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Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway

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Summary

1. Avian migrants often make substantial detours between their seasonal destinations. It is likely some species do this to make the most of predictable wind regimes along their respective flyways. We test this hypothesis by studying orientation behaviour of a long-distance soaring migrant in relation to prevailing winds along the East Atlantic Flyway.

2. We tracked 62 migratory journeys of 12 adult European Honey Buzzards *Pernis apivorus* with GPS loggers. Hourly fixes were annotated with local wind vectors from a global atmospheric model to determine orientation behaviours with respect to the buzzards' seasonal goal destinations. This enabled us to determine hot spots where buzzards overdrifted and overcompensated for side winds. We then determined whether winds along the buzzards' detours differed from winds prevailing elsewhere in the flyway.

3. Honey Buzzards cross western Africa using different routes in autumn and spring. In autumn, they overcompensated for westward winds to circumvent the Atlas Mountains on the eastern side and then overdrifted with south-westward winds while crossing the Sahara. In spring, however, they frequently overcompensated for eastward winds to initiate a westward detour at the start of their journey. They later overdrifted with side winds north-westward over the Sahel and north-eastward over the Sahara, avoiding adverse winds over the central Sahara.

4. We conclude that Honey Buzzards make seasonal detours to utilize more supportive winds further *en route* and thereby expend less energy while crossing the desert. Lifelong tracking studies will be helpful to elucidate how honey buzzards and other migrants learn complex routes to exploit atmospheric circulation patterns from local to synoptic scales.

Key-words: adaptive drift, bird migration, movement ecology, orientation, weather and migration

Introduction

Animals that move through air or water must compensate for prevailing flows in order to reach specific destinations while foraging or migrating (Åkesson & Hedenström 2007; Chapman *et al.* 2011; Tarroux *et al.* 2016). When moving short distances and through flows that do not exceed an animal's own speed, it is relatively easy for goal-navigating animals to correct for lateral flow to travel the shortest possible distance (McLaren *et al.* 2014; Sapir *et al.* 2014). However, animals engaging in long

journeys, such as migrant taxa, are likely to encounter multiple flows that can exert a strong influence on the development of migration routes and detours (Alerstam 1979, 2001; Gauthreaux, Michi & Belser 2005; Liechti 2006). Analogous to turtles and other marine migrants that allow themselves to be transported by ocean currents for parts of their journeys (Luschi, Hays & Papi 2003; Sale & Luschi 2009; Scott, Marsh & Hays 2014) migrating birds could improve the efficiency of travel by using routes that offer relatively more wind assistance than others (Alerstam 2001; McLaren *et al.* 2014; Kranstauber *et al.* 2015). At least some shorebirds, songbirds and falcons anticipate seasonal tailwinds by undertaking long trans-oceanic flights in autumn, whereas they circumvent

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those water bodies in spring (Stutchbury *et al.* 2009; Dixon, Batbayar & Purev-Ochir 2011; Gill *et al.* 2014). It is likely that predictable wind regimes drive the evolution of seasonal migration routes over land as well (Richardson 1990; Alerstam, Hedenström & Åkesson 2003; Gauthreaux, Michi & Belser 2005; Liechti 2006). In order to elucidate whether and how long-distance migrants exploit large-scale atmospheric circulation patterns, we investigate when and where orientation behaviour changes in relation to the winds they encounter along the way and the winds that prevail elsewhere in their flyway.

Most experienced migratory birds travel between individually fixed breeding and wintering sites, often via established geographical bottlenecks and stopover sites (Alerstam 2001). In windless conditions, migrants should fly along the shortest possible migration route, thus minimizing the length of the total journey (Chapman *et al.* 2011; Klaassen *et al.* 2011). This assumption allows classification of orientation behaviours at any given moment, depending on the extent to which a bird travels downwind (i.e. overdrifts) or upwind (i.e. overcompensates) from its shortest possible route. If birds utilize an alternative route due to prevailing winds, we would expect to find consistent latitudinal and seasonal patterns in orientation behaviour of individuals across years. The simplest theoretical benchmark to predict orientation behaviours along wind-dependent detours in predictable wind regimes is that of 'adaptive drift' (Alerstam 1979, 1991). 'Adaptive drift' predicts that migrants can tolerate wind drift off-course from their shortest possible route at the onset of migration, provided they can compensate for the resultant displacement towards the end of the journey. According to the original formulation of 'adaptive drift', this is the case when birds encounter randomly varying or balanced wind fields along the way. Empirical testing of adaptive drift at the scale of an entire flyway is still only feasible for medium-sized or large birds that can be tracked accurately with satellite telemetry or GPS. Most studies on the subject considered soaring raptors (usually diurnal migrants) travelling between Western Europe and western Africa along the East Atlantic Flyway and described geographical and seasonal patterns in daily orientation strategies that comply with the predictions of 'adaptive drift' (Klaassen *et al.* 2011; Limiñana *et al.* 2013; Vidal-Mateo *et al.* 2016); that is, they mainly tolerate drift at the onset of autumn and spring migration, while they compensate or overcompensate for side winds while approaching their destination. Soaring migrants also tend to overcompensate for side winds at a coastline to avoid being blown out to sea (Klaassen *et al.* 2011).

However, migrating birds encounter more complex wind fields than the scenarios from which the predictions of 'adaptive drift' were originally derived, so it is not surprising that they also demonstrate a higher degree of flexibility in orientation behaviour than expected from these models. For example, adult marsh harriers *Circus aeruginosus* react differently to winds coming from

opposing directions, and it has been suggested that the birds may gauge the local wind conditions encountered during each journey relative to the conditions they expect to find in a given area, possibly based on previous experience (Klaassen *et al.* 2011). Simulation models have shown that if birds could make perfect weather predictions, they would adopt a range of orientation behaviours in response to dynamic wind fields along their journeys when minimizing flight time, including overdrift and overcompensation with respect to the shortest possible route (McLaren *et al.* 2014). While it is improbable that birds make perfect weather predictions to achieve truly optimal orientation, it is plausible that they overcompensate and overdrift between their goals because they anticipate predictable wind conditions across the flyway. Until now no empirical study has quantified the occurrence of overdrift relative to other orientation behaviours of free-flying birds.

To understand how seasonal migratory detours relate to large-scale wind regimes, we studied the hourly orientation behaviours of adult honey buzzards *Pernis apivorus* in the East Atlantic Flyway. Most of these birds engage in a westward detour as they travel to Gibraltar in spring (Vansteelant *et al.* 2015). Moreau (1972) speculated this detour could be beneficial because climatic conditions are less harsh near the Atlantic than in the central Sahara, but also because of the occurrence of favourable winds for crossing the desert along this route. We calculated the relative frequency of five orientation behaviours (overcompensation, full compensation, partial compensation, full drift and overdrift; Chapman *et al.* 2011) by latitude. Finally, we compared the wind conditions along the birds' detours with the prevailing winds throughout the rest of the flyway. If birds take detours in anticipation of large-scale wind regimes, we expect to find that winds prevailing along the honey buzzards' seasonal detours are intuitively more favourable for migration than those elsewhere in the East Atlantic Flyway.

