

Differential flight strategies of Western Marsh Harrier *Circus aeruginosus* in relation to sex and age class during spring migration in the Central Mediterranean

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Abstract. Several bird species show differential migration in relation to age and/or sex classes, often associated with morphological and behavioural differences. The Western Marsh Harrier *Circus aeruginosus* is a partial migrant, showing a strong sexual dimorphism in size. This species migrates on a broad front, undertaking long water crossings through the Mediterranean Sea. In this study we carried out a two-year survey on the pre-breeding migration of this species at three sites located in the Central Mediterranean region: the islands of Ustica and Panarea (Tyrrhenian Sea) and the Strait of Messina (Peloritani Mountains). The aim of this study was to analyse the flight strategies of this broad front migrant in relation to wind patterns, such as in relation to different sex and age classes. Our results revealed differential flight behaviours among harriers belonging to different sex classes, with adult females less attracted to islands than adult males during a sea crossing, and adult males reaching higher altitude early in the season along a mountain chain. It is suggested that adult males, thanks to their smaller size, use to a larger extent soaring flight by exploiting even weak thermals en route. Unlike the Tyrrhenian islands, few immatures were seen passing along the Peloritani Mountains, probably because they fly at lower altitudes over mainland, passing over areas where they can eventually find prey and/or rest at stop-over site en route. In conclusion, our study shows that the location of the observation post can affect the result concerning migration survey of both sex and age classes in this species, leading to evident bias.

Key words: *Circus aeruginosus*, differential migration, sex and age classes, water crossing, wind, Mediterranean

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INTRODUCTION

Several bird species show age and/or sex dependent migration strategies which can differ in terms of speed, timing and route choice. Such differential migrations are often associated with morphological and behavioural differences (e.g. body size, dominance and breeding roles; Newton 2008). In spring, although in some species (e.g. in some waterfowl) adult males and females arrive together in the breeding areas, in most cases (e.g. in passerines) adult males arrive first to compete for territories while adult females and immatures arrive later (Briedis et al. 2019). This is the case of

raptor species in which a sex/age dependent timing of migration has been recorded to date (e.g. Eurasian Kestrel *Falco tinnunculus*, Eurasian Sparrowhawk *Accipiter nisus*, Northern Harrier *Circus hudsonius*; or a review see Newton 2008).

The Western Marsh Harrier *Circus aeruginosus* (thereafter WMH) is a partial migratory raptor, since its populations breeding in Northern and Eastern Europe are total migrants and winter in the Mediterranean region and sub-Saharan Africa (Ferguson-Lees & Christie 2001). As in other harriers, polygyny, nearly always bigamy, has been widely reported for this species, being more prevalent in certain regions and strictly related to

the abundance of food (Clarke 1995, Simmons 2000). As a result, both adult males and females are expected to reach their breeding grounds as soon as possible, males to get better territories, females to be the primary ones, since nestling mortality increases in secondary nests (Altenburg et al. 1982). The WMH shows a strong sexual dimorphism in plumage (among adults) and size (both in adults and juveniles) since, as occurs in raptors, the female is the larger sex being about 25% heavier than male (male: 0.40–0.73 kg; female: 0.54–0.96 kg; Ferguson-Lees & Christie 2001), the latter looking surprisingly slim and slender (Forsman 2016). Thanks to its relatively small body mass and morphology (relatively long wings), both allowing to reduce the energetic cost of flapping flight (Agostini et al. 2015), this species migrates on a broad front, flying also when thermal currents are weak or not available (Kerlinger 1989, Spaar & Bruderer 1997, Agostini 2021). In so doing, they spend more time flying during the day than typical soarers, and undertake the crossings of wide water bodies migrating on a broad front. For this reason, seasonal counts exceeding 1,000 individuals are recorded in few sites at traditional bottlenecks (Agostini 2021). However, studies made by radar in Israel and Italy, clearly showed that migrating WMHs are able to adopt a mixed flight strategy, similar to that of typical soarers when migrating over mainland, especially where and when updrafts current are available. In particular, they react to different thermal conditions by adjusting their gliding airspeed to the actual climbing rate in thermal circling. As a result, cross-country speed over land is related to climbing rate, and maximized in soaring-gliding flight (Spaar & Bruderer 1997). Moreover, they fly nearer to a mountain ridge aligned along their axis of migration, during strong tailwinds, perhaps since they are efficient in exploiting their support using flapping flight even during inter-thermal gliding (Chiatante et al. 2023).

Studies made by satellite telemetry on adult WMHs belonging to the populations breeding in Northern Europe, revealed that birds spend more time and energy flying in spring than in autumn, especially in unfavourable winds (e.g. in the Sahara Desert). This migration behaviour is in agreement with the time minimization strategy (see above), adopted in this period by reproductive individuals to reach as soon as possible breeding grounds (Mellone et al. 2012, Nilsson et al. 2013). In addition, among tracked birds, adult females began migrating later but reached their

breeding grounds earlier than adult males, showing a faster migration speed (193 vs 139 km/day; Strandberg et al. 2008). Although this difference appears evident, it proved to be non-significant, probably because of the small sample size. In a recent study, Sergio et al. (2014) showed that in the Black Kite *Milvus migrans* early departure seems to be the key to occupy the best breeding territories, and late departing individuals could not reach earlier ones even when showing significantly higher travel speeds. However, it could not be the case of WMHs belonging to different sex classes. In this study we hypothesize different migration strategies adopted by adult female and male WMHs in relation to wind and topography thanks to their different size. To test this hypothesis, a two-year survey on the spring migration of the WMH through the Central Mediterranean was made, carrying out simultaneous observations at four watchsites located over two small islands and along a mountain chain. In addition, data concerning age classes were recorded to analyze migration strategies of immature and adult birds.

METHODS

Study area and data collection

Observations, aided by binoculars and telescopes, were made between 09:00 and 19:00 (local time) from 11 March to 20 April 2014–2015. This period coincides with the peak of the spring migration of WMHs in the Mediterranean basin (Agostini 2021). Ustica is a small volcanic island (8.5 km²) about 60 km N of western Sicily, 270 km NE of the Cap Bon Promontory (Tunisia) and 230 km W of the Italian Peninsula. Like Ustica, Panarea is a volcanic island (3.5 km²), located approximately 65 km NW from the Strait of Messina. At each site, the monitoring was made using the observation posts of previous surveys (see Agostini et al. 2021). In particular, the two observation posts used at the Strait of Messina, along the ridge of the Peloritani Mountains, were located at different altitudes at Dinnammare (38.159°N; 15.465°E; 1,115 m a.s.l.) and Mount Ciccica (38.240°N; 15.537°E; 550 m a.s.l.; Fig. 1). In addition to the sexing and ageing WMHs, observers collected data concerning the flock size and the time of passage.

