species of migrating birds are able to compensate it (Klaassen *et al.*, 2010b). We compared numbers of raptors observed in each time slot (morning, midday, afternoon) with different wind conditions (lateral winds *versus* other winds) by using non-parametric Mann-Whitney U-test. Before the analysis, an F test was run to compare variances among samples (Fowler & Cohen 1995). Wind data were obtained from the NCEP/NCAR reanalysis project (NOAA/ OAR/ ESRL PSD, Boulder, CO, USA, <http://www.esrl.noaa.gov/psd/>).

Cross tab statistics were applied in order to compare proportions of birds belonging to different age and sex classes. Similar analysis were used to compare the circadian variation of raptors observed.

Computer simulation

To the best of our knowledge there are not available data on the literature, that allowed to compare rates of energy consumption for Western Marsh Harriers and European Honey Buzzards, during different flight styles. To somehow fill this gap of information we used *Flight* software, a published performance simulation program that is based on flight mechanics (Pennycuick, 2008). *Flight* is based on classical aerodynamics and the power estimates (energy consumption) are absolute numbers, calculated from Newtonian mechanics.

In *Flight*, a bird is described by three numbers, its mass, its wing span and its wing area; for our analysis we used measurements derived by a series of published studies (Table 1; Clark, 1999; Bruderer & Boldt, 2001). The two most important environmental variables for flight calculations are the strength of gravity and the density of the air. The benchmark for air speed is the value calculated one metre above sea-level at the minimum power speed (V_{mp}), assuming no wind; with V_{mp} being the speed for minimum mechanical power in level flight. The mechanical power is the rate at which the flight muscles have to work, while the chemical power is the rate at which fuel energy has to be consumed. The value used to test energy consumption during powered flight is the minimum chemical power, reflecting the rate at which fuel

TABLE 1. Measurements of European Honey Buzzards and Western Marsh Harriers, the energy consumption during powered and gliding flight is expressed in Watt; (1) Clark, 1999; (2) Bruderer & Boldt, 2001; Pennycuik, 2008)

SPECIES	Body mass (Kg)	Wingspan (m)	Wing area (m ²)	Aspect ratio	Powered flight (W)	Gliding flight (W)
<i>Pernis apivorus</i>	0.79 (1)	1.3 (1)	0.236 (2)	7.16	30.6	4.32
<i>Circus aeruginosus</i>	0.54 (1)	1.28 (1)	0.225 (2)	7.28	17.4	3.11

energy is required in aerobic flight when flying level is at V_{mp} . The energy required for gliding flight is calculated as the chemical power in gliding, thus it represents the sum of chemical power for tonic muscles and basal metabolic rate. The unit (Watt) is the same for both mechanical and chemical power (Pennycuik, 2008). In previous studies that have been focused on the comparison between observed data and data derived by *Flight* program predictions were realistic (Pennycuik, 1996; Spedding & Pennycuik, 2001; Pennycuik & Battley, 2003).

RESULTS

During the study period a total of 268 and 187 Western Marsh Harriers were observed, respectively at Mount Olympus and at the island of Antikythira. Comparing the migratory flow we identified no significant correlation between the passage of Western Marsh Harriers at the two sites ($r = 0.008$, $p > 0.05$). Daily variation of migratory flow showed that at the island of Antikythira Western Marsh Harriers migrated mostly during the first half of the study period, while at Mount Olympus they were observed migrating during the whole study period (Fig. 2A).

Overall, it was possible to determine age and sex classes for 118 and 162 individuals at Mount Olympus and at the island of Antikythira, respectively. Comparing the age classes at the two sites (Table 2), the proportion of juveniles was significantly higher at Mount Olympus than at the island of Antikythira (contingency table: $\chi^2 = 23.8$, d.f. = 1, $p < 0.01$). Moreover, comparing the proportion of sex classes, adult

males migrated mostly through the island of Antikythira rather than at Mount Olympus (contingency table: $\chi^2 = 3.94$, d.f. = 1, $p < 0.05$).

The analysis of the hourly variation of migratory flow demonstrated an afternoon peak at the island of Antikythira ($\chi^2 = 7.74$, d.f. = 2, $p < 0.01$) while the opposite occurred at Mount Olympus where Western Marsh Harriers were observed mostly during morning and midday ($\chi^2 = 37.8$, d.f. = 2, $p < 0.01$). During lateral winds the number of Western Marsh Harriers observed migrating at the island of Antikythira was significantly lower than with other wind directions such as headwinds and tailwinds ($U = 1625$, $p < 0.05$).

A total of 177 migrating European Honey Buzzards were counted at Mount Olympus and 120 at the island of Antikythira. The passage of this species at the two sites was strictly related ($r = 0.637$, $p < 0.05$). In particular the migration showed a peak of movement on the 10th of September (Fig. 2B; $N = 42$; 23.7%) at Mount Olympus and at the 12th-13th of September ($N = 54$; 45%) at the island of Antikythira. Based on the observed aged birds ($N = 134$), the estimated numbers of juvenile European Honey Buzzards outnumbered adults both at Mount Olympus (154 versus 23; $\chi^2 = 74.3$, d.f. = 1, $p < 0.001$) and at the island of Antikythira (97 versus 23; $\chi^2 = 25.8$, d.f. = 1, $p < 0.001$).

