ORIGINAL ARTICLE

Flight altitude of migrating European Honey Buzzards facing the open sea

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Abstract Migrating birds adjust their behaviour in order to reach their final destination safely and in a timely manner. In doing so, they fly at different altitudes, but unlike passerines, raptors do not explore all air levels searching for the best tailwind assistance. Soaring species migrate over the mainland using updrafts to optimize soaring-gliding flight and reaching higher altitudes during midday. However, there is little information on which variables affect their flight altitude when facing the open sea, where thermals are very weak and they are forced to use powered flapping flight for a long time. To fill this gap, we recorded the flight altitude of migrating European Honey Buzzards *Pernis apivorus* as they crossed the Tyrrhenian Sea (Central Mediterranean) and passed over a small island. During four migratory seasons, we recorded the altitudes of birds when they reached the NE coast of Ustica, a volcanic island between Sicily and central Italy, and analysed data in relation to several variables. The results showed that the tendency to continue migrating, flock size, and wind speed are the most important features in explaining height variation in migrating European Honey Buzzards facing the open sea.

Key words European Honey Buzzard, Flight altitude, Flocking, Migration, Sea crossing behaviour

During migration, birds adjust their behaviour in order to minimize the risk of mortality, optimize metabolic expenditure, match the phenology, cope with social factors, and avoid adverse weather conditions (Alerstam 1990; Newton 2008). As a result, the flight altitude of migrating birds greatly varies according to different factors, such as weather, geography, and avian morphology (Kerlinger 1989). Passerine migrants usually select their flight altitude according to wind conditions (Richardson 1976; Richardson 1990; Gauthreaux 1991; Bruderer & Liechti 1995; Liechti et al. 2000; Schmaljohann et al. 2009) and choose flight levels according to differences in tailwind assistance between neighbouring levels (Bruderer et al. 1995). However, migratory raptors do not adopt this strategy during water crossing and instead select for the first optimum wind they encounter when climbing, even when better winds occur at higher altitudes (Mateos-Rodríguez & Liechti 2012). Other studies that have measured the flight altitude of raptors inland (Kerlinger & Gauthreaux 1985) or close to the mainland before a sea crossing (Houghton 1971 in Kerlinger 1989; Meyer et al. 2000), have reported that raptors climbed very high using thermal currents. As previously reported, migrating raptors passing along an isthmus or along a coast, reduce the time spent soaring and, consequently, fly at lower altitude in order to decrease the probability of being drifted over water due to crosswinds (Kerlinger & Gauthreaux 1984; Panuccio et al. 2010). Larger species are more sensitive to rapid changes in wind than other species; for example, at the Bosphorus Strait (1–3 km wide) only eagles compensate for wind drift by reducing their flight altitude, while smaller species of raptors do not (Panuccio et al. 2017). In southern

Sweden, Common Buzzard *Buteo buteo* undertakes the crossing (20–45 km) between the Falsterbo peninsula and Denmark by flying at higher altitudes and being more wind selective than the smaller Eurasian Sparrowhawk *Accipiter nisus*. In particular Common Buzzards migrate mostly in weak winds and when trying to use thermal currents (Malmiga et al. 2014). But, what happens when raptors face the open sea? Few raptor species are capable of flying for hundreds of kilometres over water, because for heavier species, flapping flight is highly energetically demanding (Agostini et al. 2015). However, smaller raptors, such as falcons or small harriers, are able to fly over the sea because the difference in energy consumption between flapping and soaring-gliding is much smaller than in medium-sized and large raptors (Meyer et al. 2000). As a consequence, long detours are energetically unfavourable for small raptors, which usually do not concentrate at migratory bottlenecks. However, small falcons are not the only species of raptors able to fly over open seas. Some soaring species, such as those of the genus *Pernis*, also perform these flights. For this purpose, raptors select days with good tailwind assistance to reduce both energy and time spent over the sea (Higuchi et al. 2005; Yamaguchi et al. 2008; Agostini et al. 2016; Nourani et al. 2016, 2017; Panuccio et al. 2016). Although the migration patterns of these species have been well investigated, their behaviour, when selecting flight altitude, is unclear. In particular, it is unknown which variables affect the flight altitude of buzzards facing the open sea on migration. To answer these questions, we took measurements of flight altitudes of European Honey Buzzards, at an isolated and small island in the Mediterranean Sea where the passage of hundreds of raptors is reported each spring (Panuccio et al. 2004; Agostini et al. 2016).

