

Article

Wind effects on the migration routes of trans-Saharan soaring raptors: geographical, seasonal, and interspecific variation

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Abstract

Wind is among the most important environmental factors shaping birds' migration patterns. Birds must deal with the displacement caused by crosswinds and their behavior can vary according to different factors such as flight mode, migratory season, experience, and distance to goal areas. Here we analyze the relationship between wind and migratory movements of three raptor species which migrate by soaring–gliding flight: Egyptian vulture *Neophron percnopterus*, booted eagle *Aquila pennata*, and short-toed snake eagle *Circaetus gallicus*. We analyzed daily migratory segments (i.e., the path joining consecutive roosting locations) using data recorded by GPS satellite telemetry. Daily movements of Egyptian vultures and booted eagles were significantly affected by tailwinds during both autumn and spring migrations. In contrast, daily movements of short-toed eagles were only significantly affected by tailwinds during autumn migration. The effect of crosswinds was significant in all cases. Interestingly, Egyptian vultures and booted eagles showed latitudinal differences in their behavior: both species compensated more frequently at the onset of autumn migration and, at the end of the season when reaching their wintering areas, the proportion of drift segments was higher. In contrast, there was a higher drift at the onset of spring migration and a higher compensation at the end. Our results highlight the effect of wind patterns on the migratory routes of soaring raptors, with different outcomes in relation to species, season, and latitude, ultimately shaping the loop migration patterns that current tracking techniques are showing to be widespread in many long distance migrants.

Key words: *Neophron percnopterus*, *Aquila pennata*, *Circaetus gallicus*, wind drift, satellite telemetry, migration.

In the last decades, research on bird migration has focused on several aspects, such as flight mode, fuel deposition, predation risk, use of stopover sites, routes and detours, migration schedules, and the effect of wind (Alerstam 2011). Recently, the effect of winds upon migratory behavior has received great attention, because it is apparently the most important environmental factor influencing bird behavior in different stages of the routes (Klaassen et al. 2011;

Mellone et al. 2011a; Safi et al. 2013). The effect of wind reaches such importance that it intervenes directly in the movement vector of the bird: birds' direction and flight speed is the sum of the wind vector and the bird's own flight vector relative to the surrounding air (Alerstam 1990).

The influence of wind has been studied in different migration parameters. In some cases, the importance of wind has been

highlighted for the onset of bird migration, when individuals try to select favorable wind conditions for departure (Åkesson and Hedenström 2000), although this is not always the case (Thorup et al. 2006). Winds also influence the speed that birds can achieve (Shamoun-Baranes et al. 2003; Mellone et al. 2012), and the selection of flight altitude (Mateos-Rodríguez and Liechti 2012). Therefore, it is important to consider wind conditions in relation to migration to achieve a better understanding of migratory performance (Kemp et al. 2010; Vansteelant et al. 2015) and previous studies have suggested that wind is a strong predictor of migration speed, accounting for 10–66% of variance, depending on species (Safi et al. 2013). Within diurnal raptors, recently the effect of winds has been investigated also in relation to foraging movements (Hernández-Pliego et al. 2014).

In addition to headwinds and tailwinds, birds must also deal with crosswinds during their migrations, causing them partial or full drift from the main intended direction of their movement. Hence, in order to maintain direction birds must adjust their course according to wind direction and speed by exhibiting a compensating or even overcompensating behavior (Alerstam 2011; Klaassen et al. 2011). Furthermore, birds can vary their behavior in response to wind depending on the stage of the journey. Several studies have shown that drift is more frequent at the onset of migration when birds are further away from their goal, while compensation increases when birds are approaching their goal areas (Green et al. 2004; Klaassen et al. 2011; Limiñana et al. 2013; Mellone et al. 2015). Moreover, bird behavior is also influenced by the occurrence of natural barriers, for instance avoiding drift over the sea (Panuccio et al. 2010; Klaassen et al. 2011). These findings suggest that the response to crosswind depends not only on distance to the goal, but also on wind direction and speed. Age is also a determining factor, with juveniles being more susceptible to drift than adults (Thorup et al. 2003).

On the other hand, different flight modes may also influence the response to winds (Limiñana et al. 2013) and the flight performance (Malmiga et al. 2014). Flapping flight is the most common flight mode of small-sized birds, whereas large birds use a combination of soaring–gliding flight as the energy expenditure required for flapping increases with body mass. Hence, from the energy consumption point of view, large-sized birds take more advantage than smaller one from soaring flight, spending a low percentage of their metabolic rate for flight (Pennycuik 1975). In addition, large and medium-sized raptors use mostly a soaring–gliding flight strategy, taking advantage of thermal updrafts to gain altitude and then descending gliding in the intended direction until the next updraft (Kerlinger 1989). Other species, such as harriers, although predominantly use a flapping–gliding flight mode, also make use of flapping flight mode more often than other raptors (Spaar and Bruderer 1997).

