Species-Specific Behaviour of Raptors Migrating Across the Turkish Straits in Relation to Weather and Geography

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SPECIES-SPECIFIC BEHAVIOUR OF RAPTORS MIGRATING ACROSS THE TURKISH STRAITS IN RELATION TO WEATHER AND GEOGRAPHY

COMPORTAMIENTO ESPECÍFICO DE LA ESPECIE EN RAPACES MIGRATORIAS EN LOS ESTRECHOS DE TURQUÍA EN RELACIÓN CON LA METEOROLOGÍA Y LA GEOGRAFÍA

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SUMMARY.—Afro-Palearctic migrants move between breeding and wintering grounds along flyways determined by several factors (bird morphology, geography, behavioural adaptations) and raptors often concentrate at straits to avoid long sea crossings. Here we test the hypothesis that raptor passages across different areas of the Turkish straits are similar in species composition as well as flight behaviour. We made simultaneous observations at the Bosphorus and at the Dardanelles in autumn 2010. We tested the influence of weather, time of day and flock size on the intensity and spatial shift of migratory flow as well as the tendency to cross the Dardanelles Strait rather than follow the peninsula. We also collected information of the flight altitude of raptors using an optical range finder. The species composition observed at the two sites was completely different, with eagles predominating at the Bosphorus and small and medium-sized raptors predominating at the Dardanelles Strait. Compensation for wind drift at the Bosphorus was species-specific, with small and medium-sized raptors showing a drift effect by crosswinds, and eagles showing compensation and overcompensation. Mean flight altitude was similar among species, while the response to weather conditions varied, being mainly affected by wind. In the case of Short-toed Snake-eagles, flight ability and response to weather conditions was also age-dependent. These results show that the flight strategies of migrating raptors are species-specific even if some flight parameters may converge as a result of risk minimisation. The differences between species and flyways probably reflect interspecific differences in the ability to fly over water.

Key words: Bosphorus, Dardanelles Strait, raptor migration, Turkey, weather.

RESUMEN.—Las aves migratorias afropaleárticas se desplazan entre las áreas de reproducción e invernada a través de rutas determinadas por distintos factores (morfología corporal, geografía, adaptaciones comportamentales) y las rapaces frecuentemente se concentran en estrechos para evitar largas trayectorias sobre el mar. Aquí testamos la hipótesis de que los pasos migratorios de las rapaces a través de distintas áreas de los estrechos en Turquía son similares en cuanto a la composición de especies

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y en el comportamiento de vuelo que estas manifiestan. Para ello, hicimos observaciones simultáneas en el Bósforo y los Dardanelos en otoño de 2010. Comprobamos la influencia de la meteorología, la hora del día y el tamaño del bando sobre la intensidad y el desplazamiento espacial del flujo migratorio, así como sobre la tendencia a cruzar el estrecho de los Dardanelos en lugar de seguir la península. Recogimos también información sobre la altitud de vuelo usando un distanciómetro láser. La composición de especies observada en los dos lugares fue completamente diferente, con un predominio de águilas en el Bósforo y de pequeñas y medianas rapaces en el estrecho de los Dardanelos. La compensación por deriva por viento en el Bósforo fue específica de las especies, de forma que las pequeñas y medianas rapaces mostraron un efecto de deriva por vientos cruzados, mientras que las águilas mostraron compensación y sobrecompensación. La altitud promedio de vuelo fue similar entre especies, mientras que la respuesta a las condiciones meteorológicas varió, siendo principalmente afectada por el viento. En el caso de la culebrera europea, la habilidad en el vuelo y la respuesta a las condiciones meteorológicas dependió también de la edad. Estos resultados muestran que las estrategias de vuelo de las rapaces migratorias son específicas de las especies, incluso si algunos parámetros de vuelo pueden converger como resultado de la minimización del riesgo. Las diferencias entre especies y rutas migratorias probablemente reflejen diferencias interespecíficas en la capacidad de volar sobre el agua.

Palabras clave: Bósforo, estrecho de Dardanelos, migración de rapaces, tiempo atmosférico, Turquía.

INTRODUCTION

For many bird species, the most risky life stage occurs during migration (Klaassen *et al.*, 2014). Many species perform long-distance migrations between breeding and non-breeding grounds with tremendous energetic costs, especially when overcoming ecological barriers such as deserts, water bodies and high mountain chains. As a result, birds have evolved migration strategies that allow them to survive and reproduce successfully. In general, migrants are expected to show morphological features that minimise the cost of locomotion for efficient migration (Alerstam, 1991; Åkesson & Hedenström, 2000). For example, migration speed is increased by wings with a high aspect ratio (wingspan squared divided by wing area). However, wing shape is just one morphological parameter affecting flight performance. Theory predicts that the mechanical power required to fly increases with body mass (Pennycuick, 1975), and recent studies have shown that body mass is the main factor influencing flight style (Agostini *et al.*, 2015a; Panuccio *et al.*, 2013b). In particular, the maximum possible body mass for a bird using flapping flight is 12 kg (Hedenström, 2003). In consequence, large birds use soaring flight to gain altitude, mainly by circling in thermals and then gliding to the next thermal current (Bildstein, 2006). Since soaring species greatly vary in size and wing shape, differences in their flight behaviour may be explained by bird size and morphology, as well as different responses to weather conditions such as wind and convective thermal uplifts. In particular, eagles and vultures have a lower limit for efficient use of thermals than smaller raptors such as harriers and falcons. They are also more vulnerable to crosswinds, which cause them to refrain from migration or accept a drift (Hedenström, 1993).

However, interspecific differences in many flight parameters seem to be smaller than previously predicted (Spaar, 1997; Horvitz *et al.*, 2014; Mellone *et al.*, 2012). Our aim here was to determine whether different raptor species show similar flight strategies and responses to abiotic factors such as weather, geography and time of day. For this purpose we investigated interspecific differences in migratory behaviour of birds of prey, making visual observations at two watchsites in Turkey, the Bosphorus and the Dardanelles Strait. In this area, the migratory flow is heavier at the Bosphorus (Porter & Willis, 1968; Beaman, 1973; Beaman & Jacobsen, 1974; Bijlsma, 1987; Fülöp *et al*., 2014). However, the migratory front is wider, involving the passage of raptors also over the Sea of Marmara and the Dardanelles Strait (Nisbet & Smout, 1957; Tuncalı, 2010), where systematic observations during autumn are lacking. We tested the null hypothesis that raptor passage across different areas of the Turkish straits would be similar in species composition as well as flight behaviour under different weather conditions.