Our initial predictions are: that raptors try to gain as much altitude as possible before leaving the island so as to reduce as much as possible the amount of time spent flapping over the sea (Meyer et al. 2000). In this scenario, higher values of solar radiation and of air pressure should allow raptors to gain higher flight altitudes (Shamoun-Baranes et al. 2003) while flock size might be positively related with flight altitude because of the more efficient use of thermal currents (Bildstein 2006). Conversely, flight altitude should be negatively influenced by higher wind speeds and by crosswinds as has already been observed during migration over land and straits (Panuccio et al. 2010, 2017).

MATERIALS AND METHODS

1) Fieldwork

We used a point on the northeastern coast of the island of Ustica (38°42′41″N, 13°11′52″E) in the Tyrrhenian Sea. The island is approximately 60 km north of Sicily, 230 km southwest of the continental coast of Italy, and 260 km northeast of the Cap Bon promontory in Tunisia (Fig. 1). The island covers an area of 8.6 km² and has a circumference of 12 km (3.5 km wide). The highest relief is 244 m. a.s.l. Its isolation makes it attractive to migrating raptors, because they can stop there while crossing the sea if necessary (Panuccio et al. 2004). The watch point used was located on the highest point of the Falconiera promontory (175 m. a.s.l.) which dominates the northeast coast of the island and from where it is possible to detect a significant proportion of raptors leaving the island towards the open sea. We distinguished between flocks that continued the sea crossing and flocks that paused during migration by observing their behaviour and direction using a telescope (Panuccio et al. 2002; Agostini et al. 2005). We took measurements of the flight altitude of migrating European Honey Buzzards that passed above our post using an optical range finder (Leica Rangemaster 1600B; accuracy±1 m as stated by Leica data) with a magnification factor of 7x and an elevation scale that was set to zero at the horizon (Rosén et al. 1999; Panuccio et al. 2017). Since the flock was the sample unit in this study, we took a single random measurement for each flock (or single individual) to avoid multiple measurements on different individuals of the same flock. Data were collected between 20th April and 20th May from 2009 to 2012.
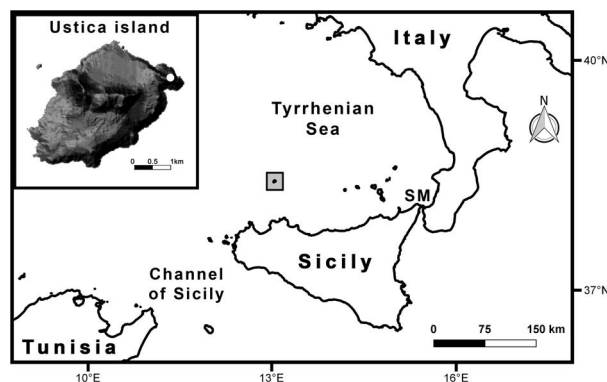

Fig. 1. The Study area. The white dot indicates the watch point. SM=Strait of Messina

2) Data analysis

In our analyses, we used the flight altitude (meters a.s.l.) of raptors as the dependent variable in a negative binomial GLM using the MASS package in R software (see Table 1 for details of explanatory variables). We treated the dependent variable as a discrete variable. Negative Binomial Regression has the same structure as a Poisson regression with an extra parameter to model over-dispersion (Venables & Ripley 2002). Flight altitude values were expressed as a whole number without decimal places. The Generalized Variance Inflation Factor (GVIF) was measured for the model with a threshold of two to test for collinearity among variables (Fox & Monette 1992; Zuur et al. 2010; Table 1).