Migration in relation to age and sex classes

Observers focused on the migration of adult males, adult females, and immatures (second calendar year birds) based on the birds' plumage attributes

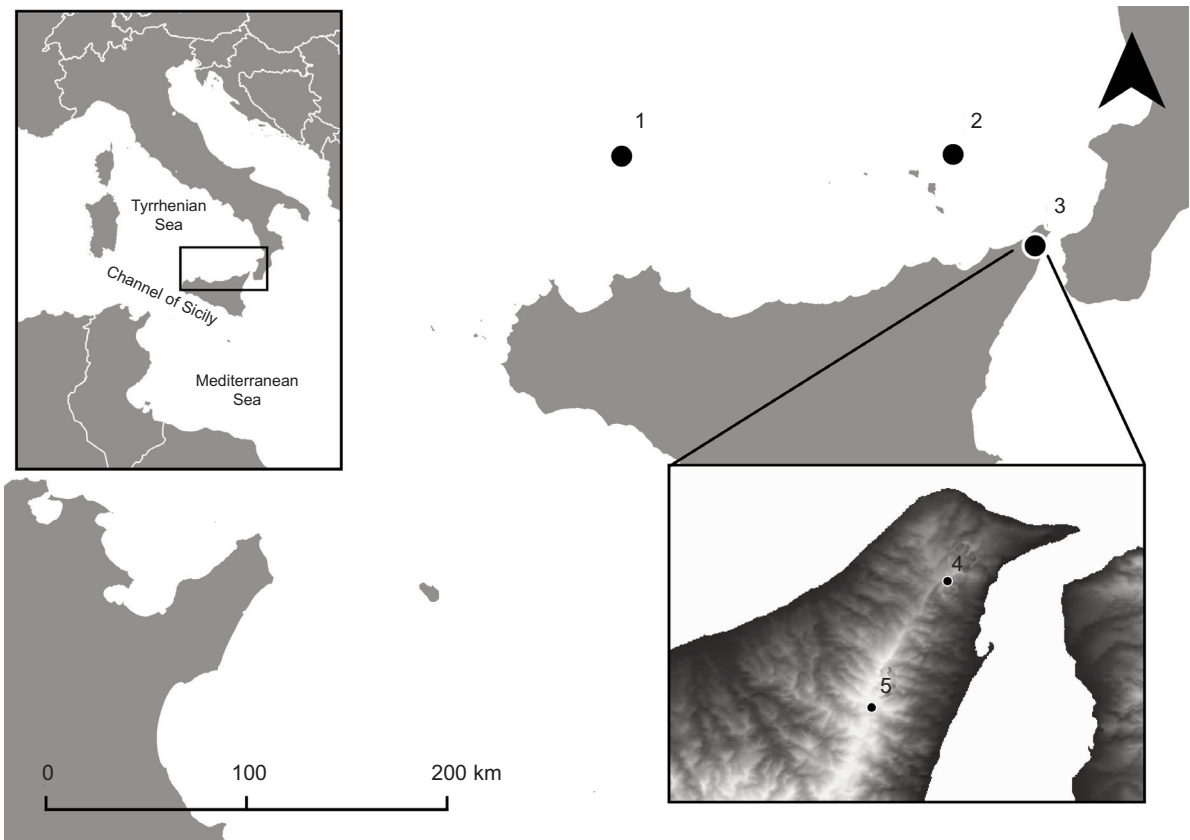


Fig. 1. The study area in the Central Mediterranean. The sites are Ustica (1), Panarea (2) and Peloritani Mountains (3; Strait of Messina). In the last site, observation posts are Mount Ciccio (4) and Dinnammare (5).

(Forsman 2016). To limit a possible bias resulting from an easier identification of adult males, the numbers of adult females and immatures were derived following the method used by Kjellén (1992) at Falsterbo. In particular, a proportion of WMHs was labelled “female/immature” meaning that they were either adult females or immatures. Then, each day the group “female/immature” was divided between adult females and immatures according to their proportions among identified individuals (see Agostini et al. 2021). For completeness, we calculated the proportion of observed and estimated females and immatures, as well as their percent difference. Data concerning the plumage of birds recorded over the two islands were pooled and reported as “Tyrrhenian islands”.

Wind data

At a regional scale, we analysed wind data in the period 1991–2020 obtained from the ERA5 reanalysis product (Hersbach et al. 2020), available in the Copernicus Climate Change Service (C3S) Climate Data Store (CDS), which provides a

reconstruction of historical atmospheric conditions at 0.25° resolution. Instantaneous hourly wind data at 100 m a.s.l. were retrieved, since most migrating raptors are detected below this altitude when flying over the open water (Kerlinger 1989) and not at the optimal flight altitude with respect to tail wind assistance (Mateos-Rodríguez & Liechti 2012). All wind statistics were computed between 07:00 GMT and 17:00 GMT.

At a local scale, we considered both horizontal and vertical winds on the same days on which observations were carried out, whose data were obtained by Movebank (www.movebank.org), a free online database of animal tracking and related environmental data, which were provided by the most relevant gridded global datasets (Dodge et al. 2013, Wikelski & Kays 2018). Thereby, for horizontal winds we used east-west (U) and north-south (V) components of the wind (provided by the Movebank ECMWF ERA-Interim weather datasets) from which we calculated direction (in degrees) and speed (in m/s). As regards vertical winds, we extracted data concerning the strength

of both thermal and orographic uplift (deflection updrafts). Both these measures were derived from the Movebank ECMWF ERA-Interim weather data; in addition, the orographic uplift was calculated with elevation from the ASTER Global Digital Elevation Model (Wikelski & Kays 2018). Movebank wind data were extracted at an altitude of 300 m a.s.l, the mean altitude of Western Marsh Harriers recorded by radar when migrating over land (Spaar & Bruderer 1997, Agostini et al. 2017).

Statistical analysis

As regards migration in relation to age and sex classes, we compared the number of adult males recorded and the number of adult females estimated (see above) by using a χ^2 test for each site (Tyrrhenian islands, Dinnammare and Mount Ciccica in the Peloritani Mountains), and the proportion of estimated immatures between sites through a contingency table. Furthermore, to understand the wind pattern at each observation post, we compared wind data between them with the χ^2 test and the non-parametric Kruskal-Wallis rank test. Then, we investigated the migration in relation to wind conditions through regression analysis. Particularly, we computed two Generalized Linear Models (GLMs) with negative binomial (Lindén & Mäntyniemi 2011) and gamma error distribution (McCullagh & Nelder 1989), for the daily counts and for the flock size respectively. As daily counts we used only days with at least one bird observed, excluding days with no observations. In addition, since the flock size is not normally distributed, even after a log-transformation (Kolmogorov-Smirnov test, $D = 0.308$, $p < 0.001$), we defined the Gamma as the best distribution by comparing the AIC (Akaike Information Criterion; Akaike 1973) of univariate distributions fitted to our data (Appendix 1). For both these regressions, we used as covariates the observation post (categorical, 4 levels), the year (categorical, 2 levels), the interaction observation post $\times$ year, the Julian date, the east-west (U) component of the wind (m/s), the north-south (V) component of the wind (m/s), the wind speed (m/s), the thermal uplift (m/s) and the orographic uplift (m/s). For the Julian date, the thermal uplift, the east-west (U) component of the wind (only for the daily count), and the north-south (V) component of the wind we investigated their quadratic effect (i.e., $y \sim x + x^2$) because a preliminary graphical analysis showed a probable non-linear effect of these variables.