This study focuses on three diurnal migrating raptors that use mostly the soaring flight mode: Egyptian vulture *Neophron percnopterus*, booted eagle *Aquila pennata*, and short-toed snake eagle *Circaetus gallicus*. All three species are trans-Saharan migratory birds: their breeding populations in Western Europe migrate to their wintering grounds located in the Sahel region (Cramp and Simmons 1980). Recent studies have provided a complete description of their migratory routes by means of GPS satellite telemetry (García-Ripollés et al. 2010; Pavón et al. 2010; Mellone et al. 2013; López-López et al. 2014). However, a detailed analysis of the effects of wind on their migratory routes is still lacking. Therefore, the main goals of this article are: 1) to assess the effect of forward and

crosswinds in the autumn and spring migration of these three raptor soaring–gliding species; 2) to analyze the different responses to wind conditions in relation to species, season, and latitude; and finally, 3) to examine the different responses of birds with regard to the origin of crosswinds (easterly or westerly winds).

Material and Methods

Study species and tagging

A total of 22 individual raptors were tagged with GPS satellite transmitters, tracking both their autumn and their spring migrations, between the breeding areas in Europe and their wintering grounds in the Sahel. As the three species are soaring–gliding migrants, they are more dependent of wind conditions to migrate than the raptors that use mostly flapping flight. In fact, since they need thermal updrafts for flying they are more selective for favorable weather conditions than species flying mainly by flapping–gliding (Limiñana et al. 2013).

Between 2007 and 2009, six adult Egyptian vultures were trapped in Castellón and Guadalajara provinces, Spain (see García-Ripollés et al. 2010; López-López et al. 2013 for further details). Nine adult booted eagles were trapped in different provinces of Spain (Madrid, Castellón, Ávila, Murcia, Barcelona, and Badajoz) between 2011 and 2013 (see Mellone et al. 2013, 2014 for more details). Concerning short-toed eagles, seven juveniles were tagged with satellite transmitters between 2008 and 2010, all trapped at their nests when were 55–60 days old: five of them in Spain and two in the Basilicata region in Italy (see Pavón et al. 2010; Mellone et al. 2011b, 2011c for more details).

All individuals were equipped with 45 g (Egyptian vultures and short-toed eagles) and 22 g (booted eagles) solar-powered GPS transmitters (Microwave Telemetry Inc.), apart from one-booted eagle which was tagged with a GPS datalogger (Telemetry Solutions Inc.). Tags were affixed to their backs using a Teflon harness, a resistant and nonabrasive material, which was tied with a cotton thread to ensure that the harness is released from the animal at the end of the transmitter's life. Transmitters' weight was <5% of birds' body mass, which is within the recommended limits (Kenward 2001). The Egyptian vultures' and short-toed eagles' tags were programmed to obtain GPS locations every 2 h 24 h per day during both autumn and spring migration (García-Ripollés et al. 2010; Pavón et al. 2010; Mellone et al. 2011b, 2011c; López-López et al. 2013). The booted eagles' tags were programmed to obtain GPS locations every hour from 06:00 h to 20:00 h (Mellone et al. 2013, 2014).

Tracking data

Overall, the dataset included 88 migratory journeys as follows: 47 journeys were recorded for Egyptian vultures (24 autumn and 23 spring journeys), 25 journeys for booted eagles (15 autumn and 10 spring journeys), and 18 journeys for short-toed snake eagles (11 in autumn and 7 in spring). Migration tracks were divided into daily segments (Limiñana et al. 2013), using one location per night included in the interval between 18:00 h and 06:00 h of the next day, trying to approach as much as possible to midnight (Klaassen et al. 2011). Segments longer than 1 day were excluded from the analysis. Segments in which birds displacement were shorter than 50 km/day, were also excluded in order to avoid including segments in which birds were not migrating (Klaassen et al. 2011; Limiñana et al. 2013; Mellone et al. 2014), as well as segments in a direction opposite to the main one. In the case of the two short-toed eagles

tagged in Italy (#56810 and #56813), the segments recorded before reaching the Iberian Peninsula were not taken into account in order to avoid any bias in the analyses, since it has been suggested that these juvenile individuals travel together with adults during this migration stretch (Mellone et al. 2011b).

For each segment, we established the coordinates (latitude and longitude) of the starting point (the coordinates of the place where the previous night the bird stopped to rest), of the ending point (corresponding to the day where the bird ended the segment), and the midpoint (the location exactly between the starting and ending coordinates).

Overall, we included in the analyses 572 daily segments for Egyptian vultures (250 in autumn and 232 in spring); 382 segments for booted eagles (204 in autumn and 178 in spring); and 230 segments for short-toed eagle (119 corresponding with the first autumn migration, 45 with the subsequent autumn migrations, and 66 recorded during spring migration).

Wind data

Wind data were obtained from the NCEP/DOE Reanalysis II dataset, using the RNCEP package (Kemp et al. 2012) for the R-software. This dataset includes wind's east-west and north-south components (expressed in m/s) which were extracted for our analyses. From the combination of these components two different vectors were obtained: direction (in degrees) and wind velocity (in m/s). East-west and north-south components have a spatial resolution of $2.5^\circ \times 2.5^\circ$ and a temporal resolution of 6 h, being available at 00:00, 06:00, 12:00, and 18:00 h UTC, so for each daily segment the components were extracted for the starting coordinates of the segment at 06:00 h, for the midpoint coordinates at 12:00 h, and for the ending coordinates at 18:00 h. Coordinates were extracted for a pressure level of 925 hPa, which corresponds to an altitude between 445 m and 1145 m (Schmaljohann et al. 2012). This pressure level has already been used in previous studies in which the effect of wind on other soaring raptors was analyzed (Klaassen et al. 2011; Mellone et al. 2012).