Weather data was recorded every hour by the meteorological station of the Italian Air Force located on the highest point of the island of Ustica. We retained the phenological variables "Julian date" and "Julian date squared" (considering the non-linear effect of Julian date on bird migration) a *priori* in our model to test for the effect of phenology despite the fact that they are highly auto correlated with each other (Knudsen et al. 2007; Lindén 2011; Lindén & Mäntyniemi 2011). We ran a set of 19 models with several possible combinations of predictors. Then we compared the models using Akaike's Information Criterion (AICc, Akaike 1973), with the best model evaluated as the model with the lowest AICc value (Burnham & Anderson 2002). We used a cross-validation technique by randomly splitting our datasets into 'training' and 'test' sets, consisting of 70% and 30% of the data, respectively. Then, we used the training data to develop the models and evaluated the models using the test data and we calculated the Pearson correlation coefficient of observed versus predicted values to evaluate the consistency of model predictions (Guisan & Zimmermann 2000). Moreover, we compared the flight altitudes of raptors under different wind conditions using paired Mann-Witney U-tests (R core development team 2015).

RESULTS

We collected 201 records (flocks and single individuals) of flight altitudes of migrating European Honey Buzzards. Of them, 159 (79%) disappeared over the sea moving NE, while 42 (21%) stopped migrating and flew back inland. Mean flock size was 5.7 ± 0.7 SE individuals (max. 70), and mean flight altitude was 279.9 ± 4.9 SE metres above sea level (max. 523 m). The flight altitude of raptors setting out on the sea crossing was higher (340.5 ± 8.7 SE) than that of birds observed returning inland (240.5 ± 12.8 SE). Crosswinds were the commonest winds during our study period (43.8%). Average wind speeds were similar for all wind categories as well as for air pressure values. Moreover, solar radiation was lower when tailwinds were blowing. During hours without wind, values of both solar radiation and air pressure were higher (Table 2). Raptors flew at higher altitudes during hours without wind (Fig. 2a) than with wind, and this difference was significant (no wind vs. headwind: $U=503$, $P<0.05$; no wind vs. tailwind: $U=663.5$, $P<0.05$; no wind vs. crosswind: $U=1139$, $P<0.001$). However, the model selection highlights that water-crossing tendency, flock size, and wind speed (regardless of its direction) were the most important variables explaining the variation in flight altitude (Table 3). In particular, raptors flew at higher altitudes when undertaking the sea crossing (Fig. 2b), when flying in weak winds (Fig. 3a),

Table 1. Variables used in GLMs explaining the variation in the flight altitude of migrating European Honey Buzzards

Variable	Type	GVIF	Details
Time of day	Categorical	1.3	Morning: 0900–1159; Midday: 1200–1459; Afternoon: 1500–sunset
Air Pressure	Numerical	1.1	hPa (100 newtons)/ (1 meter^2)
Flock size	Numerical	1.1	as counted by observers
Julian date	Numerical	1129.1	calculated as the number of days from the beginning of the year
(Julian date)^2	Numerical	1123.7	squared Julian date
Water-crossing behaviour	categorical	1.1	(1) when raptors disappeared over sea; (0) when raptors returned inland
Solar radiance	Numerical	1.2	calculated with a Campbell–Stokes recorder (10 sunny, 0 cloudy)
Wind speed	Numerical	1.7	Km/h
Wind direction	Categorical	1.7	headwind (N-NE-E); crosswind (NW, SE); tailwind (S-SW-W); no wind.
Wind direction * w. speed	Interactions	/	between the last two variables

Table 2. Average values of wind speed, air pressure, solar radiation, flight altitude ($\pm$SE), and the number of records under different wind directions.