MATERIAL AND METHODS

Fieldwork and weather data

We made observations simultaneously at two watchsites located at both ends of the Turkish straits: Bosphorus and Dardanelles. Our site at the Bosphorus was Toygar Tepe (41° 07’ 42” N, 29° 08’ 43” E, 310 m a.s.l.), a point on the Asian side about 20 km north of the Sea of Marmara and 10 km south of the Black Sea (Figure1). The Bosphorus Channel in this area is between 0.8 and 2.2 km wide. We made observations from the roof of the forestry fire-fighter service building. Woodlands dominate the northern region of both sides of the Bosphorus despite the relative

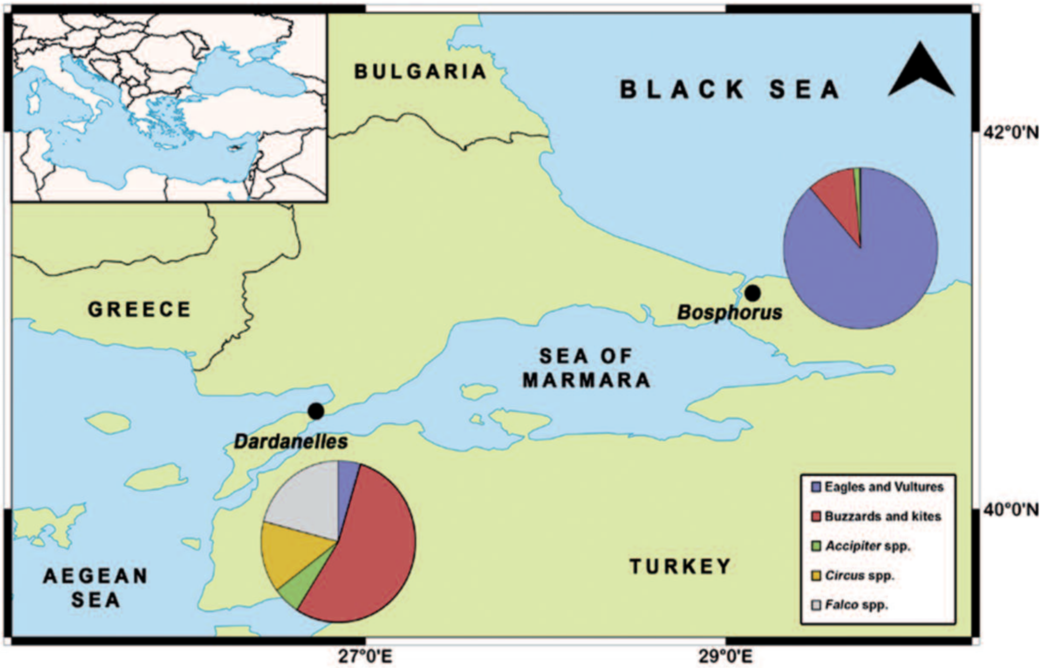

FIG. 1.—Study area with proportions of the different groups of raptors observed. Points indicate the watchpoints.

[Área de estudio con la proporción de los diferentes grupos de rapaces detectados. Los puntos indican los lugares de observación.]

density of buildings. We obtained hourly weather data for this site from the Meteorological Station at Istanbul Ataturk Airport located on the European side of the Strait (available at www.wunderground.com).

At the Dardanelles we made observations at Çimpe Kalesi (40° 29’ 47” N, 26° 44’ 03” E), a hill with ruins of a Byzantine fortress that is about 140 m a.s.l. and where the Dardanelles Peninsula is about 5 km wide. From this point it is possible to see both the Mediterranean coast and the Strait (at this point about 4 km wide). We collected weather data hourly using a portable meteorological station, with the anemometer positioned on a pole 3.5 m above ground.

At both watchsites we made observations between 07:30 and 17:30 (UTC/GMT+2h) on 41 days between 22 August and 1 October 2010. Observations were interrupted by heavy rain at the Bosphorus on 12 September and at the Dardanelles on 30 September; these days were excluded from our analysis.

Statistical models

We fitted Generalized Linear Models to explain (1) hourly counts of raptors (with Poisson or negative binomial regression, depending on the species), (2) flight altitude (with Gaussian or Poisson distribution) and (3) the tendency to cross the Dardanelles Strait (as opposed to following the peninsula) for each species. We used the following variables as independent factors: i) wind direction (categorical variable), ii) wind speed (km/h), iii) wind direction *wind speed interaction, iv) air temperature (°C), v) air pressure (mbar), vi) air humidity (%), vii) time of day and viii) flock size. To analyse variation in the migratory flow at the Bosphorus we used three categories of wind direction: northerly, southerly and other winds, since crosswinds were the commonest winds (see Results section). However, since flight altitude can be strongly influenced also by headwinds and tailwinds (Kerlinger, 1989), in this analysis we used up to five categories: northerly, southerly, easterly, westerly and light or variable winds; the number of categories varying depending on the subset of analysed data. For the Dardanelles we considered up to four categories: southerly, northerly, easterly and westerly winds. To investigate the influence of the time of the day we calculated the interval from local noon; these values were thus negative before noon and positive afterwards (Mellone *et al*., 2012).

The Variance Inflation Factor (VIF) was measured for the model with a threshold of 3 to test collinearity of variables (Zuur *et al*., 2010). In case of collinearity we deleted the variable ‘air humidity’ and thereafter, if necessary, ‘air pressure’ from the subset (tables indicate when these variables were omitted). We evaluated the model fitness checking the normal distribution of the model residuals (in the GLM with Gaussian, negative binomial or Poisson distributions) while, in the case of logistic regressions, we tested the ability of the model to distinguish between the two tested behaviours (binary dependent variable) by means of the area under the curve of the Receiver Operating Characteristic (ROC), using ROCR package in R software (Pearce & Ferrier, 2000; Boyce *et al*., 2002; Sing *et al*., 2004; Fawcett, 2006).

