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VISIBLE MIGRATION OF SHORT-TOED SNAKE-EAGLES: INTERPLAY OF WEATHER AND TOPOGRAPHICAL FEATURES

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ABSTRACT.—Migratory behavior of raptors is affected by several factors, including weather, geography, and topographical features. Here we provide information on how these factors may affect the behavior and detectability of the Short-toed Snake-Eagle (*Circaetus gallicus*). We observed passage of Short-toed Snake-Eagles at two watchsites along mountain chains in northeastern Greece (Mount Olympus) and northwestern Italy (Arenzano) during the peak periods of migration in autumn 2009 and spring 2010. More Short-toed Snake-Eagles were observed in spring than in autumn; this difference was more evident at Arenzano. Temperatures influenced the number of migrants observed. In particular, the number of individuals observed decreased drastically when temperatures were higher than 24°C during post-reproductive movements. At both sites, daily patterns showed a lower proportion of raptors observed during midday and early afternoon in autumn than in spring. These results suggest that, during autumn, individuals may pass undetected by flying at higher altitudes during midday and in early afternoon at both sites. The lack of difference in number of eagles observed during westerly (lateral) winds compared to other wind directions at Mount Olympus suggests that these birds may be able to compensate for drift effect toward the Aegean Sea. Wind strength and lateral northerly wind negatively affected the number of migrants observed at Arenzano during spring movements.

KEY WORDS: *Short-toed Snake-Eagle*; Circaetus gallicus; *geography*; *migration*; *visible migration*; *weather.*

MIGRACIÓN VISIBLE DE *CIRCAETUS GALLICUS*: INTERACCIÓN DE LAS CARACTERÍSTICAS CLIMÁTICAS Y TOPOGRÁFICAS

RESUMEN.—El comportamiento migratorio de las rapaces se ve afectado por diversos factores, incluyendo el clima, la geografía y las características topográficas. Proveemos información acerca de cómo estos factores pueden afectar el comportamiento y la detectabilidad de *Circaetus gallicus*. Observamos el paso de individuos de *C. gallicus* en dos sitios de avistaje a lo largo de las cadenas montañosas en el noreste de Grecia (Monte Olimpo) y en el noroeste de Italia (Arenzano) durante los períodos de mayor migración en el otoño de 2009 y la primavera de 2010. Durante la primavera se observaron más individuos de *C. gallicus* que durante el otoño; esta diferencia fue más evidente en Arenzano. La temperatura influyó en el número de migrantes observados. En particular, el número de individuos observados disminuyó drásticamente cuando las temperaturas fueron mayores a 24°C durante los movimientos post-reproductivos. En ambos sitios, durante el otoño los patrones diarios mostraron una proporción menor de rapaces observadas durante el mediodía y temprano en la tarde que durante la primavera. Estos resultados sugieren que, durante el otoño, los individuos pueden pasar sin ser detectados al volar a mayores altitudes durante el mediodía y temprano en la tarde en ambos sitios. La falta de diferencias en el número de águilas observadas durante

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los vientos de orientación oeste (lateral) comparada con otras direcciones del viento en el Monte Olimpo sugiere que estas aves pueden llegar a compensar el efecto de deriva hacia el Mar Egeo. La fuerza del viento y el viento lateral de dirección norte afectaron negativamente el número de migrantes observados en Arenzano durante los movimientos primaverales.

[Traducción del equipo editorial]

Most raptors migrate using one or both of two basic flight styles: flapping flight and soaring-gliding flight. When facing different weather conditions, migrants show a high degree of plasticity in their behavior (Klaassen et al. 2011, Vardanis et al. 2011). In particular, the daily movements of raptors and their detectabilities are strongly influenced by wind direction and strength, temperature, barometric pressure, and relative humidity (Kerlinger 1989, Alerstam 1990, Maransky et al. 1997, Agostini et al. 2002b, Panuccio et al. 2010, Panuccio 2011). It is generally assumed that flight strategies have been shaped by selection to minimize the costs of migration such as flight time and energy expenditure (Hedenström 1993). This latter factor influences the migration strategies of broad-winged species such as eagles and vultures (Kerlinger 1989). The Short-toed Snake-Eagle (*Circaetus gallicus*) is a long-distance migrant that uses mostly soaring-gliding flight and therefore exploits thermal currents and updrafts to reduce energetic costs. As a result, migrating snake-eagles concentrate at isthmuses, straits, and along mountain chains. In doing so, they sometimes undertake long detours overland between their wintering grounds south of the Sahara desert and their breeding grounds in Europe to cross the Mediterranean Sea at its narrowest points: the Strait of Gibraltar and the Bosphorus. Birds breeding in central-southern Greece and in the Italian Peninsula, use the so-called ''circuitous migration'' that involves movements that are opposite to the main migration direction, southward during spring and northward during autumn, at the end and at the beginning of their movements, respectively (Agostini et al. 2002a, Mellone et al. 2011, Panuccio et al. 2012).

