

Pushed by increasing air temperature and tailwind speed: weather selectivity of raptors migrating across the Aegean Sea

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Received 27 May 2015, accepted 16 May 2016

A vast number of raptors migrates between the Western Palearctic and Africa every autumn. Species and/or populations of migratory raptors that choose to cross the Mediterranean Sea need to overcome an extended ecological barrier, which is particularly extensive in the area of east–central and east Mediterranean. We tested the selectivity of two raptor species to weather and phenology analyzing the data collected on a small Greek island throughout four different years. Weather selectivity of the two species shows both similarities and differences. The intensity of migration of both studied species is positively correlated with air temperature. The European Honey Buzzard selects days with strong tailwind assistance that helps to reduce flight time over sea thus decreasing mortality risk and energy consumption during this sea crossing. On the other hand, the Western Marsh Harrier seems to be less wind selective reaching the island in good numbers also with headwinds, probably because of its higher ability in using powered-flapping flight.



1. Introduction

Migratory birds are able to match the explosion of resources during spring and summer at the high latitude thanks to their movement abilities (Alerstam 1990, Newton 2008). However, the migration between breeding and non-breeding areas involves many risks. Daily mortality during migration has been estimated to be higher than daily mortality at other times of year (Newton 2007). Klaassen *et al.* (2014) quantified the phenomenon

showing that mortality is six times higher during migration than during stationary periods. Birds face higher risks when flying over ecological barriers such as desert and sea. A recent study showed that among ten Egyptian Vultures (*Neophron percnopterus*) that attempted to cross the Mediterranean Sea, nine died while the only one that survived was assisted by tailwinds during the crossing (Oppel *et al.* 2015). Those birds were juveniles supporting the hypothesis that mortality is higher for inexperienced birds (Strandberg *et al.* 2009).

During migration powerful selective forces act and experience can lead to higher survival rates (Mellone *et al.* 2011, Sergio *et al.* 2011, 2014, Agostini *et al.* 2015).

Water surfaces are inhospitable areas for land birds. During water crossings these birds must continue flying even if weather conditions suddenly change. This is particularly evident for soaring birds since they cannot use thermal updrafts as they usually do over land (Kerlinger 1989, Bildstein 2006). The morphology of Accipitriformes allows these birds to move across landmasses at faster rates and with a relatively low amount of energy using the soaring-gliding flight (Hedenström 1993, Åkesson & Hedenström 2007). In contrast, these large and medium-sized birds require a large amount of energy when using flapping (powered) flight (Kerlinger 1989, Alerstam 2001, Penny-cuick 2008, Bildstein *et al.* 2009, Agostini *et al.* 2015).

Several studies have highlighted that birds show a high selectivity to weather conditions during migration. Many species of birds, such as passerines and shorebirds, select both days and altitudes in order to find the best tail-wind assistance (Åkesson & Hedenström 2000, Ma *et al.* 2011). With favorable wind conditions birds can increase their flight speed up to 30%, which saves a large amount of energy (Liechti & Bruderer 1998). For raptors facing long water crossings, current data suggests that these birds tend to stop migration flight in strong head and crosswinds (Kerlinger 1984, 1989, Meyer *et al.* 2000). At some Mediterranean sites, raptors do not migrate over sea at all when there are strong winds, regardless of the direction (Agostini & Duchi 1994, Agostini *et al.* 2005, Panuccio *et al.* 2002, 2011). The migration speed of raptors over land is usually higher during the central time of the day when thermal currents are stronger (Mellone *et al.* 2012) and new evidence suggests that soaring species travel faster and further with stronger average daily thermal convection (Vansteelant *et al.* 2015).

The specific weather conditions that can be considered favorable for bird migration vary greatly among regions (Liechti & Bruderer 1998) and also among species because of morphological and behavioral adaptations (Newton 2008, Malmiga *et al.* 2014). As such, this study was conducted to investigate the following question: will

raptors undertake the crossing of the Mediterranean Sea irrespective of weather conditions? Therefore we identify which weather conditions are affecting the migration over sea of two species of raptors showing different flight strategies: the European Honey Buzzard (*Pernis apivorus*), a species that largely uses soaring-gliding flight (Schmid 2000, Spaar 1997), and the Western Marsh Harrier (*Circus aeruginosus*), a species that uses both flapping and soaring-gliding flight (Spaar & Bruderer 1997a, Panuccio *et al.* 2013b, Panuccio & Agostini 2010). Here we analyze the migratory flow over the island of Antikythira in southern Greece testing the hypothesis that the two species are influenced differently by weather conditions during migration. In particular, our hypothesis is that the different morphology of European Honey Buzzards and Western Marsh Harriers leads to different weather selectivity during sea crossing. Harriers, being lighter than buzzards, should be better suited to use powered flight for longer, over sea (Panuccio *et al.* 2013b, Agostini *et al.* 2015). Hence, the predictor variables used are, air temperature, air pressure and wind conditions, variables that are rarely used together to explain the variation of the migratory behavior of raptors (Vansteelant *et al.* 2015).

