Visible autumn migration of Honey Buzzards *Pernis apivorus* in the NE Iberian Peninsula regarding horizontal winds at altitude

Ruth García & Fran Trabalon

The Honey Buzzard *Pernis apivorus* is a migratory soaring raptor that breeds in Eurasia and winters south of the Sahara. Since wind is one of the most important meteorological factors affecting bird migration, we analyzed how prevailing horizontal winds at 850 hPa (equivalent to an altitude of 1,000–1,500 m a.s.l) influenced autumn Honey Buzzard migration through La Garrotxa Volcanic Zone Natural Park (GVZNP) in the NE Iberian Peninsula in the period 2007–2012. We determined the percentage of visual migration over the GVZNP in relation to the prevailing wind direction at two different regional scales: the area surrounding the GVZNP (grid resolution of 12 km) and an area in southern France between 46°N and the border with Spain (grid resolution of 36 km). The greatest percentages of migrants detected over the GVZNP coincided in all years with north-westerly prevailing winds at a large regional scale (i.e. southern France). At a GVZNP scale, the same effect was observed in four out of the six study years. We found highly significant differences between the total migratory frequencies observed for each prevailing wind at both scales and in every year of the study. We thus suggest that *Pernis apivorus* migration in GVZNP is conditioned by the drift caused by north-westerly horizontal winds at altitude over southern France.

Key words: migration, horizontal winds at altitude, drift, *Pernis apivorus*, Garrotxa.

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Wind and rain are probably the most important meteorological factors affecting bird migration (Berthold 2001, Newton 2008). Birds usually change their migratory behaviour and decisions *en route* to take advantage of favourable winds and reduce the effect of unfavourable ones (Thorup *et al.* 2003, Klaassen *et al.* 2010, Mellone *et al.* 2012). Horizontal winds are especially influential on flight and are normally classified as either tailwinds, headwinds or crosswinds. The latter, which intersect the chosen migration route, can hamper migration by altering the selected heading, thereby causing migratory drift (Klaassen *et al.* 2010).

Much relevant information on several aspects of bird migration has been generated by the use of radars (Lack 1962, Eastwood 1967, Alerstam 1979, Bruderer *et al.* 1994) and, more recently, satellite tracking systems (Hake *et al.* 2003, Thorup *et al.* 2003, Meyburg *et al.* 2010). In spite of these technical advances, observational studies can still provide valuable information because at some sites and times, visible low-altitude movements constitute a significant fraction of the total numbers of migrant that pass over a zone (Richardson 1978).

An analysis of flight patterns is essential for understanding how birds find and follow migratory routes at different geographical scales (Alerstam 1996). It is known that geographical wind patterns have an important effect on the evolution of migratory routes (Landsberg 1948, Westernhagen 1960) since they determine the most efficient flyway from the point of view of energy consumption (Felicísimo *et al.* 2008, Agostini *et al.* 2012). Since horizontal wind is a key meteorological variable for bird migration, we expect that it will have an important effect on the migratory behaviour of this common raptor when migrating over the NE Iberian Peninsula. Thus, we tested whether the visible migration of Honey Buzzards, i.e. the number of passing individuals observed (García & Trabalon 2010), is affected by horizontal winds of different directions at different geographical scales.

Material and Methods

Study species

The Honey Buzzard is a long-distance migratory raptor. It breeds in Eurasia and during the post-nuptial period migrates to its sub-Saharan wintering territories (Cramp & Simmons 1980). At most migration watchsites, it is one of the most abundant raptors seen on passage (Westernhagen 1960, Bildstein 2006, Newton 2008).

Despite being a soaring bird, some studies indicate that it is less dependent on thermals than other raptors due to its more flexible behaviour that combines soaring, gliding and flapping flight (Bruderer *et al.* 1994). This allows the species to fly long distances into headwinds and undertake long sea crossings, occasionally even at night (Gätke 1895, Thake 1977, Bruderer *et al.* 1994, Agostini *et al.* 2005a).

It is a gregarious migratory bird that migrates relatively quickly, with records of 6,747 km covered in 42 days for adults and 64 days for juveniles (Hake *et al.* 2003). There is evidence that flocking behaviour allows birds to find thermals more quickly during migration as soaring groups can be detected from far away (Kerlinger 1989, Bildstein 2006). Inexperienced juveniles may use this technique to locate more easily their wintering grounds (Thake 1980). Nevertheless, juveniles migrate, in general, two or three weeks later than adults (Kjellén 1992, 1998; Agostini & Logozzo 1995, Forsman 1999, Schmid 2000) on a broader front and will also undertake longer sea crossings (Schmid 2000, Hake *et al.* 2003, Agostini 2004).

Tracking radar studies in Israel (Arava valley, 150 m below sea level) have shown that, although the average height of flight of this species is around 600 m above ground level (a.g.l.) (85% of individuals below 1,000 m a.g.l.), they occasionally reach exceptional heights (800–2,000 m a.g.l.) by following, for instance, the lee-waves caused by mountain ridges (Bruderer *et al.* 1994).

Study area

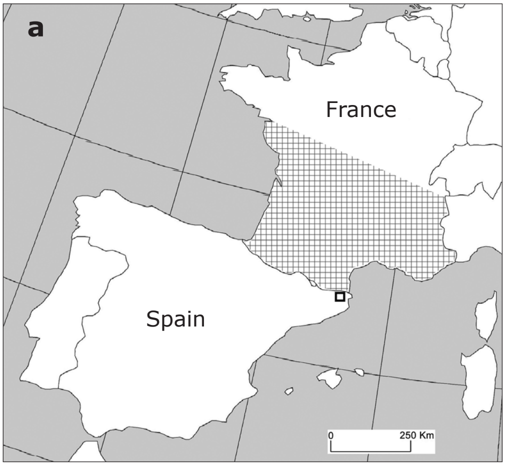
The observation point during this study was the summit of the volcano of Aiguanegra (42°20'N-2°52'E, 588 m a.s.l.) in a protected area, La Garrotxa Volcanic Zone Natural Park (GVZNP; Catalonia, Spain). The visibility from this site covers a strip of approximately 40 km wide to the north and just over 30 km wide to the south. Northward, the GVZNP shares a boundary with the Alta Garrotxa Area of Natural Interest, which is also a Special Protection Area for birds. In this northern strip, the mountain of Comanegra is the highest point (1,567 m a.s.l.).