The variation of the circadian migratory flow showed a clear midday peak at Mount Olympus ($\chi^2 = 35.5$, d.f. = 2, $p < 0.01$) while at the island of Antikythira the passage of European Honey Buzzards did not show an evident peak. Lateral winds did not influence numbers of European Honey Buzzards observed at the island of Antikythira ($U = 863$, $p > 0.05$).

TABLE 2. Estimated numbers of adults (males, females) and juveniles of Western Marsh Harriers at the two sites

	Adults (♂, ♀)	Juveniles	Total
Mount Olympus	125 (50, 75)	143	268
Antikythira	139 (80, 59)	48	187

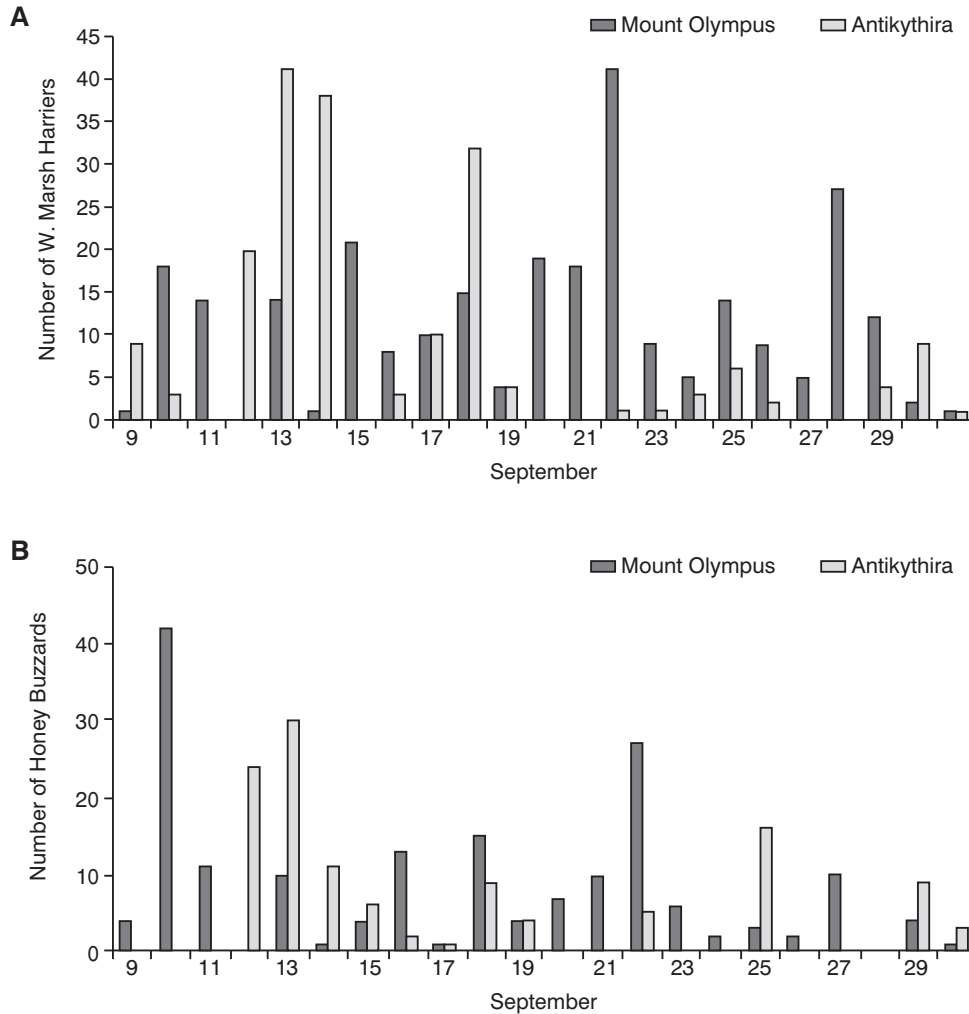


FIG. 2. Occurrence of Western Marsh Harriers (A) and European Honey Buzzards (B) at the two sites.

Despite the similar aspect ratio of Western Marsh Harrier and European Honey Buzzard (7.28 *versus* 7.16) the energy consumption during powered flight was higher for the latter species. The results provided by *Flight* program showed that during gliding flight the energy consumption was similar in both species while during powered flight it was much higher for European Honey Buzzards than for Western Marsh Harriers (Table 1). In particular, the use of powered flight for European Honey Buzzards required 7.1 times the energy used for gliding flight, while the difference was only 5.6 times for Western Marsh Harriers.

