Is there a different response to winds during migration between soaring and flapping raptors? An example with the Montagu's harrier and the lesser kestrel

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Abstract During migrations, birds have to cope with varying meteorological conditions, which shape their migratory routes and affect their performance. Amongst these, wind is the main meteorological agent influencing behaviour of birds in their migration journeys. Here we analyze the effect of winds during migrations of adult individuals of two raptor species tracked with satellite telemetry, the Montagu's harrier (*Circus pygargus*) and the lesser kestrel (*Falco naumanni*). While harriers use mostly soaring flight, kestrels principally use flapping flight and thus, wind can differently affect these birds. We found that both forward and perpendicular winds significantly affected the movements of the Montagu's harrier, which were drifted from their intended direction but also took advantage of tailwinds. On the contrary, lesser kestrels moved more regardless of forward winds, despite they were highly drifted by crosswinds. Our results also support that the drifting effect of winds at the onset of the spring migration may explain the loop migration observed for both species, with birds compensating later the effect of crosswinds to arrive to their breeding areas. Results presented here illustrate how winds can differently affect migrating birds according to their flight modes.

Introduction

Prior to migration, birds should make the decision on when begin to migrate, which is usually influenced, apart from endogenous factors (e.g., Gwinner 1996; Maggini and Bairlein 2012), by environmental conditions such as precipitation or wind (see, e.g., Richardson 1978; Liechti 2006). Once they have decided to migrate, they have to deal with the actual environmental conditions encountered during their migration journeys (e.g., Schmaljohann et al. 2008, 2009) and sometimes they are forced to rest in stopovers until better conditions for migration prevail (e.g., Thorup et al. 2006; Morganti et al. 2011). If birds are already aloft, they can take advantage of winds to achieve a higher travelling speed to reach the breeding or wintering grounds as soon as possible (Shamoun-Baranes et al. 2003; Kemp et al. 2010; Mellone et al. 2012), which may have important implications, as for example, assure a good breeding site or have higher fitness (Kokko 1999). However, this also implies that birds could be also drifted from the correct way and therefore, they should compensate for the drifting effect of wind to safely arrive to their wintering or breeding grounds (Alerstam 1979). To counteract the effect of perpendicular winds (i.e., crosswinds) while being aloft, birds have to increase their flying speed to be at least as high as wind speed or they may select a different flight altitude where better wind conditions occur, and these behaviours may represent an increased energy expenditure. However, if birds are not able to do this, they could be drifted into hazardous areas, which may

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result in increased mortality rates (e.g., Strandberg et al. 2010) or carryover other negative effects (e.g., delayed arrival or arriving in bad physical condition) to the next breeding season (see Harrison et al. 2011 for a review). Therefore, they sometimes have to change their heading to compensate (or overcompensate) the effect of crosswinds to avoid being drifted into a different area than that where they want to arrive. There is a regional variability in the extent of these different behaviours, with birds being more expected to be drifted when flying over ecological barriers such as the Sahara desert (Alerstam 1979); there is also a temporal variability on this, with birds being more prone to compensate during the last part of the migration journey to reach their specific breeding or wintering areas (Alerstam 2001; Klaassen et al. 2011a). By doing this, birds take advantage of drifting winds during the crossing of ecological barriers to minimize the overall duration of the journey but they have to compensate later (Alerstam 1979). Also, recent advances in tracking systems have provided new important insights on the role of crosswinds on the evolution of loop migrations (i.e., when birds travel along different routes in autumn and spring), which are being increasingly documented (e.g., Meyburg et al. 2003; García-Ripollés et al. 2010; Klaassen et al. 2010; Limiñana et al. 2012a, b), seeming to be more common than previously thought (Alerstam 2011).

In raptors, the effect of wind on their migratory performance is likely to depend on intrinsic individual's factors — for example, age, with adult experienced birds showing a high ability to compensate for the drifting effect of wind compared with juvenile inexperienced birds, which are more frequently drifted (Thorup et al. 2003). Moreover, adult individuals of soaring raptors usually adopt a strategy of partial drift during migrations (e.g., Klaassen et al. 2011a). In a situation of changing winds, partial drift is expected to save time and energy during the migratory journey, thus being the most suitable strategy (Alerstam and Hedenström 1998). On the other hand, raptors could also adjust this behaviour to avoid being drifted into hazardous areas during migration and, in this scenario, they may respond differently to winds coming from different directions. For example, if winds push them towards the sea, they would compensate for this effect; however, if winds come from the opposite direction, they might take advantage of these winds to increase their speed and hence they are likely to be more drifted (Klaassen et al. 2011a). Moreover, for most of the small raptors using flapping flight during migrations, energetic costs of transport may be much higher than for larger raptors that use soaring flight (e.g., Alerstam 2011), which is mainly due to their different flight style (see, e.g., Pennycuick 1989; Rayner 1990). Therefore, and to achieve larger daily ranges, small raptors using flapping flight may extend their diurnal flights into the night, at least during desert crossings, where wind conditions are generally more benign (Alerstam 2009), as it has been observed in the Levant Sparrowhawk *Accipiter brevipes* (Spaar et al. 1998),

the Eurasian Hobby *Falco subbuteo* (Strandberg et al. 2009) or the Eleonora's Falcon *Falco eleonorae* (López-López et al. 2010). Hence, these flapping species may be differently affected by winds during day and night, and they probably may take advantage of forward winds only during one of these periods (i.e., day or night), when they are more likely to be drifted from their intended direction.