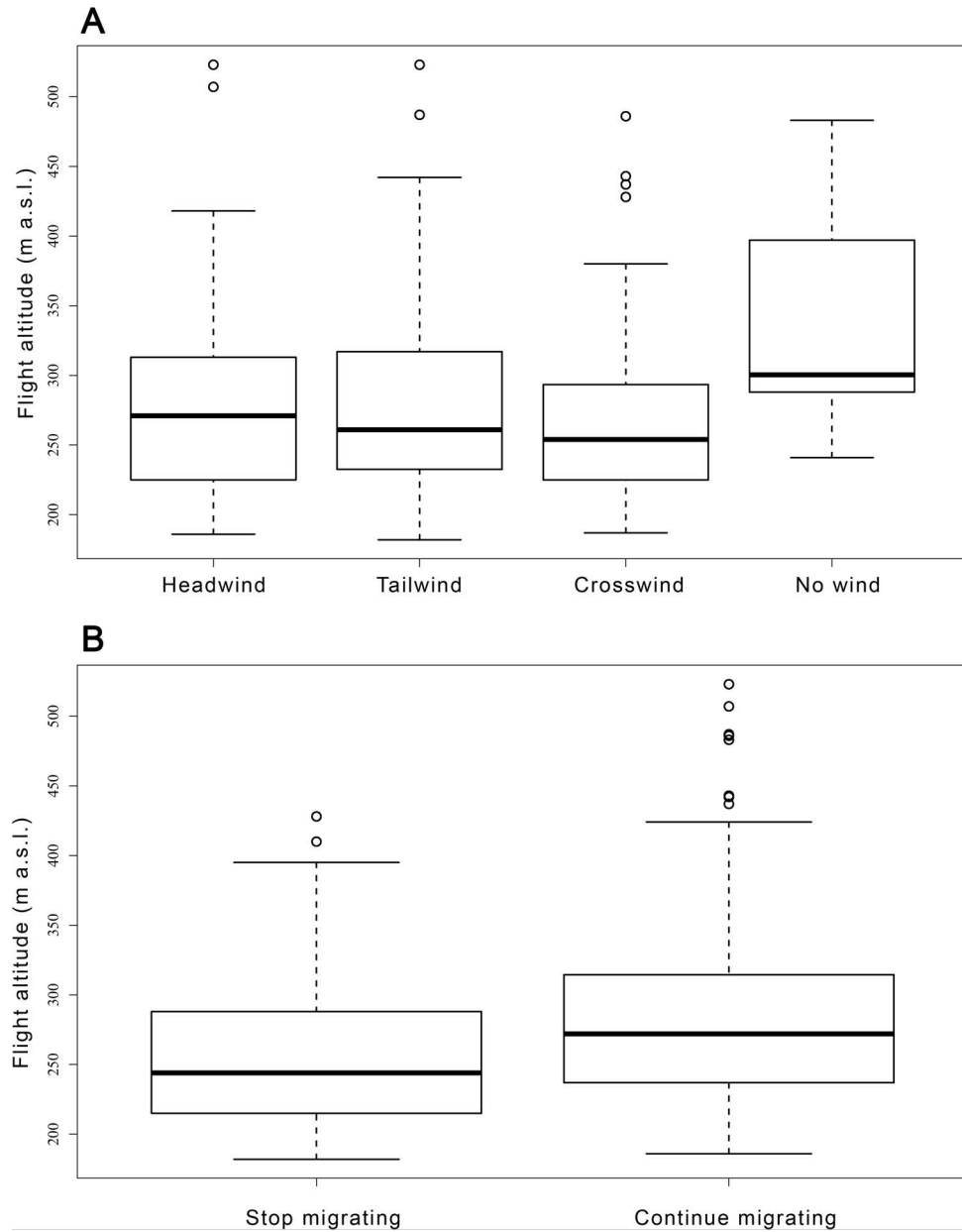| Wind direction	Wind speed (km/h)	Air Pressure (hPa)	Solar radiation	Flight altitude (m a.s.l.)$\pm$SE	Number of records
Headwind	7.6	979.2	7.9	282.3$\pm$11.8	42
Crosswind	9.1	986.2	8.4	267.6$\pm$6.5	88
Tailwind	9.1	985.8	5.6	280.7$\pm$9.9	55
No wind	0	994.7	8.8	338.3$\pm$18.5	16