Data analysis

We analysed data only for the most abundant species, in the period when the 95% of the individuals of each species was counted. For analyses of the Bosphorus data we considered European Honey-buzzards *Pernis apivorus*, Lesser Spotted Eagles *Clanga pomarina*, Common/Steppe Buzzards *Buteo buteo*, Booted Eagles *Hieraaetus pennatus*, Short-toed Snake-eagles *Circaetus gallicus* (adults and juveniles) and also accipiters (Eurasian Sparrowhawks *Accipiter nisus*, Levant Sparrowhawks *A. brevipes* and unidentified *Accipiter* spp.) these last considered together because of their similar morphology and behaviour (Porter & Willis, 1968; Pennycuick, 2008; Vansteelant *et al.*, 2014). Unlike the other species, Short-toed Snake-eagles varied in the proportion of juveniles and adults during the study period, with a greater number of juveniles recorded during the later period of observations. Since migration strategy in relation to wind drift is age-dependent in some species (Thorup *et al.*, 2003), we tested whether different proportions of juveniles influenced the behavioural analysis. For this reason we divided the migration period into two sectors: the Short-toed Snake-eagle early period (up to 24 September), when most observed individuals were adults, and the Short-toed Snake-eagle late period (from 25 September), when the proportion of juveniles increased (Contingency table: $\chi^2 = 35.2$, $P < 0.001$; aged individuals: N = 527). For the analyses of the Dardanelles data, we considered the following species: falcons (Red-footed Falcon *Falco vespertinus*, Common Kestrel *Falco tinnunculus*, Eurasian Hobby *Falco subbuteo*), buzzards and kites (European Honey-buzzard, Common/Steppe Buzzard and Black Kite), eagles (Lesser Spotted Eagle, Short-toed Snake-eagle, Booted Eagle, Eastern Imperial Eagle *Aquila heliaca* and *Aquila* spp.) and harriers (Western Marsh-harrier *Circus aeruginosus*, Montagu's Harrier *C. pygargus* and Pallid Harrier *C. macrourus*, as well as unidentified harriers) pooled because of similar morphology and behaviour (Spaar & Bruderer, 1997; Panuccio, 2011; Vansteelant *et al.*, 2014).

Variation in migratory flow

We tested the effect of time of day and weather variables (including the interaction between wind speed and direction) on the variation in migratory flow at the two sites using GLMs. We used the hourly numbers of raptors of each species as the dependent variable. In order to keep our analysis as conservative as possible, we did not consider hours in which no raptors were recorded, since this could have been related to factors occurring outside our study area (Agostini *et al.*, 2015b; Panuccio *et al.*, 2010).

To cross the strait or to follow the peninsula?

For migration at the Dardanelles, we tested whether raptors showed a species-specific tendency to follow the peninsula rather than to cross the strait when passing close to our watch-site. To do this, we used a logistic regression (Boyce *et al.*, 2002; Keating & Cherry, 2004; Rushton *et al.*, 2004) where the dependent variable was *crossing the sea/following the peninsula* (1/0), and the independent variables were those described above. We analysed which variables affected this behaviour for all the species together and, separately, for the two most commonly observed species: Western Marsh-harrier and European Honey-buzzard. For the latter, we distinguished (as a covariate) between early and late periods because, as expected, until 10 September we observed mostly adults (57 *vs.* 46) while after 11 September juveniles predominated (18 *vs.* 93; contingency table: $\chi^2 = 35.9$, $P < 0.001$, N = 214; see also Agostini & Panuccio, 2005). This was in contrast to our Bosphorus observations, where we saw few European Honey-buzzards (only 43 individuals) after 10 September.

Variation of flight altitude of raptors

We investigated the variation of flight altitude of raptors at the Bosphorus by using an optical range finder to measure the vertical distance between observer and bird when it was flying directly overhead. It was possible to collect sufficient data for four species: Lesser Spotted Eagle (N = 172), Booted Eagle (N = 55), Short-toed Snake-eagle (N = 126) and Common/Steppe Buzzards (N = 72). We compared the median altitudes of the four species with a Kruskal-Wallis test and used GLMS with Gaussian or Poisson distribution, depending on the distribution of the data, to test which variables (see the Statistical Models section) affected flight altitude variation of each species.

RESULTS

Wind conditions at the two straits

At the Bosphorus, excluding 16 observation hours with variable direction, winds had a northerly component (average speed 22.6 km/h) for 64.6% of observation hours, a southerly component (average speed 11.9 km/h) for 31% of observation hours; the remaining 4.4% of observation hours had winds blowing from the east (headwind; average speed 24.6 km/h) or west (tailwind; average speed 12.2 km/h).

At the Dardanelles Strait, prevailing winds had an easterly component (average speed 24.3 km/h) for 63% of observation hours, a northerly component (average speed 21.5 km/h) for 20% of observation hours, westerly (average speed 14.7 km/h) for 11% and southerly (average speed 15 km/h) for 6%.

Bosphorus

At the Bosphorus we counted a total of 24,701 raptors of 25 species (Table 1). The Lesser Spotted Eagle was the most common (78.2% of observed individuals), followed by the Short-toed Snake-eagle (8.2%) and the Common/Steppe Buzzard (7.9%).

Intensity of migratory flow

The GLMs explaining variation in the hourly number of raptors observed showed inter-specific differences in the effect of different variables (Table 2). As a general pattern, crosswinds were the most important factors influencing the number of counted raptors, affecting six of the seven species or species-groups considered (Table 2). Hourly numbers of *Accipiter* spp., Common/Steppe Buzzards, European Honey-buzzards and juvenile Short-toed Snake-eagles were lower with northerly winds (Figure 2). Additionally, when wind became stronger, the number of Lesser Spotted Eagles observed increased (estimate: 0.2 ± 0.1). The same tendency was marginally apparent also in adult Short-toed Snake-eagles (estimate: 0.05 ± 0.04). Moreover the interaction between wind direction and speed influenced the passage of Lesser Spotted Eagles, with the effect of wind speed being stronger under northerly than southerly winds (estimates: northern 0.3 ± 0.1; southerly 0.08 ± 0.01). The wind speed*wind direction interaction also affected the number of Booted Eagles and Common/Steppe Buzzards; in these species, and in contrast with Lesser Spotted Eagles, the interaction shows that the effect of wind speed was stronger under southerly winds than northerly winds, this effect being more marked for buzzards (estimates: northerly –0.5 ± 0.3; southerly 0.7 ± 04) than for Booted Eagles (estimates: northerly –0.02 ± 0.06; southerly 0.2 ± 0.09).