Because the migratory behavior of raptors often changes in relation to weather conditions and topographical features, monitoring methods that rely on direct observation may be biased by these factors. In addition, weather-related variables may differ between spring and autumn, affecting migration counts in the two periods differently. In this study, we document the influence of wind, temperature, barometric pressure, relative humidity, and time of the day on the number of Short-toed Snake-Eagles observed migrating along two mountain chains, through systematic observations at watchsites located on the slopes of Mount Olympus (northeastern Greece) and at Arenzano (northwestern Italy) during both autumn and spring migration.

STUDY AREA AND METHODS

At Mount Olympus, in northeastern Greece, the mountain chain (approx. 40°01′N, 22°29′E) runs parallel to and approximately 7 km from the coast, forcing migrants to concentrate over a narrow corridor of land between the sea and the mountain (Panuccio et al. 2012). North of Mount Olympus there is a large flat area and the mountain chain continues southward (Fig. 1). At Arenzano, in Italy, the observation site was at the northernmost point of the mid-western Mediterranean basin (44°25′N, 8°40′E), where the ridge of the Ligurian Apennines, after running parallel to the coast, reaches its closest proximity to the sea (6 km; Fig. 1). Observations were made with telescopes and binoculars from 9 September to 1 October 2009 at Mount Olympus, from 8 to 29 September 2009 at Arenzano, from 6 to 26 March 2010 at Mount Olympus, and from 8 to 29 March 2010 at Arenzano; these periods corresponded to the peak times of autumn and spring migration of the Short-toed Snake-Eagle in the Mediterranean basin (Agostini et al. 2002b, Baghino and Premuda 2007, Baghino et al. 2009). Observations were discontinued during heavy rain or snow. Each day was divided into four 2-hr periods: 9:00–10:59 H, 11:00–12:59 H, 13:00–14:59 H, and 15:00 H–sunset (solar time). We used weather data collected from the Litochoro (for Mount Olympus) and Genoa (for Arenzano) meteorological stations every hour. These stations are both located less than 15 km from the watchpoints and provided data on local weather conditions.

In our statistical analysis we used hourly numbers of observed Short-toed Snake-Eagles and hourly weather data. In particular, we examined the effect of the following weather variables: main wind directions, wind strength (km/h), temperature (°C), air pressure (mbar), and air humidity (%). First we used Mann-Whitney and Kruskal-Wallis tests to compare weather data across the two seasons for both sites. Then we divided our data set into four subsets