Currently, the use of recent technological advances, such as satellite telemetry, has enabled the study of migrating birds' behaviour in more detail, which would have been otherwise very difficult (Thorup et al. 2010). In particular, tracking the movements of individual birds whose breeding and wintering areas are known, and thus also the intended direction of migration, enables us to analyze how deviations from this overall direction correlates with wind speed and direction during their migration journeys, avoiding the problems arising as a consequence of pseudo-drifts (when the final destination of birds is not known; Green and Alerstam 2002). In this study, we analyze the effect of wind during migrations of satellite tracked adult Montagu's harriers *Circus pygargus* and lesser kestrels *Falco naumanni*. These species have similar ecology (they both live in open habitats and have similar feeding habits and preys during the breeding and wintering season, and show similar migration timing and pathways; see Cramp and Simmons 1980 for a more detailed description), but they mainly differ in their flight modes. Despite the fact that Montagu's harriers use mainly soaring flight during migration, they also use flapping–gliding flight more frequently than pure soaring raptors. Hence, harriers are more independent of environmental factors such as thermal activity or wind to migrate than those pure soaring species, which allows them to migrate under unfavourable wind or thermal conditions (Spaar and Bruderer 1997). The lesser kestrel, mostly using flapping flight during migrations, is even less dependent on thermal updrafts for migration.

To date, interspecific variation of the response to weather conditions in relation to species morphology has been a poorly studied topic (but see Saino et al. 2010). According to this general background on the topic, we predict that: (a) Montagu's harriers take more advantage of forward winds than lesser kestrels, since the former species uses a high proportion of soaring flight than the later during migrations; (b) also as a consequence of their different flight modes, lesser kestrels are more drifted than harriers, showing a behaviour more similar to that of passerines than that of larger raptors; (c) both species may respond differently to crosswinds coming from different direction (easterly vs. westerly winds), and consequently their behaviour is related to this; (d) both species are more drifted at the onset of their journeys, whereas they show a high proportion of (over)compensation when approaching to their breeding/wintering grounds.

Materials and methods

Study species and tagging

The Montagu's harrier is a medium-sized migratory raptor, with breeding populations from Western Europe to Asia. Whereas breeding populations of Western Europe (such as the one studied here) spend the winter in western Sahel (Trierweiler and Koks 2009; Limiñana et al. 2012b, c), other Eastern Europe and Asian population have wintering grounds in eastern Sahel and India (Cramp and Simmons 1980). The species is a typical diurnal migratory raptor (Limiñana et al. 2007) and hence, it uses mostly soaring flight during migrations, although flapping flight could be also used (Spaar 1997). The lesser kestrel is a small migratory raptor with breeding populations from Spain and northern Africa to China; they also migrate between breeding areas in Western Europe and wintering areas in western Sahel (Rodríguez et al. 2009; Catry et al. 2011; Limiñana et al. 2012a), and between Eastern Europe and Eastern Africa (Cramp and Simmons 1980; Rodríguez et al. 2011). Contrary to harriers, lesser kestrels are also able to migrate during the night, especially in spring (Limiñana et al. 2012a), since they use flapping flight to a higher extent than harriers, being thus more independent of the existence of thermals to migrate (Kerlinger 1989). For both species, a more westerly route during spring compared to that in autumn has been described (Limiñana et al. 2012a, b).

Between 2006 and 2011, a total of 14 adult Montagu's harriers and five lesser kestrels were tracked by satellite telemetry along their migration routes between Spain and sub-Saharan Africa, some of them during several years (see Limiñana et al. 2007, 2012a, b for a complete description of routes). Birds were trapped using a dho-gaza net with a stuffed eagle owl *Bubo bubo* used as a decoy, placed close to their nests (25–50 m). To prevent nest abandonment, birds were only trapped in the late stage of incubation or when they had small nestlings (Limiñana et al. 2012a, c). Montagu's harriers were tagged using 9.5-g solar PTTs and lesser kestrels were tagged with 5-g solar PTTs (both from Microwave Telemetry Inc., Columbia, MD, USA). Duty cycle for harrier tags was 6 h ON/16 h OFF and for kestrel tags it was 8 h ON/15 h OFF. Satellite tags were affixed to the back of birds using a Teflon harness, a non-abrasive material (e.g., Kenward 2001), which was sew with a cotton thread in a single point to enable its liberation when the thread is wear out (both the PTT and the harness). Weight of PTTs was below the recommended 5 % of the bird's body mass (Kenward 2001; for Montagu's harrier: mean percentage±SD=3.27±0.42 %, N=14, range=2.64–3.96 %; for lesser kestrels: mean percentage±SD=3.95±0.52 %, N=5, range=3.13–4.46 %). Birds were released in a maximum of 40 min after capture and they were visually tracked to make

sure that they resumed their normal activities. We did not observe any adverse effect of the PTTs on behaviour or reproduction of the tagged birds and, to our knowledge, no negative effects of these devices on birds have been described in previous studies. Indeed, individuals of other migratory raptors tracked with PTTs have been proved to complete their migration journeys and breed successfully while carrying the satellite tags (e.g., Alerstam et al. 2006).

Tracking data

Both species were tracked using the Argos system, which assigns a measure of reliability to every location obtained (known as location class or LC); locations belonging to high-quality LCs (3, 2 or 1, with nominal errors up to 1.5 km; Argos 2011) were always initially used to define the migration tracks, whereas lower-quality LCs 0, A and B (nominal errors cannot be usually estimated, but this does not mean that errors are always large; Argos 2011) were included if they were well within the routes and its inclusion did not result in unrealistic flight speeds (López-López et al. 2010; Klaassen et al. 2011a; Limiñana et al. 2012a). Overall, we tracked a total of 49 and 15 migration journeys for harriers and kestrels, respectively, which are used here (28 autumn and 21 spring journeys for harriers, and eight autumn and seven spring journeys for kestrels; see Online Resource 1). Migration tracks were divided into segments to assess the effect of wind along the migration route (Thorup et al. 2003). We did this at two different time scales: a daily scale and an hourly scale. For both species, we defined the "daily segments" by selecting nighttime locations (between 1800 and 0600 hours, according to local time). From every night, we selected the best quality location closest to midnight. Duty cycle of the PTTs used for lesser kestrels allowed to get at least one location per night during the whole migratory period and hence, daily distances (i.e., distance covered in a day) were always calculated between two consecutive nights. However, for Montagu's harriers there were nights without locations during the migration period and therefore, we also used segments up to 3 days long (i.e., where birds were migrating up to 3 consecutive days) for the analyses (see also Klaassen et al. 2011a); for these segments of 2 or 3 days, we calculated a mean daily distance by dividing the total distance covered in the period by the number of days used to achieve that distance. Segments longer than 3 days were not included in the analyses, as wind conditions may change in such long periods (Klaassen et al. 2011a). Additionally, we only used segments of at least 50 km/day long, to exclude from the analyses those segments that may belong to stopovers (Klaassen et al. 2011a). Overall, we identified a total of 250 segments between 1 and 3 days long for Montagu's harriers (144 in autumn and 106 in spring), when birds

always migrated during the daytime (for every night when more than one location was obtained, birds always remained stationary). For lesser kestrels, a total of 104 daily segments were used for the analyses (52 in autumn and 52 in spring), and some of these included to some extent a part of nocturnal migration (24 out of the 104). We performed the same analyses using only the segments that did not include partially nocturnal migration, and similar results were obtained; therefore, we present here the results based in the complete dataset (see Online Resource 2).