Analysis

Calculation of the intended directions

For every bird and migration journey, we calculated the overall intended direction of migration, which was estimated by dividing the entire migratory journey into two different stages: for autumn migrations, we calculated the angle between the nest (or the first location in the Pyrenees in the case of short-toed eagles born in Italy) and the Strait of Gibraltar, and the angle between the Strait of Gibraltar and the first location at wintering grounds in the Sahel. For the spring migrations, we calculated the angle between the last location at wintering grounds and the Strait of Gibraltar, and also between the Strait of Gibraltar and the nest. In the case of the Egyptian vultures, one of the birds (#89730) headed to a vulture feeding station during both autumn and spring migration, so we took it into account as the intended direction calculation. In the case of autumn migrations of short-toed eagles, juveniles (1st calendar year) were analyzed separately from older birds (2nd and 3rd calendar year), since in the first case the individuals do not know the place they are going, so we considered a general South direction (180°) from the Strait of Gibraltar to the Sahel. Instead, older birds head to previously known wintering areas, and therefore we took the coordinates of such areas into account, in the same way as for the other species. In addition, we considered a general North

direction (0°) for the calculation of the intended direction during spring migration, since the analyzed short-toed eagles spent summer in Northern Africa (Mellone et al. 2011c).

Forward and perpendicular components of the movement and wind

We calculated the forward and perpendicular components of the movement for each daily segment of migration in kilometres per day in relation to the estimated intended directions (Klaassen et al. 2011). Equally, the forward (tailwind) and perpendicular (crosswind) components were calculated with regard to the intended direction. We calculated these components at the beginning of each daily segment (06:00 h), at the midpoint (12:00 h), and at the end point (18:00 h). Finally, to simulate the effect of wind experienced along a whole migration segment, we calculated an overall forward wind and an overall perpendicular wind for every daily segment with these three values, giving more importance to the wind at the midpoint of the segment (see Klaassen et al. 2011 and Limiñana et al. 2013 for a similar approach). Therefore, for the tailwind (TW) calculation we used the formula: $TW_{\text{segment}} = (TW_{\text{onset}} + 2 * TW_{\text{midpoint}} + TW_{\text{end}}) / 4$, proceeding in the same way for the crosswinds (CW): $CW_{\text{segment}} = (CW_{\text{onset}} + 2 * CW_{\text{midpoint}} + CW_{\text{end}}) / 4$.

To assess the effect of winds on bird's movement rates, we performed a regression analysis relating the forward rate of movement to tailwinds and the perpendicular rate of movement to crosswinds for daily segments (Thorup et al. 2003; Klaassen et al. 2011; Limiñana et al. 2013). These regressions were conducted for autumn and spring migrations of each species. In the case of short-toed eagles, we separated the segments corresponding to their first autumn migration from the following migrations, in order to differentiate between data coming from birds with different degrees of experience. We also checked whether the slopes of forward and perpendicular regressions were significantly different according to 95% confidence intervals. Using regression slopes, we calculated the drift effect by dividing the forward slope coefficient by the perpendicular slope coefficient.

Types of behavior

Daily segments were classified into three different behavioral categories depending on the relationship between perpendicular movement component and crosswinds (Klaassen et al. 2011; Limiñana et al. 2013): 1) drift segments, when the perpendicular movement component was higher than 50 km/day or lower than -50 km/day with equal sign than for perpendicular winds; 2) compensation segments: when the perpendicular movement component was between 50 km/day and -50 km/day; and 3) overcompensation segments: when the perpendicular movement component was higher than 50 km/day or lower than -50 km/day (as for the drift segments) with opposite sign between this component and the perpendicular wind. We considered the distance of 50 km/day as a notably variation from the intended direction for the three species, according to their normal daily travel rates (mean daily distance for travelling days recorded in this study: 203.98 + 101.72 km/day; 194.88 ± 84.83 km/day and 191.12 ± 97.45 km/day for Egyptian vulture, booted eagle and short-toed eagle, respectively).

We evaluated the behavioral response to wind conditions among species, seasons, and regions using chi-squared tests in contingency tables (Limiñana et al. 2013). To this end, journeys were divided into three different regions, thus building three sub-samples to make comparisons among the first, middle, and final segments of the migration itself: latitudes higher to 36° N (those corresponding with

Europe), latitudes between 36° N and 28° N, and latitudes below 28° N. We also evaluated whether there was an effect of age in the frequency of the different segments for the short-toed snake eagle, comparing the first autumn migration with the subsequent ones. Finally, we analyzed birds' behavior in relation to the origin of winds (i.e., easterly or westerly winds), in order to test for differences in the proportion of these types of segments for both cross-wind directions.