Field sampling

The study was conducted from August 25 to September 25 every year between 2007 and 2012 (total sampling = 178 days). The sampling effort was constant and was performed by a single observer between 10:00 and 14:00 h, who counted all visible raptors on migration with the aid of a telescope (20–60×) and binoculars (8×40). This time period was selected because during a pilot study in 2002, a greater frequency of migratory passage was detected in the morning, as has been found by other studies (e.g. Bruderer *et al.* 1994). Overall, information from 12 days was discarded due adverse weather conditions that prevented observation, and from two further days due to a lack of meteorological information.

Wind data

We used data for horizontal winds at 850 hPa of admospheric pressure. Models of wind dynamics at 850 hPa indicate the direction and intensity of winds at heights at 1,000–1,500 m a.s.l. They provide information based on real data regarding large areas and free of the topographical distortions (Erni *et al.* 2005). An analysis of surface winds was discarded because birds rarely migrate so low, especially over land (Kerlinger 1989).



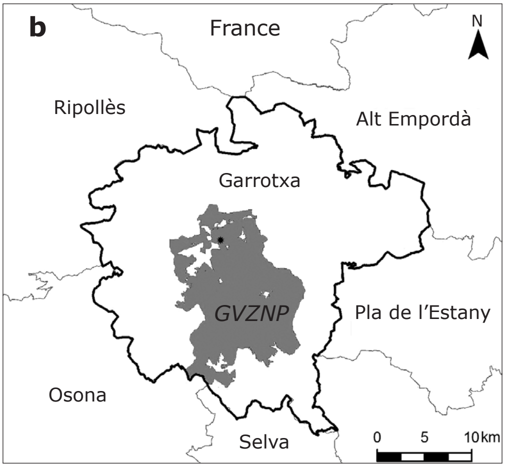


Figure 1. (**a**) Map of southwest Europe. The striped area of southern France was used in the analyses of the horizontal winds at 850 hPa, while the observation zone is shown in a black square. (**b**) Map in detail of the observation zone. The thick black line shows La Garrotxa region boundary. The GVZNP is the grey area, and Aiguanegra volcano is the black star.
*(**a**) Mapa del sud-oest d'Europa. La superfície del sud de França pintada amb quadrícula va ser la considerada pels anàlisis dels vents horitzontals a 850hPa. El quadrat negre limita la zona d'estudi. (**b**) Mapa en detall de la zona d'estudi. Els límits comarcals de la Garrotxa vénen donats per la línia negra gruixuda, el PNZVG és l'àrea grisa, i el volcà Aiguanegra està senyalitzat per l'estrelleta negra.*

We considered winds at two regional spatial scales. As a larger regional scale, we selected an area of southern France covering roughly 220,000 km^2 between 46°N and the Spanish border (Figure 1a). Honey Buzzards are obliged to pass over this region before reaching our study site. We selected the size of the area based on known travel distances for the study species. Although its mean travelling speed is usually around 40 km/h (Bruderer *et al.* 1994), Honey Buzzards can in fact exceed 80 km/h under exceptional circumstances and, consequently, can cover over 450 km in a single day (Bruderer *et al.* 1994, Hake *et al.* 2003, Meyburg *et al.* 2010). Therefore, exceptionally, an individual departing at sunrise (07:00) about 450 km north of our study site could reach Aiguanegra by the end of our daily census. This distance coincides approximately with a straight line drawn between 46°N and the border with Spain and so this surface area was considered to be the maximum possible area of horizontal wind influencing the migrant Honey Buzzards recorded at our observation site.

As a smaller regional scale, we analyzed the winds in the GVZNP (roughly 150 km^2; Figure 1b). Both studied areas were not abutting because the Pyrenean strip was discarded due to the distortions in horizontal wind directions provoked by the topography (mountains over 1,500 m a.s.l.). Our observation site was located about 15 km in a straight line south of the Spanish/French border.

The meteorological models employed were the MM5 (Fifth-Generation NCAR/Penn State Mesoscale Model) with a resolution of 36 km for southern France and the MM5 with a resolution of 12 km for the GVZNP. We obtained the daily wind maps at 850hPa at 12:00 h (Universal Coordinated Time) from the Meteorological Service of Catalonia (http://www.meteo.cat/servmet/index.html#) for the period 2007–2012 (e.g. Figure 2). These maps are updated every day and are only available on-line in real time. This information can be requested, however, from the Meteorological Service of Catalonia.