Materials and methods

TRACKING HONEY BUZZARDS

We tracked 12 adult honey buzzards that nested in mixed forests of the Veluwe in the centre of the Netherlands that were faithful to specific sites in western Africa in the winter. The birds were tracked using GPS trackers (Bouten *et al.* 2013) at a 3 s – 1-h resolution over two to five complete migration cycles each. Erroneous fixes were removed according to procedure of Vansteelant *et al.* (2015). The University of Amsterdam Bird Tracking System (www.UvA-BiTS.nl) uses local remote downloading of data, so we only retrieved data for birds that completed an entire migration cycle, that is birds that returned to the study area in one or more years.

The honey buzzards in our study population avoid long over-water flights across the Mediterranean Sea by travelling over the Strait of Gibraltar in order to benefit from overland thermals as much as possible (Fig. 1a; Vansteelant *et al.* 2015). In addition,

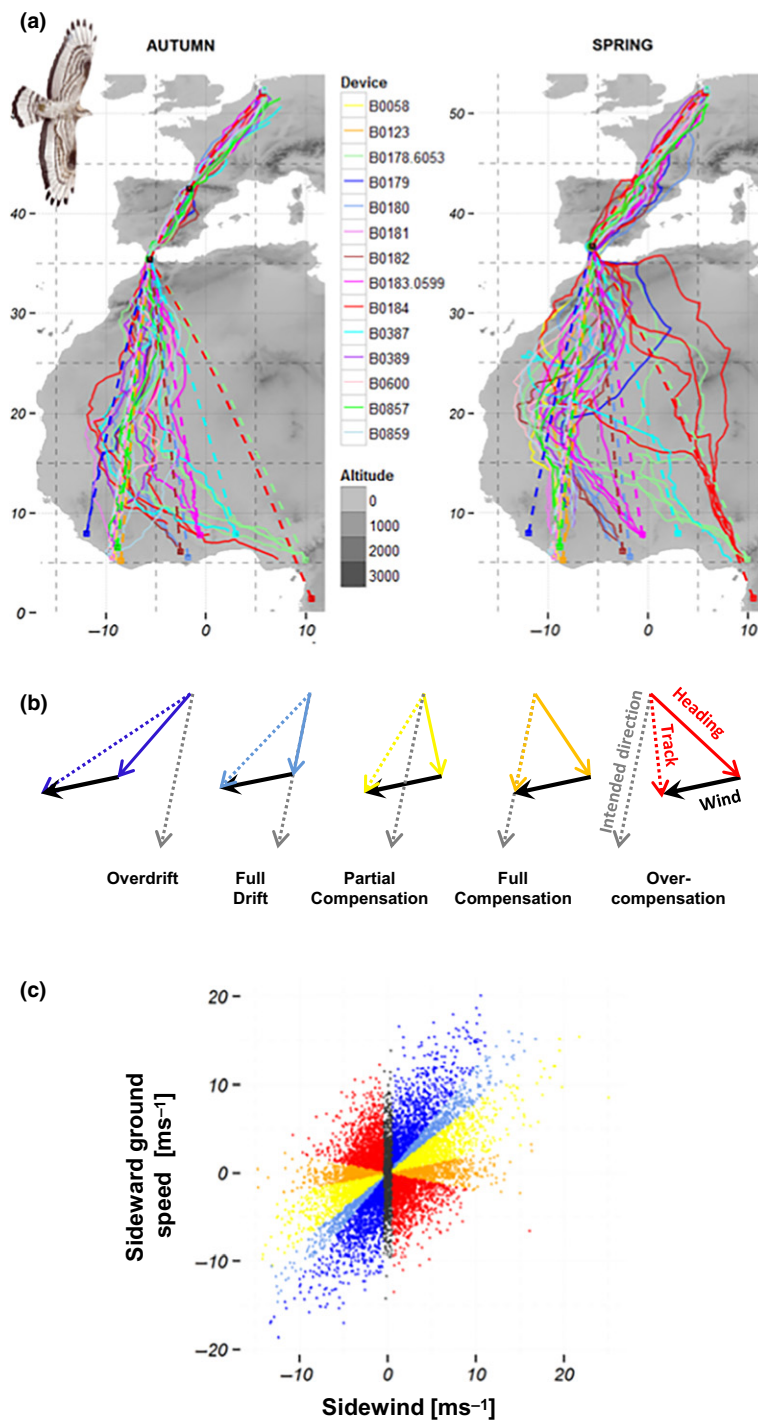


Fig. 1. Goal-directed migrations of adult honey buzzards between summer 2010 and summer 2014 and classification of their orientation behaviours. (a) We tracked 62 migratory journeys of 12 adult honey buzzards that travelled between individually fixed breeding and wintering sites (colour code) via the western Pyrenees in autumn and over the Strait of Gibraltar in both seasons. (b) Birds may use any of five orientation behaviours with respect to local wind conditions at any point. (c) We categorized these behaviours for each hourly travel segment, based on the sideward speed of a bird and the side wind it encountered relative to its shortest possible travel direction, except when side wind speed $< 0.5 \text{ ms}^{-1}$ (black).

they take large detours over land along which we expect the birds to encounter predictably favourable wind conditions.

DATA PROCESSING

Honey buzzards move considerable daily distances during migration while commuting between staging sites in Africa, and while flying to pre-migratory stopover sites and from post-migratory stopover sites (Strandberg *et al.* 2008; Vansteelant *et al.* 2015). Based on a histogram of daily travel distances (i.e. the distance along a great-circle route from the first to the last location obtained on each day), we distinguished travel days (daily dist.

$> 25 \text{ km}$) from stationary days (daily dist. $\leq 25 \text{ km}$) across the annual cycle. We then partitioned the annual cycle into uninterrupted periods of travel days and stationary days. To identify migration, we then assumed that birds were not migrating as long as they remained stationary for at least three consecutive days within the wintering range (south of 10°N) in spring or in the breeding range (north of 51°N) in autumn. Migration stopped when a bird was stationary for a period of at least three consecutive days in the breeding range in spring and in the wintering range in autumn.

In order to analyse orientation strategies at the same temporal scale across all migrations, we resampled our data into hourly

segments between the first and last GPS-fix at which a bird was travelling on each day. We first determined whether a bird was travelling by calculating ground speeds along a great-circle route from each location to the next. The threshold ground speed for active travel in this thermal-soaring species was set at 1.5 ms^{-1} . We then resampled hourly segments (with a maximum deviation of 10 min) using actual GPS-fixes between the location where a bird started travelling on each day until the first fix following the last location where a bird was travelling on that day. We calculated ground speeds for each hourly segment and excluded stationary segments (ground speed $<1.5 \text{ ms}^{-1}$). Finally, flight altitude above ground was determined by subtracting surface elevation, which was extracted using the srtm3 global elevation model (<http://srtm.csi.cgiar.org>), from the GPS-determined flight altitude above sea level (Bouten *et al.* 2013).