Results

Relationship between forward movement and forward winds

Daily movements of Egyptian vultures and booted eagles were significantly affected by tailwinds (Table 1). During autumn migrations, Egyptian vultures increased their forward rate of movement on average 16.38 km/day for every meter per second of tailwind, with a forward daily rate of movement of 214.35 km/day in absence of wind. This advantage was higher than in spring (Figure 1), when for every meter per second of tailwind the forward rate of movement increased by 9.79 km/day, showing rates of 181.81 km/day in absence of wind. Booted eagles took a similar advantage of tailwinds in autumn and spring, increasing their rate of movement on average by 8.98 and 10.35 km/day for every meter per second of wind. In the case of the short-toed eagles, the effect of tailwinds was significant both in their first and the following autumn migrations, being somewhat higher the advantage obtained by experienced individuals (2nd and 3rd calendar year birds: 14.90 km/day for every m/s of tailwind versus 10.82 km/day for every m/s of wind in the case of the juveniles). The relationship between the rate of forward movement and the tailwinds was not significant ($P=0.061$) for the short-toed eagle spring migrations (Figure 1).

Relationship between perpendicular movement and crosswinds

The effect of crosswinds in perpendicular movement rates was significant in all cases (Table 1), and similar for autumn and spring migrations of each species (Figure 2).

According to the ratio between slopes (perpendicular/forward), the drift experienced by Egyptian vultures and short-toed eagles was higher during spring migrations, while in the case of the booted

eagles there was only a slight difference between spring and autumn. Nevertheless, these values were not significant for most cases at an $\alpha=0.05$ level (Table 1).

Differences between frequencies of drift, compensation, and overcompensation segments

There were no differences in the proportions of segment type (drift, compensation, and overcompensation) among seasons (Egyptian vulture: $\chi_2^2=2.41$, $P=0.300$; booted eagle: $\chi_2^2=2.12$, $P=0.346$; short-toed eagle: $\chi_2^2=1.21$, $P=0.174$). Similarly, there were no significant differences among species neither in autumn ($\chi_4^2=5.12$, $P=0.423$), nor in spring ($\chi_4^2=4.07$, $P=0.142$), nor combining both seasons ($\chi_4^2=8.18$, $P=0.146$). Juvenile short-toed eagles in their first autumn migration did not show significant differences in the proportions of segments in comparison to subsequent migrations ($\chi_2^2=5.16$, $P=0.190$). Proportions of these segments were significantly different when considering the latitude for Egyptian vultures and booted eagles (Figure 3). Both species compensated more frequently at the onset of autumn migration rather than at the end, especially the Egyptian vulture (Egyptian vulture: $\chi_4^2=20.75$, $P<0.001$; booted eagle: $\chi_4^2=20.94$, $P<0.001$). Egyptian vultures and booted eagles also experienced a higher drift at the onset of the spring migration (Table 2) while, at the end of migration, already in Europe, the proportion of compensation segments was higher (Egyptian vulture: $\chi_4^2=35.07$, $P<0.001$; booted eagle: $\chi_4^2=31.87$, $P<0.001$). These latitudinal differences were not observed in short-toed eagles neither in autumn ($\chi_2^2=4.13$, $P=0.127$) nor in spring ($\chi_2^2=3.838$, $P=0.508$).

Concerning differences between frequencies of segments according to wind direction (easterly and westerly winds), there were no significant differences for any species neither in autumn (Egyptian vulture: $\chi_2^2=0.79$, $P=0.671$; booted eagle: $\chi_2^2=5.82$, $P=0.054$; short-toed eagle: $\chi_2^2=3.86$, $P=0.144$), nor in spring (Egyptian vulture: $\chi_2^2=0.68$, $P=0.712$; booted eagle: $\chi_2^2=3.63$, $P=0.163$; short-toed eagle: $\chi_2^2=3.93$, $P=0.140$) nor considering both seasons combined (Egyptian vulture: $\chi_2^2=1.56$, $P=0.457$; booted eagle: $\chi_2^2=2.67$, $P=0.263$; short-toed eagle: $\chi_2^2=3.56$, $P=0.169$). The analyses were also performed combining compensation and overcompensation segments, therefore comparing drift against (over)compensation segments, but differences between segments were not significant in any case.

Table 1. Linear regressions between the rate of forward movement (km/day) and the forward wind component (m/s), and between the rate of perpendicular movement and the perpendicular wind component

		n	Forward movement				Perpendicular movement				Test between slopes	Ratio between slopes
			Slope	95% Confidence interval	Intercept (km/day)	Sig.	Slope	95% Confidence interval	Intercept (km/day)	Sig.		
Egyptian vulture	Autumn	250	16.37	11.97–20.77	214.3	0.000	10.78	7.78–13.78	–0.1	0.000	*	0.66
	Spring	322	9.78	7.73–11.83	181.8	0.000	8.69	6.57–10.82	13.9	0.000	n.s.	0.89
Booted eagle	Autumn	204	8.97	4.61–13.34	173.3	0.000	6.77	4.07–9.47	–10.1	0.000	n.s.	0.75
	Spring	178	10.34	7.15–13.54	156.0	0.000	8.07	5.74–10.41	2.9	0.000	n.s.	0.78
Short-toed eagle	Autumn	45	14.90	6.73–23.07	163.9	0.001	10.53	5.54–15.52	8.3	0.000	n.s.	0.71
	Spring	66	5.87	–0.28–12.04	176.9	0.061	10.96	6.14–15.79	22.9	0.000	n.s.	1.87
	Juvenile	119	10.81	5.26–16.37	142.4	0.000	7.00	2.30–11.71	–1.3	0.004	n.s.	0.65