2. Materials and methods

2.1. Study area and data collection

We analyzed the influence of weather conditions on the passage of the two most abundant raptor species passing through southern Greece during autumn migration (Lucia *et al.* 2011, Panuccio *et al.* 2013a): the European Honey Buzzard and the Western Marsh Harrier. Daily observations were made in the following periods: from 24 August to 20 September 2007, from 21 August to 20 September 2008, from 4 September to 20 October 2009 and from 17 August to 28 September 2013.

Antikythira is a small island (20 km²; max. altitude 378 m.a.s.l.) in southern Greece and is located 32 km southeast of the island of Kythira and 33 km northwest of Crete which in turn is located approximately 300 km northeast of the Cyrenaica Peninsula (Libya; Fig. 1). Antikythira is oriented in a northwest–southeast direction and during autumn

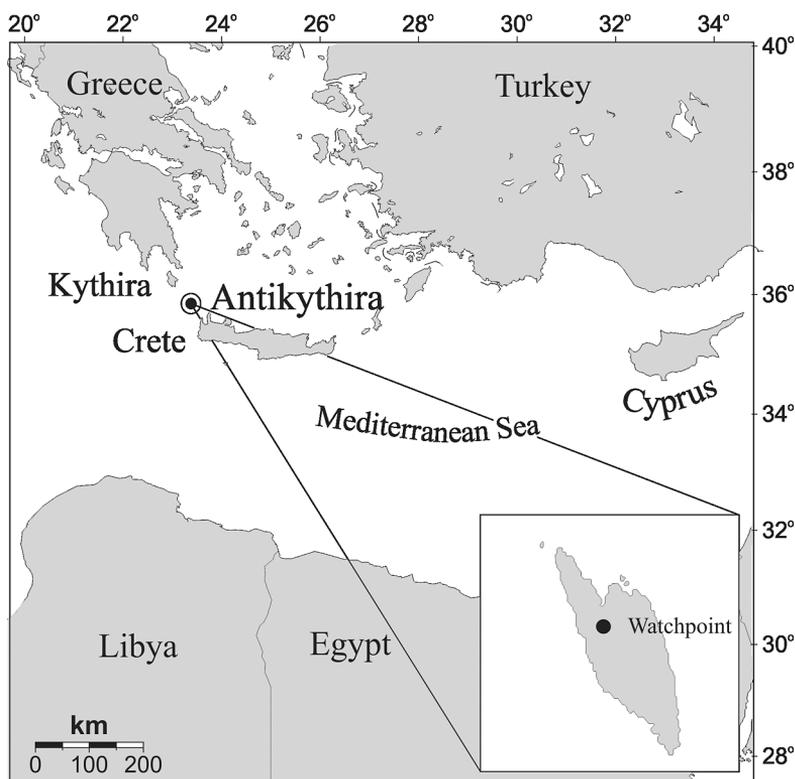


Fig. 1. Location of the study site in relation to the mainland Greece and the African coast.

migrating raptors approach the island from the northwest and depart heading southeast apparently toward the island of Crete (Lucia *et al.* 2011). Observations were made from a watch-point ($35^{\circ}5'48''\text{N}$; $23^{\circ}17'50''\text{E}$) located on the northern side of the island at an approximate elevation of 220 m above the sea level. From the watch-point it was possible to detect birds approaching the island from the north. Roosting birds or individuals moving in reverse migration were not considered in the count.

2.2. Data analysis

To avoid bias due to the migratory phenology, only the peak periods of migration were considered in the analysis for both studied species: days from 20 August to 10 September were taken into account for the European Honey Buzzards and between 5 September and 20 September for the Western Marsh Harrier.

Two analytic methods were used to assess the influence of weather conditions on the migration

of the two studied species. Firstly, we used a Binary Logistic Regression Analysis (hereafter BLRA) to evaluate if the peak days of migration occur with particular weather conditions, or if these peak days are only influenced by phenology. Thereafter, to better understand if the intensity of migration (number of observed birds) in southern Greece was related with meteorological features, Generalized Linear Models (hereafter GLM) were applied, using daily numbers of counted raptors as a continuous dependent variable.

We used BLRA (*logit* link function) (Boyce *et al.* 2002, Keating & Cherry 2004, Rushton *et al.* 2004) to compare days with a high intensity of migration ($N = 18$ and 14 , for European Honey Buzzards and Western Marsh Harrier, respectively) with days of lower migration intensity. A day with high intensity of migration is defined as one where at least 6% (a value that is just above the conventional threshold of significance; Fowler & Cohen 1993) of the total number of individuals observed in each season were counted. In the model, the dependent variable was high intensity/low intensity days (1/0), while the covariates were air tempera-