Fig. 2. a) Flight altitude of European honey buzzards under different wind conditions. b) Flight altitude of raptors observed continuing the migration over open sea and individuals coming back from the sea.

Table 3. Generalized linear model analysis for flight altitude. Parameter estimates±standard errors are shown for models with ΔAICc<2 (in bold).

Model	AIC$_c$	ΔAIC$_c$
Water crossing tendency (continue migration: 0.3±0.1), wind speed (−0.04±0.008)	**2182.08**	**0**
Water crossing tendency (continue migration: 0.3±0.1), wind speed (−0.04±0.008), flock size (0.005±0.001)	**2182.94**	**0.86**
Water crossing tendency, flock size, wind speed, wind direction	2184.96	2.88
Water crossing tendency, flock size, wind speed*wind direction	2186.43	4.35
Water crossing tendency, flock size, wind speed*wind direction, Julian date	2188.08	6
Water crossing tendency, flock size, wind speed*wind direction, Julian date, Julian date squared	2189.93	7.85
Water crossing tendency, flock size, wind speed*wind direction, Julian date, Julian date squared, air pressure	2191.86	9.78
Water crossing tendency, flock size, wind speed*wind direction, Julian date, Julian date squared, air pressure, sun irradiation	2193.83	11.75
Water crossing tendency, flock size, wind speed*wind direction, Julian date, Julian date squared, air pressure, solar radiation, time of day	2197	14.92
Wind speed, flock size	2224.1	42
Wind speed, wind direction, flock size	2225.4	43.2
Wind speed	2226	43.9
Wind speed, wind direction, flock size, wind speed*wind direction	2226.24	44.16
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date	2227.4	45.32
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date, air pressure	2229.3	47.22
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date, air pressure	2229.3	47.2
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date, air pressure, Julian date squared	2231.3	49.2
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date, air pressure, Julian date squared, sun irradiation	2233.3	51.22
Wind speed, wind direction, flock size, wind speed*wind direction, Julian date, air pressure, Julian date squared, solar radiation, time of day	2235.9	53.82

and when migrating in larger flocks (Fig. 3b). Model evaluation using cross-validation showed that the model fitness was appropriate (Rho=0.5, P<0.001).

DISCUSSION

Our results partly confirm our initial expectations as we found that, as expected, those European Honey Buzzards continuing to migrate tend to fly at higher altitudes than those pausing on migration. Usually, raptors leaving a mainland for the sea tend to fly at higher altitudes (Kerlinger 1984; Meyer et al. 2000). Previous studies have given two different explanations for this, based either on the need for raptors to see the opposite coastline or because of topographical features, such as very high reliefs on the coast they are leaving. However, neither of the two explanations fit in our case; the first because the opposite shore is more than 200 km away and out of