Prevailing winds were classified as either N, W, S or E, or NW, SW, SE and NE. For each study day, the prevailing wind over southern France was determined as the direction with the maximum number of wind barbs on the relevant weather map (Figure 2a). If the difference in number between the two wind directions with the highest number of wind barbs was less than three, the prevailing wind was determined to be the direction closest to the study site. In these cases, we selected the direction from the areas nearest the study site, even if it had fewer wind

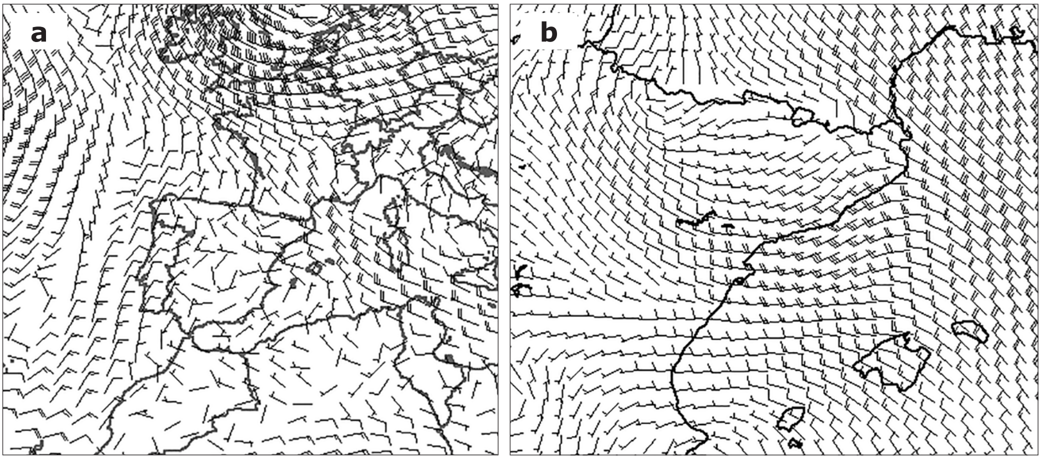


Figure 2. Wind map at 850 hPa at 12:00 h Universal Coordinated Time. Example of the MM5 models at 36 km (**a**) and 12 km resolutions (**b**) on 29 August 2010. Wind barbs indicate wind direction over each cell.
*Mapa de vent a 850hPa a les 12:00h Horari Universal Coordinat. Exemples del Model MM5 de resolució 36 km (**a**) i 12 km (**b**) pel 29 d'agost de 2010. Les fletxes indiquen la direcció del vent a cadascuna de les cel·les.*

barbs due to the probability that the target Honey Buzzards were most affected by prevailing winds in the southernmost part of France. When three or more wind directions affected similar areas of southern France, the days were classified as 'no prevailing wind' (NPW). The wind direction counts were carried out twice for each map to ensure an exact estimation. Finally, the prevailing wind in the GVZNP was determined simply by the single wind barb depicted over the area (Figure 2b) or the closest to it. Wind analysis models were obtained for the period 2007–2012.

Data analyses

Firstly, the percentage of migratory flow for each prevailing wind at both scales was calculated (a) for each year and (b) cumulatively for the period 2007–2012. In order to test for differences in the migratory flows with respect to the prevailing winds, we performed a χ^2 test (Fowler & Cohen 1999) for every year studied and for both analyzed wind scales.

Results

Honey Buzzard migration

A total of 4,627 individuals were counted during the period 2007–2012. There was a notable interannual variability with a range of 288 (2008) to 1,301 (2007) individuals (Table 1). After discarding 14 sampling days (mainly due to bad weather), the total number of sampling days was 178 that gave, in all, a total of 712 census hours.

The phenology of autumn migration peaked between late August and early September (Figure 3), which was usually followed by another small peak around mid-September, which can probably be attributed to the passage of juvenile birds (Kjellén 1992, 1998; Agostini & Logozzo 1995).

Effect of the winds over southern France

The highest percentage of migrants was recorded when the prevailing wind in southern France came from the NW. This relationship was observed both for the whole period 2007–2012 (Figure 4a) and for each year (Table 1). These values ranged from 48.9% in 2011 to 80.0% in 2010. In five out of six years, the Honey Buzzards recorded during this prevailing wind exceeded 50% of the total annual number of observations. Percentages reported during southerly winds were the lowest: for instance, SW winds blew every study year for more days than the other southerly winds but for this wind annual migration records ranged from just 1.76% in 2010 to 17.4% in 2011. These findings indicate that there is a clear preference for northerly and westerly winds; χ^2 tests for each individual year showed highly significant differences in migration numbers between all the different prevailing winds (total $p < 0.001$, Table 3).

Effect of wind over the GVZNP

Likewise, in the GVZNP, most Honey Buzzards were counted when the prevailing winds were from the NW. This was true for the whole period 2007–2012 (Figure 4b) and for four out of six years (Table 1). Only in two years (2009 and 2011) did the percentage of total observations for NW winds account for less than 50%. Interestingly, in both 2007 and 2010 over 85% of individuals were observed with prevailing NW winds. Southerly winds never blew for more than 36.7% of days (2012) and observations never exceeded 20.3% (2011, Table 1).

Highly significant differences in the migration numbers according to the different prevailing winds were found (χ^2 tests, all $p < 0.001$, Table 3).

Discussion

Migration peaks recorded during this study agree with phenology of adult migration in southern Italy (which peaks between August 24 and September 9) (Agostini and Logozzo 1995). Juveniles cross the Mediterranean Sea on a wider front than adults (Schmid 2000, Hake *et al.* 2003) which may explain why the second

Table 1. Number of days of each prevailing wind direction and the number of Honey Buzzards recorded in each one. Total numbers and their percentages for both wind scales (southern France and the GVZNP) are shown for the years 2007–2012. NPW = No prevailing wind; IS = Days of incomplete sampling due to adverse weather conditions; P. A. = *Pernis apivorus*; * Excluding the days in which sampling was not possible due to weather conditions.
*Nombre de dies per a cadascuna de les direccions predominants dels vents i el nombre d'Aligots vespers observats a cadascuna d'elles. Els nombres totals i seus percentatges es donen per a les dues escales de vent (sud de França i el PNZVG) durant el període 2007-2012. NPW = Sense component predominant, IS = Dies d'incompliment de les hores de mostreig per causes meteorològiques, P. A.=*Pernis apivorus*, * Sense els dies que no es va realitzar el seguiment per causes meteorològiques.*