DEFINING SEASONAL GOAL DESTINATIONS

We determined the coordinates of individual breeding and wintering sites as the average position of each bird during the core breeding (July) and early wintering periods (November), respectively. Migration routes converged over the western Pyrenees in autumn and at the Strait of Gibraltar in autumn and spring. In order to calculate orientation behaviour and side winds relative to these goals, we assumed the birds' intended destination was a location in the middle of their migration corridor just beyond each of these goals. We thus assumed that they intended to travel to 42.50°N , 1.66°W until they crossed the western Pyrenees ($<42.50^\circ\text{N}$) in autumn and that they intended to travel towards a point just to the south (35.40°N , 5.64°W) or just to the north (36.70°N , 5.58°W) of the Strait of Gibraltar, until they completed half of the sea crossing in autumn and spring, respectively.

QUANTIFYING DETOURS

To quantify detours, we assumed that migration consists of two distinct stages, one from the starting point of each journey to the Strait of Gibraltar and one from the Strait of Gibraltar to the final destination of each journey. We calculated the shortest possible route as the great-circle distance between seasonal goal destinations, taking into account the starting and end points of each separate journey. We also calculated the cumulative distance travelled over Europe and Africa during each journey, and averaged the great-circle and cumulative travel distances over Europe and Africa for each individual in autumn and spring. These metrics enabled us to calculate the average straightness of the autumn and spring migration routes for each individual (Benhamou 2004). We did not calculate detours with respect to the western Pyrenees in autumn, because the intermediate goal destination is already situated on a great-circle route between our study population and the Strait of Gibraltar (Fig. 1a, black squares).

DETERMINING LOCAL WIND CONDITIONS

We estimated local wind vectors at every hourly location and flight altitude using the European Centre for Medium-Range Weather Forecasts (ECMWF) high-resolution (HRES) model (ECMWF 2016). To do this, we first determined zonal (u-) and meridional (v-) wind components at the surface and at 925-, 850- and 700-mb pressure levels by linearly interpolating wind components to the coordinates of each hourly location. For each

location, we then determined wind components at the bird's flight altitude by linearly interpolating wind components between the two nearest pressure levels using geopotential height to estimate the altitude at each pressure level. For the remainder of this paper, we describe wind conditions in terms of the direction which the wind is blowing *towards* (the convention in meteorological studies is the direction which the wind is blowing *from*), in order to allow for a more intuitive comparison with the flight direction of the birds.

DETERMINING ORIENTATION BEHAVIOURS IN SIDE WINDS

We assumed that in very light winds honey buzzards intend to fly to the next goal destination (Fig. 1a, black squares) along the shortest possible (i.e. great-circle) route from their current location. We can then classify orientation behaviours in windy conditions relative to this hypothetical *intended* travel direction. To do this, we first derived the forward and sideward ground speeds of the birds, as well as their tailwind and side wind speeds, relative to the shortest possible route to their next goal. We then determined the birds' 'drift ratio' (DR), that is the ratio between the sideward ground speed of the bird and the side wind speed (Fig. 1b,c), and classified five types of orientation behaviour. We distinguished between 'overdrift' ($\text{DR} \geq 1.2$), 'full drift' ($0.8 < \text{DR} < 1.2$) and 'partial compensation/drift' ($0.2 < \text{DR} \leq 0.8$) as distinct types of 'drift' behaviour, in addition to 'full compensation' ($-0.2 \leq \text{DR} \leq 0.2$) and 'overcompensation' ($\text{DR} < -0.2$). We classified cases with no side winds separately ($<0.5 \text{ ms}^{-1}$, Fig. 1c).

DETERMINING LATITUDINAL SHIFTS IN ORIENTATION BEHAVIOURS

In order to gain insight into large-scale orientation strategies, we identified hot spots of overdrift and overcompensation behaviours that indicated areas where honey buzzards generally do not travel along the shortest possible migration route. We first mapped orientation behaviours throughout the entire flyway for each season and then quantified the relative frequency of overdrift, overcompensation and other orientation behaviours across geographical bands of 5° latitude. Using chi-square tests, we determined whether latitudinal deviations in the frequency of overdrift and overcompensation with respect to the combined frequency of the other orientation behaviours were significant with respect to the flyway average (cf. Klaassen *et al.* 2011).

LATITUDINAL SHIFTS IN WIND CONDITIONS *EN ROUTE* AND WIND REGIMES THROUGHOUT THE FLYWAY

In order to understand how wind shapes detours and geographical patterns in orientation behaviour, we looked for concomitant geographical patterns in the wind conditions that birds encountered *en route* and the average wind regimes throughout the entire flyway. To do this, we created separate maps of the hourly orientation strategies in which birds encountered winds blowing westward or eastward (cf. Klaassen *et al.* 2011). The density of hourly locations on each map helps to identify hot spots where birds encountered westward or eastward winds. In addition, we created a heat map of the relative frequency of westward or

eastward winds across Western Europe and western Africa, as described in more detail below.

Heat maps of zonal wind regimes

While wind conditions encountered by the birds were determined using the ECMWF HRES model (see above), we used National Centres for Environmental Prediction (NCEP) reanalysis-II data ($2.5^\circ \times 2.5^\circ$, Kalnay *et al.* 1996) to determine large-scale and long-term wind regimes throughout the rest of the flyway. NCEP reanalysis-II data were obtained and processed using the RNCEP package (Kemp *et al.* 2012). The average proportion of days with eastward/westward winds during the honey buzzard migration season was calculated at every node in the NCEP grid based on wind conditions at 12:00 UTC each day at the 925-mb pressure level (corresponding to an average altitude of ca. 750 m for migrating honey buzzards; Vansteelandt *et al.* 2015). We then produced heat maps by linearly interpolating the seasonal proportion of westward or eastward wind days across the NCEP grid. We focused on zonal wind components, that is the westward or eastward movement of the air, because this constituted most of the side wind influence in the latitudinal migration of the honey buzzards.

Wind roses

In order to help interpret the latitudinal changes in wind conditions that were encountered by the birds, and within the entire flyway, we determined frequency distributions of wind direction and speed (i.e. wind roses) encountered by the birds and wind direction and speed throughout the rest of the flyway for each geographical band of 10° latitude. To determine wind conditions within the flyway, we only took into account the NCEP nodes that were situated within the longitudinal range of the honey buzzards in each latitudinal band.