To select the most important variables, first, sets of a priori models were built using all the combinations of the covariates measured. Then, for each model, the Akaike Information Criterion (AIC) was calculated and the best models with the lowest AIC were selected (Burnham & Anderson 2002). Specifically, we considered as the best, models included within the '95% confidence set' based on cumulative Akaike weights (Burnham & Anderson 2002). These models were averaged (through the 'subset' method) and the importance of each variable in the set *sw* was calculated as the sum of Akaike weights of models (Burnham & Anderson 2002). We calculated the Variance Inflation Factor (VIF) with a threshold of 3 to test the collinearity of variables (Fox & Monette 1992, Zuur et al. 2010). The normality of the model residuals was tested both graphically and by the Kolmogorov-Smirnov test (Legendre & Legendre 1998). The goodness-of-fit of the model obtained was assessed by the Pearson's χ^2 test (Legendre & Legendre 1998, Agresti 2007) and by correlating expected and observed values with Pearson's correlation test. Considering the different units of measurements used in the analysis, the independent variables were standardized by normalization; that is, each variable had a mean of zero and a standard deviation of one (Quinn & Keough 2002). Statistical analyses were computed with R software version 4.1.1 (R Core Team 2021) and the packages *MuMIn* (Bartoń 2018) and *car* (Fox & Weisberg 2011).

RESULTS

Migration counts

During the fieldwork, we had 143 and 123 days with at least one WMH observed, in 2014 and 2015 respectively. In general, more WMHs passed over the Peloritani Mountains (Strait of Messina) than over Tyrrhenian islands, particularly over Mount Ciccica (Table 1, Fig. 2). The flock size was quite similar between sites, ranging on average from 2.2 to 3.0 WMHs/flock, with a maximum of 97 birds in a single flock observed over Mount Ciccica (Table 1).

Migration in relation to sex and age classes

Over the Tyrrhenian islands, 2143 WMHs were aged/sexed or at least labelled as "female/immature" (adult males = 922; adult females = 313; immatures = 590; female/immature = 318) during the two-year study. In this sample, the passage of

Table 1. Descriptive statistics of daily counts and flock size of Western Marsh Harriers passed during the spring migration at four observation posts in Central Mediterranean Sea in 2014–2015. WMH_{tot} — total number of WMHs observed in 2014 and 2015, SD — Standard deviation, Max — maximum value, N — sample size.

Site	WMH_{tot}		Mean $\pm$ SD	Daily count		Flock size		
	2014	2015		Max	N	Mean $\pm$ SD	Max	N
Ustica	653	990	22.0 $\pm$ 31.1	214	80	2.2 $\pm$ 2.5	28	719
Panarea	624	499	17.9 $\pm$ 30.2	180	64	2.4 $\pm$ 3.1	32	477
M. Ciccica	2544	2188	65.7 $\pm$ 153.8	1207	72	3.0 $\pm$ 5.3	97	1564
Dinnammare	1870	1005	50.4 $\pm$ 103.5	747	57	2.5 $\pm$ 3.1	31	1134

438 adult females and 783 immatures was estimated; the proportions of female and immature (0.35 and 0.65 respectively) identified in the field were very similar to those of estimates (0.36 and 0.64 respectively), with a difference of 1.5–2.9% between them. At these sites, both adult males ($\chi^2 = 173.27$, $df = 1$, $p < 0.001$) and immatures ($\chi^2 = 97.89$, $df = 1$, $p < 0.001$) outnumbered adult females (Fig. 3). Finally, adult males migrated slightly earlier (Median dates: adult males = 30 March; adult females = 1 April; immatures = 2 April; Fig. 4).

At Dinnammare, it was possible to observe the plumage of 2565 birds (adult males = 1139; adult females = 666; immatures = 181; female/immature = 579) estimating the passage of 1135 adult females and 291 immatures; also in this case, the proportions of female and immature (0.79 and 0.21 respectively) identified in the field were very similar to those of estimates (0.80 and 0.20 respectively), with a difference of 1.3–4.8% between them. At Mount Ciccica, in a sample of 3437 birds (adult males = 1463; adult females = 662; immature = 103; female/immature = 1209), a total of 1727 adult females and 245 immatures were

estimated; the proportions of females and immatures (0.87 and 0.13 respectively) identified in the field were very similar to those of estimates (0.88 and 0.12 respectively), with a difference of 1.1–7.7% between them. Therefore, at Mount Ciccica adult females outnumbered adult males ($\chi^2 = 21.99$, $df = 1$, $p < 0.001$) while at Dinnammare their numbers were almost the same. In addition, when comparing the estimations made along the Peloritani Mountains (Strait of Messina) with those made over the Tyrrhenian islands, a considerably higher proportion of adult females was reported at both the observation posts located along this mountain chain, while the proportion of immatures dramatically decreased (Contingency tables; Dinnammare/Tyrrhenian islands: $\chi^2 = 523.5$, $df = 2$, $p < 0.001$; M. Ciccica/Tyrrhenian islands: $\chi^2 = 921.9$, $df = 2$, $p < 0.001$; Fig. 3). Interestingly, at Dinnammare the median date of the passage of adult males was recorded one week earlier than that of adult females (adult males = 22 March;

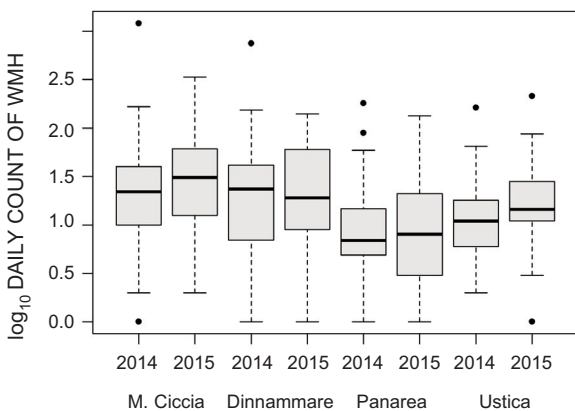


Fig. 2. Daily number of Western Marsh Harriers migrating in spring at three sites in Central Mediterranean Sea in 2014–2015. Data are shown in $\log_{10}$ scale.