For the hourly scale, we defined as "hourly segments," for both species, those between 2.5 and 8 h long, in which birds moved at least 50 km with speeds higher than 10 km/h, to avoid including in the analyses segments where birds remained stationary. The main intention of using these short segments was to assess the possible effect of wind in the nocturnal migration of lesser kestrels. As harriers only migrate during daytime, we expect that similar results are obtained at both scales for this species; hence, we consider that the analyses for lesser kestrels to assess the nocturnal migration in kestrels should not be biased if these similar results for Montagu's harriers at both scales are actually found. We classified these hourly segments for this species in diurnal and nocturnal segments according to the status at median time (nocturnal segments were those for which at least half the time length occurred after sunset or before sunrise, whereas the remaining segments were considered to be diurnal; López-López et al. 2010). The exact time of sunrise and sunset (when the sun is 0.833° below the horizon) for the midpoint of each segment were calculated using the Sunrise/Sunset spreadsheet downloaded at: http://www.ecy.wa.gov/programs/eap/models. html, which is based on the calculation procedure by the National Oceanic and Atmospheric Administration (NOAA).

Wind data and analyses

Wind data was obtained from the NCEP/DOE Reanalysis II data set (Kanamitsu et al. 2002, hereafter R-II), using the RNCEP package (Kemp et al. 2012) for R-software (R Development Core Team 2010). These data consists of several atmospheric variables at several pressure values, which are available in a raster format having a spatial resolution of 2.5×2.5° and a temporal resolution of 6 h (0000, 0600, 1200 and 1800 hours UTC). We extracted u-winds (west–east) and v-winds (south–north), in m/s, at a pressure of level of 925 hPa, which corresponds to altitudes between 445 and 1,145 ma.s.l. (see, e.g., Schmaljohann et al. 2012). We used the same pressure level for both species, as falcon and harrier species have been recorded migrating at similar altitudes in other radar studies, and usually below 1,000 ma.s.l. (e.g., Meyer et al. 2000; Mateos-Rodríguez and Liechti 2012). Moreover, this pressure level has been previously used to assess the effect of winds on migration patterns of several satellite-tracked raptor

species (Thorup et al. 2003; Klaassen et al. 2010, 2011a). Hence, as most of the migration of both species is likely to occur within this pressure level and also to compare our results with those from other raptors tracked with satellite telemetry during migration, we present here results achieved using the 925 hPa pressure level.

Nevertheless, as flapping birds are likely to migrate higher than soaring ones, and given that maximum flight altitudes observed for falcons are usually higher than those of harriers (Meyer et al. 2000), we also downloaded wind data at other pressure levels for lesser kestrels (850 hPa: from 1,145 to 2,375 m; 700 hPa: from 2,375 to 4,000 m; see Schmaljohann et al. 2012). We found that tailwinds and crosswinds (see below) calculated at these pressure levels were correlated (Spearman $r_s > 0.25$, $p < 0.05$ in all cases; see Online Resource 3) and hence using the selected pressure level of 925 hPa for our analyses is not likely to significantly bias the overall results presented here. In any case, we computed the same regression analyses using tailwinds and crosswinds at these pressure levels (Online Resource 4). Moreover, we computed also the regressions taking into account that flapping birds may select an "optimum" migration altitude each day, where they find favourable tailwind assistance (Online Resource 4); to do that, we considered that birds did not explore the entire air column to select the best overall migration altitude, but they select the lowest altitude where they find favourable tailwind assistance (Mateos-Rodríguez and Liechti 2012). Hence, we selected as optimum altitude for every daily segment the lowest altitude with positive tailwinds between 925 and 700 hPa; if no positive tailwind occurred, we selected as optimum the altitude with lowest headwinds (i.e., negative tailwinds closer to zero). For crosswinds, we used those that occurred at the optimum altitude according to tailwinds. These analyses considering the "optimum" altitude are also presented in the Online Resource 4.

On the other hand, as data from R-II was only available until 31 July 2011 at the time of downloading the data and doing the analyses, wind data for autumn 2011 and spring 2012 migrations of lesser kestrels was extracted from the NCEP/NCAR Reanalysis I data set (hereafter R-I), which has the same spatial and temporal resolution that Reanalysis II data set, although it is updated on a daily basis. To do that, we first compared u- and v-winds data from R-I and R-II (when both were available) obtained for locations defining the daily segments of lesser kestrels (starting point, midpoint and ending point; see below), and results indicated that u and v-winds extracted from both data sets were highly correlated (with R^2 ranging from 0.63 to 0.86 and $p < 0.001$ in all cases). Hence, combining data from R-I and R-II is not expected to significantly influence the main results achieved with our analyses. For every daily segment, wind data (u and v winds) was extracted from the grid data set at 0600 hours at the starting coordinates and day of the segment, at 1200 hours at

the midpoint coordinates and day of the segment (for segments of 2 or 3 days of harriers, u and v vectors were extracted at the mid coordinates for all these 2 or 3 days) and at 1800 hours at the ending coordinates and day of the segment. For the short segments, we used the real time at the starting, ending and midpoint coordinates of the segments to download u- and v-wind vectors.