Latitudinal shifts in wind conditions

We quantified to what extent the frequency of eastward/westward winds that were encountered by the birds differed from the average frequency of eastward/westward winds within the flyway. We used two-sided Kolmogorov–Smirnov tests ($P < 0.05$) to test for significant differences between the cumulative frequency distribution of zonal wind speeds encountered by the birds and the cumulative frequency distribution of zonal wind speeds within the flyway, across each band of 5° latitude. To determine cumulative frequency distributions of zonal wind speeds across the flyway, we only took into account the NCEP nodes within the longitudinal range used by honey buzzards in each band of 5° latitude.

The decision to use bands of 5° and 10° latitude was made partly because higher resolution resulted in unnecessarily complex figures and tables. All of the analyses were conducted using the R Language for Statistical Programming (R.3.0.2, R Core Development Team 2013), and all of the figures were prepared using the ggplot2-package (Wickham 2009).

Results

We used 5501 autumnal and 6308 vernal hourly travel segments in our analyses (Table S1, Supporting

Information). The number of journeys and the average number of hourly travel segments and travel days recorded on each journey are summarized per season for each of the 12 honey buzzards we studied in the online Table S1.

DETOURS DURING AUTUMN AND SPRING IN EUROPE AND AFRICA

The honey buzzards stayed within a rather narrow migration corridor along the great-circle route between the Netherlands and Gibraltar in Europe, whereas they made substantial detours between Gibraltar and their wintering areas in Africa that increased the migration distance by 10–30% (Fig. 1a, Table S2). The detour over western Africa was further west and was more concave than S-shaped in spring than in autumn (Fig. 1a).

LATITUDINAL SHIFTS IN HOURLY ORIENTATION BEHAVIOUR AND PREVAILING WINDS

Hourly orientation strategies and wind conditions encountered by the birds as well as prevailing winds within the entire flyway are shown for autumn in Fig. 2 and for spring in Fig. 3. There were clear hot spots of overcompensation and overdrift by latitude in both seasons (Figs 2a and 3a). Deviations in the frequency of each orientation strategy by latitude with respect to the flyway average were significant during autumn ($\chi^2 = 271.63$, $P < 0.01$) as well as during spring ($\chi^2 = 627.92$, $P < 0.01$).

While full compensation was a rare strategy that mainly occurred at the end of migration, the honey buzzards exhibited highly flexible orientation behaviours, overdrifting and overcompensating more than half of the time throughout their journey (Figs 2a and 3a). In both seasons, the honey buzzards overcompensated more frequently than on average when arriving at a geographical bottleneck such as the Strait of Gibraltar (latitude 35°N Figs 2a and 3a; Table 1) and when approaching their breeding or wintering destinations (Figs 2a and 3a; Table 1). This effect was particularly evident at the end of the spring migration, when all of the birds converged in the same general breeding area (latitude 52°N Fig. 3a), as opposed to autumn, when the birds travelled to widely dispersed wintering grounds (latitude $5\text{--}10^\circ\text{N}$, Fig. 2a).

Migration over Europe

The honey buzzards changed orientation behaviours frequently across Europe, either drifting, partially compensating or fully compensating for side winds more than they did on average throughout the flyway (Table 1, 'Other'). Europe is dominated by winds with an eastward component in both seasons (heat maps $40\text{--}50^\circ\text{N}$ Figs 2b and 3b). These winds mainly blow from the south-west to the north-east (wind roses $40\text{--}50^\circ\text{N}$ in flyway Figs 2c and 3c). For the honey buzzards, this wind regime implies