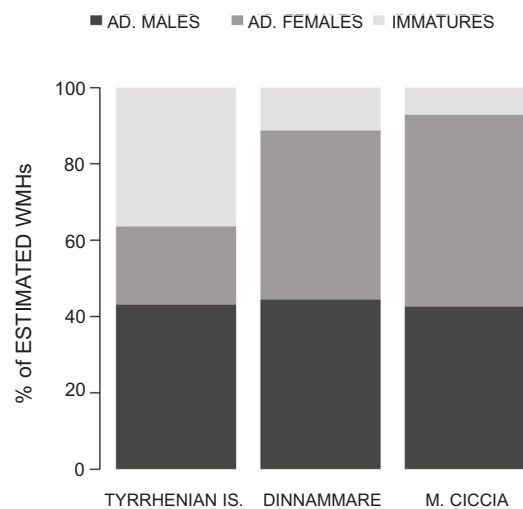


Fig. 3. Estimated Western Marsh Harrier divided by sex/age categories migrating through the Central Mediterranean in spring 2014–2015.

adult females = 29 March; immatures = 7 April), while at Mount Ciccia, the median dates of adults occurred the same day (adults males and females = 26 March; immatures = 8 April; Fig. 4).

Wind pattern in the study area

At a local scale, during the whole observation period the strength of thermals was different between the four observation posts (Kruskal-Wallis test,

$\chi^2 = 119.14$, $df = 3$, $p < 0.001$), as well as the orographic uplift (Kruskal-Wallis test, $\chi^2 = 15.599$, $df = 3$, $p = 0.001$). At a regional scale, despite winds with variable directions blow over the Central Mediterranean, they showed a higher frequency of west and north-westerly winds both in March and April (Fig. 5). At a local scale, wind direction was different between observation posts ($\chi^2 = 72.328$, $df = 21$, $p < 0.001$), except for E/S/NW winds; at Ustica frequencies of all winds were not different ($\chi^2 = 9.895$, $df = 7$, $p = 0.195$). In addition, wind speed was different between observation posts (Kruskal-Wallis test, $\chi^2 = 22.234$, $df = 3$, $p < 0.001$).

Migration in relation to winds

The wind pattern of the study area affected the daily counts of Western Marsh Harriers passing during the spring migration. Particularly, there was a negative effect of the strength of the thermal uplifts and a clear quadratic effect of both the Julian date and the V component of the wind, showing a more consistent passage between March 26 and April 6 and without/weak north-south winds (Table 2, Fig. 6, Appendix 2). The observation post was an important covariate, showing higher passage at the posts located

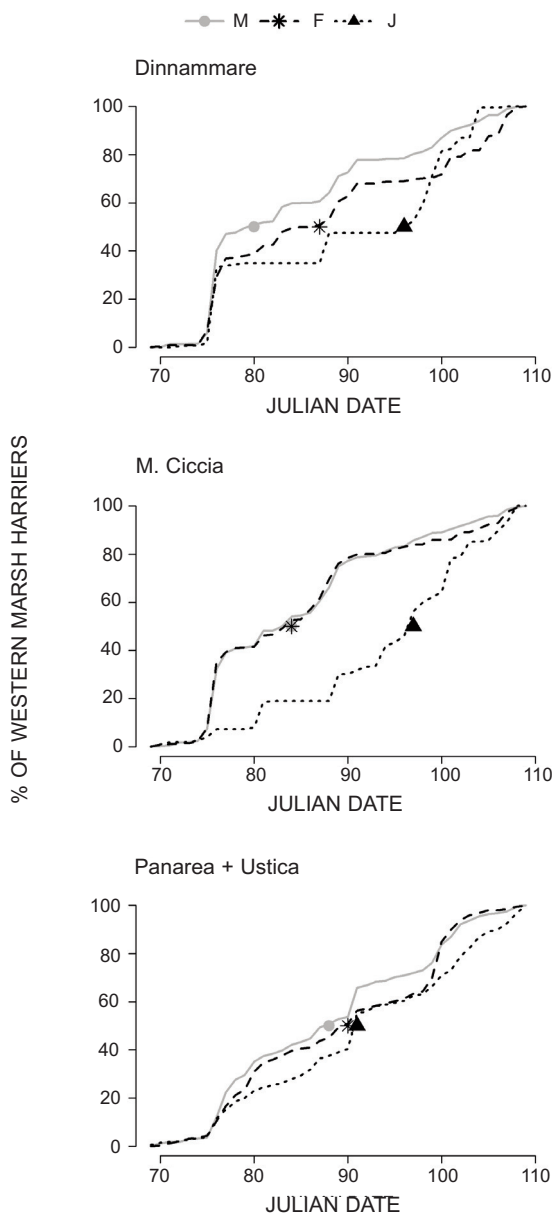


Fig. 4. The cumulative percentage of Western Marsh Harriers divided by sex/age categories migrating through the Central Mediterranean in spring between 2014 and 2015. Markers indicate the median of passage.

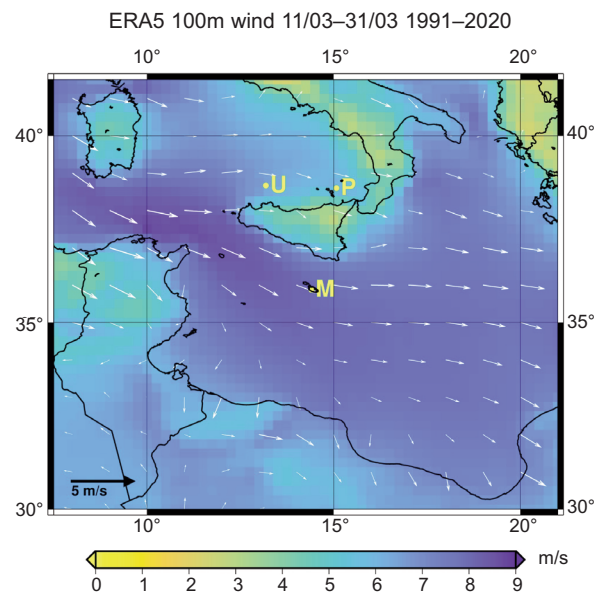


Fig. 5. 100 m wind patterns in the Central Mediterranean between 11–31 March, and 1–20 April in the years from 1991 to 2020. The colour map indicates the average value of the modulus of the hourly wind; the arrows represent the composite hourly wind vector over the averaging period. The letters "U", "P" and "M" label the islands of Ustica, Panarea and Malta, respectively. Wind data were obtained from the ERA5 reanalysis product, as described in the text.