Air pressure had a negative effect on passage of both European Honey-buzzards (Table 2, estimate: –0.3 ± 0.07) and Common/Steppe Buzzards (estimate: –0.2 ± 0.04). The latter was also negatively affected by air humidity (estimate: –0.04 ± 0.01). The Lesser Spotted Eagle was influenced also by air temperature (Table 2, estimate: 0.2 ± 0.006). Finally the time of day influenced the number of *Accipiter* spp. and Lesser Spotted Eagles, with migration intensity being lower later in the day (estimates: –0.1 ± 0.06 and –0.1 ± 0.004 respectively).

TABLE 1

Raptor species observed during the present study.
[Especies de rapaces observadas en el presente estudio.]

Species	Bosphorus	Dardanelles
Griffon Vulture, *Gyps fulvus*	1	0
Egyptian Vulture, *Neophron percnopterus*	11	2
White-tailed Eagle, *Haliaaetus albicilla*	2	0
Lesser Spotted Eagle, *Clanga pomarina*	19325	20
Greater Spotted Eagle, *Clanga clanga*	4	1
Golden Eagle, *Aquila chrysaetos*	0	2
Eastern Imperial Eagle, *Aquila heliaca*	5	3
Steppe Eagle, *Aquila nipalensis*	1	0
Aquila spp.	1	1
Booted Eagle, *Hieraaetus pennatus*	497	20
Short-toed Snake-eagle, *Circaetus gallicus*	2034	26
Osprey, *Pandion haliaetus*	0	3
European Honey-buzzard, *Pernis apivorus*	456	646
Black Kite, *Milvus migrans*	20	44
Red Kite, *Milvus milvus*	1	0
Common/Steppe Buzzard, *Buteo buteo*	1958	173
Long-legged Buzzard, *Buteo rufinus*	7	15
Levant Sparrowhawk, *Accipiter brevipes*	180	84
Northern Goshawk, *Accipiter gentilis*	1	0
Eurasian Sparrowhawk, *Accipiter nisus*	134	6
Accipiter spp.	20	2
Western Marsh-harrier, *Circus aeruginosus*	9	167
Hen Harrier, *Circus cyaneus*	9	0
Pallid Harrier, *Circus macrourus*	1	1
Montagu's Harrier, *Circus pygargus*	2	63
Lesser Kestrel, *Falco naumanni*	1	0
Eurasian Hobby, *Falco subbuteo*	19	33
Common Kestrel, *Falco tinnunculus*	1	26
Red-footed Falcon, *Falco vespertinus*	1	280

TABLE 2

GLMs explaining variation of hourly numbers of raptors of different species counted at the Bosphorus. Asterisks indicate significant terms.
[GLMs para explicar la variación en los conteos de las distintas especies de rapaces detectadas en el Bósforo. Los asteriscos indican términos significativos.]

Species	**Covariates**	**F**	**d.f.**	***P***
Accipiter spp.	Wind direction	11.6	2	0.01*
	Wind speed	0.0003	1	0.9
	Wind dir.*speed	0.9	2	0.4
	Air humidity	3.5	1	0.06
	Air temperature	0.3	1	0.6
	Air pressure	0.08	1	0.7
	Time of the day	5.5	1	0.02*
European Honey-buzzard	Wind direction	3.3	2	0.04*
	Wind speed	1.8	1	0.2
	Wind dir.*speed	1.6	2	0.2
	Air humidity	1.5	1	0.2
	Air temperature	0.1	1	0.7
	Air pressure	8.3	1	0.007*
	Time of the day	0.006	1	0.9
Common/Steppe Buzzard	Wind direction	4.5	2	0.01*
	Wind speed	2.1	1	0.2
	Wind dir.*speed	8.4	2	0.0004*
	Air humidity	6.7	1	0.001*
	Air temperature	0.4	1	0.5
	Air pressure	15.1	1	0.0002*
	Time of the day	0.8	1	0.4
Booted Eagle	Wind direction	1.4	2	0.2
	Wind speed	1.1	1	0.3
	Wind dir.*speed	4.2	2	0.02*
	Air temperature	2.3	1	0.09
	Air pressure	0.3	1	0.6
	Time of the day	1.2	1	0.3
Lesser Spotted Eagle	Wind direction	1.1	2	0.3
	Wind speed	12.2	1	0.0007*
	Wind dir.*speed	7.9	2	0.0006*
	Air humidity	1.3	1	0.2
	Air temperature	7.4	1	0.008*
	Air pressure	0.04	1	0.8
	Time of the day	5.5	1	0.02*

Species	Covariates	F	d.f.	*P*
Short-toed Snake-eagle - Adults	Wind direction	0.3	2	0.7
	Wind speed	2.8	1	0.08
	Wind dir.*speed	0.1	2	0.9
	Air temperature	0.4	1	0.5
	Air pressure	0.1	1	0.7
	Time of the day	1.3	1	0.3
Short-toed Snake-eagle - Juveniles	Wind direction	3.7	2	0.04*
	Wind speed	2.3	1	1.1
	Wind dir.*speed	0.8	2	0.5
	Air humidity	0.2	1	0.7
	Air temperature	1.2	1	0.3
	Air pressure	0.09	1	0.8
	Time of the day	0.5	1	0.5