The slope, 95% confidence interval, intercept, and significance levels are shown for each species and season. Significance level of the difference between the slopes according to the 95% confidence interval are also shown (* $P<0.05$, n.s.: not significant). The results of the juvenile short-toed eagle (1st calendar year) are separated from 2nd and 3rd calendar year. All Egyptian vultures and booted eagle were adults.

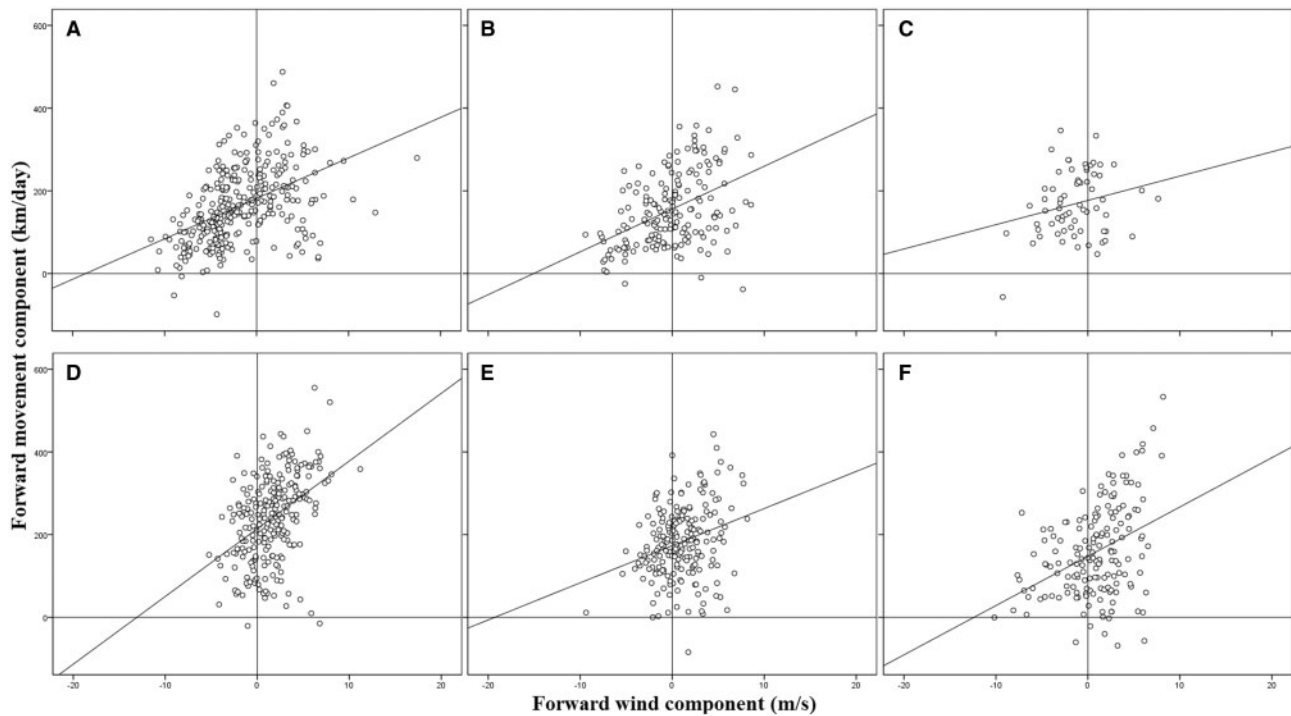


Figure 1. Regression analysis between forward rate of movement and forward wind during spring (upper graphics) and autumn migration (lower graphics) for Egyptian vulture (A, D), booted eagle (B, E), and short-toed snake eagle (C, F).