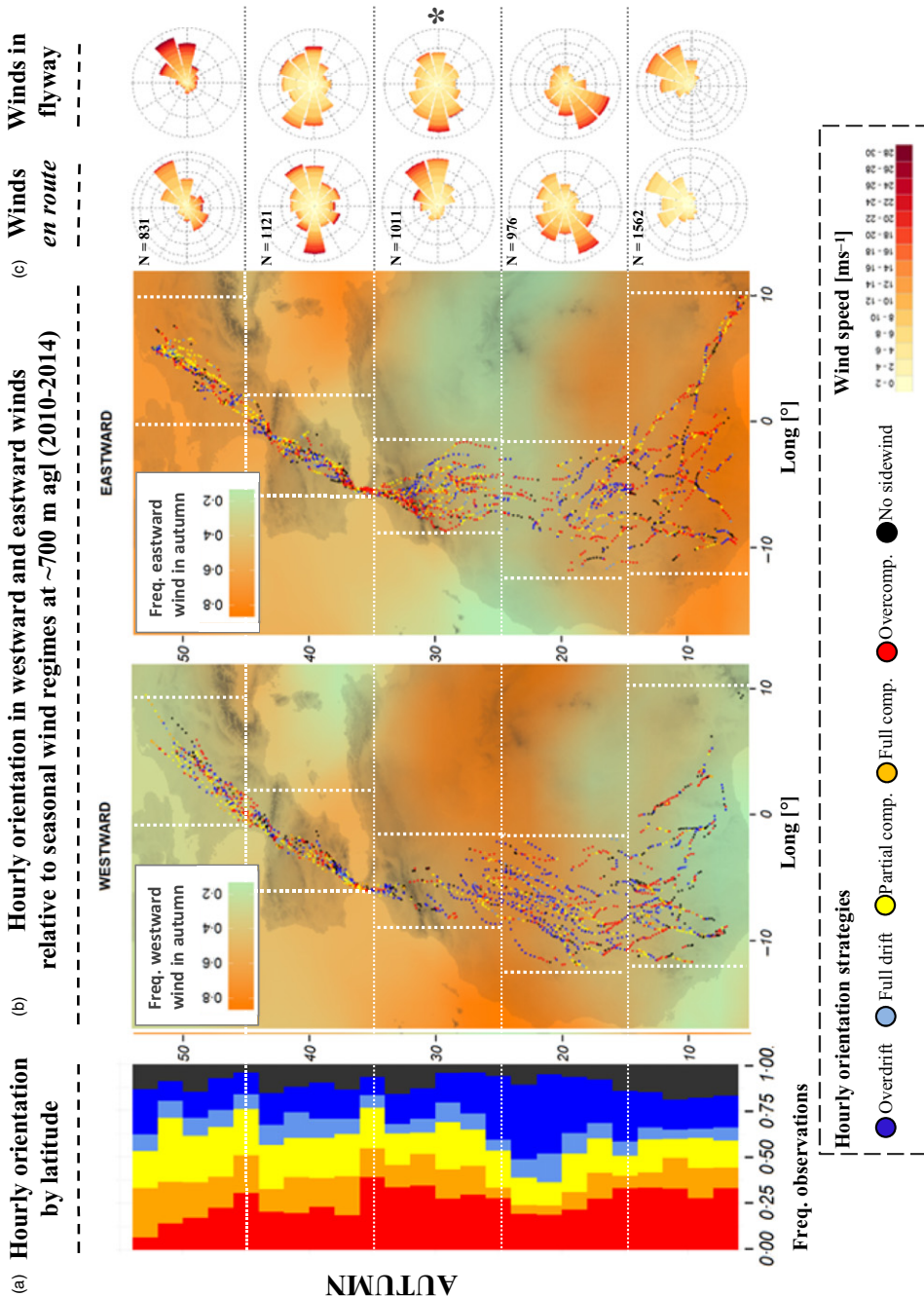


Fig. 2. Geographical flexibility in hourly orientation strategies, wind conditions encountered *en route* and wind conditions prevailing within the entire flyway during *autumn migration*. (a) Barplot showing the relative frequency of each orientation behaviour and cases with negligible side winds by latitude (binwidth 2°). A high proportion of blues indicates frequent drift and overdrift while reds signify overcompensation behaviour (legend). (b) We plotted the starting points of all hourly travel segments, on separate maps depending on whether birds experienced a wind with a westward component (left map) or with an eastward component (right map). All points were coloured for orientation behaviour using the same colour code as in the barplot. The green-orange heatmap represents wind regimes over Western Europe and Africa, showing the relative frequency of westward ($U < 0$, left map) and eastward ($U > 0$, right map) winds thought the flyway during the honey buzzard migration season. If the density of hourly locations was higher in orange areas than in green areas within each latitudinal band on each map, then the wind direction that birds encountered was comparable to the wind direction that prevailed within that part of the flyway. (c) Wind conditions that birds encountered *en route* and wind conditions within the rest of the flyway are summarized across consecutive bands of 10° latitude. The latter were summarized across the date range and longitudinal range (vertical white dashed lines) used by the birds within each latitudinal band. Wind roses show the frequency of winds depending on speed (colour legend) and the direction towards which winds were blowing. Asterisks indicate latitudinal bands in which the birds encountered significantly different wind conditions along their migration routes compared to the average conditions within the entire flyway.

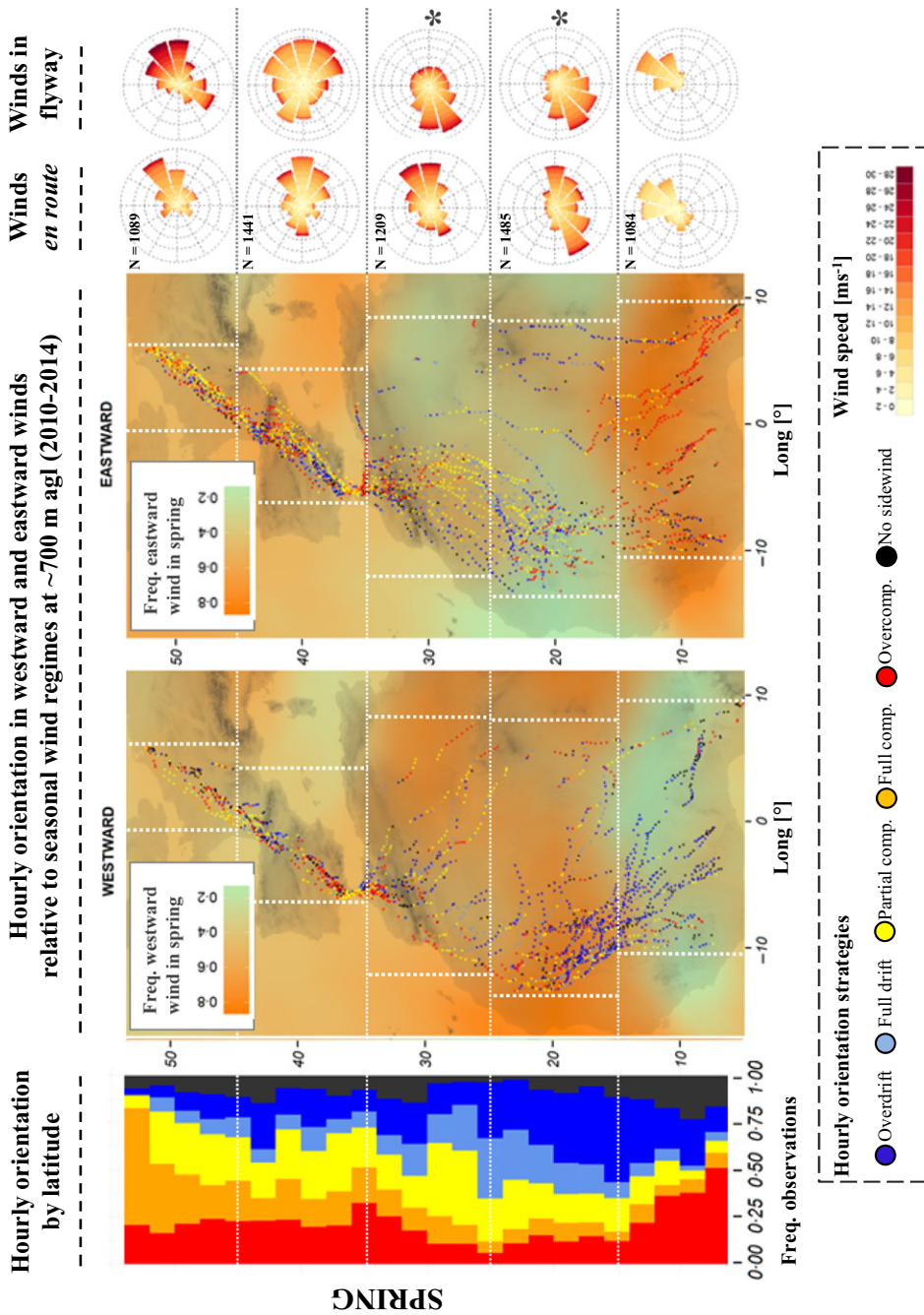


Fig. 3. Geographical flexibility in hourly orientation strategies, wind conditions encountered *en route* and wind conditions prevailing within the entire flyway during *spring migration*. (a) Barplot showing the relative frequency of each orientation behaviour and cases with negligible side winds by latitude (binwidth 2°). A high proportion of blues indicates frequent drift and overdrift, while reds signify overcompensation behaviour (legend). (b) We plotted the starting points of all hourly travel segments, on separate maps depending on whether birds experienced a wind with a westward component (left map) or with an eastward component (right map). All points were coloured for orientation behaviour using the same colour code as in the barplot. The green-orange heatmap represents wind regimes over Western Europe and Africa, showing the relative frequency of westward ($U < 0$, left map) and eastward ($U > 0$, right map) winds thought the flyway during the honey buzzard migration season. If the density of hourly locations was higher in orange areas than in green areas within each latitudinal band on each map, then the wind direction that birds encountered was comparable to the wind direction that prevailed within that part of the flyway. (c) Wind conditions that birds encountered *en route* and wind conditions within the rest of the flyway are summarized across consecutive bands of 10° latitude. The latter were summarized across the date range and longitudinal range (vertical white dashed lines) used by the birds within each latitudinal band. Wind roses show the frequency of winds depending on speed (colour legend) and the direction towards which winds were blowing. Asterisks indicate latitudinal bands in which the birds encountered significantly different wind conditions compared to the average conditions within the entire flyway.