Table 2. The average models obtained by GLM investigating the effect of wind pattern on the daily counts of the Western Marsh Harrier during the spring migration at three sites in Central Mediterranean Sea in 2014–2015. SE — standard error; LCI 95% — 95% lower confidence interval; UCI 95% — 95% upper confidence interval; sw — sum of model weights. The most important variables (sw = 1.00) are in bold. The reference level for the observation post is M. Ciccìa.

Variable		Estimate	SE	LCI 95%	UCI 95%	sw
Intercept		4.147	0.150	-	-	-
Observation post	Dinnammare	-0.358	0.188	-0.727	0.012	1.00
	Panarea	-1.639	0.242	-2.116	-1.163	
	Ustica	-1.261	0.240	-1.732	-0.789	
Julian date		-1.948	1.118	-4.139	0.243	1.00
Julian date²		-4.625	1.145	-6.880	-2.370	
U wind		-2.351	1.205	-4.726	0.024	0.90
U wind ²		-2.935	1.336	-5.567	-0.304	
V wind		-3.201	1.435	-6.015	-0.388	1.00
V wind²		-5.474	1.273	-7.982	-2.967	
Thermal uplift		-6.210	1.689	-9.535	-2.884	1.00
Thermal uplift²		-1.077	1.164	-3.369	1.216	
Orographic uplift		-0.069	0.099	-0.264	0.127	0.27

on the Peloritani Mountains (M. Ciccìa and Dinnammare; Strait of Messina) than on the

islands (Ustica and Panarea). The residuals were normally distributed (Kolmogorov-Smirnov test, $D = 0.13$, $p = 0.435$) and there was no collinearity between the variables ($VIF < 3$). Furthermore, the goodness-of-fit of the model was good ($\chi^2 = 223.44$, $df = 222.60$, $p = 0.344$) and the expected values are correlated to the observed values ($r = 0.487$, $p < 0.001$).

The wind pattern also affected the flock size of WMHs. Particularly, considering vertical winds, there was a negative effect of the strength of both the thermal and the orographic uplifts. As regards horizontal winds, there was a negative effect of the east-west (U) component of the wind, with smaller flock when the wind was strong. Finally, the Julian date affected negatively the flock size, with a short plateau at the beginning of the period (Table 3, Fig. 7, Appendix 3). Similarly

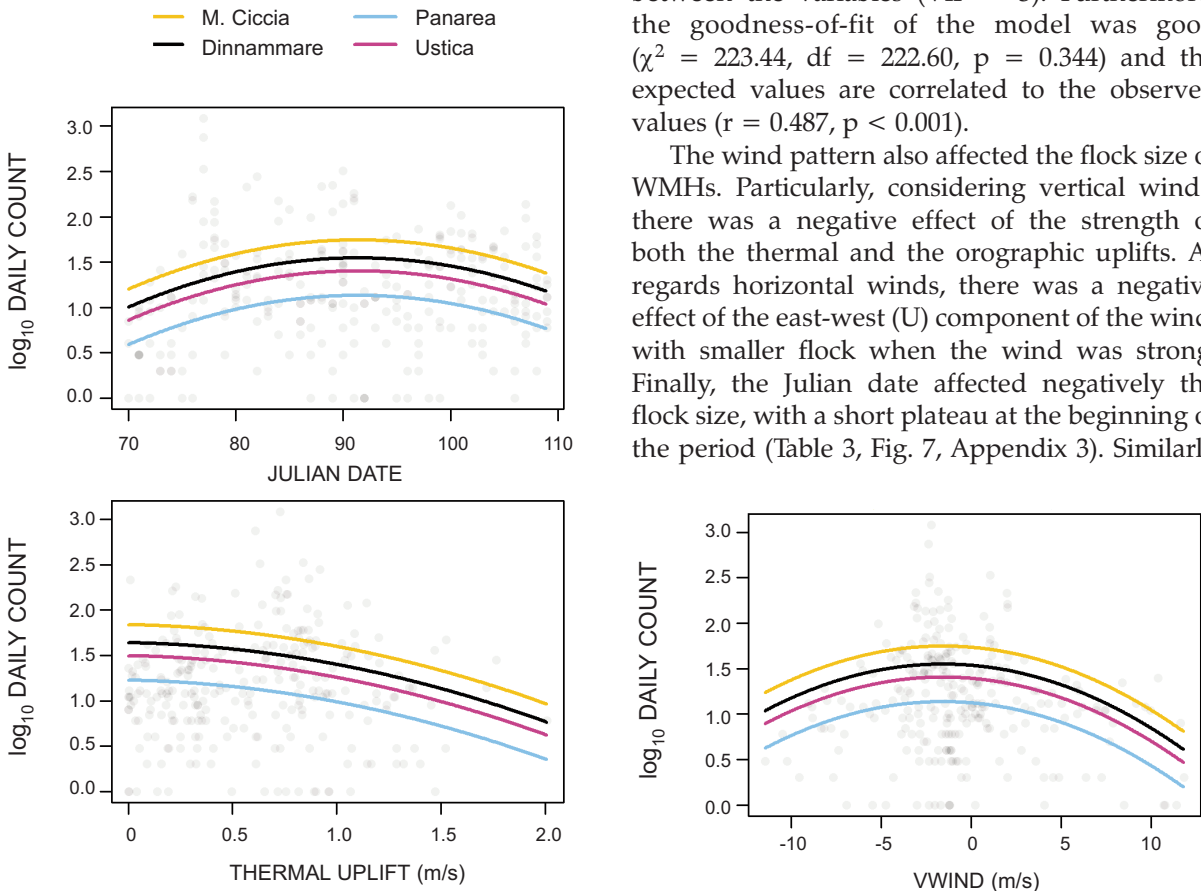


Fig. 6. Response curves of the most important variables (sw = 1.00) affecting the daily counts of the Western Marsh Harrier during the spring migration at three sites in Central Mediterranean Sea in 2014–2015. Lines are predictions of the best model fit, points are the raw data.

Table 3. The average models obtained by GLM investigating the effect of the wind pattern on the flock size of the Western Marsh Harrier during the spring migration at three sites in Central Mediterranean Sea in 2014–2015. SE — standard error; LCI 95% — 95% lower confidence interval; UCI 95% — 95% upper confidence interval; sw — sum of model weights). In bold we marked the most important variables (sw = 1.00). The reference level for the observation post is M. Ciccia.