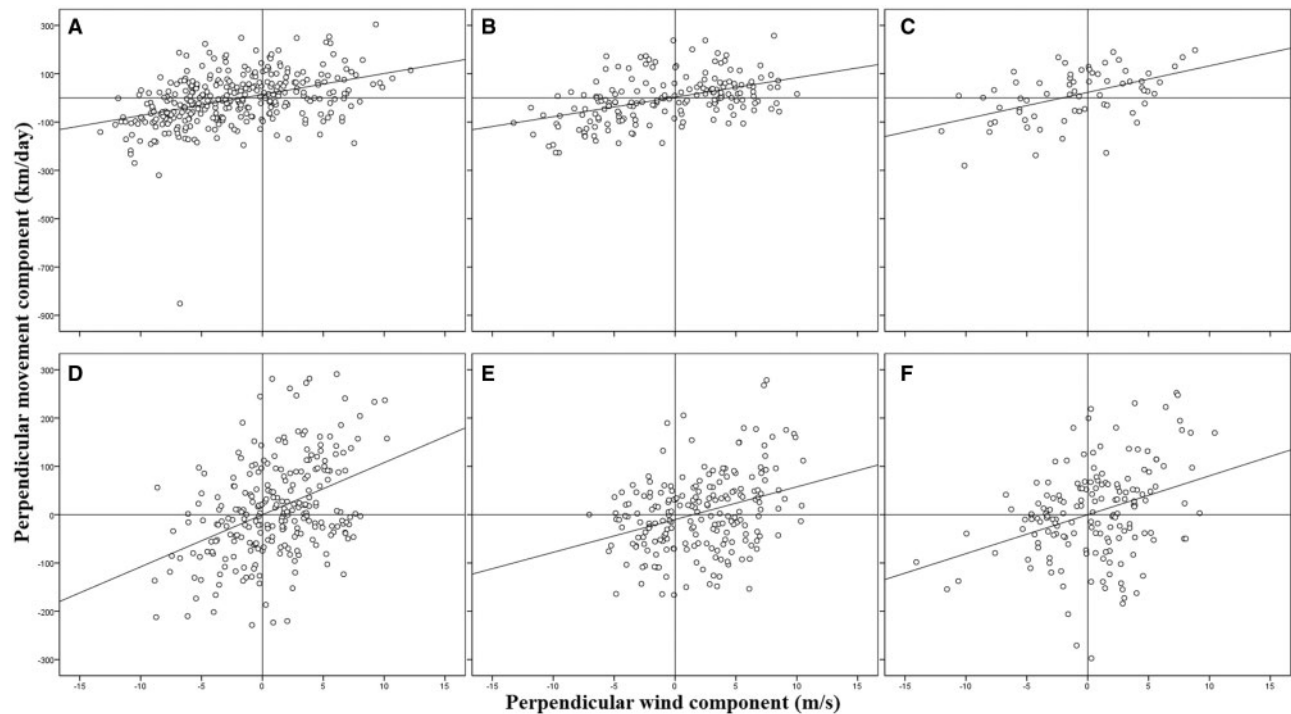


Figure 2. Regression analysis between perpendicular rate of movement and perpendicular wind during spring (upper graphics) and autumn migration (lower graphics) for Egyptian vulture (A, D), booted eagle (B, E), and short-toed snake eagle (C, F).

Discussion

Tailwinds affected Egyptian vultures, booted eagles, and short-toed eagles in a similar way, enhancing their forward movements at a daily scale. These results agree with previous studies carried out with other

raptors (Klaassen et al. 2010; Limiñana et al. 2013). For example, Limiñana et al. (2013) reported a higher effect of tailwinds during autumn migration in the Montagu's harrier, a species that besides soaring flight uses a flapping flight mode with higher frequency than other