Table 1. Residual frequencies of overcompensation (OC), overdrift (OD) in comparison with the remaining orientation behaviours ('Other') across each band of 5° latitude during autumn and spring migrations

Latitude [°]	Autumn			Spring		
	OC	Other	OD	OC	Other	OD
50	-6.16	8.60	-3.94	-1.1	5.4	-7.7
45	-0.96	2.34	-1.87	1.4	0.9	-2.9
40	-3.65	4.79	-1.95	0.8	0.9	-2.2
35	1.41	1.44	-3.38	4.2	0.4	-4.9
30	3.06	-0.83	-2.36	-3.0	2.9	-1.8
25	-0.25	-4.72	6.22	-7.0	3.0	2.0
20	-3.44	-4.44	9.42	-4.5	-1.7	7.1
15	4.01	-5.12	1.97	-2.4	-5.5	11.4
10	2.85	-0.89	-2.05	8.1	-5.3	0.7
5	2.46	-1.71	-0.59	6.9	-2.4	-2.9

Residual frequencies (observed – predicted) within each latitudinal band were determined relative to the average frequency of each behavioural class across the entire flyway for each season using a *chi-square* test. Significantly higher frequencies of OC and OD than the seasonal flyway averages are highlighted in bold.

moderate headwinds at the onset of the autumn migration in contrast to favourable tailwinds at the end of spring migration (wind roses 40–50°N *en route* Figs 2c and 3c).

Autumn migration over western Africa

In contrast to patterns observed over Europe, we found strong latitudinal shifts in orientation behaviour and wind regimes over Africa in both seasons (heat maps Figs 2b and 3b, Table 1). In autumn, the birds frequently overcompensated south-westward after crossing the Strait of Gibraltar until they passed the Atlas Mountains (latitude 25–30°N Fig. 2a,b; Table 1). The birds most frequently encountered winds blowing towards the north-east over north-western Africa (30–25°N, Fig. 2b) and they encountered such winds significantly more frequently along their route than we would expect from the average frequency of eastward winds within the flyway at latitude 30–25°N (Fig. 4, Table S3). After entering the Sahara, they increasingly drifted and overdrifted (latitude 25–20°N Fig. 2a,b; Table 1) south-westward (25–20°N, Fig. 2b). South-westward winds were by far the most common winds anywhere across the desert in autumn (Fig. 4, Table S3). After completing the desert crossing, honey buzzards increasingly overcompensated towards their individual wintering sites (latitude 5–15°N Fig. 2a,b; Table 1). At this stage, they encountered weak north-eastward winds (wind roses 10°N Fig. 2c) slightly less frequently than expected from the average wind regime within the flyway at 10°N (Fig. 4, Table S3).

Spring migration over western Africa

In spring, honey buzzards frequently overcompensated at the onset of migration, thereby initiating a westward

detour (latitude 5–15°N Fig. 3a,b; Table 1) against the prevailing eastward winds over tropical Africa (10°N, Fig. 3b, wind roses Fig. 3c, Table S3). The conditions encountered by the birds can be expected to occur every year based on the average wind regime in the flyway at 10°N (Fig. 4, Table S3). We also noted that the winds in tropical Africa were weaker than elsewhere along the migration route (there was a lack of high wind speeds, dark colours in the colour scale, in wind roses at 10°N, Fig. 3). When entering the Sahel, the birds started overdrifting north-westward (10–20°N Fig. 3a,b; Table 1) with winds blowing towards the south-west (wind rose *en route* Fig. 3c). They continued moving north-westward until they reached the desert at approximately 20°N where they changed travel direction towards the north-east (Fig. 3b) and continued overdrifting with side winds. At this latitude, they usually encountered a change in wind direction towards the north-east at 20°N (note the number of points in the westward vs. eastward winds just south and north of 20°N in spring, Fig. 3b,c). Moreover, these north-eastward winds occur within a relatively small region near the Atlantic coast of north-western Africa (heat maps Fig. 3b), whereas south-westward winds prevail elsewhere over the desert (20–30°N, Fig. 4, Table S3). Using this corridor of north-eastward winds, honey buzzards entered the desert while overdrifting with side winds significantly more frequently than they did at any other stage of spring migration (20–30°N Fig. 3a,b; Table 1).

Discussion

The 12 adult honey buzzards studied revealed remarkably flexible orientation behaviours that can be understood in the context of regional and seasonal wind regimes within the East Atlantic Flyway. They made larger detours over Africa than over Europe, and overdrifted or overcompensated very frequently during certain parts of their journeys. Most notably, they travelled in a north-westward direction immediately upon leaving the wintering areas, taking on a headwind by overcompensating for weak north-eastward winds. We they used this detour to catch a tailwind by overdrifting north-westward in winds blowing from the north-east to the south-west across the Sahel, and by overdrifting north-eastward in winds blowing from the south-west to the north-east across the Sahara.

The wind estimates we used to classify orientation behaviour are subject to some error because the wind data have a coarser resolution than our movement data. However, we focused on synoptically driven patterns in prevailing winds that are generally resolved well by the numerical models and reanalysis data we used here (Kalnay *et al.* 1996; ECMWF 2016). We also do not expect this large-scale detour to be determined by other environmental factors that are otherwise of interest to soaring migrants. While soaring birds do adjust migration routes to thermal availability at local to regional scales (Leshem & Yom-Tov 1998; Bohrer *et al.* 2012; Duerr *et al.* 2014;