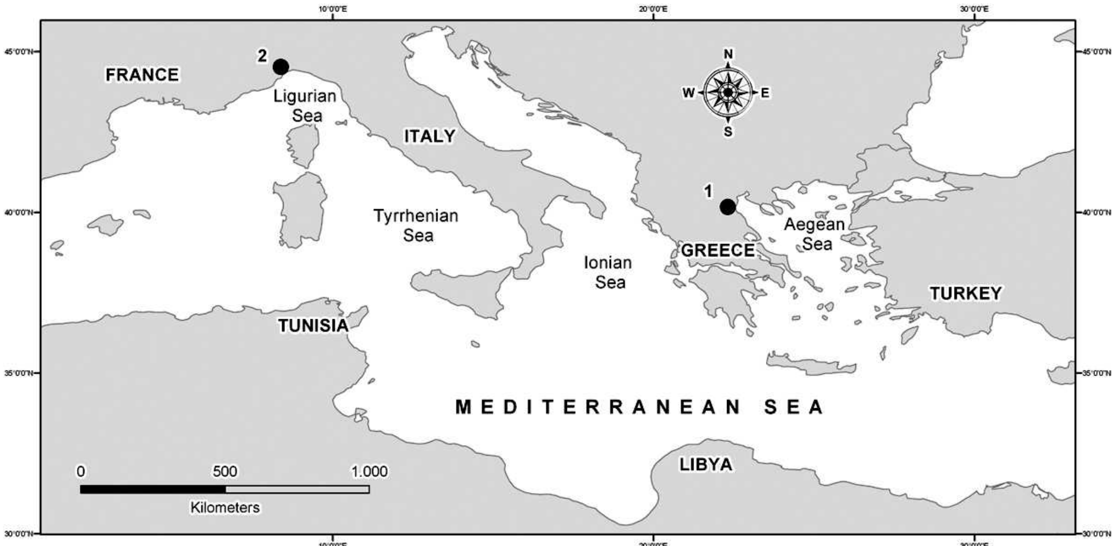

Figure 1. The study area: (1) Mount Olympus, (2) Arenzano on the Ligurian Apennines.

for season (autumn, spring) and site (Mount Olympus, Arenzano). For each series of data, we determined 33rd and 67th percentiles in order to divide each series (i.e., wind strength, temperature, air pressure and air humidity) into low, medium and high weather conditions. Because we made this classification for each season and site, the classes were not absolute but relative. We used Kruskal-Wallis tests to verify whether hourly numbers of eagles varied significantly within the different classes; to do this we ran Kruskal-Wallis tests for each season and site. When analyzing the average numbers of birds passing through the study area per hour with different wind directions, we used the Z test after the F test run to compare variances. We used logarithmic transformation of original data when variances were not homogeneous (Fowler and Cohen 1996).

RESULTS

Mount Olympus. *Weather variables.* Barometric pressure and relative humidity (both higher in spring than in autumn) and temperatures (higher in autumn than in spring) differed significantly between the two seasons (Table 1). Winds from NE-NNE-N-NNW-NW (headwinds in autumn and tailwinds in spring) and SE-SSE-S-SSW-SW (tailwinds in autumn and headwinds in spring) commonly occurred in both periods, whereas in autumn prevailing winds were also from WNW-W-WSW (lateral). Wind speed was weak (<15 km/h) for all wind directions during both spring and autumn. In autumn, there was no significant difference in the strength of headwinds, tailwinds, or westerly winds (Kruskal-Wallis $H = 10.02$, $P > 0.05$). In spring, tailwinds were stronger than headwinds (U-test = 2049, $P < 0.01$; Table 2).

Migration flight. We observed 367 (maximum daily count: 107 birds on 19 September) and 602 (maximum daily count: 258 birds on 24 March) Short-toed Snake-Eagles at Mount Olympus heading NNE in autumn and SSW in spring, respectively. At this site, wind strength did not affect the number of migrants observed (autumn: $H = 3.52$, $P > 0.05$; spring: $H = 3.01$, $P > 0.05$). Comparison of mean hourly counts of eagles during different wind conditions (Table 4) indicated that wind direction did not affect the number of raptors detected at the site during either autumn (headwind vs. tailwind: $Z = 0.11$, $P > 0.05$; westerly wind vs. headwind + tailwind: $Z = 1.79$, $P > 0.05$) or spring (headwind vs. tailwind: $Z = 0.32$, $P > 0.05$). The passage of Short-toed Snake-Eagles was affected by temperature in both seasons (autumn: $H = 7.6$, $P < 0.05$; spring: $H = 24.29$, $P < 0.001$). In particular, during autumn higher numbers of eagles were observed migrating between 22° and 24°C, whereas with lower and higher temperatures numbers of migrating raptors decreased. During spring, hourly numbers of migrating raptors increased with increasing temperature (Fig. 2a). The number of migrants recorded did not show a daily peak in autumn. Conversely, during spring, the number of migrants recorded appeared

Table 1. Temperature, barometric pressure and relative humidity recorded during the two seasons at Mount Olympus and Arenzano. Values reported are: minimum, maximum, median, and mean values of each variable for both sites and seasons. The columns on the right give results of Mann-Whitney tests used to compare weather variables in the two season for both sites.