For every bird and migration journey, we calculated the overall intended direction of migration. To do that for autumn migrations, we calculated the angle between the breeding area and the first location at the wintering grounds (i.e., at the end of the migration track); for spring, we calculated the angle between the last location at the wintering grounds and the breeding area. Then, for every migration segment (both at the daily and hourly scales), we calculated the forward and perpendicular components of the movement in the segment (in km/day and km/h for daily and hourly segments, respectively), according to the intended directions of migration (Thorup et al. 2003; Klaassen et al. 2011a). Similarly, with the u- and v-winds of every daily and hourly segment, also according to the intended direction, we calculated the tailwinds (forward component of the wind vector) and crosswinds (perpendicular component of the wind vector) experienced by birds at the onset, at the midpoint and at the end of every segment. These variables, both movement and wind components are two-dimensioned variables, as they include information on both direction and speed, to avoid the possible pitfalls of using one-dimensioned variables in this kind of wind analysis (Shamoun-Baranes et al. 2007). To simulate the effect of wind experienced along a whole migration segment, we calculated an overall tailwind and an overall crosswind component for every segment, giving more importance to the wind at the midpoint of the segment, as birds are more likely to be found (i.e., they spend more time) at any point closer to the midpoint than on the starting or ending point during every migration day (see also Klaassen et al. 2011b). For daily segments of 1 day of duration (all daily segments recorded for kestrels and some of the harriers), we calculated an average tailwind and crosswind value giving twice much weight to the wind at the midpoint and dividing by four: $TW_{segment} = (TW_{onset} + 2*TW_{midpoint} + TW_{end})/4$ (the same for crosswinds). For daily segments of 2 or 3 days of duration (all belonging to harriers), we also gave twice much weight to the wind at the midpoint of the segment for the 2 or 3 days that lasted the segment (assuming the midpoint to be the same for those 2 or 3 days but using wind data downloaded for every those days), and calculated the average value by dividing by six or eight for segments of 2 and 3 days, respectively (e.g., tailwind for a segment of 3 days was calculated as: $TW_{segment} = (TW_{onset} + 2*TW_{midpoint\ day\ 1} + 2*TW_{midpoint\ day\ 2} + 2*TW_{midpoint\ day\ 3} + TW_{end})/8$). Average tailwinds and crosswinds for both species and seasons are presented in Online Resource 5. For hourly

segments, we used the same calculations than for daily segments of 1 day of duration (see the formula above). 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 both hourly and daily segments (Thorup et al. 2003; Klaassen et al. 2011a). In these analyses, we used data from several years for some of the individuals (see Online Resource 1). We do this because there is likely to be more differences in migration routes and timing for the same individuals between years than for different individuals within the same year for these species (Limiñana et al. 2012a, b; see also data presented here) and hence, using repeated data of the same individuals is not likely to significantly influence the overall results (see also Thorup et al. 2003 and Klaassen et al. 2011a, who used the same approach when using these analyses).

Following Klaassen et al. (2011a), we classified the daily segments into three segment types, according to the relationship between perpendicular movement and crosswinds: (1) drift segments, when perpendicular movement was more than 50 km/day in one or other direction (i.e., more than 50 km/day or less than −50 km/day), and this sign is the same than for crosswinds; (2) compensation, when perpendicular movement was between −50 and 50 km/day; and (3) overcompensation, when perpendicular movement was as for drift segments, but with opposite sings of perpendicular movement and crosswinds. We used the value of 50 km/day only for Montagu's harriers, as we considered this distance to be a significant deviation from intended direction, according to normal daily travel rates of the species (mean daily distance for travelling days observed in the present study ± SD=220.93± 112.74 km/day, N=250; see also Limiñana et al. 2007, 2012b). However, lesser kestrels achieve longer daily distances during migrations (mean daily distance for travelling days observed in the present study ± SD=302.38±221.79 km/day, N=104; see also Limiñana et al. 2012a) and hence, we used a threshold of 75 km/day to classify the daily segments into the three abovementioned categories. For both species, the threshold used represent ca. 25 % of their normal daily travelling rates (see also Klaassen et al. 2011a). We tested whether the proportions of these segment types varied between seasons and also between species during the same season. Similarly, we also evaluated whether birds responded differently to crosswinds coming from the east (i.e., blowing towards the west; easterly winds) or the west (i.e., blowing towards the east; westerly winds), according to the proportions of these types of segments recorded for both crosswind directions (easterly and westerly). Finally, we also tested whether birds showed a different proportion of drift segments vs. (over)compensation between the onset and the end of their journeys; to do that, we divided the

journeys in two legs: latitudes lower or higher than 28°N, which corresponds to the mid latitude of the migration tracks for both species. All these comparisons were done using chi-square tests in contingency tables.

Results

Daily scale

Daily movements of Montagu's harriers were significantly affected by both tailwinds and crosswinds, whereas lesser kestrels were significantly affected by crosswinds but not by tailwinds (Table 1). Montagu's harriers increased their forward rate of movement on average 12.26 km/day for every m/s of tailwind, showing mean daily rates of forward movement of 195 km/day in absence of wind (intercept). Harriers took more advantage of forward winds in autumn than in spring, although the forward rates of movement in absence of wind were quite similar. The effect of perpendicular winds on perpendicular movements was gentler, with the latter increasing on average only by 4.95 km/day for every m/s of perpendicular wind, and this effect was similar in both seasons (Table 1). Lesser kestrels, although not significant, seemed to take a similar advantage of forwards winds in autumn and spring, and also covered longer mean distances in absence of winds (ca. 260 km/day; Fig. 1). The effect of crosswinds in perpendicular daily movement rates was significant and similar in both seasons, overall moving laterally 13.78 km/day for every m/s of perpendicular wind. Overall, harriers and kestrels allowed a 90 % drift in their daily movements; according to the 95 % confidence intervals of the regressions' slopes, the effect of crosswinds

was higher for both species in spring than in autumn (although not significantly) and significantly higher for kestrels than for harriers in both seasons (Table 1).