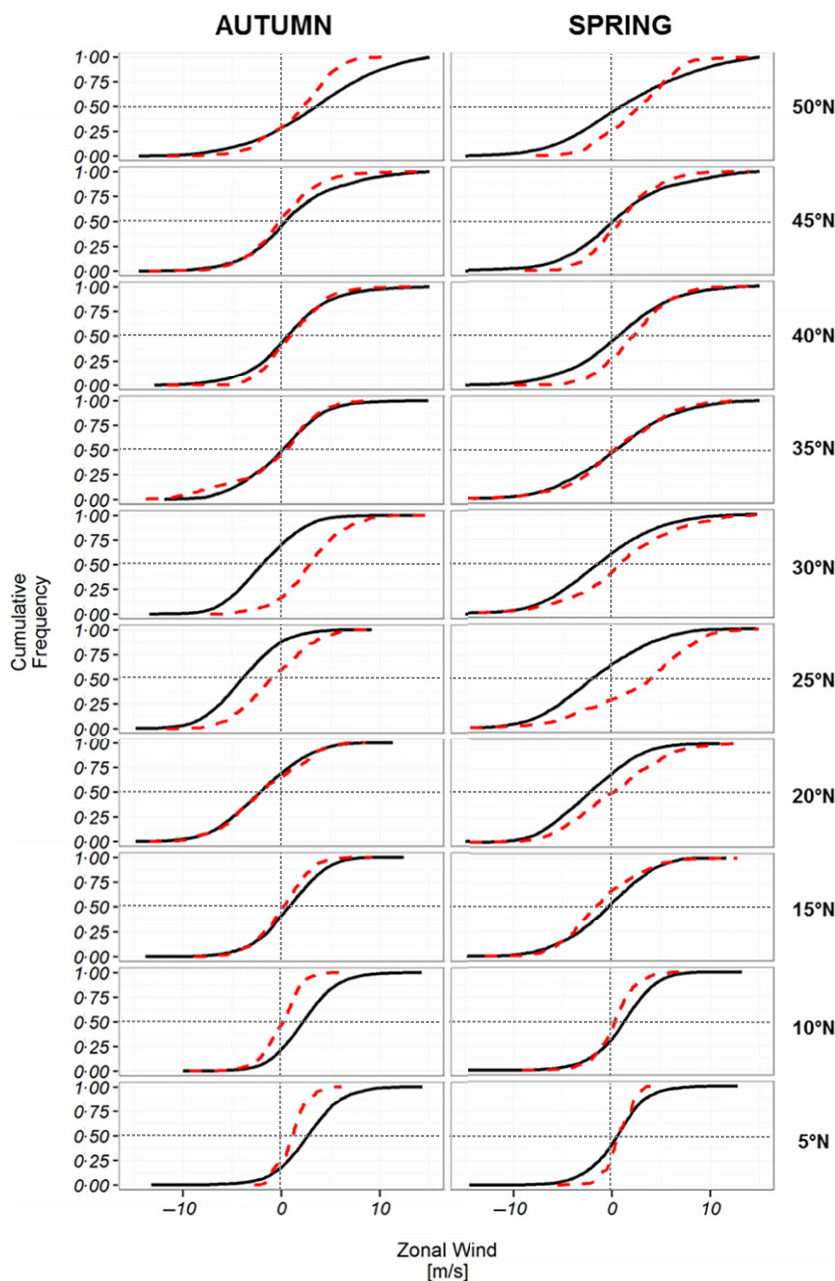


Fig. 4. Cumulative frequency distributions (CFDs) of zonal (i.e. westward/eastward) wind speeds that were encountered by the birds (red dashed lines) and those that occurred throughout the entire flyway (black solid lines) within each band of 5° latitude. If cumulative frequency >0.5 at zonal wind speed <0 ms⁻¹, then winds were blowing predominantly westward. For example, at latitude 30°N in autumn, bird most frequently encountered winds blowing eastward, while winds were predominantly blowing westward within the flyway at that latitude. The largest deviations in the frequency of westward/eastward winds *en route* compared to those within the flyway occurred at latitudes 30–25°N in autumn and 20–30°N in spring, which were hot spots of overdrift behaviour (Fig. 2, Table 1).

Vansteelant *et al.* 2014), thermals tend to be strong and ubiquitous in the tropics (Careau *et al.* 2006) and so we do not expect thermal selectivity would justify large detours across western Africa. Moreover, while many migrants may benefit from better feeding opportunities over the western Sahel to fatten up before the desert crossing (Moreau 1972; Åkesson, Bianco & Hedenström 2016), this is unlikely to be the case for honey buzzards that rarely engage in long stopovers before the desert (Vansteelant *et al.* 2015).

It has been suggested that birds drift with side winds over desert landscapes because it is more difficult to navigate and to estimate wind conditions, and thus to compensate for side winds, in the absence of clear landmarks (Alerstam 2001; Klaassen *et al.* 2011). However, the

Sahara has a rich topography including many aeolian land forms (e.g. dunes and ergs) that have existed for thousands of years (Mainguet 1978). Migrant birds, at least diurnal migrants, may use such landmarks for orientation as well as navigation (Holland 2003; Biro *et al.* 2007). Consequently, we do not think that honey buzzards detour downwind over western Africa because they are unable to compensate for side winds, but because they rely on an alternative, more favourable wind-assisted detour (Felicísimo, Muñoz & González-Solis 2008; Kransstauber *et al.* 2015).

The honey buzzards did not converge at a specific location at the start of the desert crossing in spring, in contrast to the sea crossing at Gibraltar, and the extent of the westward displacement varied between years for every

bird, probably due to variations in the wind conditions encountered during each trip. Nevertheless, they picked up on winds blowing from the south-west to the north-east, that were conducive for migration, within the same general area almost every trip. Moreover, individuals that entered the desert at roughly the same date and longitude followed highly similar routes, even if they were too far apart to be flying in the same flock (Fig. S1). Such a high consistency in flight behaviour between nearby individuals supports the notion that honey buzzards negotiate regional wind fields using a uniform strategy (Lanzone *et al.* 2012). Their strategy somewhat resembles the strategy of ‘compass-biased downstream orientation’ of migrating insects that rely on favourable winds to reach a broad target area (Chapman *et al.* 2010, 2011). While insects rely on vector-based orientation, the buzzards navigate to specific goals and could compensate for relatively strong winds if needed (Alerstam *et al.* 2011; Chapman *et al.* 2015). Consequently, the tendency of migrant birds and insects to travel downwind arises through fundamentally different processes. Nevertheless, the appearance of convergent behaviour, tuning migration routes to prevailing winds, emphasizes the importance of ambient flows in the migration ecology of volant and natant creatures (Gauthreaux, Michi & Belser 2005; Felicísimo, Muñoz & González-Solis 2008; Chapman *et al.* 2011, 2015).

THE ADVANTAGES OF DETOURS IN THE CONTEXT OF PREVAILING WINDS

The strong south-westward trade winds that dominate above the Sahara desert are known as the ‘Harmattan’ (Hayward & Oguntuyinbo 1987) and make up a formidable barrier for spring migrants (Moreau 1972; Gatter 1987; Zwarts *et al.* 2009; Strandberg *et al.* 2010; Klaassen *et al.* 2014). These desert winds collide with cooler air that is drawn in from the Gulf of Guinea at the Intertropical Convergence Zone (ITCZ) and the latter is deflected westward near the earth’s surface at the ITCZ (Hayward & Oguntuyinbo 1987; Schneider, Bischoff & Haug 2014). The ITCZ moves northward over Africa in spring (March–July) and southward in autumn (September–November), such that the position of the ITCZ roughly coincides with the border between the Sahel and the Sahara at approximately 20°N during the peak honey buzzard migration in autumn as well as in spring. In autumn, honey buzzards can hitch a ride on the Harmattan winds to cross the desert no matter where they start the crossing. In spring, however, honey buzzards are better off travelling towards the Atlantic side of the Sahara before crossing the desert, because they are most likely to find a window of opportunity to catch a tailwind across the desert there. This is because in westernmost Africa cyclones frequently move onshore from over the Atlantic during the boreal winter (Lamb & Pepler 1987; Knip-pertz, Christoph & Speth 2003). Consequently, in westernmost Africa, winds blow from the south-west to the

north-east on average 60% of the days in the honey buzzard spring migration period.