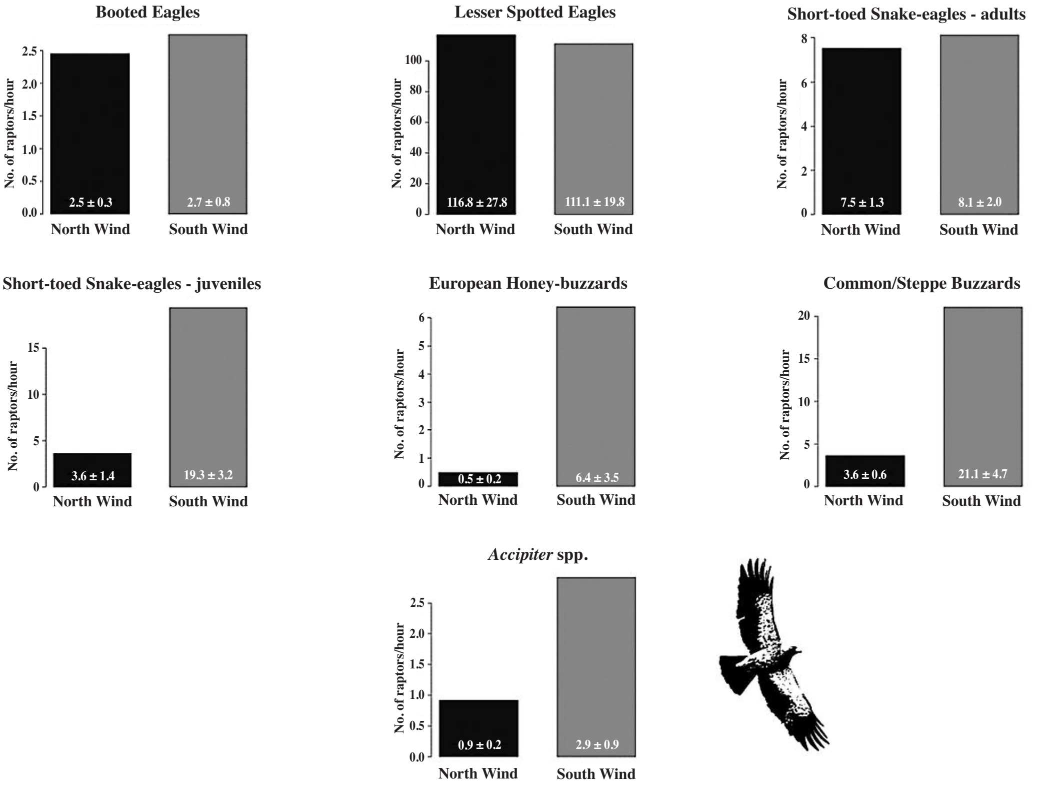

FIG. 2.—Hourly numbers of raptors observed at the Bosphorus under the two different crosswind conditions (northerly and southerly winds). Hourly means ± SE are reported for each category.

[Número por hora de rapaces observadas en el Bósforo bajo dos diferentes condiciones de viento (de componentes norte y sur). Se indican las medias (± SE) para cada hora en cada categoría.]

Variation in flight altitude

Flight altitudes of the four most commonly recorded species, Common/Steppe Buzzard, Booted Eagle, Lesser Spotted Eagle, Short-toed Snake-eagle, were similar (Kruskal-Wallis test; $H = 5.9$, d.f. = 3, $P > 0.05$; Figure 3). In general, with the wind speed increase, raptors tended to fly at lower altitudes and passed below our watchpoint (Figure 4). Table 3 shows the results of the statistical analyses explaining variation in flight altitude of different species. Wind direction significantly explained flight altitude for all species except Common/Steppe Buzzards. All the eagle species flew lower during tailwinds: Booted Eagle (estimates: tailwind –124.7 ± 99.5; headwind 57.1 ± 123.6; northerly 49.9 ± 86.8; southerly 77.1 ± 172), Lesser Spotted Eagle (estimates: tailwind –38.5 ± 29.5; headwind 53.5 ± 255.9; northerly 2.8 ± 42.6; southerly 37.7 ± 49.4); Short-toed Snake-eagle (estimates: tailwind –205.6 ± 71.9; headwind –126.6 ± 489.5; northerly –145.2 ± 86.8; southerly –171.2 ± 60.7). The flight altitude of Common/Steppe Buzzards decreased with air temperature (Table 3, estimate: –10.2 ± 5.3). Finally air pressure had a negative effect on flight altitude of Lesser Spotted Eagles (estimate: –4.5 ± 2.0), as well as marginally the time of day (estimate: –3.8 ± 1.9).

Dardanelles Strait

At the Dardanelles Strait watchsite, we detected a total of 1,601 raptors of 20 species (Table 1). The European Honey-buzzard was the most commonly recorded (39.9% of observations), followed by the Red-footed Falcon (17.3%), Common/Steppe Buzzard (10.9%) and Western Marsh-harrier (10.3%).

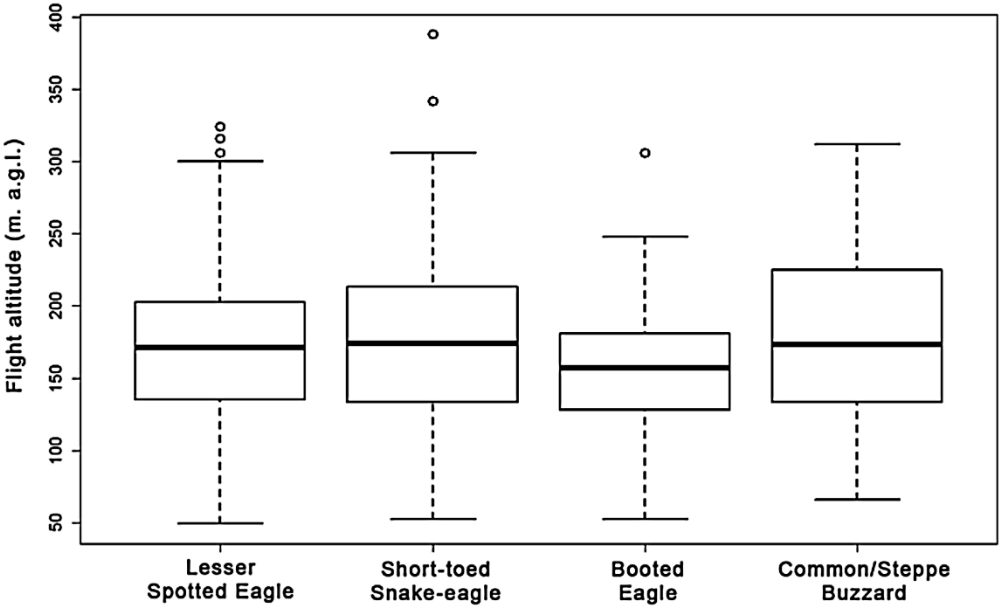

FIG. 3.—Flight altitudes of four species observed at the Bosphorus.
[Altitudes de vuelo de cuatro especies observadas en el Bósforo (de izquierda a derecha: águila pomerana, culebrera europea, águila calzada, busardo ratonero / de estepa.]