Variable		Estimate	SE	LCI 95%	UCI 95%	sw
Intercept		3.919	0.131	-	-	-
Observation post	Dinnammare	0.619	0.186	0.255	0.983	1.00
	Panarea	1.039	0.308	0.434	1.643	
	Ustica	1.312	0.316	0.692	1.932	
Julian date		61.110	5.984	49.378	72.842	1.00
Julian date²		14.779	5.411	4.171	25.388	
Wind speed		0.202	0.186	-0.162	0.566	0.39
U wind		0.475	0.119	0.241	0.708	1.00
V wind		9.454	8.104	-6.435	25.343	0.73
V wind ²		34.003	10.123	14.157	53.849	
Thermal uplift		43.645	6.853	30.210	57.080	1.00
Thermal uplift²		14.297	7.418	-0.247	28.343	
Orographic uplift		0.615	0.146	0.329	0.900	1.00

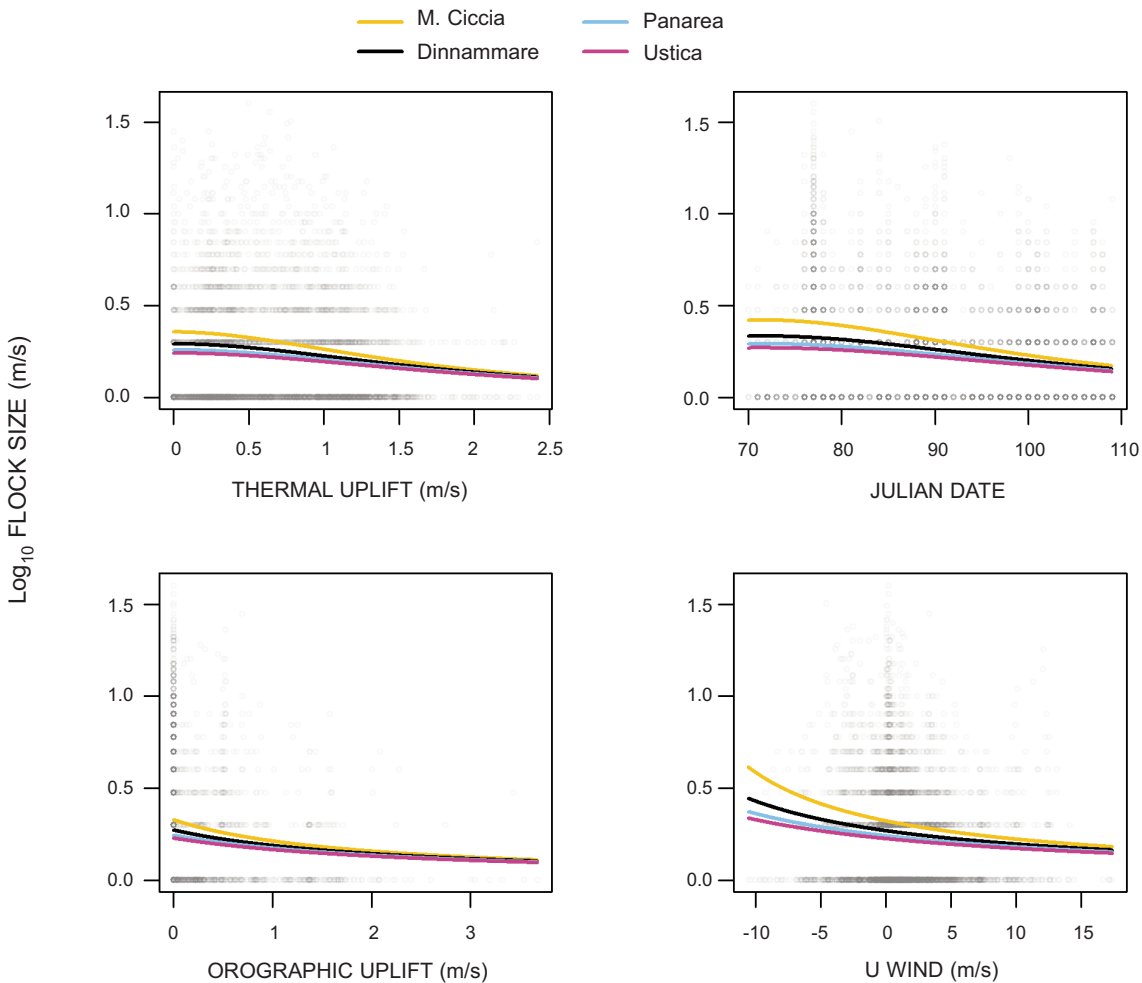


Fig. 7. Response curves of the most important variables (sw = 1.00) affecting the flock size of the Western Marsh Harrier during the spring migration at three sites in Central Mediterranean Sea in 2014–2015. Lines are predictions of the best model fit, points are the raw data.

to the daily count, the observation post was an important covariate, showing larger flocks passing at the posts located on the Peloritani Mountains (M. Ciccìa and Dinnammare; Strait of Messina) than on the islands (Ustica and Panarea). The residuals were normally distributed (Kolmogorov-Smirnov test, $D = 0.04$, $p = 0.761$) and there was no collinearity between the variables ($VIF < 3$). Furthermore, the goodness-of-fit of the model was good ($\chi^2 = 111.52$, $df = 111.15$, $p = 0.218$) and the expected values are correlated to the observed values ($r = 0.304$, $p < 0.001$).

DISCUSSION

Several studies showed both intra and interspecific flight strategies adopted by migrating raptors affected by weather, geography and topography en route (for a review see Panuccio et al. 2021). In the case of the WMH, daily counts recorded in this survey, higher along the Peloritani Mountains (Strait of Messina) than over the islands of Ustica and Panarea, suggest that mountain reliefs when passing over the mainland are more attractive than islands when crossing water bodies. However, our results partially agree with those of the radar study made in southern Israel showing that WMHs behave like typical soarers when and where thermals are available (Spaar & Bruderer 1997) since, as expected for a species migrating on a broad front, daily counts were not positively affected by the strength of thermals. When focusing on the passage in relation to sex classes to test our hypothesis concerning a differential migration strategy between adult males and females, our observations along the Peloritani Mountains (Strait of Messina) reveal that the former reached higher altitudes in early season, probably exploiting even weaker thermals at the higher ridges (Dinnammare, in this case). This flight behaviour could be facilitated, in the case of adult males, by their lighter body mass and, presumably, lower wing load (Spaar 1997). Such potential differential strategies, would explain why adult males were seen passing one week earlier than females at Dinnammare, but not at Mount Ciccìa. Moreover, since at the last observation post adult females outnumbered adult males, it is reasonable that a substantial number of adult males reaching higher altitudes at Dinnammare, soon after undertook the crossing of the Strait of Messina, as observed in the case of European Honey Buzzards *Pernis apivorus* migrating in the same area (Agostini et al.