		Southern France				GVZNP			
Year	**Wind**	**Days**	**P. A.**	**%Wind**	**%P. A.**	**Days**	**P. A.**	**%Wind**	**%P. A.**
2007	NW	8	692	28.6	53.4	13	1,116	46.4	86.0
	W	–	–	–	–	1	23	3.6	1.8
	SW	7	98	25.0	7.6	7	88	25.0	6.8
	S	–	–	–	–	2	15	7.1	1.2
	SE	2	4	7.1	0.3	2	4	7.1	0.3
	E	1	5	3.6	0.4	–	–	–	–
	NE	5	54	17.9	4.2	1	3	3.6	0.2
	N	–	–	–	–	2	48	7.1	3.7
	NPW	5	444	17.9	34.2	–	–	–	–
	Total	**28**	**1,297**	**100.0**	**100.0**	**28**	**1,297**	**100.0**	**100.0**
	No Map	1	0			1	0		
	IS	3	4			3	4		
	Overall total	**32**	**1,301**			**32**	**1,301**		
2008	NW	9	167	28.1	58.0	11	147	34.4	51.0
	W	1	10	3.1	3.5	3	51	9.4	17.7
	SW	12	41	37.5	14.2	11	50	34.4	17.4
	S	1	1	3.1	0.3	–	–	–	–
	SE	–	–	–	–	2	14	6.3	4.9
	E	1	5	3.1	1.7	–	–	–	–
	NE	4	39	12.5	13.5	2	1	6.3	0.3
	N	–	–	–	–	2	20	6.3	6.9
	NPW	4	25	12.5	8.7	1	5	3.1	1.7
	Overall total	**32**	**288**	**100.0**	**100.0**	**32**	**288**	**100.0**	**100.0**

►

Year	Wind	Southern France				GVZNP			
		Days	P. A.	%Wind	%P. A.	Days	P. A.	%Wind	%P. A.
2009	NW	9	480	29.0	50.9	6	323	20.7	34.3
	W	2	337	6.5	35.7	2	137	6.9	14.6
	SW	7	22	22.6	2.3	4	2	13.8	0.2
	S	2	1	6.5	0.1	5	16	17.2	1.7
	SE	3	34	9.7	3.6	1	0	3.4	0.0
	E	–	–	–	–	–	–	–	–
	NE	7	6	22.6	0.6	6	68	20.7	7.2
	N	–	–	–	–	1	0	3.4	0.0
	NPW	1	63	3.2	6.7	4	395	13.8	42.0
	Total	**31**	**943**	**100.0**	**100.0**	**29**	**941**	**100.0**	**100.0**
	IS	1	6			1	6		
	No Map	–				2	2		
	Overall total	**32**	**949**			**32**	**949**		
2010	NW	14	816	48.3	80.0	12	869	41.4	85.2
	W	4	55	13.8	5.4	1	3	3.4	0.3
	SW	5	18	17.2	1.8	6	24	20.7	2.4
	S	–	–	–	–	1	0	3.4	0.0
	SE	1	6	3.4	0.6	3	84	10.3	8.2
	E	1	35	3.4	3.4	–	–	–	–
	NE	1	40	3.4	3.9	1	2	3.4	0.2
	N	1	10	3.4	1.0	1	10	3.4	1.0
	NPW	2	40	6.9	3.9	4	28	13.8	2.7
	Total	**29**	**1,020**	**100.0**	**100.0**	**29**	**1,020**	**100.0**	**100.0**
	IS	2	2			2	2		
	Overall total	**31***	**1,022**			**31**	**1,022**		
2011	NW	10	214	35.7	48.9	6	83	21.4	18.9
	W	3	35	10.7	8.0	4	143	14.3	32.6
	SW	8	76	28.6	17.4	8	89	28.6	20.3
	S	1	5	3.6	1.1	6	65	21.4	14.8
	SE	–	–	–	–	3	51	10.7	11.6
	E	–	–	–	–	–	–	–	–
	NE	–	–	–	–	–	–	–	–
	N	–	–	–	–	1	7	3.6	1.6
	NPW	6	108	21.4	24.7				
	Total	**28**	**438**	**100.0**	**100.0**	**28**	**438**	**100.0**	**100.0**
	No Map	1	24			1	24		
	IS	1	1			1	1		
	Overall total	**30***	**463**			**30**	**463**		
2012	NW	6	461	20.0	71.9	5	467	16.7	72.9
	W	1	2	3.3	0.3	3	6	10.0	0.9
	SW	16	79	53.3	12.3	11	82	36.7	12.8
	S	–	–	–	–	2	4	6.7	0.6
	SE	–	–	–	–	3	3	10.0	0.5
	E	–	–	–	–	–	–	–	–
	NE	3	63	10.0	9.8	2	2	6.7	0.3
	N	4	36	13.3	5.6	4	77	13.3	12.0
	Overall total	**30***	**641**	**100.0**	**100.0**	**30**	**641**	**100.0**	**100.0**