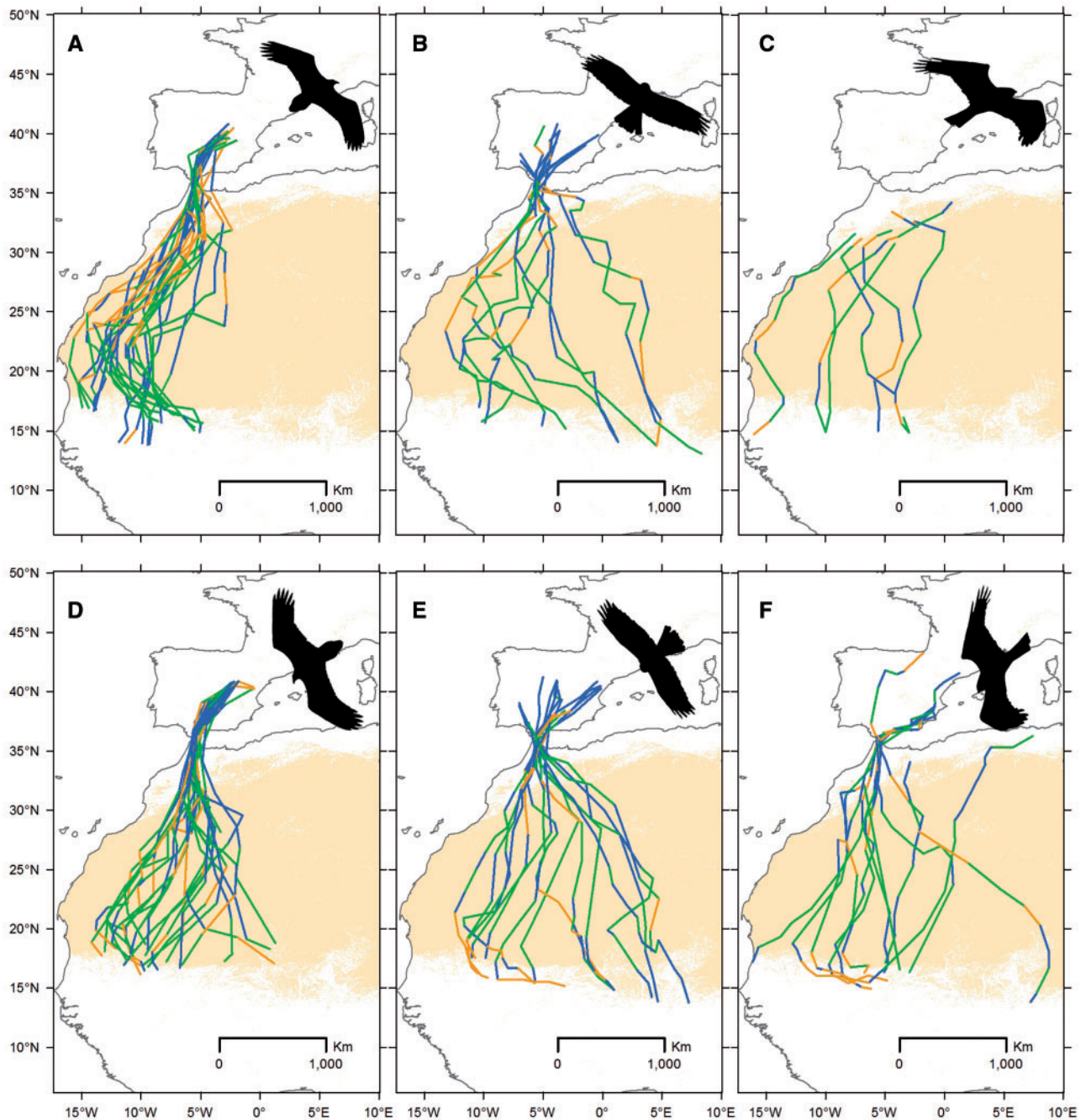


Figure 3. Response of three migratory raptors to crosswinds in spring (upper panel) and autumn (lower panel). Egyptian vulture's routes are shown in (A) and (D); booted eagle's routes in (B) and (E); and short-toed snake eagle's routes in (C) and (F). Colors indicate drift (green), compensation (blue), and overcompensation (orange) in daily segments.

soaring birds. In fact, favorable winds blow predominantly during autumn, in contrast to spring, when winds blow mainly against the main migration direction (Spaar and Bruderer 1997; Mellone et al. 2012; see Figure 2 and Table A1 for a summary of tailwind speeds). In our study, which includes three soaring species, the same effect was observed in Egyptian vultures and short-toed eagles, but not in booted eagles. Short-toed eagles stopped in northern Africa in their first spring migrations (that includes all spring migrations analyzed), and hence they were not exposed to the different wind conditions that occur in the Iberian Peninsula as Egyptian vultures and booted eagles do experience. Differences in morphometric characteristics could explain the

differences observed between Egyptian vultures and booted eagles (Mellone et al. 2012), with Egyptian vultures showing higher wing loading than booted eagles (Kirmse 1998; Mellone et al. 2012), thus allowing higher glide speed (Spaar 1997). Assuming absence of wind during autumn, the Egyptian vulture speed was notably higher than that recorded in booted eagles, probably due to the different wing loading and wind conditions given, in the booted eagle there were no significant seasonal differences concerning the effect of tailwinds in the forward rate of movement.

Crosswinds significantly affected the rate of perpendicular movement in all three species both in autumn and in spring, in agreement

Table 2. Percentage of drift, compensation and overcompensation segments in relation to latitude of three long-distance migratory raptors

Comparison		Segments (%)			<i>n</i>	χ^2	<i>P</i>
		Drift	Compensation	Overcompensation			
Egyptian vulture Autumn	> 36°	20.8	62.5	16.7	250	20.75	< 0.001
	36–28°	40.8	45.1	14.1			
	< 28°	52.3	30.8	16.8			
Egyptian vulture Spring	< 28°	50	36.3	13.7	322	25.07	< 0.001
	36–28°	32.9	32.9	34.2			
	> 36°	20.6	58.8	20.6			
Booted eagle Autumn	> 36°	13	75.1	10.9	206	20.94	< 0.001
	36–28°	40.4	49.1	10.5			
	< 28°	35.6	39.6	24.8			
Booted eagle Spring	< 28°	56.4	34	9.6	178	31.86	< 0.001
	36–28°	23.1	53.8	23.1			
	> 36°	5.3	84.2	10.5			
Short-toed eagle Autumn	> 36°	–	–	–	45	4.12	0.127
	36–28°	33.3	61.9	4.8			
	< 28°	50.0	33.3	16.7			
Short-toed eagle Spring	< 28°	50.0	30.3	19.7	66	1.35	0.508
	36–28°	50.0	22.2	27.8			
	> 36°	–	–	–			

n refers to the total number of segments per species and season, and the χ^2 and their significance are specified for the differences between the proportions of segment type for each species and season.

with previous studies (Thorup et al. 2003; Klaassen et al. 2011; Limiñana et al. 2013). There were no differences in the frequencies of drift, compensation, and overcompensation segments between seasons for any of the three species. Previous studies showed a relationship between latitude and migration behavior (Shamoun-Baranes et al. 2003; Klaassen et al. 2011), and how the proximity or distance to the goal areas influences the response to wind (Green et al. 2004). Similar differences in the behavioral response to wind conditions were also recorded for Egyptian vulture and booted eagles in our study.