2021). Anyway, our study shows that the location of the observation post chosen to make a survey can affect the result concerning the migration phenology of adult males and females in this species, leading to evident bias. A differential flight strategy among adults belonging to different sex classes apparently occurs also during the crossing of the Tyrrhenian Sea, when birds are forced to use longer the flapping flight because of weaker thermal conditions over water. In particular, the low estimated number of adult females passing over Panarea and Ustica suggests that they are less attracted than males to islands, where it is possible to gain higher altitudes before continuing migrating over sea. However, if birds concentrate over the islands to gain higher altitudes, why were daily count negatively affected by the strength of thermals? In the case of the Tyrrhenian islands, although such result may appear contradictory, better thermal conditions form during ideal weather conditions for the sea crossing (sunny days with high atmospheric pressure and stable weather), and perhaps better thermal conditions over water can be exploited to some extent (Nourani et al. 2021), making islands less attractive for migrants. In addition, considering horizontal winds, fewer WMHs were seen passing over the Tyrrhenian islands, such as along the Peloritani Mountains, during a strong N-S component. As regards Tyrrhenian islands, since the wind regime at a regional scale shows a higher frequency of lateral winds with a tail component (westerlies) in this Central Mediterranean area, we suggest that WMHs choose to follow in a higher number of individuals more direct flyway en route to continental Italy when exploiting a stronger tail support, bypassing the islands en route.

A differential migration strategy in relation to sex classes at a fine scale, with adult males using at a larger extent soaring flight by exploiting even weaker thermals, would explain the faster migration speed of adult females revealed by the satellite study (see above). As a matter of fact, interspecific differences are expected to occur among species able to use a mixed flight strategy (soaring-gliding/flapping flight), with those using at a larger extent flapping flight, and exploiting the soaring-gliding flight only when strong thermals are available, being expected to reach a faster migration speed (Hedenström 1993). If such an interspecific difference occurs, we suspect that it could also occur among individuals of the same species, especially in those showing a marked sexual dimorphism in size (see above) and

morphology (Forsman 2016). Moreover, heavier females could actively select stronger thermals also because heavier birds reach faster ground speed in inter-thermal gliding, maximizing cross-country speed (Spaar 1997). Another factor could affect inter-individual differences in the migration speed of WMHs. Studies made in the breeding grounds showed that older males return earlier and have higher success than the younger ones (Altenburg et al. 1987). Since older males are expected to be dominant on the younger ones at the non-breeding grounds, it is possible that different body condition due to bad foraging conditions at their non-breeding sites, especially towards the end of the non-breeding season, further affect their migration speed, forcing some birds (probably younger individuals) to long stopovers en route (see also Vansteelant et al. 2020). In addition, as shown by other raptor species, migratory performance develops gradually over time with younger birds, often performing suboptimal flight strategies than older ones (López-López et al. 2014, Sergio et al. 2014, 2022, Vansteelant et al. 2017). Nevertheless, due to their larger size, adult females are expected to be dominant on both older and younger males at their non breeding sites, probably reaching even better body conditions which favour a faster northwards movements. As mentioned above, a strong competition among females, forcing them to reach as soon as possible their breeding grounds, is expected in polygynous species, primary females having more success than secondary ones (Altenburg et al. 1982).

Finally, why were immatures observed in large numbers over the Tyrrhenian islands, while fewer were seen flying along the Peloritani Mountains? Although some WHSs breed in their second calendar year (Clarke 1995), immatures are not expected to adopt a time minimization strategy to reach earlier breeding grounds, to the extent that those arriving earlier in the season and taking a territory, probably because migrating on shorter distances (Agostini 2001), are often ousted at a later date by adults (Newton 2010). In the same way, they could be ousted from the better non-breeding areas by adults, perhaps reaching a worse body condition before spring migration. A ringing recovery analysis of birds wintering in Sub-Saharan Africa showed differential wintering areas in relation to age classes, with juveniles wintering further west than adults (Panuccio et al. 2013). In that study, the authors suggested that such differential distribution in wintering areas

could be related to the different ability of non-experienced individuals to compensate for the wind drift of dominant easterly winds during migration over the desert in autumn. In fact, juveniles do not know non-breeding areas and do not have a precise goal to reach during their first autumn migration (see also Thorup et al. 2003). As mentioned above, our results suggest that immatures do not concentrate along a mountain chain to reach higher altitudes when passing over mainland; being less motivated than adults by reproduction, they probably prefer to fly more slowly and at lower altitudes over areas where they can eventually find prey and/or rest at stop-over site en route, especially after or during a long water crossing (see also Vansteelant et al. 2020). Unfortunately, until now no satellite tracking was carried out on the spring migration of immature WMHs, and further studies are needed to investigate in detail their flight strategy when returning to breeding grounds.

WMHs mostly migrate solitary or in small loose flocks, although flocks of few dozens of individuals have been reported (Agostini 2021). Unlike typical soarers, it has been suggested that they do not use flocking to locate stronger thermals. As a matter of fact, a radar study made in southern continental Italy during autumn migration, reported larger flocks flying at lower altitudes (Agostini et al. 2017). Our results seem to support this conclusion, since smaller flocks were detected during stronger vertical winds. Such as the strength of thermal and orographic uplift, also the strength of east-west component (U) of the wind negatively affected flock size at all observation posts. Satellite studies showed that WMHs leave a drift effect when flying in stronger crosswinds, exploiting their tail support to migrate faster especially during spring migration (Mellone et al. 2012, Vansteelant et al. 2020). Moreover, visual observations made at the Cap Bon Promontory (NE Tunisia), showed that WMHs facing the open sea undertake the crossing even in strong side winds (Agostini & Duchi 1994), prevailing in early spring over the Channel of Sicily (see also Agostini et al. 2022). In this picture, it is reasonable to assume that during strong winds, having with higher frequency a side component in the study area in early spring, WMHs would tend to fly more dispersed in space, thus forming even smaller flocks.

In conclusion, our study shows how sex and age differences in counts of migrating birds can be noticed by direct visual observations at a small

spatial scale (e.g. within the Strait of Messina or Tyrrhenian islands), highlighting that the location of the observation posts chosen to make a survey can affect the result concerning the migration phenology of adult males and females in this species, leading to evident bias.

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STRESZCZENIE

[Zróznicowane strategie przelotu w zależności od płci i wieku podczas wiosennej migracji błotniaka stawowego w środkowej części Morza Śródziemnego]

Wiele gatunków ptaków wykazuje zróżnicowanie strategii wędrówek w zależności od wieku i/lub płci, co często związane jest z różnicami morfologicznymi i behawioralnymi. Błotniak stawowy

jest częściowym migrantem, wykazującym silny dymorfizm płciowy pod względem wielkości (samice są cięższe od samców o ok. 25%). Gatunek ten migruje szerokim frontem, podejmując przeloty nad Morzem Śródziemnym. Autorzy zakładali, że dorosłe samce i samice tego gatunku, ze względu na różnicę w wielkości ciała, mogą różnić się strategiami wędrówkowymi związanymi z topografią terenu oraz charakterystyką wiatru.