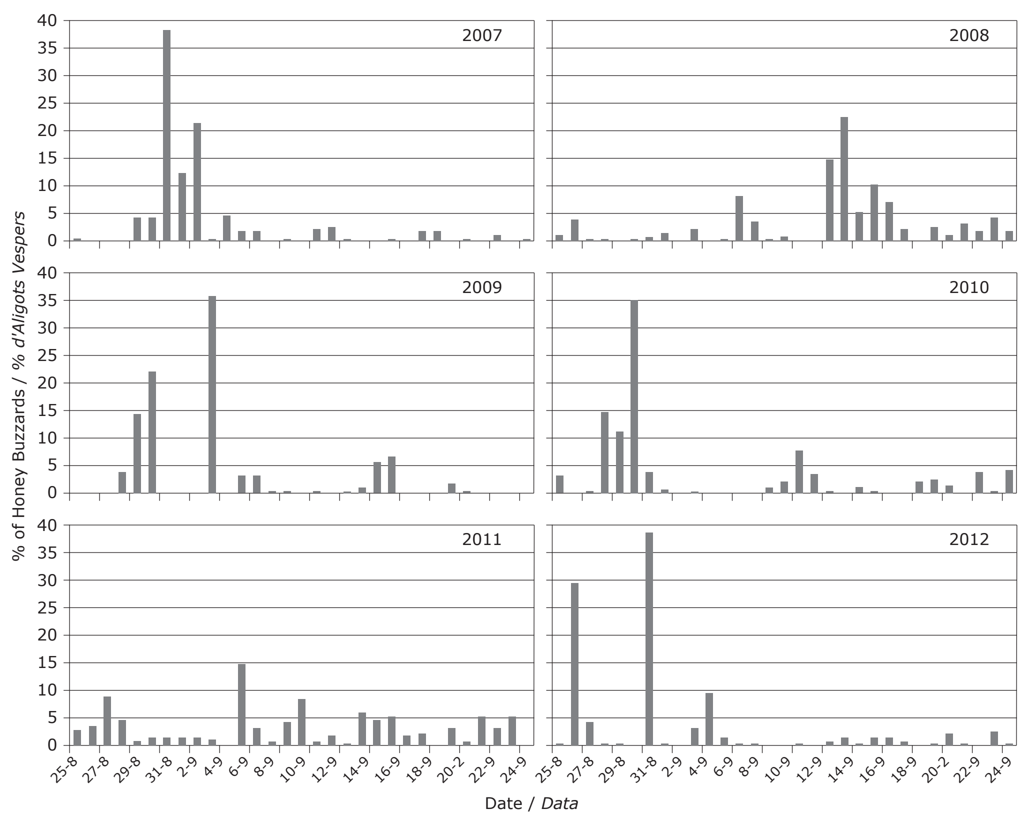


Figure 3. Percentages of daily observations of Honey Buzzards in post-nuptial migration over the GVZNP during the study years.
Percentatges de les observacions diàries d'Aligots Vespers en migració postnupcial a través del PNZVG durant els anys d'estudi.

peak, i.e. the juvenile peak, was generally less pronounced (Figure 3).

For the whole study period and at the scale of both southern France and the GVZNP, we found that there was an important autumn migratory passage of Honey Buzzards associated with prevailing NW winds at 850 hPa. The migratory pattern detected over the GVZNP might therefore be conditioned by the drift effect of NW winds in southern France and in the study area. There is probably an optimal wind direction for Honey Buzzard migration irrespective of the scale. NW winds over southern France consistently had a greater effect on the number of individuals passing over the study site than the winds blowing over the GVZNP, although this difference could be due to a greater stochasticity associated with the estimation of the prevailing wind direction at the smaller scale of the GVZNP.

It is important to highlight the marked inter-annual variability in the numbers of migrating Honey Buzzards (García & Trabalon, 2010). This is due, possibly, to the fact that winds with a NW component are often accompanied by precipitation in the Pyrenees, which is known to negatively affect bird migratory behaviour, especially soaring (Richardson 1978 and references therein, Elkins 1988). Certain methodological biases may also create further sources of variability since large migrants flocks can gather in just a few hours and may not always coincide with the monitoring time schedule. Finally, variation in wind strength between years may account for some differences in the observed numbers. Birds regulate their flying height in terms of the

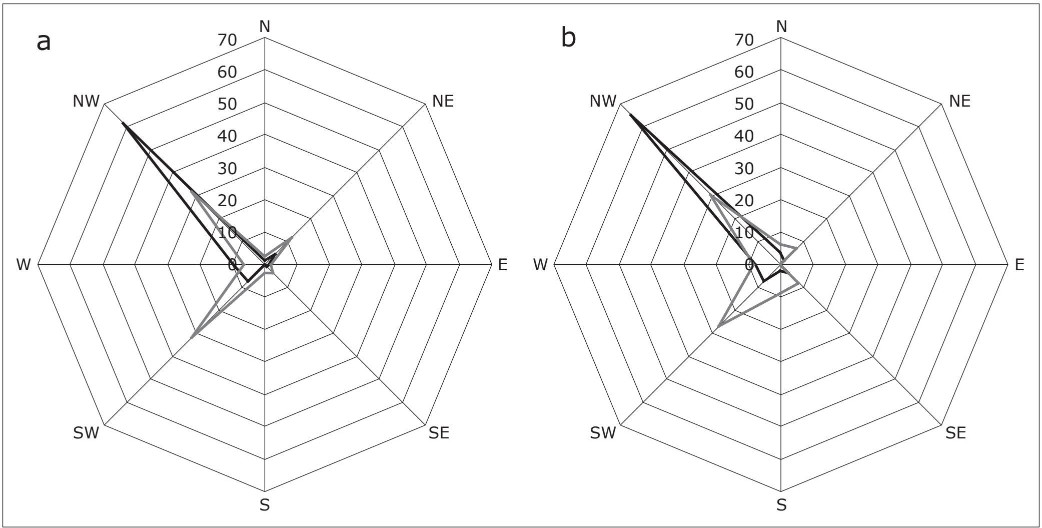


Figure 4. Percentages of Honey Buzzards observed in the GVZNP with each prevailing wind (black line) and percentages of each prevailing wind (grey line) for the period 2007–2012. (**a**) Southern France (n = 178 days); 14.7% of individuals observed with NPW; NPW = 10.1% of total days. (**b**) The GVZNP (n = 176 days); 9.3% of individuals observed with NPW; NPW = 5.1% of total days.
*Percentatges d'Aligots vespers observats al PNZVG amb cada component de vent predominant (línia negra) i percentatges de cada component predominant (línia grisa) per al període 2007-2012. (**a**) Per al sud de França (n = 178 dies), 14.7% dels individus observats sense component predominant (SCP), SCP = 10.1% dels dies totals. (**b**) Per al PNZVG (n = 176 dies), 9.3% dels individus observats SCP, SCP = 5.1% dels dies totals.*

wind strength and, for example, fly lower in the event of strong winds (Klaassen *et al*. 2010, Panuccio *et al.* 2010, Duerr *et al.* 2012, Lanzone *et al.* 2012). In the case of the Honey Buzzard, a recent study reported a higher proportion of birds passing at lower altitudes along an isthmus during strong lateral winds and low barometric pressure (Panuccio *et al*. 2010). Likewise, birds have been found to fly at greater heights with tailwinds and at lower heights with headwinds and/or crosswinds (Trowbridge 1902, Deelder & Tinbergen 1947, Rudebeck 1950, Berthold 2001 and references therein), and this factor may affect their detectability.