Overall, there were no significant differences in the frequencies of the different types of segments (drift, compensation and overcompensation) between autumn and spring for both harriers ($\chi_2^2=2.39$, $p=0.302$) and kestrels ($\chi_2^2=4.68$, $p=0.10$). Similarly, no significant differences on this between species were found, either in autumn ($\chi_2^2=3.02$, $p=0.221$), spring ($\chi_2^2=3.76$, $p=0.152$) or both seasons combined ($\chi_2^2=4.02$, $p=0.134$). We repeated these same analyses comparing drift vs. (over)compensation segments (two segment types), and the same results were obtained for all of the abovementioned comparisons ($p>0.08$ in all cases).

Regarding the differences between frequencies of these segment types in different wind directions (easterly and westerly winds), there was only a slightly significant difference for harriers when considering both seasons combined ($\chi_2^2=6.00$, $p=0.049$), which was more evident when comparing drift vs. (over)compensation ($\chi_1^2=5.24$, $p=0.022$), with birds showing a high proportion of drift segments with easterly winds. These differences may be due to differences in autumn (three segment types: $\chi_2^2=5.46$, $p=0.065$; two segment types: $\chi_1^2=4.17$, $p=0.041$), as no significant differences were found in spring (three segment types: $\chi_2^2=3.77$, $p=0.152$; two segment types: $\chi_1^2=0.41$, $p=0.523$). For kestrels, no differences in frequencies of segments related to wind direction were found, either when considering three types of segments or two types of segments in any of the seasons ($p>0.13$ in all cases).

Finally, both species were more frequently drifted at the onset of the spring migration, showing a higher proportion of compensation and overcompensation when reaching the

Table 1 Regressions of daily forward and perpendicular movement rates (km/day) in relation to forward and perpendicular winds (m/s), respectively, for Montagu's harriers and lesser kestrels

		n	Forward movement			Perpendicular movement			Test between slopes	Ratio slopes (perp/fwd)
			Slope	(95 % confidence interval)	Intercept	Slope	(95 % confidence interval)	Intercept		
Montagu's harrier	All seasons	250	**12.26**	7.54 to 16.99	195.15	**4.95**	2.25 to 7.65	−8.09	*	0.40
	Autumn	144	**24.31**	15.37 to 33.25	185.83	**6.02**	1.72 to 10.31	−19.66	*	0.25
	Spring	106	**6.2**	0.51 to 11.89	185.69	**6.09**	2.08 to 10.09	7.26	ns	0.98
Lesser kestrel	All seasons	104	6.11	−3.98 to 16.2	259.95	**13.78**	8.34 to 19.2	13.07	ns	2.26
	Autumn	52	16.17	−5.23 to 37.58	196.1	**15.24**	5.26 to 25.23	−14.4	ns	0.94
	Spring	52	13.75	−2.57 to 30.07	315.13	**18.93**	10.47 to 27.39	54.16	ns	1.38
Overall (both species and seasons)		354	**9.22**	4.46 to 13.98	214.79	**8.31**	5.73 to 10.89	−3.25	ns	0.90

For every regression, the slope, the 95 % confidence interval of the slope and the intercept area presented. Slopes of significant regressions are given in bold. We also tested if slopes of forward and perpendicular regressions are significantly different (according to 95 % confidence intervals; *: $p<0.05$, ns: not significant). The last column gives an overall estimation of the drift effect (perpendicular slope/forward slope)

Fig. 1 *Upper panel*: relationship between forward rate of movement (km/day) and tailwinds (m/s). *Lower panel*: relationship between perpendicular rate of movement (km/day) and crosswinds (m/s). Both graphs include data from both seasons (spring and autumn) and species (*black dots* Montagu's harrier, *open dots* lesser kestrel)
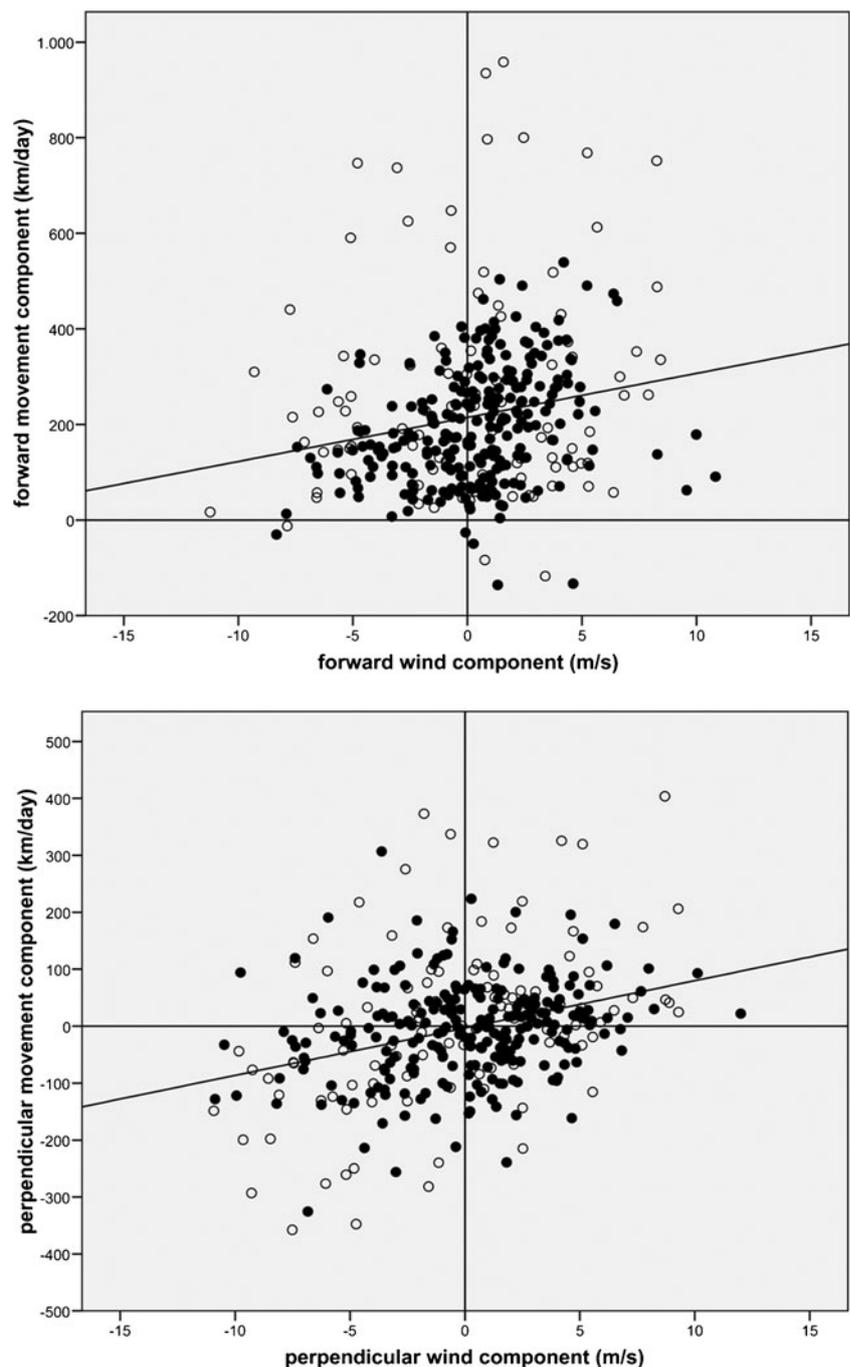
breeding grounds (harriers: $\chi_2^2=10.71$, $p=0.005$ when considering three segment types and $\chi_1^2=5.74$, $p=0.017$ when considering two segment types; kestrels: $\chi_2^2=17.35$, $p=0.0002$ when considering three segment types and $\chi_1^2=9.65$, $p=0.002$ when considering two segment types; see Fig. 2). However, in autumn, these differences related to distance to wintering areas were not generally observed for both species; the only significant difference was observed when considering three segment types for harriers ($\chi_2^2=13.67$, $p=0.001$), which was due to differences in the proportion of compensation and overcompensation segments, as when considering only drift vs. (over)compensation, no differences were observed ($\chi_1^2=0.15$, $p=0.703$), i.e., they showed similar percentages of drift segments during the whole journey (Fig. 2).