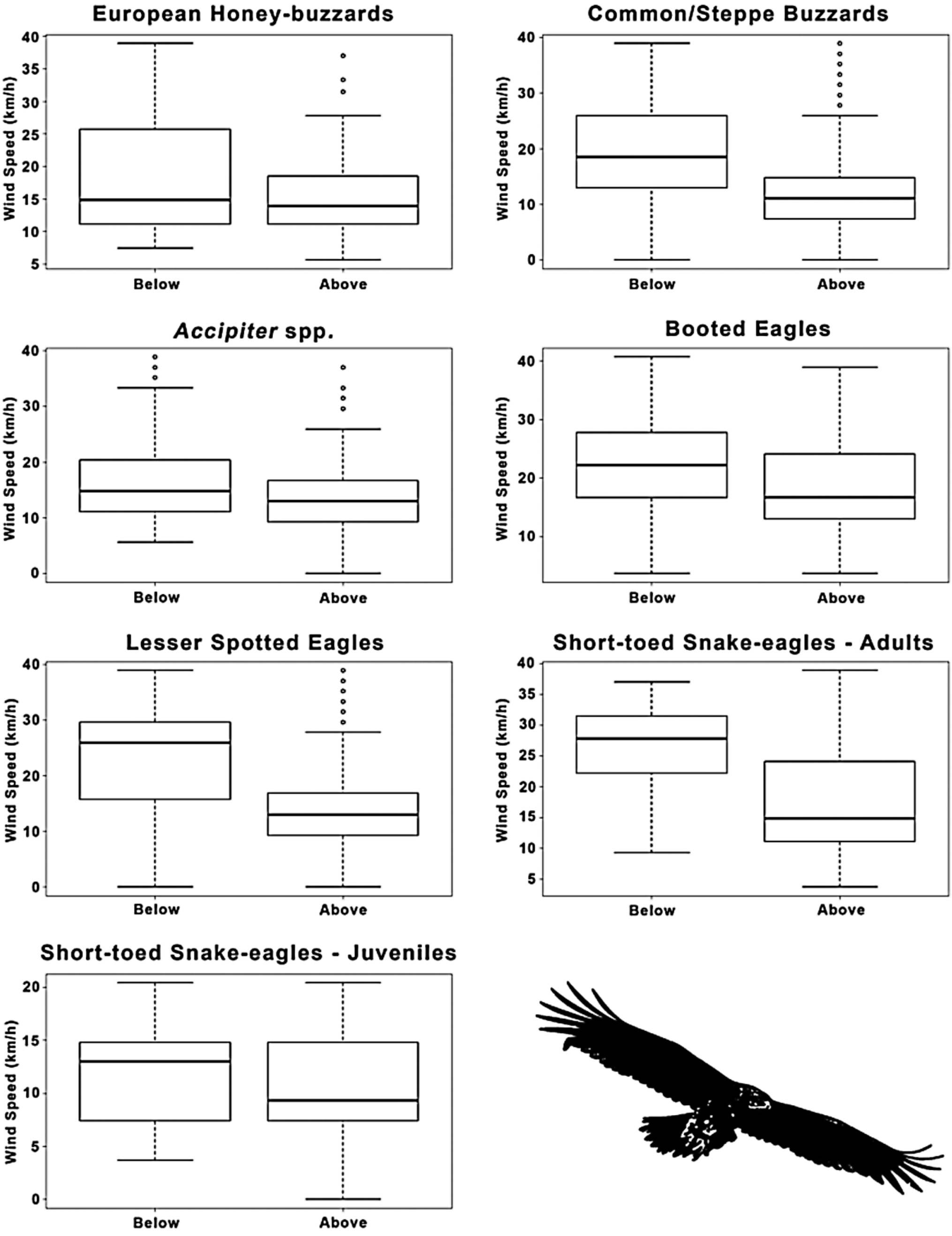

FIG. 4.—Box-plots showing the proportion of raptors observed passing above and below our watchpoint at the Bosphorus in relation to wind speed.

[Diagramas de cajas que muestran la proporción de rapaces observadas pasando por encima y por debajo del punto de observación en el Bósforo en relación con la velocidad del viento.]

Intensity of migratory flow

Table 4 shows results of the GLMs explaining the hourly variation in migratory flow. None of the considered variables significantly explained variation for *Circus* spp. The passage of European Honey-buzzards was positively influenced by air pressure (estimate: 0.2 ± 0.05) and, marginally significantly, by air temperature (estimate: 0.2 ± 0.07). On the other hand, falcons (mostly Red-footed Falcons) were more commonly observed when air humidity was higher (estimate: 0.09 ± 0.02) and when air pressure was lower (estimate: –0.2 ± 0.06). Finally the hourly passage of Common/Steppe Buzzards was negatively influenced by wind speed (estimate: –0.07 ± 0.01).

TABLE 3

GLMs explaining the variation in flight altitudes of raptors at the Bosphorus. Asterisks indicate significant terms. *[GLMs para explicar la variación en la altitud de vuelo de rapaces detectadas en el Bósforo. Los asteriscos indican términos significativos.]*

Species	**Covariates**	**F**	**d.f.**	***P***
Common/Steppe Buzzard	Wind direction	0.7	3	0.6
	Wind speed	0.6	1	0.5
	Wind dir.*speed	0.3	3	0.8
	Air humidity	0.9	1	0.3
	Air temperature	3.7	1	0.05
	Air pressure	0.7	1	0.4
	Flock size	0.5	1	0.5
	Time of the day	1.1	1	0.3
Booted Eagle	Wind direction	2.6	4	0.04*
	Wind speed	0.08	1	0.8
	Wind dir.*speed	0.6	3	0.6
	Air temperature	2.8	1	0.1
	Flock size	0.008	1	0.9
	Time of the day	0.05	1	0.8
Lesser Spotted Eagle	Wind direction	2.4	4	0.04*
	Wind speed	0.9	1	0.3
	Wind dir.*speed	0.6	4	0.7
	Air temperature	0.09	1	0.8
	Air pressure	5.1	1	0.03*
	Flock size	0.05	1	0.8
	Time of the day	3.7	1	0.06
Short-toed Snake-eagle	Wind direction	2.9	4	0.02*
	Wind speed	1.9	1	0.2
	Wind dir.*speed	2.2	4	0.07
	Air humidity	1.1	1	0.3
	Air temperature	1.4	1	0.2
	Air pressure	1.4	1	0.2
	Flock size	1.3	1	0.3
	Time of the day	0.7	1	0.4

TABLE 4

GLMs explaining variation of hourly numbers of raptors of different species counted at the Dardanelles. Asterisks indicate significant terms.
[GLMs para explicar la variación en los conteos de las distintas especies de rapaces detectadas en los Dardanelos. Los asteriscos indican términos significativos.]