SITE	WEATHER VARIABLE		AUTUMN	SPRING	U-TEST	P	n
Mount Olympus	Temperatures (°C)	Min.	16	0	38528	<0.001	398
		Median	23	11			
		Mean	22.8	10.7			
		Max.	28	19			
	Barometric Pressure (hPa)	Min.	1009	1010	14514.5	<0.001	398
		Median	1018	1021			
		Mean	1018	1021			
		Max.	1027	1035			
	Relative Humidity (%)	Min.	29	26	14177.5	<0.001	398
		Median	56	66			
		Mean	56.1	63.6			
		Max.	100	94			
Arenzano	Temperatures (°C)	Min.	17	3	30945	<0.001	352
		Median	24	13.5			
		Mean	24.2	12.3			
		Max.	30	19			
	Barometric Pressure (hPa)	Min.	1008	1006	15299.5	>0.05	352
		Median	1018	1018			
		Mean	1018	1018			
		Max.	1025	1032			
	Relative Humidity (%)	Min.	31	28	12184.5	<0.001	352
		Median	57	67			
		Mean	59.6	65			
		Max.	100	94			

to peak in the early afternoon (contingency table: $\chi^2 = 191.78$; df = 3; $P < 0.001$; Fig. 3a). Higher barometric pressures favored the passage of Short-toed Snake-Eagles in autumn but not in spring (autumn: $H = 7.87$, P < 0.05; spring: $H = 2.5$, P > 0.05). Interestingly, barometric pressure was negatively correlated with temperature in autumn ($r = -0.26$; $P < 0.01$) but positively correlated with temperature in spring ($r = 0.23$; $P < 0.01$). Finally, relative humidity affected the number of migrants observed at Mount Olympus in spring (higher numbers with mean values) but not in autumn (autumn: $H = 3.24$, $P > 0.05$; spring: $H = 6.93$, $P < 0.05$). On the peak autumn migration day, temperature did not exceed 23°C with weak lateral winds; the peak spring migration day occurred on a day with very little wind and warm temperatures (up to 19°C).

Arenzano. *Weather variables.* Relative humidity (higher in spring than in autumn) and temperatures (higher in autumn than in spring) differed significantly between the two seasons but barometric pressure did not (Table 1). At this watchsite, wind strength was higher than at Mount Olympus in both seasons (autumn: $U = 11069$, $P < 0.001$; spring $U = 5314$, $P < 0.001$). During autumn, the difference between strengths of prevailing winds (headwind vs. lateral northerly wind) was not significant; however, during spring, lateral northerly winds were stronger than lateral southerly ones (Table 3). Finally at this site, as at Mount Olympus, barometric pressure was positively correlated with temperature in spring ($r = 0.31$; $P < 0.001$).

Migration flight. We observed 896 (maximum daily count: 302 birds on 19 September) and 2250 (maximum daily count: 830 birds on 17 March) Short-toed Snake-Eagles at Arenzano in autumn and spring, respectively. When comparing the proportions of eagles observed at each site in the two seasons, we recorded a greater difference between spring and autumn at Arenzano than at Mount Olympus (contingency table: $\chi^2 = 30.29$; df = 1; $P < 0.001$). Eagles reached the observation post from the ENE-E and left the site heading SW in autumn and vice versa during spring. As at Mount

Table 2. Wind strength of prevailing winds in spring and autumn at Mount Olympus during the study periods. Wind categories shown are minimum, maximum, median, and mean wind speeds. Columns on the right give results of tests (Mann-Whitney and Kruskal-Wallis) comparing wind speeds under different directions. Dashes indicate that such wind conditions were negligible in the study period.

SEASON	WIND SPEED MEASURE	LATERAL (WESTERLY) WIND (km/h)	HEADWIND (km/h)	TAILWIND (km/h)	TEST RESULTS
Autumn	Min.	5.6	3.7	5.6	KW = 10.02
	Median	11.1	11.2	14.8	$P > 0.05$
	Mean	11.7	12.9	14.1	$n = 193$
	Max.	21.1	27.8	22.2	
Spring	Min.		1.6	1.7	U-test = 2049
	Median	—	8.0	9.7	$P < 0.01$
	Mean		8.6	12.3	$n = 119$
	Max.		47.9	48.2	