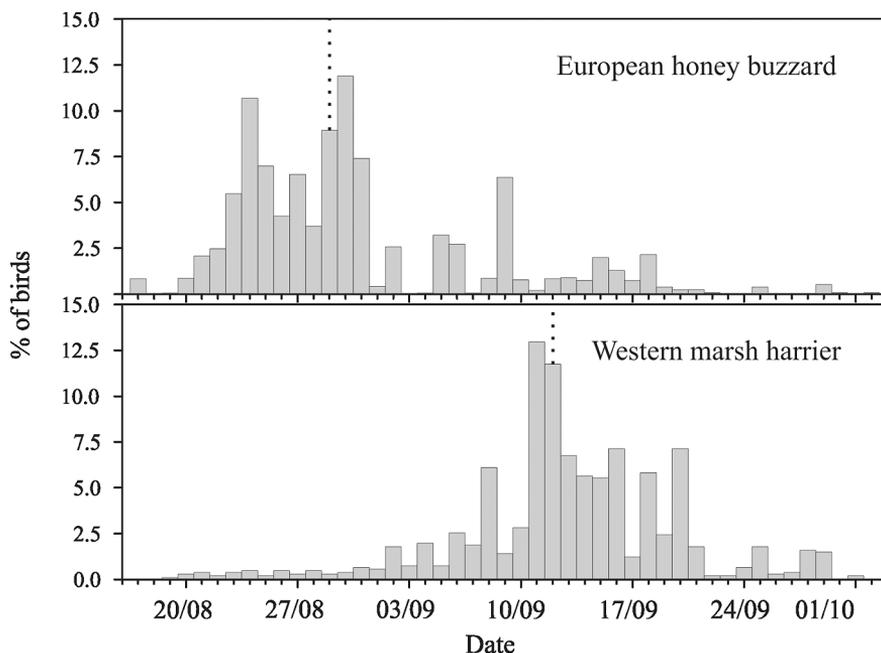


Fig. 2. Timing of autumn migration of the European Honey Buzzard and the Western Marsh Harrier at Antikythira. Dashed line represents the median date of passage.

ture ($^{\circ}\text{C}$), air pressure (mbar), the interaction between wind speed (m/s) and wind direction (headwind, tailwind, and crosswind) and the Julian date, calculated as the number of the day from the beginning of the year (January 1st being day number 1). We excluded from the analyses the low number of days with headwind ($N = 1$) and lateral wind ($N = 6$), for European Honey Buzzard and Western Marsh Harrier, respectively. Moreover considering the non-linear effect of Julian date on bird migration the squared Julian date was used as covariate as well (Knudsen *et al.* 2007, Lindén 2011, Lindén & Mäntyniemi 2011).

We ran a set of 8 models with all the possible combinations of predictors retaining *a priori* the phenological covariates (Julian date and the squared Julian date) in order to evaluate the influence of phenology on the migratory behavior of raptors. Then we compared models with the second-order Akaike Information Criterion (AIC_c , Akaike 1973), with the best model evaluated as the model with the lowest AIC_c value (Burnham & Anderson 2002).

We tested the ability of the model to distinguish between *high intensity days* and *other days* by means of the area under the curve of the Receiver Operating Characteristic (ROC) plot (Pearce & Ferrier 2000, Boyce *et al.* 2002, Fawcett

2006). This area provides a measure of discrimination ability, varying from 0.5 for a model with a discrimination ability no better than random, to 1.0 for a model with perfect discriminatory ability. A rough guide for classifying the accuracy of this diagnostic test is the traditional academic point system (Swets 1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.00 = fail. The Variance Inflation Factor (VIF) was measured for the model with a threshold of 3 to test collinearity of variables (Zuur *et al.* 2010).

Moreover, as mentioned above, we modeled the total daily numbers of individuals observed in relation to the meteorological and phenological data using a GLM (McCullagh & Nelder 1989, Dobson 1990) with negative binomial error distribution (*log* link function) (Bliss & Fisher 1953; White & Bennets 1996). In the same way of the BLRA, we ran the set of 8 models with all the possible combination of variables (air temperature, interaction between wind speed and wind direction; Julian date and squared Julian date were retained *a priori*) comparing the different models by the AIC_c value. The goodness of fit of the model obtained was assessed by the Pearson's χ^2 test (White & Bennets 1996, Agresti 2007) and the VIF was calculated to prevent covariates collinearity.

Table 1. Meteorological conditions in the study area between August and September in 2007–2009 and 2013. Average (minimum–maximum) air temperature and wind speed are shown.

Year	Period	Temperature (°C)	Wind speed (m/s)	Wind direction
2007	August 1–15	25.7 (23.6–27.0)	6.5 (4.5–8.6)	W–NW
	August 16–31	27.2 (25.8–29.3)	5.6 (2.9–7.4)	NW–N
	September 1–15	24.5 (22.1–27.9)	5.9 (3.7–8.1)	W–NW
	September 16–30	23.4 (20.6–25.6)	5.5 (1.0–8.2)	NW–N
2008	August 1–15	26.0 (24.7–27.4)	6.6 (4.1–7.8)	NW–N
	August 16–31	26.4 (25.3–27.7)	5.9 (3.8–8.0)	NW–N
	September 1–15	25.5 (23.8–27.1)	4.9 (2.2–6.5)	NW–N
	September 16–30	22.6 (20.4–25.0)	4.9 (0.7–10.1)	W–N
2009	August 1–15	25.9 (24.6–27.0)	6.3 (4.4–7.6)	NW–N
	August 16–31	25.7 (25.0–27.0)	6.0 (3.7–8.2)	NW–N
	September 1–15	24.5 (22.9–26.4)	4.7 (1.6–8.4)	W–N
	September 16–30	23.2 (21.3–25.1)	4.4 (1.4–6.3)	NW–NE
2013	August 1–15	26.7 (25.8–27.3)	5.8 (4.7–6.5)	NW–N
	August 16–31	26.0 (24.3–27.1)	5.4 (2.8–8.3)	NW–N
	September 1–15	25.0 (23.9–26.0)	4.6 (1.8–7.2)	NW–N
	September 16–30	24.1 (22.7–25.8)	5.0 (1.8–7.4)	W–NW