sight, and the second because the island's relief is not very high. Meyer et al. (2000) estimated the energy consumption of European Honey Buzzards during flapping-gliding flight over water to be six times higher than energy consumption during soaring-gliding over land. Moreover, when using the algorithm created by Pennycuick (2008), the energy consumption during full flapping flight is 7.1 times higher than during gliding flight (Panuccio et al. 2013b). Therefore, it is likely that raptors that are strongly motivated to continue the sea crossing will aim to commence gliding at higher altitudes so as to save as much energy as possible before using powered flapping flight over the sea (Kerlinger 1989). Flocking behaviour is another variable explaining variation in flight altitude. Indeed, flock size is positively related to water-crossing tendency (Agostini et al. 1994; Agostini & Duchi 1994; Panuccio & Agostini 2010; Panuccio et al. 2017). Bildstein (2006) underlined
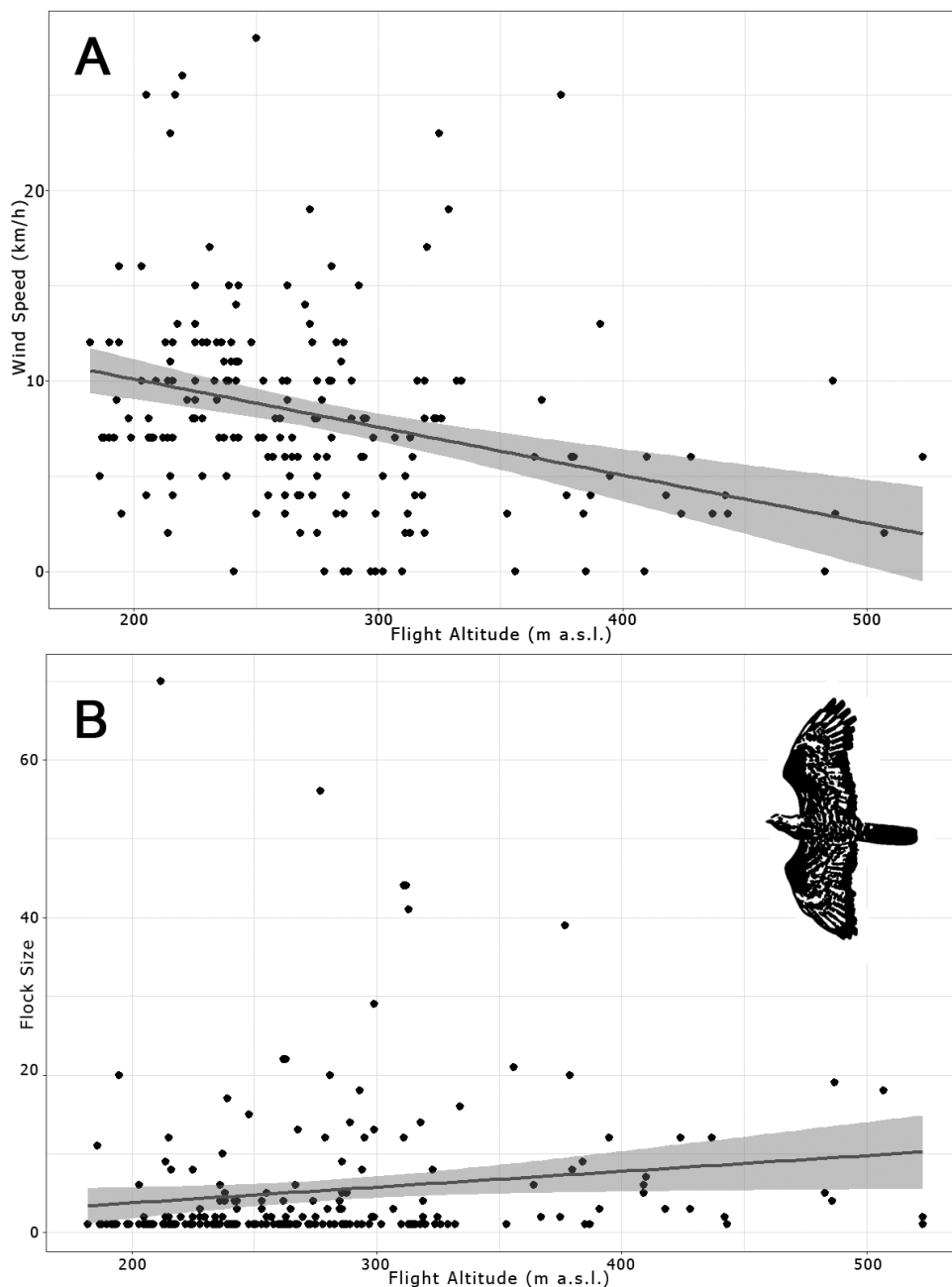
Fig. 3. Linear relationships between the flight altitude of European honey buzzards and a) wind speed, b) flock size.