Olympus, passage of Short-toed Snake-Eagles was influenced to a similar extent by temperature in both seasons (Fig. 2b; autumn: $H = 5.49$, $P < 0.05$; spring: $H = 25.12$, $P < 0.001$). Along the Ligurian Apennines, wind strength influenced the number of migrants recorded during spring migration ($H = 24.99$, $P < 0.001$) but not during autumn ($H = 3.68$, $P > 0.05$). The comparison of mean hourly passage of eagles during prevailing wind conditions (Table 4) indicated that wind direction affected the number of raptors detected at the site during spring (lateral northerly wind vs. lateral southerly wind: $Z = 2.67$, $P < 0.05$) but not during autumn (tailwind vs. lateral northerly wind: $Z = 1.01$, $P > 0.05$). During autumn migration, the number of migrants increased during the day, whereas during spring the number of migrants appeared to peak during midday (contingency table: $\chi^2 = 105.9$; df = 3; $P < 0.001$; Fig. 3b). Unlike at Mount Olympus, barometric pressure affected the number of raptors observed during spring, with higher numbers of eagles observed with high air pressure ($H = 10.42$, $P < 0.001$), while it did not occur in the autumn ($H = 2.68$, $P > 0.05$). Similarly, relative humidity affected the passage of Short-toed Snake-Eagles in spring, with higher numbers observed with mean values ($H = 22.81$, $P < 0.001$), but it did not affect the migration in autumn ($H = 3.35$, $P > 0.05$).

As at Mount Olympus, the day of peak autumn passage was characterized by weak lateral winds and relatively cool temperatures for the season (up to 23°C). In contrast, the day of peak passage in spring was characterized by strong winds (up to 25.9 km/h) coming from southern and eastern quadrants (ESE-SSE) and temperatures cooler than at Mount Olympus (up to 14°C).

Table 3. Wind strength of prevailing winds in spring and autumn at Arenzano during the study periods. Wind categories shown are minimum, maximum, median, and mean wind speeds. Columns on the right give results of tests (Mann-Whitney and Kruskal-Wallis) comparing wind speeds under different directions. Dashes indicate that such wind conditions were negligible in the study period.

SEASON	WIND SPEED MEASURE	LATERAL (NORTHERLY) WIND (km/h)	TAILWIND (km/h)	LATERAL (SOUTHERLY) WIND (km/h)	TEST RESULTS
Autumn	Min.	7.4	5.6		U-test = 2146
	Median	18.5	22.2	—	$P > 0.05$
	Mean	19.3	20.8		$n = 123$
	Max.	33.3	29.6		
Spring	Min.	11.1		7.3	U-test = 2654
	Median	25.9	—	20.4	$P < 0.01$
	Mean	25.3		21.0	$n = 137$
	Max.	46.3		38.9	

Table 4. Hourly means counts of Short-toed Snake-Eagles observed with different wind directions at Mount Olympus and Arenzano in both seasons. Dashes in the columns indicate that such wind conditions were negligible in the study period.

Site		Hourly Mean ± SE (*n*) Autumn	Spring
Mount Olympus	Headwind	2.1 ± 1.09 (55)	4.8 ± 1.83 (40)
	Tailwind	1.3 ± 0.46 (56)	4 ± 0.45 (79)
	Lateral (westerly) wind	1.9 ± 0.38 (82)	—
Arenzano	Lateral (northerly) wind	3.4 ± 0.7 (73)	6.4 ± 2.2 (44)
	Tailwind	4.6 ± 0.9 (50)	—
	Lateral (southerly) wind	—	18.4 ± 3.9 (93)

Discussion

Effects of Wind on Migration. The lack of difference between numbers of eagles observed during westerly (lateral) winds and during other wind directions (headwinds + tailwinds) in autumn at Mount Olympus suggests that migrants compensated for the drift effects of such lateral winds when passing through that study area, to avoid being blown out over the Aegean Sea. As reported in previous studies, raptors are able to compensate for drift effects of lateral winds by changing their heading and/or limiting the use of soaring-gliding flight, in particular when migrating through or near an ecological barrier (Kerlinger 1989, Klaassen et al. 2011, Panuccio et al. 2010). Also, tailwinds and headwinds did not affect counts at the site during spring and autumn, which may be explained by the fact that such winds were weak during our observation periods; although, during spring, tailwinds were significantly stronger than headwinds.