Badania prowadzono w okresie szczytu wędrówki wiosennej (11 marca–20 kwietnia) w basenie Morza Śródziemnego w latach 2014–2015. Obserwacje wędrujących ptaków z podziałem na płeć i klasy wieku (dorosłe i młodociane), oraz zapisując wielkość stad, prowadzono na trzech stanowiskach: na wyspach Ustica i Panarea na Morzu Tyrreńskim oraz w Cieśninie Mesyńskiej (dwa punkty obserwacyjne: Dinnammare i Ciccina w Górach Pelorytańskich, w płn.-wsch. Sycylii) (Fig. 1). W analizach wpływu wiatrów uwzględniano dwa kierunki poziomych ruchów powietrza — wschód-zachód (U) oraz północ-południe (V), oraz prądy wznoszące.

Stwierdzono, że więcej ptaków wędrowało nad Górami Pelorytańskimi niż nad wyspami Ustica i Panarea (Tab. 1, Fig. 2). Średnia wielkość stad ptaków w poszczególnych punktach obserwacyjnych była podobna i niewielka (Tab. 1). Wśród ptaków wędrujących nad wyspami Ustica i Panarea przeważały samce i osobniki młodociane, podczas gdy nad Górami Pelorytańskimi, w zależności od punktu obserwacyjnego, nie było różnic w liczebności dorosłych samic i samców lub samice były liczniejsze (Fig. 3). Nad wyspami Ustica i Panarea oraz w punkcie Dinnammare samce wędrowały wcześniej niż pozostałe grupy, a nad górą Ciccina samce i samice wędrowały w tym samym czasie (Fig. 4). Stwierdzono, że na liczbę błotniaków obserwowanych dziennie wpływał kierunek wiatru, siła prądu wznoszącego typu termicznego a także data i miejsce obserwacji (Tab. 2, Apendyks 2). Najwięcej wędrujących ptaków obserwowano między 26 marca a 6 kwietnia, przy słabszych prądach wznoszących typu termicznego oraz braku lub słabym wietrze w kierunku północ-południe (Fig. 6), nad Górami Pelorytańskimi. Również wielkość migrujących stad zależała od kierunku i siły wiatru (Tab. 3). Stada były tym mniejsze im silniejsze były wznoszące prądy powietrza typu termicznego i orograficznego (wznoszący prąd powietrza powstający po napotkaniu pionowej przeszkody) oraz im silniej wiał wiatr w kierunku

wschód-zachód (Fig. 7). Także data i miejsce obserwacji miały wpływ na wielkość stad błotniaków (Tab. 3, Fig. 7, Apendyks 3). Uzyskane wyniki wskazują na zróżnicowane strategie błotniaków podczas przelotów przez morze, z dorosłymi samicami mniej chętnie niż dorosłe samce lecącymi nad niewielkimi wyspami Morza Tyrreńskiego. Autorzy sugerują, że dorosłe samce, dzięki swoim mniejszym rozmiarom, w większym stopniu używają lotu szybowego, wykorzystując nawet słabe prądy wstępujące napotymane na

trasie przelotu. W przeciwieństwie do obu małych wysp, niewiele młodocianych osobników było widzianych przelatujących wzdłuż Gór Pelorytańskich, prawdopodobnie dlatego, że lecą one na niższych wysokościach, przez obszary, gdzie mogą znaleźć zdobycz i/lub odpocząć po drodze. Uzyskane wyniki wskazują także, że lokalizacja punktu obserwacji wędrujących błotniaków może istotnie wpływać na wnioski dotyczące wędrówek tych ptaków w zależności od płci, czy klas wiekowych.

Appendix 1. AIC comparison of univariate distributions fitted to flock size of Western Marsh Harriers crossing the Central Mediterranean Sea during the spring migration at three sites. Distributions are ordered by AIC; AIC was calculated in R with the package *fitdistrplus* (Delignette-Muller et al. 2017).

Data distribution	AIC
Gamma	14 108.87
Exponential	14 500.87
Negative binomial	15 248.42
Poisson	17 657.36
Normal	19 100.44
Uniform	27 363.48

Delignette-Muller M.-L., Dutang C., Pouillot R., Denis J.-B., Siberchicot A. 2017. Package *fitdistrplus*: Help to fit of a parametric distribution to non-censored or censored data. Available at: www.cran.r-project.org, Wien.

Appendix 2. The best models (cumulative sum of $w_i = 0.95$) explaining the effect of the wind on the daily counts of Western Marsh Harrier during spring migration at three sites in central Mediterranean Sea in 2014–2015. For each model, we show the log-Likelihood (logLik), the AIC_c and its difference with the minimum AIC_c in the set (ΔAIC_c) and the Akaike's weights (w_i).

Model	logLik	AIC	ΔAIC	w_i
Observation post + Julian date + Julian date ² + U wind + U wind ² + V wind + V wind ² + thermal uplift + thermal uplift ²	-1159.52	2346.49	0.00	0.60
Observation post + Julian date + Julian date ² + U wind + U wind ² + V wind + V wind ² + thermal uplift + thermal uplift ² + orographic uplift	-1159.27	2348.21	1.73	0.25
Observation post + Julian date + Julian date ² + V wind + V wind ² + thermal uplift + thermal uplift ²	-1163.62	2350.28	3.79	0.10

Appendix 3. The best models (cumulative sum of $w_i = 0.95$) explaining the effect of the wind on the flock size of Western Marsh Harrier during spring migration at three sites in Central Mediterranean Sea in 2014–2015. For each model, we show the log-Likelihood (logLik), the AIC_c and its difference with the minimum AIC_c in the set (ΔAIC_c) and the Akaike's weights (w_i).

Model	logLik	AIC	ΔAIC	w_i
Observation post + Julian date + Julian date ² + U wind + V wind + V wind ² + thermal uplift + thermal uplift ² + orographic uplift	5218.41	-10 410.72	0.00	0.49
Observation post + Julian date + Julian date ² + wind speed + U wind + V wind + V wind ² + thermal uplift + thermal uplift ² + orographic uplift	5218.48	-10 408.85	1.87	0.20
Observation post + Julian date + Julian date ² + wind speed + U wind + thermal uplift + thermal uplift ² + orographic uplift	5216.36	-10 408.64	2.07	0.18
Observation post + Julian date + Julian date ² + U wind + thermal uplift + thermal uplift ² + orographic uplift	5214.55	-10 407.03	3.69	0.08