The prevailing wind direction during most of the Honey Buzzard passage in our study fully agrees with the prevailing tailwinds occurring during the migration of soaring birds found by previous studies (Richardson 1978 and references therein, 1990, Elkins 1988, Bruderer *et al*.

Table 2. Peak numbers of Honey Buzzards recorded during post-nuptial migration and the prevailing winds on that date at both wind scales analyzed. NW = North-western, W = Western, NPW = No prevailing wind.
Valors màxims registrats per campanya d'Aligots vespers en migració postnupcial i les components predominants aquell dia a les dues escales de vent analitzades. NW = nord-oest, W = oest, NPW = cap direcció predominant.

Date	Peak number	Prevailing Wind Over Southern France	Prevailing Wind Over the GVZNP
31/08/2007	495	NW	NW
13/09/2008	65	NW	NW
03/09/2009	336	W	NPW
30/08/2010	359	NW	NW
05/09/2011	68	NW	W
31/08/2012	247	NW	NW

Years	Southern France		GVZNP	
	Df	χ^2	Df	χ^2
2007	5	1888,3	6	5483,2
2008	6	485,9	6	376,3
2009	6	1652,2	7	1473,5
2010	7	4264,4	7	4969,7
2011	4	298,1	5	139,2
2012	4	1106,5	6	1879,5

Table 3. Results of χ^2 test on the total observed frequencies of Honey Buzzards with each prevailing wind for all study years and at both wind scales analyzed (all $p < 0.001$).
Resultats del test χ^2 sobre el total de freqüències observades d'Aligots vespers amb cada component de vent predominant per a cada any d'estudi i les dues escales de vent analitzades (tots $p < 0,001$).

1994, Berthold 2001). Other reports have also revealed the importance of favourable winds for the success of migration (Erni *et al*. 2005 and references therein); the striking differences in the number of individuals observed for each wind direction suggest that the migration strategy of the Honey Buzzard has been strongly shaped by the characteristics of this environmental force. The selection for specific wind directions seems to be robust even if some soaring birds may escape detection during favourable weather, especially towards midday when strong thermals occur (Heintzelman 1975, Bruderer *et. al*. 1994).

An important portion of migrating Honey Buzzards cross the Pyrenees between late August and early September. This may be due, in part, to the leading line effect of mountain ridges (Geyr 1929), which create updrafts that favour soaring birds (Robbins 1956, Ulfstrand 1960, Bildstein 2006). The drift generated by NW in southern France on these migratory routes might increase the number of birds flying over the GVZNP.

Our results support the idea of horizontal wind as a key factor in the final route of migratory flyways (Mueller & Berger 1967, Richardson 1978, Alerstam & Hedenström 1998). Alerstam (1979) established that partial drift might be an adaptive strategy against wind as a selective agent, especially when migrating over inhospitable regions. In particular, some studies conducted in southern Italy indicate that Honey Buzzards change their migration strategy in terms of the wind drift when migrating over the Channel of Sicily and form a broad front of migration over water (Agostini *et al*. 2005b, 2007; Panuccio *et al*. 2010). Some raptors change migratory strategies depending on the site and the period as a response to crosswinds (Klaassen *et al*. 2010); this is the case of the Western Marsh-harrier *Circus aeruginosus,* which drifts when westerly winds blow at latitudes of 30-40° and compensates the route with easterly winds. These, and other reports, show the importance of extending the geographical scope of research on the influence of prevailing winds on birds' migratory flyways. Monitoring changes could be of great transcendence given the onset of global change and associated climatic shifts (Weimerskirch *et al.* 2012).

In conclusion, the results of this study were fairly consistent over years and geographic scales. This finding suggests that – despite the methodological drawbacks such as the way in which the prevailing winds were determined using maps, which are a snapshot of weather conditions and may not exactly match the height of flight we assumed for the Honey Buzzard – horizontal wind maps at 850 hPa may constitute a useful tool in the study of bird migratory behaviour, especially in case of species that depend most on gliding flight when migrating. Therefore, regardless of the possible limitations of a methodology based on visual observations (Richardson 1978), this study provides information that could be incorporated into the design of more complex and interdisciplinary studies of the optimization of migratory behaviour, and be combined with different sampling techniques (e.g. satellite radio-tracking). Indeed, several researchers have stressed the need to perform integrated migration studies that incorporate various scientific disciplines including meteorology (Alerstam & Hedenström 1998, Shamoun-Baranes *et al*. 2010a) and that use new technologies and theoretical models, all within the context of animals' annual cycles (Bowlin *et al.* 2010).