We used data pooled between years to reduce the bias related to small sample size and because no significant differences were observed among them. In particular no differences were observed between years both in the number of birds observed (for European Honey Buzzard: Kruskal–Wallis test, $\chi^2 = 1.484$, $df = 2$, $P = 0.476$; for Western Marsh Harrier: Kruskal–Wallis test, $\chi^2 = 5.177$, $df = 3$, $P = 0.159$) and in the number of high intensity/low intensity days (for European Honey Buzzard: $\chi^2 = 0.188$, $df = 2$, $P = 0.910$; for Western Marsh Harrier: $\chi^2 = 0.373$, $df = 3$, $P = 0.946$).

Meteorological data between the islands of Kythira and Antikythira (36°0'41.70"N, 23°14'56.59"E) at about 100 meters above sea level were obtained from the NCEP/NCAR reanalysis project (NOAA/OAR/ESRL PSD, Boulder, CO, USA; Kalnay *et al.* 1996) using the specific package 'RNCEP' for R (Kemp *et al.* 2012). These data are freely available state-of-the-art gridded reanalysis data sets with global coverage of many relevant atmospheric variables spanning 1957 to present. These data have a spatial resolution of 2.5° × 2.5° and a temporal resolution of 6 h (00, 06, 12, 18 h UTC) (Kemp *et al.* 2012). In the analysis we used daily weather data taken at 12:00 (solar time). Statistical analyses were made with R soft-

ware version 3.0.2 (R Development Core Team 2010).

3. Results

3.1. Weather conditions

Table 1 shows the average air temperatures, wind speeds, and wind directions during the peak periods of migration in the study area. In the Aegean Sea the prevailing wind during autumn is the “Meltemi wind” blowing from northern quadrants and this was particularly evident during the migration of European Honey Buzzards. Consequently, at least for this latter species, we should consider the wind of the present study almost as a tailwind (Fig. 3; see also Agostini *et al.* 2012). During the study period, there were not days with no wind at all (wind speed = 0).

3.2. Timing and phenology of autumn migration

In total 4,513 European Honey Buzzards and 1,065 Western Marsh Harriers were logged during the four autumn seasons. The earliest European

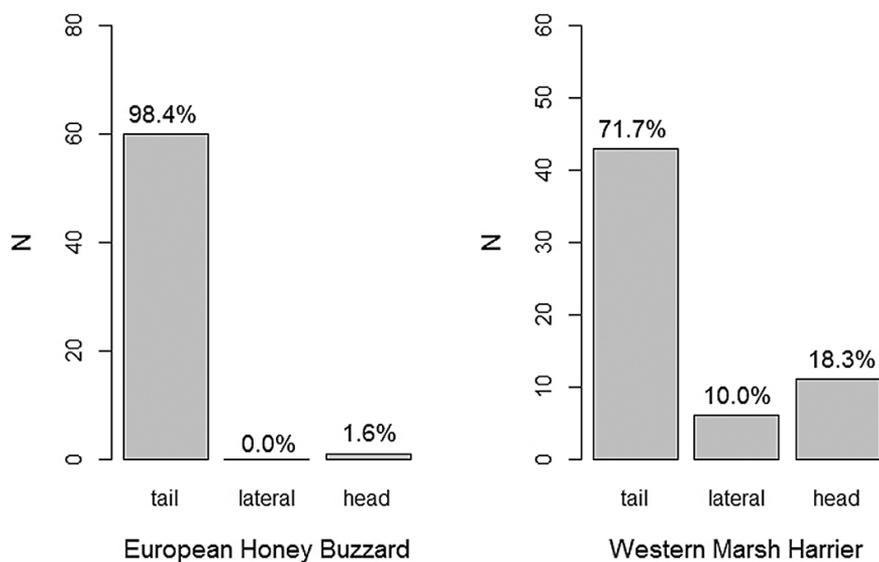


Fig. 3. Direction of winds occurring during the study period (N = days). Days from 20 August to 10 September and from 5 September to 20 September were taken into account for European Honey Buzzard and Western Marsh Harrier, respectively.

Table 2. Binary logistic regression analysis for European Honey Buzzard. The best model is marked in bold. Parameters estimates \pm standard errors are shown for models with $\Delta AIC_c < 2$.

MODEL	AIC_c	ΔAIC_c	w_i
intercept(-1.346 \pm 0.537), air temperature (1.427 \pm 0.507), wind speed (0.829 \pm 0.395), Julian date (-0.239 \pm 0.412) + Julian date² (0.071 \pm 0.382)	64.43	0.00	0.47
intercept (-1.353 \pm 0.552), air temperature (1.241 \pm 0.520), air pressure (-0.463 \pm 0.467), wind speed (0.769 \pm 0.399), Julian date (-0.232 \pm 0.417) + Julian date ² (0.028 \pm 0.386)	65.87	1.44	0.23
air temperature, Julian date + Julian date ²	66.94	2.51	0.14
air temperature, air pressure, Julian date + Julian date ²	67.46	3.03	0.10
air pressure, Julian date + Julian date ²	70.42	6.00	0.02
air pressure, wind speed, Julian date + Julian date ²	70.74	6.31	0.02
wind speed, Julian date + Julian date ²	72.86	8.43	0.01
Julian date + Julian date ²	73.99	9.56	0.00

Table 3. Generalized linear model analysis for the European Honey Buzzard. The best model is marked in bold. Parameters estimates \pm standard errors are shown for models with $\Delta AIC_c < 2$.