Species	**Covariates**	**F**	**d.f.**	***P***
European Honey-buzzard	Wind direction	1.7	3	0.2
	Wind speed	0.7	1	0.4
	Wind dir.*speed	0.3	3	0.8
	Air humidity	0.4	1	0.5
	Air temperature	2.9	1	0.07
	Air pressure	4.9	1	0.03*
	Time of the day	0.7	1	0.4
Circus spp.	Wind direction	1.2	3	0.3
	Wind speed	0.2	1	0.6
	Wind dir.*speed	0.7	3	0.5
	Air humidity	0.07	1	0.8
	Air temperature	0.01	1	0.9
	Air pressure	0.002	1	0.9
	Time of the day	1.3	1	0.3
Falco spp.	Wind direction	0.5	3	0.7
	Wind speed	0.5	1	0.5
	Wind dir.*speed	0.8	2	0.5
	Air humidity	7.9	1	0.008*
	Air temperature	0.08	1	0.8
	Air pressure	4.6	1	0.03*
	Time of the day	0.01	1	0.9
Common/Steppe Buzzards	Wind direction	0.7	3	0.6
	Wind speed	3.5	1	0.04*
	Wind dir.*speed	0.03	2	0.9
	Air humidity	3.2	1	0.08
	Air temperature	0.02	1	0.9
	Air pressure	1.8	1	0.2
	Time of the day	0.01	1	0.9

Following the peninsula or crossing the sea?

In the logistic regression model, comparing all raptors together, *species* was the most important significant term (Table 5), with *Circus* spp. and European Honey-buzzards crossing the Strait close to our watchpoint more than other species that were more likely to follow the peninsula (estimates: *Circus* spp. 2.4 ± 1.0; European Honey-buzzards 1.2 ± 1.0; *Falco* spp. –0.8 ± 1.5; Common/Steppe Buzzards –0.05 ± 1.2). The same GLM shows that raptors were more likely to cross the Dardanelles Strait when migrating in large flocks (estimate: 0.1 ± 0.03), with higher temperatures (estimate: 0.2 ± 0.09) and higher air pressure (estimate: 0.2 ± 0.06).

The tendency of harriers to undertake the sea crossing was positively influenced by air temperature (Table 5, estimate: 0.3 ± 0.1). Increasing wind speed discouraged European Honey-buzzards from crossing (Table 5, estimate: –0.2 ± 0.1) while they preferred not to start crossing in the early morning (estimate: 0.4 ± 0.2). Finally adults were more likely to undertake the crossing than juveniles (estimate: juveniles –3.2 ± 2.0).

TABLE 5

Results of the logistic regression explaining the tendency to cross the Dardanelles Strait (as opposed to following the peninsula). Asterisks indicate significant terms.
[Resultados de la regresión logística para explicar la tendencia a cruzar el estrecho de los Dardanelos (en lugar de seguir la península). Los asteriscos indican términos significativos.]

Species	**Covariates**	**Wald**	**d.f.**	***P***
All species	Wind direction	1.1	3	0.8
	Wind speed	1.2	1	0.3
	Wind dir.*speed	1.2	3	0.7
	Air humidity	2.7	1	0.1
	Air temperature	5.6	1	0.02*
	Air pressure	5.4	1	0.02*
	Flock size	9.1	1	0.003*
	Species	23.2	4	0.0001*
	Time of the day	0.6	1	0.4
European Honey-buzzard	Wind direction	3.4	3	0.3
	Wind speed	4.0	1	0.04*
	Wind dir.*speed	3.4	3	0.3
	Air humidity	0.08	1	0.8
	Air temperature	1.7	1	0.2
	Air pressure	0.05	1	0.8
	Flock size	3.3	1	0.05
	Age	3.9	1	0.05
	Time of the day	4.6	1	0.03*
Circus spp.	Wind direction	0.8	3	0.9
	Wind speed	0.05	1	0.8
	Wind dir.*speed	0.2	3	0.9
	Air humidity	1.7	1	0.2
	Air temperature	4.9	1	0.03*
	Air pressure	1.2	1	0.3
	Flock size	3.7	1	0.06
	Time of the day	0.2	1	0.7

Discussion

The results do not support our predictions. Species composition shows marked differences at the two straits. Moreover, responses to weather conditions and time of day vary among the studied species, while flight altitudes of the four most common species converge to similar values.

Different flyways

Eagles predominate at the northern end of the Bosphorus whereas medium-sized and small raptors are the most common species at the Dardanelles. Large soaring birds avoid crossing the Dardanelles during autumn, preferring a safer flight over the narrower Channel of Bosphorus, even though the Dardanelles provides a shorter route to winter quarters for some raptor populations, e.g. Short-toed Snake-eagles breeding in Greece and migrating along the northern coast of the Aegean Sea (Panuccio *et al*., 2012; Panuccio *et al*., 2013a; Schindler *et al*., 2015). Birds migrating along this flyway have to head ENE to reach the Bosphorus from the Greek coasts. The species composition at the Dardanelles is similar to that reported at other Mediterranean watchsites such as the island of Antikythira in southern Greece, where hundreds of European Honey-buzzards and harriers are regularly observed (Lucia *et al*., 2011; Panuccio *et al*., 2013a, 2016).

Reaction to weather conditions and spatial variation of migratory flow

Our results suggest that the intensity of the migratory flow across the Bosphorus Channel varies from north to south depending on crosswinds. Raptor responses to crosswinds are strongly species-specific with smaller species being more likely to drift with the wind, whereas eagles compensate or overcompensate for wind drift. Juvenile Short-toed Snake-eagles are an exception, probably due to their limited experience: inexperienced birds cannot have, during their first migration, the positional information that allows adults to detect, and correct for, lateral displacement (Thorup *et al*., 2003). Booted Eagles and Common/Steppe Buzzards show an intermediate behaviour apparently drifting more when crosswinds become stronger, as suggested by the significant interaction between wind direction and speed. Interspecific differences indicate that drift compensation is influenced by a raptor species' ability to fly over water. For instance, the European Honey-buzzard is more likely to undertake water crossings than larger birds such as eagles, probably because large birds incur huge energy expenditure during powered flapping flight (Agostini *et al*., 2015a). The Sea of Marmara (20-65 km wide) is not a significant barrier for European Honey-buzzards and perhaps *Accipiter* spp., but it is for eagles. As shown in different studies, large raptors such as Short-toed Snake-eagles and Lesser-spotted Eagles have an innate reluctance to fly over water, even when approaching relatively short stretches of sea (Meyburg *et al*., 2002; Agostini *et al*., 2016; Mellone *et al*., 2016). Thus, since northerly winds are dominant during autumn at the Bosphorus (Porter and Willis, 1968; Van Den Bossche and Lens, 1994), we suggest that large numbers of European Honey-buzzards accept significant wind drift towards the Marmara Sea, the Princes' Islands and the southern region of the Bosphorus (Çamlicas area; Beaman and Bijlsma, 1987). This migration strategy would explain why we counted few European Honey-buzzards along the northern region of this strait, in comparison with counts made in the Çamlicas area during autumn (5,527 individuals in 2005, 5,515 in 2006; Smith and Yardım unpublished data). In addition, since approximately 10,000 European Honey-buzzards migrate through the northern region of the Bosphorus during spring migration (Üner *et al*., 2010), these raptors may concentrate in this area when facing the Black Sea, a wider water barrier than the Sea of Marmara.