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Resum

Migració de tardor visible de l'Aligot vesper *Pernis apivorus* al NE de la península Ibèrica en relació als vents horitzontals en altura

L'Aligot vesper *Pernis apivorus* és una rapinyaire planadora migratòria que nidifica a Euràsia i hiverna al sud del Sàhara. Ja que el vent és un dels factors meteorològics més importants que afecta a la migració de les aus, es va analitzar com el vent horitzontal predominant a 850 hPa (equivalent a una alçada de 1.000-1.500 m s.n.m.) va influir sobre el pas migratori postnupcial detectat al Parc Natural de la Zona Volcànica de la Garrotxa (PNZVG), nord-est de la península Ibèrica, durant el període 2007-2012. Es va calcular el percentatge de migració visual sobre el PNZVG per a cada component de vent predominant sobre dues escales regionals diferents: els voltants del PNZVG (pas de malla de 12 km de resolució) i l'àrea precedent del sud de França entre el paral·lel 46°N i la frontera amb Espanya (pas de malla de 36 km de resolució). Els percentatges de migrants més elevats detectats sobre el PNZVG van coincidir tots els anys amb vents predominants de nord-oest a l'escala regional més gran (sud de França). A l'escala del PNZVG, el mateix efecte es va observar en quatre dels sis anys estudiats. Es van trobar diferències altament significatives entre les freqüències totals de pas migratori amb cada component de vent predominant sobre totes dues escales i per a cada any d'estudi. Se suggereix que la migració de *Pernis apivorus* al PNZVG podria estar condicionada per la deriva causada pels vents horitzontals en alçada de component nord-oest sobre el sud de França.

Resumen

Migración visible en otoño del Abejero europeo *Pernis apivorus* en el NE de la península Ibérica en relación a los vientos horizontales en altura

El Abejero europeo *Pernis apivorus* es una rapaz planeadora migratoria que cría en Eurasia e inverna al sur del Sahara. Dado que el viento es uno de los factores meteorológicos más importantes que afecta a la migración de las aves, se analizó cómo el viento horizontal predominante a 850 hPa (equivalente a una altura de 1.000-1.500 m s.n.m.) influenció el paso migratorio postnupcial detectado en el Parque Natural de la Zona Volcánica de la Garrotxa (PNZVG), noreste de la península Ibérica, durante el período 2007-2012. Se calculó el porcentaje de migración observada a través del PNZVG con cada componente de viento predominante sobre dos escalas regionales diferentes: los alrededores del PNZVG (malla de resolución de 12 km) y el área precedente del sur de Francia situada entre el paralelo 46°N y la frontera con España (malla de resolución de 36 km). Los mayores porcentajes de migrantes detectados sobre el PNZVG coincidieron en todos los años con viento de noroeste como componente predominante en la escala regional más grande (sur de Francia). En la escala del PNZVG el mismo efecto se observó en cuatro de los seis años estudiados. Se encontraron diferencias altamente significativas entre las frecuencias totales de paso migratorio con cada componente de viento predominante para ambas escalas y cada uno de los años de estudio. Se sugiere que la migración observada de *Pernis apivorus* en el PNZVG podría estar condicionada por la deriva provocada por los vientos horizontales en altura de componente noroeste sobre el sur de Francia.

References

Agostini, N. & Logozzo, D. 1995. Autumn migration of Honey Buzzards in southern Italy. *J. Raptor Res.* 29: 275–277.

Agostini, N. 2004**.** Additional observations of age-dependent migration behaviour in western Honey Buzzards *Pernis apivorus*. *J. Avian Biol.* 35: 469–470**.**

Agostini, N., Panuccio, M. & Massa, B. 2005a. Flight behaviour of Honey Buzzards (*Pernis apivorus*) during spring migration over the sea. *Buteo* 14: 3–10.

Agostini, N., Premuda, G., Mellone, U., Panuccio, M., Logozzo, D., Bassi, E. & Cocchi, L. 2005b. Influence of wind and geography on orientation behaviour of adult Honey Buzzards (*Pernis apivorus*) during migration over water. *Acta Ornithol.* 40: 71–74.

Agostini, N., Gustin, M. & Cardelli, C. 2007. Factors shaping pathways of European Honey-buzzards (*Pernis apivorus*) during spring migration in the central Mediterranean basin. *J. Raptor Res.* 41: 57–61.

Agostini, N., Lucia, G., Mellone, U., Panuccio, M., Von Hardenberg, J., Evangelidis, A. & Kominos, T. 2012. Loop migration of adult European Honey Buzzards (*Pernis apivorus* Linnaeus, 1758) through the Central-Eastern Mediterranean. *Ital. J. Zool.* 79: 280–286.

Alerstam, T. 1979. Optimal use of wind by migrating birds: combined drift and overcompensation. *J. Theor. Biol.* 79: 341–53.

Alerstam, T. 1996. The geographical scale factor in orientation of migrating birds. *J. Exp. Biol.* 199: 9–19.

Alerstam, T. & Hedenström, A. 1998. The development of bird migration theory. *J. Avian Biol.* 29: 343–369.

Berthold, P. 2001. *Bird migration: a general survey*. Oxford: Oxford University Press.

Bildstein, K. L. 2006. *Migrating raptors of the world: their ecology and conservation*. New York: Cornell University.

Bowlin, M.S., Bisson, I-A., Shamoun-Baranes, J., Reichard, J.D., Sapir, N., Marra, P.P., Kunz, T.H., Wilcove, D.S., Hedenström, A., Guglielmo, C.G., Åkesson, S., Ramenofsky, M. & Wikelski, M. 2010. Grand challenges in migration biology. *Integr. Comp. Biol.* 50: 261–279.

Bruderer, B., Blitzblau, S. & Peter, D. 1994. Migration and flight behaviour of Honey Buzzards (*Pernis apivorus*) in southern Israel observed by radar. *Ardea* 82: 111–122.

Cramp, S. & Simmons, K.E.L. 1980. *The Birds of the Western Palearctic.* Vol.2. Oxford: Oxford University Press.

Deelder, C.L. & Tinbergen, L. 1947. Waarnemingen over de vlieghoogte van trekkende Vinken, *Fringilla coelebs* L., en Spreeuwen, *Sturnus vulgaris* L. *Ardea* 35: 45–78.