MODEL	AIC_c	ΔAIC_c	w_i
intercept (3.555 \pm 0.299), air temperature (0.847 \pm 0.241), wind speed (0.418 \pm 0.213), Julian date (-0.322 \pm 0.239) + Julian date² (0.268 \pm 0.225)	565.43	0.00	0.47
intercept (3.848 \pm 0.301), air temperature (0.780 \pm 0.248), Julian date (-0.315 \pm 0.246) + Julian date ² (0.059 \pm 0.223)	567.13	1.70	0.20
air temperature, air pressure, wind speed, Julian date + Julian date ²	567.53	2.09	0.16
air temperature, air pressure, Julian date + Julian date ²	568.54	3.11	0.10
air pressure, Julian date + Julian date ²	570.60	5.16	0.04
air pressure, wind speed, Julian date + Julian date ²	571.43	6.00	0.02
Julian date + Julian date ²	573.41	7.98	0.01
wind speed, Julian date + Julian date ²	574.18	8.75	0.01

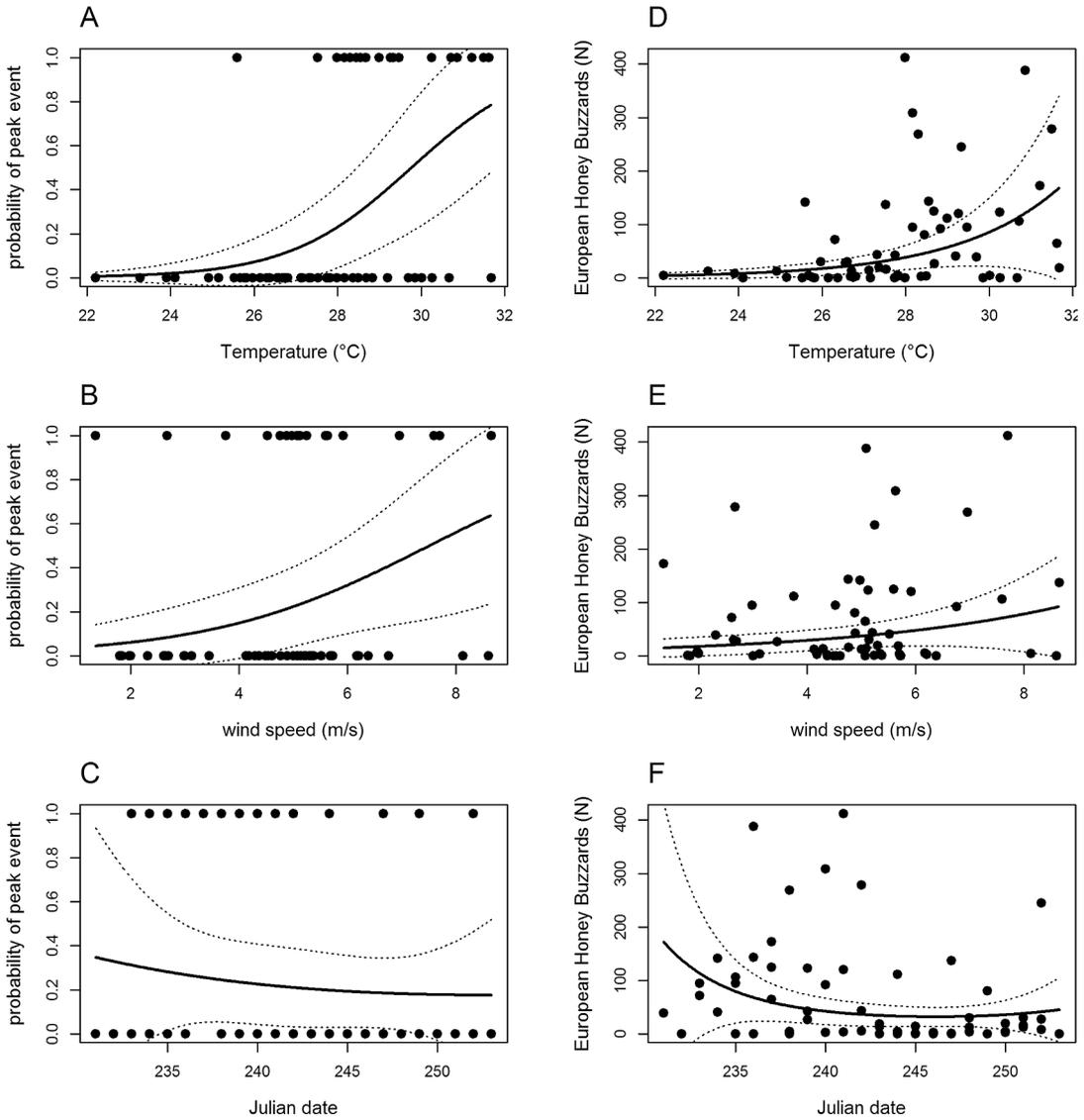


Fig. 4. Effect of air temperature (A), wind speed (B), and Julian date (C) on peak days of migration of European Honey Buzzard, and the effect of air temperature (D), wind speed (E), and Julian date (F) on the number of European Honey Buzzards observed. In both cases continue line represents the fitted values; the dashed lines show the 95% confidence intervals.