Fig. 2 Responses of Montagu's harriers and lesser kestrels to crosswinds in autumn and spring (**a** Montagu's harriers in autumn; **b** Montagu's harriers in spring; **c** lesser kestrels in autumn; **d** lesser kestrels in spring). Drift (*green*), compensation (*blue*) and overcompensation (*orange*) daily segments are depicted for both species and seasons
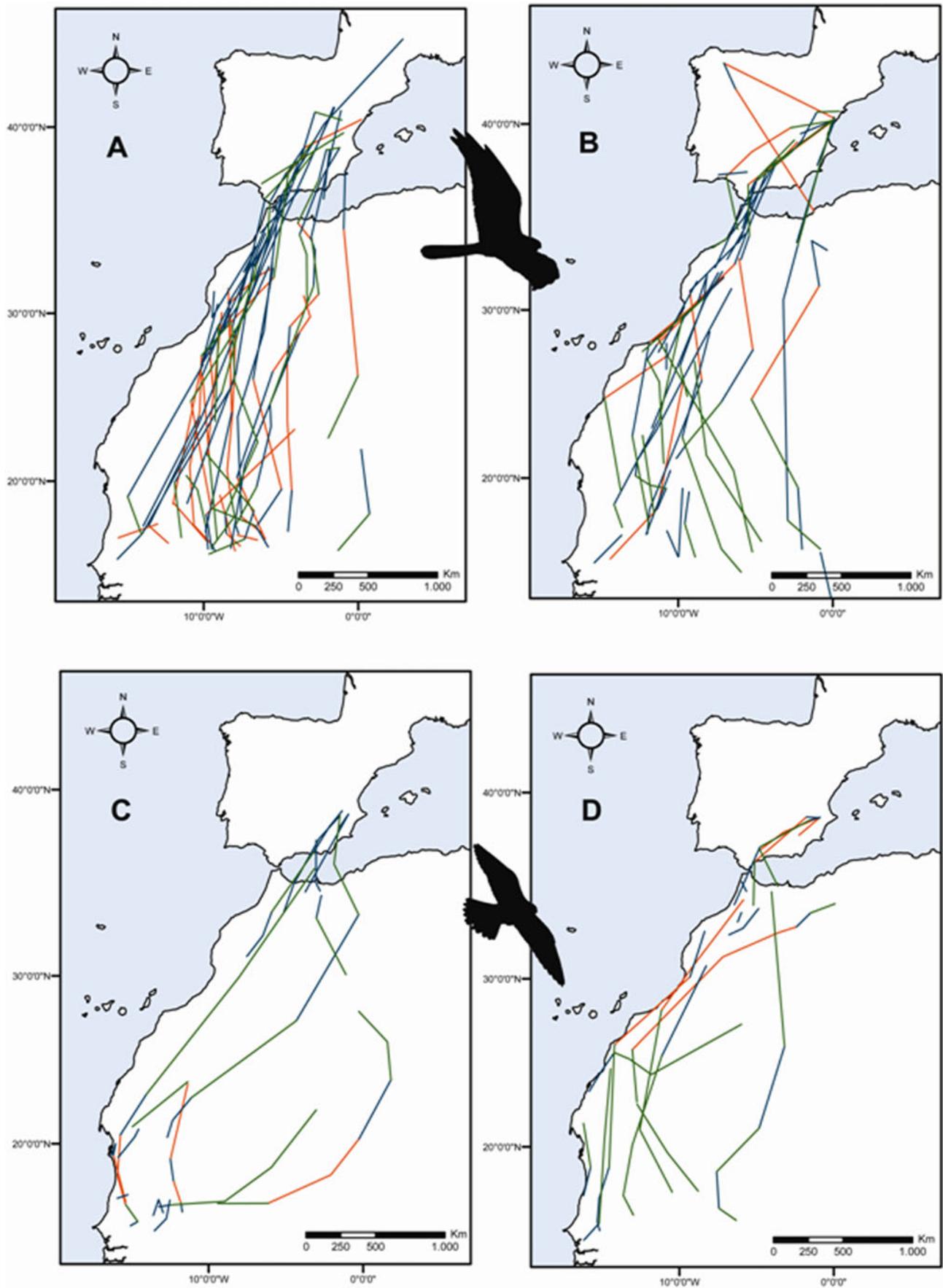
Hourly scale

At this scale, the same results than for the daily scale were found for the Montagu's harrier, whose movements were significantly affected by both tailwinds and crosswinds (Table 2); these effects were similar among seasons, although regression slopes were slightly steeper in spring, especially for crosswinds.