At Arenzano during spring migration, few Short-toed Snake-Eagles were observed during strong winds with lateral northerly components. Perhaps, in this period, strong lateral winds pushed migrants toward the coastline, slowed their travel speed and/or influenced them to fly at very low altitudes (below our observation post) to avoid being blown out over the Ligurian Sea, thus passing undetected. The influence of north winds, however, may have similar effects on visible migration at this site also in autumn (see also Baghino 2008, Baghino et al. 2009).

Effects of Air Temperature. During autumn (but not spring) migration, adult and juvenile Short-toed Snake-Eagles from the populations breeding in Greece and Italy tend to migrate at the same time, increasing the number of migrants expected to pass the observation sites during post-breeding-season movements (Agostini et al. 2002a, Panuccio et al. 2012). However, in our study, larger numbers of migrants were seen during the spring than during the autumn migration at both sites and such difference between the two seasons was more evident at Arenzano. Detectability rates may have been affected by different thermal conditions in the two seasons along the two mountain chains. In particular, the temperature in northern Greece and northwestern Italy was higher, and consequently, thermal conditions stronger, in September than in March. During spring, as expected for a soaring bird (Maransky et al. 1997), the number of Short-toed Snake-Eagles observed increased with temperature. Conversely, in autumn, the number of migrants detected decreased dramatically with higher temperatures. Because raptors increase their travelling speed with higher temperatures, faster cross-country speeds are generally attained soon after local noon (Mellone et al. 2012). Therefore, Short-toed Snake-Eagles would have had to increase their travelling speed during favorable thermal conditions, showing a daily peak during midday and early afternoon in both seasons (Kerlinger 1989, Panuccio et al. 2010). However, during our study, this pattern was reported during spring but not during autumn migration. Because the most important factor influencing detectability of migrants is their distance from the observers (Kerlinger 1989), we suggest that during midday and early afternoon, when stronger thermal conditions occurred, large numbers of Short-toed Snake-Eagles may have passed out of sight at both sites. This daily pattern of migration was described at other watchsites and called ‘‘midday lull’’ (Heintzelman 1975, Bruderer et al. 1994). Migrating broad-winged raptors become difficult to see at altitudes higher than 600 m above ground level (Kerlinger 1989). Previous radar studies made both in the United States and Israel showed that the flight altitude of raptors

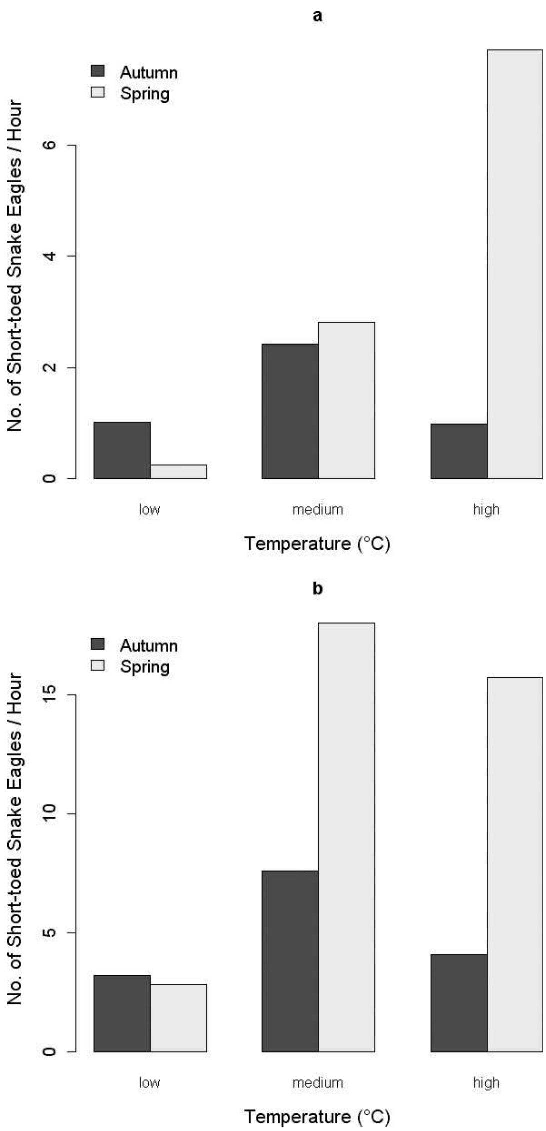

Figure 2. Hourly numbers of Short-toed Snake-Eagles seen migrating at (a) Mount Olympus and (b) Arenzano during autumn and spring in the three different classes of air temperatures.