Honey Buzzard was recorded on 17 August 2013, the maximum count took place on 30 August 2013 ($N = 412$) while the median passage date for the species over the island was 29 August (pooled data; Fig. 2).

Both the best models (Tables 2 and 3) showed that the number of European Honey Buzzards decreased over time, underlining the negative effect of the Julian date (Fig. 4C, Fig. 4F).

The first Western Marsh Harrier was recorded on 19 August 2013, the maximum count took place on 20 September 2013 ($N = 66$) while the median passage date for the species over the island was 12 September (pooled data; Fig 2). Furthermore, as confirmed by the best models obtained (Tables 4 and 5) there was a non-linear effect of the Julian date, with an increase of Western Marsh Harriers observed until the peak of passage was

reached (i.e., day 256, equal to 12–13 September) and then a decrease over time (Fig. 5A, Fig. 5C).

3.3. European Honey Buzzard

The best BLRA model obtained showed that both air temperature and wind speed positively affected the high intensity days of migration (Table 2; Fig. 4). The probability that a day was a high intensity day is higher when the air temperature was greater than 29.8°C and the speed of the wind was greater than 7.5 m/s. The AUC of this model was 0.851 ($P < 0.001$), suggesting good accuracy of the model. The variables in the model showed no issues of collinearity ($VIF < 3$).

The best GLM model showed that both air temperature and wind speed positively affected the number of European Honey Buzzards, supporting the results of the BLRA (Table 3; Fig. 4). When the air temperature was greater than 31.9°C and the predicted speed of tailwind was higher than 11.4 m/s, the number of European Honey Buzzards observed was greater than 184 (i.e., the average number of individuals on the high intensity days). There was no collinearity between the variables in the model ($VIF < 3$). The goodness of fit test shows that the model was appropriate ($\chi^2 = 2,340.00$, $df = 2301$, $P = 0.281$).

3.4. Western Marsh Harrier

The best BLRA obtained showed that only the Julian date affected the high intensity days of migration (Table 4; Fig. 5A). Indeed the AUC of the model was 0.705 ($P = 0.014$), so the accuracy of the model was sufficient. Moreover increasing air temperature and increasing headwind speed positively influenced the passage of harriers over the island as shown by the two following models with $\Delta AIC_c < 2$ (Table 4).

The best GLM model showed that the number of Western Marsh Harriers was positively affected by the air temperature during migration (Table 5; Fig. 5B). The number of individuals observed was greater than 42 (i.e. the average number of individuals in the high intensity days) when the air temperature was higher than 29.4°C. The goodness of fit test shows that the model was appropriate ($\chi^2 = 1,404.00$, $df = 1378$, $P = 0.307$).

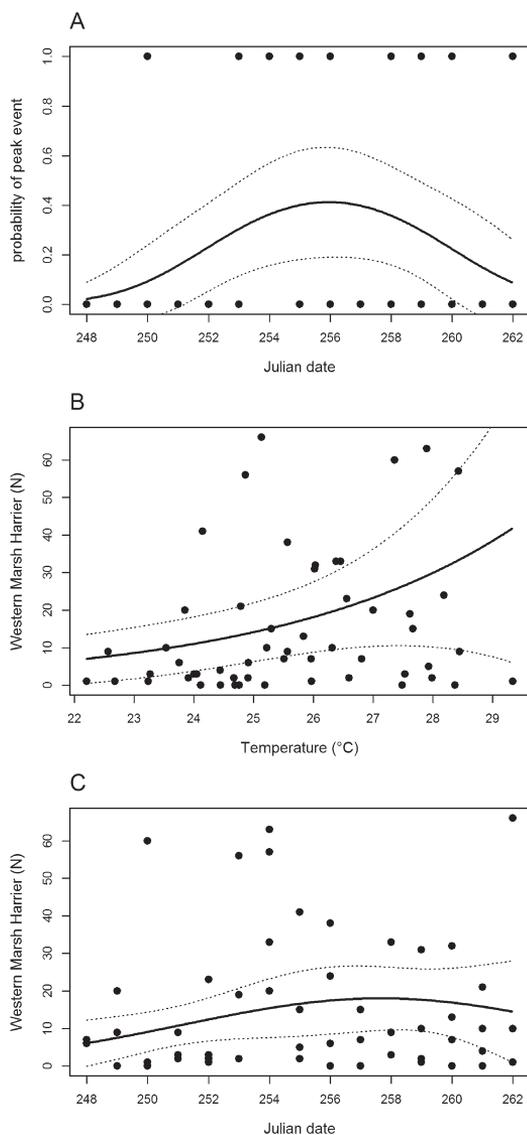


Fig. 5. Effect of Julian date on peak days (A) (fitted values and 95% confidence intervals are shown) and the effect of air temperature (B) and Julian date (C) on the observed number of migrating Western Marsh Harriers.