Duerr, A.E., Miller, T.A., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K., Maisonneuve, C., Tremblay, J. & Katzner, T. 2012. Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. *PLoS ONE* 7: e35548.

Eastwood, E. 1967. *Radar ornithology*. London: Methuen.

Elkins, N. 1988. *Weather and bird behaviour*. Calton: T. & A.D. Poyser.

Erni, B., Liechti F. & Bruderer, B. 2005. The role of wind in passerine autumn migration between Europe and Africa. *Behav. Ecol.* 16: 732–40.

Felicísimo, A. M., Muñoz, J. & González-Solis, J. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* 3, e2928.

Forsman, D. 1999. *The raptors of Europe and the Middle East*. London: T.& A.D. Poyser.

Fowler, J. & Cohen, L. 1999. *Estadística básica en ornitología*. Madrid: SEO/BirdLife.

García, R. & Trabalon, F. 2010. Seguiment de rapinyaires en migració postnupcial al Parc Natural de la Zona Volcànica de la Garrotxa (2003-2008). *Anals de la Delegació de la Garrotxa de la Institució Catalana d'Història Natural* 4: 107–112.

Gätke, H. 1895. *Heligoland as an ornithological observatory. The result of fifty years experience*. Edinburgh: David Douglas.

Geyr von Schweppenburg, H. 1929. Zugstrassen-Leitlinien. *J. Ornith*. II: 17–32.

Hake, M., Kjellén, N. & Alerstam, T. 2003. Age-dependent migration strategy in Honey Buzzards (*Pernis apivorus*) tracked by satellite. *Oikos* 103: 385–396.

Heintzelman, D.S. 1975. *Autumn hawks flight: the migration in eastern North America*. New Brunswick: Rutgers University Press.

Kerlinger, P. 1989. *Flight strategies of migrating hawks*. Chicago: University of Chicago Press.

Kjellén, N. 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scand.* 23: 420–434.

Kjellén, N. 1998. Annual variation in numbers, age and sex ratios among migration raptors at Falsterbo, Sweden from 1986-95. *J. Ornithol.* 139: 157–171.

Klaassen, R.H.G., Hake, M., Strandberg, R. & Alerstam, T. 2010. Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proc. R. Soc. B*, 278, 1339–1346.

Lack, D. 1962. Migration across the southern North Sea studied by radar. *Ibis* 104: 74–85.

Landsberg, H. 1948. Bird migration and pressure patterns. *Science* 108: 708–709.

Lanzone, M.J., Miller, T.A., Turk, P., Brandes, D., Halverson, C., Maisonneuve, C., Tremblav, J., Cooper, J., O'Malley, K., Brooks, R.P. & Katzner, T. 2012. Flight responses by a migratory raptor to changing meteorological conditions. *Biol. Lett*. 8: 710–713.

Meyburg, B.-U., Ziessemer, F., Martens, H.D. & Meyburg, C. 2010. On the biology of the Honey Buzzard (*Pernis apivorus*)-results of satellite tracking. *7th International symposium ecology of raptors and owls.* Halberstadt, Germany 21–24.10.2010.

Mellone, U., Klaassen, R.H.G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., Strandberg, R., Urios, V., Vardakis, M. & Alerstam, T. 2012. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PloS ONE* 7: e39833.

Mueller, H.C. & Berger, D.D. 1967. Wind drift, leading lines, and diurnal migration. *Wilson Bull.* 79: 50–60.

Newton, I. 2008. *The migration ecology of birds*. London: Academic Press.

Panuccio, M., Agostini, N., Lucia, G., Mellone, U., Wilson, S., Ashton-Booth, J., Chiatante, G. & Todisco, S. 2010. Local weather conditions affect migration strategies of adult Western Honey Buzzards (*Pernis apivorus*) through an isthmus area. *Zool. Stud.* 49: 651–656.

Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224–272.

Richardson, W.J. 1990. Timing of bird migration in relation to weather: updated review. In Gwinner, E. (ed.). *Bird Migration*. Pp. 78–101. Berlin: Springer-Verlag.

Robbins, C.S. 1956. Hawk watch. *Atlantic Naturalist* 11: 208–217.

Rudebeck, G. 1950. Studies on bird migration. *Var Fagelvärld* I.

Schmid, H. 2000. GetrennteWege: Der Herbstzug von juvenilen und adulten Wespenbussarden *Pernis apivorus* - eine Synthese. *Der Ornithologische Beobachter* 97: 191–222.

Shamoun-Baranes, J., Bouten, W. & van Loon, E.E. 2010a. Integrating meteorology into research on migration. *Integr. Comp. Biol.* 50: 280–292.

Thake, M.A. 1977. Synoptic scale-weather and Honey Buzzard (*Pernis apivorus*). migration across the central Mediterranean. *Il-Merril* 18: 19–25.

Thake, M.A. 1980. Gregarious behaviour among migrating Honey Buzzard (*Pernis apivorus*). *Ibis* 122: 500–505.

Thorup, K., Alerstam Th., Hake, M. & Kjellén, N. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. R. Soc. B*. 270: S8–S11.

Trowbridge, C.C. 1902. The relation of wind to bird migration. *Amer. Nat*. 36: 735-753.
Ulfstrand, S. 1960. Migration of African kites *Milvus migrans* (Bodd.)-*M. aegyptius* Sharpe & Bouvier, and Wahlberg's Eagles *Aquila wahlbergi* Sund., at Lake Tanganyika. *Kungl. Fysiografiska Sällskapets I Förhandlingar* 30:31–39.
Weimerskirch, H., Louzao M., de Grissac, S. & Delord, K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335: 211–214.
Westernhagen, W.V. 1960. Sobre el vuelo inmigratorio del Halcón Abejero (*Pernis apivorus*) a través de Gibraltar. *Ardeola* 6: 293–300.