that flocking is not only related to thermal localization (i.e. migrating raptors tend to join other individuals that are already soaring), but also that flight efficiency depends on flocking because the larger the flock the lower the flapping rate. However, we cannot exclude that, in our study case, flock size increases might be due to birds gathering at optimal migratory conditions. At the island of Ustica, larger flocks can

reach higher flight altitudes and are more likely to continue flight over the sea than smaller flocks and solitary migrants. The last variable entering the most parsimonious models was wind speed regardless of its direction. In particular, when winds are faster, flight altitudes are lower. This behaviour might be a response to avoid faster winds aloft (Alerstam 1979; Richardson 1976, 1990). Depending on the site, spe-

cies, and wind direction, there are threshold values of wind speed beyond which it becomes difficult for a bird to fly. When crosswinds are blowing, birds must compensate for wind drift by adjusting their heading, but when crosswinds are too strong, compensation becomes too difficult and energy demanding. In headwinds, the effort needed to move is energetically unfavourable and clearly increases with the wind speed; indeed, it is well known that migrating birds select tailwinds when possible to save both time and energy (Alerstam 1990; Richardson 1990; Liechti & Bruderer 1998; Weber & Hedenström 2000; Liechti 2006; Mellone et al. 2012; Vansteelant et al. 2014; Panuccio et al. 2016). However, there is also a limit in the case of tailwinds. In particular, in the case of soaring birds, research has shown that they do not fly as fast as they can, but glide in a risk-sensitive manner to avoid the risk of grounding or having to shift harshly from gliding to flapping flight (Horvitz et al. 2014). This behaviour might be more evident over the sea where raptors cannot land and splashing down into water means death (Agostini et al. 2016). When there is no wind blowing over the island (that is rare on islands), raptors probably spend more time soaring to reach higher altitudes. In contrast to most previous studies, at the island of Ustica we did not find that time of day or solar radiation affected the flight altitude of migrating European Honey Buzzards. Among soaring birds, flight altitude is generally positively related to the intensity and depth of thermals (Shamoun-Baranes et al. 2003), which are usually stronger at midday (Kerlinger & Gauthreaux 1985; Spaar 1995; Spaar & Bruderer 1996; Mellone et al. 2012; Panuccio et al. 2013a). The different behaviour shown by European Honey Buzzards in our study may have been caused by the different geography and topography of our study area. Ustica is a small island with low relief and limited ground extension. In this context, soaring opportunities might be of less importance than wind characteristics in influencing the behaviour of migratory raptors as already observed in other studies (Mellone et al. 2012; Vansteelant et al. 2014; Nourani et al. 2016; Panuccio et al. 2017).

In conclusion, with respect to our predictions, European Honey Buzzards migrating through the island of Ustica increase their flight altitude when undertaking the sea crossing probably in order to reduce the time spent flapping as much as possible; they also increase their flight altitude when migrating in large flocks thanks to the more efficient use of upward air currents, and they fly at lower altitude or tend to stop migrating when the wind speed increases so as to avoid stronger winds aloft (in the case of crosswinds) or to avoid falling into the sea (in the case of tailwinds). Taken together, these findings confirm the high plasticity of European Honey Buzzard behaviour, showing that the species may modulate its flight behaviour according to different weather, geographical and topographical conditions encountered en route and in relation to ecological barriers such as the Mediterranean Sea. Further studies may advance our understanding of the migratory behaviour of this species during sea crossing by using radar equipment and/or high definition GPS.

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