Because atmospheric circulation patterns over western Africa are largely driven by synoptic phenomena that have existed for millennia (Hayward & Oguntuyinbo 1987; Lamb & Pepler 1987; Johanson & Fu 2009), a wide range of migrants may have evolved behaviours to exploit predictable winds in this region (Moreau 1972; Gatter 1987). In fact, trade winds along the ITCZ even affect the routes and timing of seabirds engaging in trans-equatorial migrations offshore western Africa (Felicísimo, Muñoz & González-Solis 2008). For migrant landbirds, the advantages of flying with the wind are probably exacerbated by the extremely harsh environmental conditions in the Sahara, including high temperatures and arid conditions (Moreau 1972; Gatter 1987; Klaassen *et al.* 2010, 2014; Åkesson, Bianco & Hedenström 2016). Moreover, the desert crossing seems to be more risky in spring, when the desert has widened by several 100 km and powerful dust storms rage across the desert (Goudie & Middleton 2001; Goudie 2009; Klaassen *et al.* 2014; Vansteelant *et al.* 2015). Nevertheless, we also emphasize that migrants can overcome ecological barriers so long as they are supported by favourable winds. Indeed, migrant landbirds can cross entire seas and oceans relying on predictable winds (Dixon, Batbayar & Purev-Ochir 2011; Bulte *et al.* 2014; Gill *et al.* 2014; Nourani *et al.* 2016), and we found that honey buzzards are able to cross the Pyrenees across a wide front when they benefit from tailwinds over Europe in spring (Kemp *et al.* 2010), whereas they must circumvent this obstacle in autumn.

DEVELOPMENT OF COMPLEX MIGRATION ROUTES

Not all individuals in our study used the westward detour in all years. Three birds (B0178/B6053, B0184 and B0387) that wintered east of 5°E in central Africa crossed the central Sahara instead of using the western detour in half of their journeys (Fig. 1a, Fig. S1). The profitability of migratory detours is limited by a trade-offs between time, energy and safety (Alerstam & Lindström 1990; Alerstam 2001), which will be influenced by travel distance and the wind support that birds accumulate along the way (Alerstam 1979, 2001; McLaren *et al.* 2014); and thus birds that winter further east are more likely to use an alternative migration route than their conspecifics that winter in western Africa. Nevertheless, we expect that in most years crossing the central Sahara in spring entails great risks for migrant birds, and loggers with GSM or satellite-based data transmission capabilities should allow to verify this by comparing mortality between different flyways in the future (Klaassen *et al.* 2014; Hewson *et al.* 2016).

The benefits of detouring with prevailing winds will also differ between species. For example, Montagu’s harriers *Circus pygargus*, which breed and winter at

comparable longitudes as honey buzzards, tend to migrate directly over the central Sahara and the central Mediterranean in spring (Trierweiler *et al.* 2014). This might be because they are more powerful flyers than honey buzzards (Vansteelant *et al.* 2015), but also large obligate soaring migrants such as short-toed eagles *Circus gallicus* and booted eagles *Aquila pennata* cross the central Sahara during spring (Vidal-Mateo *et al.* 2016). Perhaps honey buzzards cannot afford the energy to battle the winds because they usually do not feed on migration (Panuccio *et al.* 2006), because they are less well adapted to survive in Sahelian and Saharan climate, or because they travel longer distances than the aforementioned species. However, field observations indicate the westward detour is used by many other migrant birds (Moreau 1972; Gatter 1987), at least partly because there are more feeding opportunities in the western Sahel, compared to the central Sahelian zone (Hahn *et al.* 2014; Åkesson, Bianco & Hedenström 2016). Ultimately, comparative tracking research is needed to understand what environmental trade-offs shape complex migration routes in species that differ in their foraging habits, movement capacity and navigational abilities (Nathan *et al.* 2008; Thorup *et al.* 2010; Hahn *et al.* 2014).

On the whole, we expect that honey buzzards are able to learn complex detours in anticipation of predictable winds mostly because they live long and because they tend to migrate gregariously. Other long-lived species are known to improve migratory performance as they age (Sergio *et al.* 2014). This is also true for honey buzzards that travel according to an innate vector-based orientation programme on their first outbound migration (Thorup *et al.* 2003) and later learn to circumvent the Mediterranean via geographical bottlenecks by following experienced conspecifics (Hake, Kjellen & Alerstam 2003). Considering that ecological barriers promote risk avoidance, we expect young honey buzzards eventually also learn the westward detour over western Africa by following elders (Maransky & Bildstein 2001; Mellone *et al.* 2011; Opper *et al.* 2015). Considering they are the most numerous soaring migrant in the Afro-Paleartic flyways (Shirihai *et al.* 2000; Bensusan, Garcia & Cortes 2007; Verhelst, Jansen & Vansteelant 2011) young, inexperienced honey buzzards are likely to encounter experienced conspecifics moving westwards shortly upon leaving the wintering grounds.

CONCLUSION

Honey buzzards have evolved a complex orientation strategy whereby they detour downwind from the shortest trans-Saharan migration route, apparently to reduce the energetic cost of migration by benefiting from wind assistance further along their journey. Tracking devices are now elucidating animal movement at an accelerating pace (Bridge *et al.* 2011; Kays *et al.* 2015), and opportunities

for integrating meteorology into movement research are growing fast (Shamoun-Baranes, Bouten & van Loon 2010; Kemp *et al.* 2012; Bouten *et al.* 2013; Dodge *et al.* 2013; Treep *et al.* 2015). We expect these developments will enable the discovery of many more complex behavioural adaptations of migrant birds and other animals to exploit atmospheric circulation patterns, oceanic currents and other predictable features of the earth's energy landscape at multiple scales (Chapman *et al.* 2011; Shepard *et al.* 2013; McLaren *et al.* 2014).

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Data accessibility

The honey buzzard tracking data are available from the UvA-BiTS Virtual Lab (www.uva-bits.nl/virtual-lab/; Bouten *et al.* 2013). The tracking data were annotated with ECMWF HRES wind data (<http://www.ecmwf.int/en/forecasts/datasets/set-i>; ECMWF 2016) and srtm3 global elevation data (<http://srtm.csi.cgiar.org>), and all processed data are made available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.ph2p2> (Vansteelant *et al.* 2016). NCEP-II reanalysis data (Kalnay *et al.* 1996) can be downloaded for free using the RNCEP package (Kemp *et al.* 2012).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Metadata honey buzzard migration dataset.

Table S2. Quantifying detours over Europe and Africa.

Table S3. Differences in the frequencies of zonal wind speeds *en route* and within the flyway.

Fig. S1. Annual timing and routes of the honey buzzards.