DISCUSSION

The results of our research suggested that Western Marsh Harriers and juvenile European Honey Buzzards use different flyways across the study area. In

particular, differences concerning both migration timing and water crossing behaviour, but also the observed differences in age and sex classes (in the case of Western Marsh Harriers), showed that the two species use different migration strategies when crossing the Mediterranean Sea.

Western Marsh Harrier

Our results suggest that during post-reproductive movements, Western Marsh Harrier tends to move along parallel NE-SW flyways using parallel migration paths over water and over land; a pattern that has also been observed in the Central Mediterranean region (Fig. 1A; Agostini *et al.*, 2001, 2003; Panuccio *et al.*, 2005a; Agostini & Panuccio, 2010). In particular, the different timing of migration at the two watchsites of the present study, indicate that migratory flow patterns are not correlated (Fig. 1A). This hypothesis is fur-

ther supported by considering the recorded difference in age and sex classes observed at the two sites.

The higher percentage of adult males observed at the island of Antikythira seems to confirm that adult males, in autumn, tend to migrate earlier and over longer distances than adult females. Some authors hypothesized (Panuccio *et al.*, 2005b) a latitudinal segregation of sexes in the entirely migratory population of this species, with adult females wintering mostly in the Mediterranean area and adult males wintering mostly in Africa south of Sahara according to Bergmann's rule which predicts that larger individuals (i.e. females in this case) are better adapted to survive in colder climates (Cristol *et al.*, 1999). In agreement, observations in Greece show that during winter, adult males are extremely rare (Handrinos & Akriontis, 1997). The higher number of juveniles observed to migrate in continental Greece rather than in Antikythira is likely to reflect the tendency of juvenile Western Marsh Harriers to follow leading lines of the mainland during their first migration, as has been observed in Sweden and in Southern Italy (Kjellén, 1992; Panuccio *et al.*, 2005a). The higher percentage of Western Marsh Harriers observed at the island of Antikythira during the afternoon is consistent with the hypothesis that they use the island like a stop-over site as shown also by observed roosting birds ($N=27$; 14.4%).

Our analysis demonstrated that lower numbers of Western Marsh Harriers were observed during lateral winds rather than with other wind directions at the island of Antikythira. Based on this finding we could suggest that during water crossing Western Marsh Harriers do not compensate the drift effect of lateral winds, perhaps because they are not attracted by this island being equipped to migrate over the Mediterranean Sea using powered flight (Spaar & Bruderer, 1997b; Agostini & Panuccio, 2010; Panuccio *et al.*, 2002). The Western Marsh Harrier shows high degree of flexibility in space during migration also by modulating their response to lateral winds at different places and times (Klaassen *et al.*, 2010a, b; Vardanis *et al.*, 2011).

European Honey Buzzard

The notable correspondence between the migration of European Honey Buzzards at Mount Olympus and at the island of Antikythira is not consistent with the hypothesis that juveniles of this species migrate along parallel routes as Western Marsh Harriers do. On the

contrary, the analysis of the migration at the two sites suggests that at least some of the individuals that migrate through continental Greece, once arrived in southern Peloponnesus follow the fingers of the peninsulas and cross the sea between the islands of Kythira, Antikythira and Crete en route to Libya (Fig. 1B). Moreover, the analysis of the migration in relation to wind direction is likely to suggest that juvenile European Honey Buzzards, differently from Western Marsh Harriers, compensate the drift effect of lateral winds during the sea crossing between Kythira and Antikythira. For this species, the ability to compensate wind drift is age-dependent (Thorup *et al.*, 2003). However, since the island of Antikythira is almost always visible from the island of Kythira, we suggest that juvenile European Honey Buzzards flying over the sea, can compensate the drift caused by crosswinds being attracted by the sight of Antikythira, where they can use thermal currents.

Studies made in the Central Mediterranean showed a similar behaviour of migrating juvenile European Honey Buzzards in autumn. A broad migration front involves many islands while hundreds of individuals migrating along the western coast of Central Italy deviate eastwards avoiding the crossing of the Tyrrhenian Sea and following the mainland of the Italian Peninsula. After that they cross the Mediterranean Sea between Southern Sicily and Libya passing over the island of Malta (Agostini *et al.*, 2002, 2004).

CONCLUSIONS

Our results confirmed that the two studied species use different migration strategies across the Mediterranean Sea, indicating that when possible, the European Honey Buzzard attempts to cover the longest landway of its autumn migration using gliding-soaring flight, while the Western Marsh Harrier is more likely to undertake long water crossings. These two different migratory behaviours could be a result of different skills in the exploitation of soaring-gliding flight and/or a result of different rates in energy consumption during powered flight as shown by the computer calculation (Spaar, 1997; Åkesson & Hedenström, 2007). Since their aspect ratio is similar, body mass that is quite different in the two species could be considered as the morphologic trait that drives such differences and could also explain why the powered flapping flight is particularly more disadvantageous for the European Honey Buzzard rather than for the Western Marsh Harrier.

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