For the lesser kestrel, we also found similar results for the hourly scale than for the daily scale. The effect of tailwinds on migratory movements at this scale was significant only in autumn and it was higher (although not significantly, according to the 95 % confidence interval of the slope) during the night that during the day (Table 2). Regarding crosswinds, a significant effect during the day was found in both seasons, but only significant during the night in autumn; this suggests that lesser kestrels are overall most affected by crosswinds in autumn than in spring but they were not significantly more drifted during the night than during the day in any of the seasons.

Discussion

In agreement with our first prediction, forward winds affected both species differently in their daily movements. While Montagu's harriers took a significant advantage of these winds, the effect of tailwinds on lesser kestrels was lower or non significant (i.e., their movements were not related to tailwinds). Overall, Montagu's harriers were more dependent on the forward winds, achieving higher daily ranges with stronger tailwinds, whereas lesser kestrels also covered large daily ranges with weaker tailwinds and even with headwinds (see Fig. 1). This result indicate that lesser kestrels do not need as favourable tailwinds to migrate as harriers do, being able to achieve also high forward movement rates even with headwinds (see Fig. 1). These differences could be attributed to the different flight modes of the species, since kestrels are more used to fly actively and hence, less influenced by wind.

Montagu's harriers took more advantage of forward winds in autumn than in spring. This is the result of the existence of more favourable tailwinds during autumn compared to spring (Online Resource 5), when more headwinds in Africa are encountered, resulting in lower travel rates, as it has been observed also in other birds using this flyway (Shamoun-Baranes et al. 2003; Mellone et al. 2012). It has been reported that harriers are generally flexible in choosing a mode of flight, being able to migrate by flapping or soaring flight according to weather conditions; therefore, in autumn, when winds are more favourable, harriers would use soaring flight as the more profitable strategy, while in spring, when forward winds are less favourable (Online

Resource 5), these birds would use flapping flight to a higher extent (Spaar and Bruderer 1997). In autumn, lesser kestrels experienced even more favourable tailwinds than harriers (see Online Resource 5), but their movements were not related to these winds and hence, it is not likely that kestrels obtained an advantage of these more favourable tailwinds in this season. At the hourly scale, a significant effect of tailwinds in forward movement in autumn arose in the lesser kestrel, both during the day and night. This indicates that lesser kestrels may take advantage of tailwinds in some specific moments during the autumn migration, probably during the Sahara Desert crossing, where they can use soaring flight, as it happens in the Eurasian Hobby (Strandberg et al. 2009). However, this does not happen in spring, when kestrels achieve high speeds with headwinds (with these headwinds being higher than for harriers), which implies using flapping flight. This would result in higher energy expenditure in spring, which may be an explanation for the long stopovers that lesser kestrels may perform in northern Africa, after the Sahara desert crossing and before reaching the breeding areas (Limiñana et al. 2012a), as birds would need to recover the energy that has been used to counteract the effect of prevailing headwinds during the Sahara crossing in the spring migration (Shamoun-Baranes et al. 2003). Also, these stronger headwinds may have prevented lesser kestrels from migrating and hence, this could be another reason for forward movement rates not being related to forward winds in this season. Nevertheless, there may also be that, in spring, lesser kestrels may have selected a higher altitude to migrate. If that was the case, this may explain the significant correlation between forward movements and forwards winds observed at higher altitudes (850 and 700 hPa; see Online Resource 4), where it seems that they may have found a higher tailwind support (this was not observed in autumn at any altitude). However, it is not likely that they have completed the whole migratory journey flying at such altitudes, as this is not common for raptors during migration (Meyer et al. 2000; Mateos-Rodríguez and Liechti 2012), as well as it is not likely that they have searched the altitude with most favourable tailwinds every day (forward movement and forward wind at the "optimum" altitude were not significantly related). However, they may have selected those higher altitudes during some specific moments along the route. This may also explain that maximum daily ranges observed for lesser kestrels occurred in spring (see also Limiñana et al. 2012a), taking advantage of forward winds only during some specific moments along the whole spring journey by flying at higher altitudes. In any case, the possible effect that forward winds may have on daily movements of lesser kestrels is not as clear as it is on Montagu's harriers.

Daily movements of both species were significantly influenced by crosswinds in autumn and spring. In agreement with our second prediction, the effect of crosswinds on

Table 2 Regressions of hourly forward and perpendicular movement rates (km/h) in relation to forward and perpendicular winds (m/s), respectively, for Montagu's harriers and lesser kestrels

		n	Forward movement			Perpendicular movement			Test between slopes	Ratio slopes (perp/fwd)
			Slope	(95 % confidence interval)	Intercept	Slope	(95 % confidence interval)	Intercept		
Montagu's harrier	All seasons	151	**1.32**	(0.75 to 1.8)	23.22	**1.47**	(0.91 to 2.03)	−0.42	ns	1.11
	Autumn	92	**1.36**	(0.52 to 2.2)	22.69	**1.15**	(0.41 to 1.9)	−1.62	ns	0.85
	Spring	59	**1.42**	(0.54 to 2.3)	23.99	**1.97**	(1.02 to 2.92)	2.54	ns	1.39
Lesser kestrel	All seasons	118	0.31	(−0.288 to 0.913)	23.011	**1.704**	(0.962 to 2.447)	1.539	*	5.50
	Autumn	71	**1.506**	(0.729 to 2.283)	16.733	**2.002**	(1.146 to 2.858)	−0.97	ns	1.33
	Spring	47	0.456	(−0.756 to 1.668)	28.464	**1.769**	(0.379 to 3.159)	5.024	ns	3.88
	All seasons day	61	0.693	(−0.113 to 1.500)	19.129	**1.95**	(0.974 to 2.925)	0.546	*	2.81
	Autumn day	39	**1.082**	(0.124 to 2.039)	16.357	**2.722**	(1.225 to 4.219)	0.073	*	2.52
	Spring day	22	0.866	(−1.003 to 2.734)	23.094	1.246	(−0.007 to 2.484)	0.985	ns	1.44
	All seasons night	57	0.17	(−0.688 to 1.028)	26.934	**1.525**	(0.388 to 2.662)	2.853	*	8.97
	Autumn night	32	**1.949**	(0.519 to 3.379)	16.557	**1.604**	(0.462 to 2.745)	−0.95	ns	0.82
	Spring night	25	0.977	(−0.739 to 2.693)	35.559	2.151	(−0.168 to 4.470)	8.829	ns	2.20