Lesser Spotted Eagles and adult Short-toed Snake-eagles were observed in higher numbers with increasing wind speed. Under such atmospheric conditions they may reduce the time spent soaring to avoid the drift effect of crosswinds and become more detectable since they reduce their flight altitude (Panuccio *et al*., 2010; Malmiga *et al*., 2014). The interaction between wind direction and speed shows positive estimate values in the case of Lesser Spotted Eagles that, unlike Common/Steppe Buzzards and Booted Eagles, perhaps overcompensate during strong northerly crosswinds (Klaassen *et al*., 2010; Vidal-Mateo *et al*., 2016). In addition, the positive effect of temperature on the intensity of migratory flow of this large soaring raptor is expected, because it is associated with thermal activity (Shamoun-Baranes *et al*., 2003). Our results confirm that *Accipiter* spp. and Lesser Spotted Eagles are more likely to cross the Bosphorus at its northern end during early morning (Van Den Bossche and Lens, 1994). This is likely due to the vicinity of the Belgrade Forest, an important roosting site for migrant raptors (Van Den Bossche and Lens, 1994).

The negative effect of humidity on the passage of Common/Steppe Buzzards may be linked with unstable weather and rain. On the other hand it is unclear why increasing air pressure had a negative effect on the passage of European Honey-buzzards and Common/Steppe Buzzards. However, higher air pressure is associated with fair-weather periods and stronger thermals and therefore we cannot exclude that significant numbers of birds passed undetected during such atmospheric conditions (Kerlinger, 1989; Panuccio *et al*., 2013c).

Variation of flight altitude

The recorded flight altitude of raptors was similar for all species. Here too the wind direction is of paramount importance in explaining the flight altitude. All the three eagle species decreased their flight altitude when flying in tailwinds. Since large soaring birds do not fly as fast as they can, gliding in a risk-sensitive manner (Horvitz *et al*., 2014), tailwinds may decrease their altitude by slowing the movement of air along the outline of the wings and decreasing the aerodynamic lift (Kerlinger, 1989; Agostini, 1992; Pennycuick, 2008).

Moreover, when considering the numbers of raptors that passed above or below our watchsite in relation to wind speed (Panuccio *et al*., 2010), we noted that eagles (other than juvenile Short-toed Snake-eagles) and Common/Steppe Buzzards limit the use of soaring flight, passing below the watchpoint much more than did European Honey-buzzards and *Accipiter* spp. In our study, flight altitudes were lower than those previously reported by radar at other watchsites (Bruderer *et al*., 1994; Spaar & Bruderer, 1997; Mateos-Rodríguez & Liechti, 2012). We suggest that this is because strong winds, and consequently weaker thermal currents, do not allow raptors passing over the Bosphorus to reach high altitudes. Similar results were recorded in southern Sweden, where the flight altitude of migrating raptors was strongly limited by weather conditions (Malmiga *et al*., 2014). In this regard, our study agrees with Spaar (1995) in showing that the flight characteristics of different species are more similar under the same meteorological conditions than the behaviour of individuals of the same species under different conditions.

Influence of weather conditions on raptor migration at the Dardanelles Strait

At the Dardanelles Strait, wind speed negatively affected numbers of Common/Steppe Buzzards, probably because this species is particularly wind selective (Panuccio *et al*., 2011; Malmiga *et al*., 2014). Here, unlike at the Bosphorus, we observed larger numbers of European Honey-buzzards both with higher air pressure and higher temperature, ideal weather conditions for thermal activity. That is probably because at the Dardanelles many European Honey-buzzards reached the study area after crossing the Gulf of Saros, a larger water body than Bosphorus. In doing so they were expected to decrease their flight altitude becoming more visible to the observers. On the other hand Red-footed Falcons were recorded with high levels of air humidity and lower air pressure. Unlike soaring species, falcons cross the Mediterranean on a broad front and they probably concentrate at the Dardanelles during unfavourable weather conditions caused by the passage of low pressure cells (Meyer *et al*., 2000; Panuccio *et al*., 2002; Mellone *et al*., 2011).

Flock size affected the behaviour of raptors in relation to the water barrier. In our case larger flocks were more likely to cross the strait close to our watchsite as already observed both in USA and Europe (Kerlinger, 1989; Panuccio & Agostini, 2010). Conversely, the tendency to follow the peninsula at this site was more evident in *Falco* spp., than in *Circus* spp. and in European Honey-buzzards, probably because falcons tend to migrate following an innate NE-SW axis that is also the orientation of the Gallipoli Peninsula. Similarly, among European Honey-buzzards, juveniles were more likely to follow the peninsula than adults because they orientate along an innate compass during their first migration (Hake *et al*., 2003; Agostini, 2004). The same tendency occurs in larger soaring species such as eagles and Common/Steppe Buzzards, in this case because they are reluctant to fly over sea (Agostini *et al*., 2015a). The positive effect of temperature on the water crossing tendency of harriers is in agreement with a recent study made in the southern Aegean Sea (Panuccio *et al*., 2016). European Honey-buzzards did not undertake the water crossing during strong wind conditions, instead probably waiting for better weather conditions.

CONCLUSIONS

Raptors migrating in autumn across the Turkish straits between Europe and the Middle East use different flyways probably because of different degrees of dependence on the use of thermal currents. They react differently to different weather conditions and in particular to crosswinds at the Bosphorus. Flight altitude is similar among species, but varies under different wind directions. Our study shows species-specific differences in the flight strategies of raptors during migration despite the convergence of some flight parameters, probably as a result of a risk-minimisation strategy (Horvitz *et al*., 2014).

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