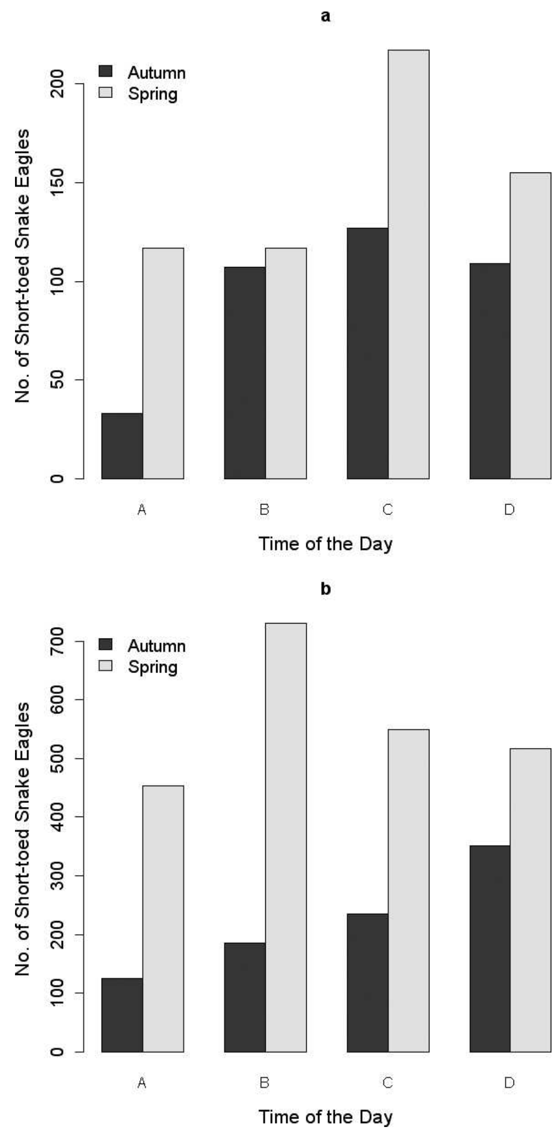

Figure 3. Number of Short-toed Snake-Eagles migrating throughout the day (A = 9:00–10:59 H, B = 11:00–12:59 H, C = 13:00–14:59 H, D = 15:00 H to sunset; solar time) during autumn and spring at (a) Mount Olympus and (b) Arenzano.

increases linearly with time of the day until the afternoon (Kerlinger and Gauthreaux 1985, Bruderer et al. 1994, Spaar 1995). Moreover, during such temperature conditions, eagles (i.e., Steppe Eagles [*Aquila nipalensis*]) appear to be less likely to fly at low altitudes than smaller species of raptors (European Honey-Buzzards [*Pernis apivorus*] and Common Buzzards of the subspecies termed Steppe Buzzards [*Buteo buteo vulpinus*]; Spaar and Bruderer 1996). Data collected by radar in Israel also showed that migrating birds flew at higher altitudes in autumn than in spring, particularly in early spring when flight altitudes were much lower (Spaar et al. 2000, Dinevich and Leshem 2010). Kerlinger (1989) reported that ''*Thermals are the predominant source of lift most migrants use.*'' This statement was confirmed by a recent study comparing flight performances of migrating Golden Eagles (*Aquila chrysaetos*) using ridge lifts and thermal currents. In that study, flight speed of the eagles was slower when using slope-soaring, and they also drifted off their migratory direction. In contrast, eagles exploiting thermals stayed on course and had faster gliding speeds (Duerr et al. 2012).

Conclusions. It appeared that air temperatures influenced the visible migration of Short-toed Snake-Eagles more than wind direction and wind strength during our study. Thus, it is possible that visual counts of Short-toed Snake-Eagle migration along mountain chains may be biased by season due to differences in thermal conditions. As a caveat, we also cannot exclude the possibility that slight differences in migration routes may have influenced differences in counts between spring and autumn.

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