For lesser kestrels, regressions were also performed separately for nocturnal and diurnal segments (see text for details). Column descriptions are as in Table 1

daily movements was higher for lesser kestrel than for Montagu's harriers in both seasons (according to regression slopes; see Table 1). However, there were no differences in the proportions of drift segments between species in any of the seasons. This indicates that both species are drifted during migrations roughly to the same extent, but lesser kestrels are displaced longer distances than harriers from their intended direction by crosswinds of the same strength. A possible explanation for this could be that as lesser kestrels travel also during the night, they could have been more drifted that soaring birds travelling only during the day, as it happens with passerines that may not be able to properly orientate during the night, at least when landmarks are not fully visible (e.g., Liechti 2006). However, results of the hourly scale analysis showed that the effect of crosswinds in lateral movement of kestrels was similar between day and night, thus not being mainly drifted during the nocturnal migration. This suggests that landmark recognition is not an important cue used by these birds to navigate, as has been suggested for other long distance migratory raptors (Alerstam et al. 2006; Mellone et al. 2011; Vardanis et al. 2011) and they are likely to use other orientation mechanisms, at least during the nocturnal migration. However, it might also be that some of these landmarks could be seen in certain conditions during the night (e.g., when migrating under moonlight conditions), at least for large-scale orientation. On the other hand, the smaller size and lighter weight of lesser kestrels (i.e., high wing load) compared to those of Montagu's harriers may also have an influence on the higher drifting effect of crosswinds on the formers (Elkins 2004), highlighting the importance of wing load as a determinant of the effect of wind in raptor's movements during migrations.

Regarding to the effect of crosswinds coming from different directions (our third prediction) on daily movements, we only found a higher percentage of drift segments when the wind came from the east in the Montagu's harrier, especially in autumn. This is in agreement with an scenario of maximizing migration speed over ecological barriers (as migration routes of individuals travelling from Spain occur almost exclusively over the Sahara desert), taking advantage of forward winds even whether birds are drifted (Alerstam 1979). In autumn, winds coming from the east in Africa are the most prevailing (Liechti 2006) and therefore, migrating harriers can take advantage of tailwinds that also moves them to the west, as they need to travel to wintering areas located mainly in western Sahel, following an overall migration direction from the northeast to the southwest (Limiñana et al. 2007, 2012b). This is in agreement with recent studies suggesting that general wind patterns have played an important role in shaping the migratory routes that are more efficient for migrating birds (e.g., Felicísimo et al. 2008; Klaassen et al. 2010). Raptors migrating between western Sahel and northern Europe have been found to compensate for the effect of wind to avoid being drifted into the ocean during the spring migration, and to do that, they should respond differently to winds coming from different directions (Klaassen et al. 2011a).

Finally, in relation with our fourth prediction, looking at the proportions of drift, compensation and overcompensation segments along migration routes, we also found that both species showed a higher percentage of drift segments in the first half of their migration routes in spring, (over)compensating later to

reach their specific breeding areas (Fig. 2). However, this did not happen in autumn, when both species showed similar percentages of drift and (over)compensation regardless of their distance to wintering areas. Therefore, in autumn, birds are able to compensate for the effect of winds as soon as they start to migrate, probably because the prevailing crosswinds are not as strong as those in spring (Liechti 2006). Additionally, wintering areas are distributed over a wide range of locations within the Sahel and both species are thought to track locust swarms along this range (Trierweiler and Koks 2009; Catry et al. 2011) and thus, they show a relatively large individual wintering home ranges (Limiñana et al. 2012a, c). In this scenario, it is probable that wind may determine to a point where autumn migration ends, but birds may move later to track known areas with adequate food conditions (Trierweiler and Koks 2009). On the other hand, these stronger crosswinds in spring may explain, at least partially, the existence of loop migrations in both species, supporting the influence of winds in the more westerly route during spring, compared to that in autumn that has been described for both species (Limiñana et al. 2012a, b). This clockwise loop migration arise as birds are significantly more drifted to the west at the onset of the spring migration, as it also happens with the Marsh harrier *Circus aeruginosus*, also using the same flyway as these species in the same time window (Klaassen et al. 2010, 2011a). The wider loop showed by lesser kestrels compared to Montagu's harriers may be due to the great influence that crosswinds have in the perpendicular movement of lesser kestrels, as described here. Overall, these loop migrations seem to have evolved as an adaptation to minimize migration timing in relation to wind patterns, even if this increases the total distance covered during migrations (Gauthreaux et al. 2005; Klaassen et al. 2010).

General meteorological and environmental conditions are expected to change as a consequence of global change, and this may have an important effect on birds' movements overall. For example, it has been recently shown that changes in wind patterns may have, in the long term, a negative effect on the behaviour and population dynamics of some bird species (Weimerskirch et al. 2012). However, migrating birds can be flexible in their reaction to wind, taking advantage of dynamic and heterogeneous atmospheric conditions to exploit favourable winds during their migrations (e.g., Alerstam 1979; Chapman et al. 2010). Nevertheless, there is still much to be analyzed to obtain a detailed picture on how winds affect migration performance or even survival (Liechti 2006). In this scenario, studies aimed at comparing the effect of wind in several species migrating in the same flyways and in the same time window, as well as those comparing age classes within the same species could help

in obtaining a more complete picture on how birds deal with winds during migrations.

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