4. Discussion

The results partially support our starting hypothesis since the movements of the two studied species are influenced by weather conditions in both similar and different ways: the two species pass over the island of Antikythira when air temperatures are hot, whereas each of the two species appears to be

Table 4. Binary logistic regression analysis for Western Marsh Harrier. The best model is marked in bold. Parameters estimates \pm standard errors are shown for models with $\Delta AIC_c < 2$.

MODEL	AIC _c	ΔAIC_c	w_i
intercept (-0.396 ± 0.458), Julian date (0.402 ± 0.439) + Julian date² (-0.977 ± 0.500)	60.72	0.00	0.33
intercept (-0.492 ± 0.475), air temperature (0.408 ± 0.375), Julian date (0.476 ± 0.460) + Julian date ² (-0.930 ± 0.508)	61.82	1.10	0.19
intercept (-0.457 ± 0.480), wind speed \times wind direction (for tailwind -0.466 ± 0.460 , for headwind 1.480 ± 1.308), Julian date (0.439 ± 0.468) + Julian date ² (-0.846 ± 0.513)	62.25	1.53	0.15
intercept (-0.346 ± 0.465), air pressure (-0.262 ± 0.327), Julian date (0.365 ± 0.445) + Julian date ² (-1.049 ± 0.517)	62.41	1.69	0.14
air temperature, air pressure, Julian date + Julian date ²	63.87	3.15	0.07
air temperature, wind speed \times wind direction, Julian date + Julian date ²	63.97	3.25	0.06
air pressure, wind speed \times wind direction, Julian date + Julian date ²	64.67	3.95	0.05
air temperature, air pressure, wind speed \times wind direction, Julian date + Julian date ²	66.60	5.88	0.02

Table 5. Generalized linear model analysis for the Western Marsh Harrier. The best model is marked in bold. Parameters estimates \pm standard errors are shown for models with $\Delta AIC_c < 2$.

MODEL	AIC _c	ΔAIC_c	w_i
intercept (2.813 ± 0.260), air temperature (0.432 ± 0.176), Julian date (0.255 ± 0.175) + Julian date² (-0.209 ± 0.201)	400.80	0.00	0.45
intercept (2.909 ± 0.267), Julian date (0.164 ± 0.179) + Julian date ² (-0.239 ± 0.205)	402.84	1.96	0.17
air temperature, air pressure, Julian date + Julian date ²	403.22	2.33	0.14
air temperature, wind speed \times wind direction, Julian date + Julian date ²	404.50	3.62	0.07
wind speed \times wind direction, Julian date + Julian date ²	404.86	3.98	0.06
air pressure, Julian date + Julian date ²	405.00	4.12	0.06
air temperature, air pressure, wind speed \times wind direction, Julian date + Julian date ²	407.07	6.18	0.02
air pressure, wind speed \times wind direction, Julian date + Julian date ²	407.09	6.21	0.02

affected differently by the wind. European Honey Buzzards favored sea crossings in high air temperature and strong tailwind speed. Peak days of Western Marsh Harriers occur in the central part of the migration season and are less influenced by wind while the intensity of the migratory flow is positively influenced by air temperature.

4.1. Effect of wind

European Honey Buzzards pass over the island during days with good tailwind assistance confirming that this species travels faster and further in tailwinds (Vansteelant *et al.* 2015) also when flying over open sea. Tailwinds allow a faster and energetically less expensive flight over water for migrating birds (Liechti & Bruderer 1998). For raptors in particular, studies using different methods (visual observations, tracking radar, satellite

telemetry) converge showing that tailwinds allow a faster migration in soaring birds (Spaar & Bruderer 1997b, Mellone *et al.* 2012, Panuccio *et al.* 2013c). Previous research (Agostini 1992) reported a threshold value of tailwind of 35 km/h (about 9.7 m/s) beyond which European Honey Buzzards showed abnormal flight being unable to maintain a steady forward flight. However, since wind speeds were rarely stronger than 8 m/s during our study period (Tab. 1), we suggest that buzzards were able to undertake the sea crossing almost every day. In this regard although our best GLM predicted the highest number of European Honey Buzzards passing during tailwind stronger than 11.4 m/s it is likely that in case of winds exceeding 10 m/s raptors are forced to stop the migration. A recent study showed that soaring birds, when migrating over land, do not fly as fast as they can but decrease their gliding speed to limit the risk of grounding (Horvitz *et al.* 2014). We can assume

that this behavior would be more evident over sea (see also Agostini *et al.* 2016).

In the case of Western Marsh Harriers the positive influence of headwinds can confirm that under less favorable wind conditions raptors tend to limit their flight over open sea by following land masses and passing over islands (Panuccio *et al.* 2002, Panuccio *et al.* 2011).