During the first stage of autumn migration, when birds were still in the Iberian Peninsula, the frequency of compensation segments was higher, whereas drift segments increased at the end of migration (Figure 3). During spring, the opposite was observed, with a high percentage of drift segments at departure when birds were far away from the goal. The proportion of drift segments decreased when birds arrived to the Iberian Peninsula, in agreement with previous studies with other raptor species (Klaassen et al. 2011). At the beginning of autumn migrations, given that these raptors have low aspect ratio and they must avoid crossing waters, they have to go to the Strait of Gibraltar, a major migratory bottleneck, in order to cross to the African continent (see also Agostini et al. 2015). This could explain the compensation behavior observed in this part of the journey. Once in Africa, birds experience higher frequency of drift, especially in the case of the Egyptian vulture during the last stage of migration, which is not surprising since this species occupies large areas with no fixed territory during winter (García-Ripollés et al. 2010; López-López et al. 2013). In spring, the proportion of drift segments also decreases in the middle of the journey, because the birds are known to home on the Strait of Gibraltar.

In the case of the short-toed eagles (both in their 1st year and 2nd and 3rd year), differences in the proportions of segments types were not observed neither in autumn nor spring, although their capability to react to different wind conditions has been observed at a local scale, avoiding for example being displaced over the sea (Panuccio and Agostini 2013). This is possibly due to the inexperience of the

tagged individuals (Thorup et al. 2003) and due to the fact that in their first spring migrations immature short-toed eagles spent the summer season in vast areas of northern Africa and therefore they do not need to navigate towards narrow goal areas such as the Strait of Gibraltar (Mellone et al. 2011c).

Previous studies have shown different bird responses according to the westerly versus easterly direction of crosswinds (Klaassen et al. 2011; Limiñana et al. 2013). Birds avoid being drifted when wind comes from directions that do not benefit them, for example in the Sahara desert easterly winds could bring them closer to the ocean. However, birds can also take advantage of these winds in some steps of their journey: as other species (Limiñana et al. 2012b), Egyptian vultures, booted eagles, and short-toed eagles have their wintering areas located in western Sahel, so they could take advantage of easterly winds (see Table 1 for a summary of wind directions) to move to the west with lower energetic expenditure, following more easterly routes in autumn than in spring. These responses highlight the importance of wind in shaping the migratory routes. Even so, our results are not consistent with these earlier findings, suggesting no differences between drift, compensation, and overcompensation in any of the three species according to the direction of crosswinds.

In summary, our analysis reveals undocumented features of three raptor species migrating between Southern Europe and Central Africa. First, we have shown the relevance of tailwinds and crosswinds on migration of three raptor species that mainly use the soaring–gliding flight, and secondly how they show a different behavior in terms of drift, compensation or overcompensation according to the geographic region and season across they are flying. The influence of wind on migration routes has been argued as a possible explanation of the loop migration pattern exhibited by the three species studied here as well as other similar loop migration patterns exhibited by other raptor species (Klaassen et al., 2010; Limiñana et al., 2012a, 2012b) or by other bird species in different scenarios (Bradley et al., 2014). Finally, our results suggest that changes in weather conditions due to global change may affect the

geometry of bird migration and their behavior, especially during the Sahara crossing, which could result in possible carry over effects during the annual cycle (see Drake et al., 2014). With the information provided by the analyses of wind influence on individual migration tracks hopefully it will be possible to predict such effects.

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Appendix

Table A1. Summary of tailwind speeds and crosswinds direction recorded for each species according to season and region

Species	Season	Region	Tailwind speed (m/s)	Wind direction (degrees)
Egyptian vulture	Autumn	>36°	1.16 ± 2.12	259.67 ± 28.55
		36–28°	1.31 ± 2.24	157.52 ± 18.77
		<28°	2.04 ± 3.09	235.35 ± 17.31
	Spring	<28°	–3.06 ± 3.60	234.384 ± 15.87
		36–28°	0.92 ± 3.97	346.396 ± 41.58
		>36°	0.48 ± 5.16	287.086 ± 63.70
Booted eagle	Autumn	>36°	0.23 ± 2.84	288.75 ± 80.10
		36–28°	0.53 ± 2.08	233.61 ± 78.32
		<28°	1.61 ± 2.75	245.69 ± 16.05
	Spring	<28°	–0.84 ± 3.90	242.08 ± 15.94
		36–28°	0.73 ± 3.29	72.06 ± 20.43
		>36°	0.38 ± 4.34	95.34 ± 24.56
Short-toed eagle	Autumn	>36°	–	–
		36–28°	–1.89 ± 3.57	59.59 ± 18.44
		<28°	2.23 ± 3.18	194.29 ± 10.43
	Spring	<28°	–1.81 ± 2.63	223.94 ± 20.27
		36–28°	–0.24 ± 3.80	65.66 ± 66.32
		>36°	–	–
	Autumn 1 st year	>36°	–0.77 ± 4.04	73.36 ± 48.92
		36–28°	2.03 ± 2.08	173.03 ± 12.79
		<28°	1.73 ± 2.88	236.81 ± 12.08