4.2. Effect of air temperature

Higher temperatures lead to stronger convection and, consequently, to a better travel performance being a strong support to efficient soaring-gliding flight (Shamoun-Baranes *et al.* 2003, Vansteelant *et al.* 2015). Radar and satellite tracking studies over land have highlighted that, when strong thermals are available, soaring birds can climb higher and glide over longer distances, and therefore faster migration speeds are obtained (Spaar 1995, Lanzone *et al.* 2012, Mellone *et al.* 2012). Thus, our results suggest that raptors may be attracted to the island in days with stronger thermal activity when they can find good soaring opportunities. Previous research on the influence of weather on the migration of Short-toed Snake Eagles (*Circaetus gallicus*) showed that when air temperature rises above 24°C, the observed number of eagles decreased probably as a consequence of the increasing flight altitude of raptors that therefore are out of sight from the observers based along mountain chains (Panuccio *et al.* 2013c). At the island of Antikythira we did not find this pattern because flying raptors approach the island from the sea where they usually fly at low altitude (Kerlinger 1989).

4.3. The flight over sea

The few studies that simultaneously consider wind and thermal soaring conditions show that both variables affect the migration of raptors over land, although tailwind had the largest effect on migratory speeds (Mellone *et al.* 2012, Vansteelant *et al.* 2015). Over water, evidence of important factors influencing migration is more heterogeneous probably because of the different geographical

context and seasons in which the different studies have been conducted. For example, most raptors show higher migration speed during spring rather than during summer/autumn as a result of a more time-constrained strategy to reach breeding territories as soon as possible (Mellone *et al.* 2012, 2015, Nilsson *et al.* 2013). In addition, the length of the water-crossing probably affects bird strategies under specific weather conditions differently. Previous studies have stated that strong wind discourage water crossings, in particular strong headwinds and crosswinds (Kerlinger 1984, Meyer *et al.* 2000, Panuccio *et al.* 2002, Agostini *et al.* 2005).

A recent radar study from southern Italy suggested that raptors crossed the Strait of Messina (3–15 km wide) with good tailwind assistance, despite they did not select the best flight altitude in relation to wind (until 2,500 m a.g.l.; Mateos-Rodríguez & Liechti 2011) while other researchers suggested that with tailwinds, raptors bypass the Strait flying a more direct route and undertaking a longer water-crossing (Agostini *et al.* 2007, 2016, Panuccio 2011). In any case, we can expect that raptors undertaking sea crossings reach higher flight speeds than they do over land in order to minimize the time spent over the water barrier (Vansteelant *et al.* 2015).

4.4. Conclusions

Raptors migrating in autumn through the Aegean Sea must reach the coast of northern Africa located about 350 km south of the continental coast of Greece and therefore they migrate by island hopping via the islands of Kythira, Antikythira and Crete (Bildstein 2006, Agostini *et al.* 2012, Panuccio *et al.* 2013b). For this migration, the two species selected hot days and stable weather conditions in order to minimize both mortality risk and energy consumption during this long sea crossing. When considering the winds during migration, the European Honey Buzzard migrated mostly with strong tailwind assistance while the Western Marsh Harrier was less wind selective probably because of its higher ability in using powered-flapping flight (Spaar & Bruderer 1997a, Agostini *et al.* 2015).

Acknowledgments. We thank Andreas Lindén, María Mateos-Rodríguez, Wouter Vansteenlant and both an anonymous referee and the Associate Editor for their comments to earlier drafts of the manuscript. We are grateful to all the people who made observations at the island of Antikythira and in particular: Ugo Mellone, Giuseppe Lucia, Diego Tarini, Teodoros Kominos. We wish to thank MEDRAPTORS (www.raptormigration.org), a network of ornithologists involved in the research and the protection of migrating birds of prey through specific projects and observation camps. We thank Christian Christodoulou-Davies and Victoria Saravia Mullin for language editing on earlier versions of this manuscript. This is contribution n. 20 from Antikythira Bird Observatory – Hellenic Ornithological Society. Antikythira Bird Observatory is funded from the A.G. and A.P Leventis Foundation.

Lämmin ilma ja myötätuli edesauttavat petolintujen muuttoa Egeanmeren yli

Joka syksy, suuri määrä petolintuja muuttaa länsipalearktiselta alueelta Afrikkaan. Ne lajit ja populaatiot, joiden muuttoreitti kulkee Välimeren kautta, joutuvat ylittämään varsin mittavan ekologisen esteen, varsinkin Välimeren keski-itäosissa. Tutkimme kahden petolintulajin – mehiläishaukan ja ruskosuohaukan – muuton ajoittumista suhteessa päivittäiseen säävaihteluun ja vuodenaikaan analysoimalla neljän vuoden aineistoa pieneltä kreikkalaiselta saarelta.

Tutkittujen lajien sääolosuhteiden valinnassa on sekä yhtäläisyyksiä että eroavaisuuksia. Muutto on molemmilla lajeilla voimakkaampaa silloin kun ilman lämpötila on korkea. Mehiläishaukka muuttaa mieluiten päivinä jolloin myötätuulesta on apua merenylityksen lentoajan lyhentämisessä, mikä pienentää myös kuolleisuusriskiä ja energiankulutusta. Sitä vastoin ruskosuohaukka on vähemmän vaateliias tuulen suhteen ja saattoi muuttaa suurissa määrin myös vastatuulella. Tämä joutune ruskosuohaukan suuremmasta taipumuksesta käyttää aktiivista lepattavaa lentoa muuttaessaan.

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