

## Repeated large scale loop migrations of an adult European Honey Buzzard

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**Abstract** – During migration birds adopt flight strategies that often differ between spring and autumn. This behaviour can lead to differences in migratory paths as well as in flight performances between seasons, and may help to explain seasonal differences in the numbers of birds passing through migratory bottlenecks. Visual observations have revealed that larger numbers of adult European Honey Buzzards *Pernis apivorus* pass through the Central Mediterranean region during spring rather than during autumn migration, while the opposite occurs at the Strait of Gibraltar. It suggested that substantial numbers of birds, probably belonging to the population breeding in eastern Europe, use an anticlockwise loop migration performing a risk-minimization strategy during autumn and a time minimization strategy during spring migration to maximize their fitness. In this study we analyze for the first time three autumn and three spring migrations of an adult bird belonging to this population tracked by satellite telemetry, also in relation to wind conditions. Each year the bird used the large-scale loop migration between the breeding site located in northern Hungary and the wintering ground in northern Cameroon, showing a higher overall migration speed, shorter paths and longer water crossings during spring movements. The bird benefited from a more efficient tail wind support during spring, while compensated the effect of lateral winds mostly at the onset of both autumn and spring migration. Finally, the bird initiated the spring sea-crossing at the same location each year, but showed remarkable flexibility in route choice across the sea in response to annual differences in different wind conditions. These results support the idea that the stronger aggregation of adult European Honey Buzzards in Central Mediterranean bottlenecks in spring vs autumn largely consists of adults breeding in central-eastern Europe that return to their nesting sites along a relatively direct route.

**Key-words:** loop migration, navigation, *Pernis apivorus*, biologging, water crossing, wind drift.

### INTRODUCTION

During spring birds are expected to minimize the duration of migration to reach their breeding grounds as soon as possible. That is because individuals can increase their reproductive performance by arriving early and occupying high-quality breeding sites (van Noordwijk *et al.* 1995, McNamara *et al.* 1998, Kokko 1999, Moore *et al.* 2005). In several species the migration speed is higher during spring than during autumn, but others show the opposite (Fransson 1995, Shamoun-Baranes *et al.* 2003, Mosbech *et al.* 2006, Yohannes *et al.* 2009, Karlsson *et al.* 2012, Bustnes *et al.* 2013, López-López *et al.* 2014, Nuijten *et al.* 2014, DeLuca *et al.* 2015, Alves *et al.* 2016, Kölzsch *et al.* 2016). Migration speed can be affected by stopover duration and/or daily travel speed, while differences between spring and autumn could be affected by less or more favourable weather conditions during the two seasons (Nilsson *et al.*

2013). In a recent review Schmaljohann (2018) analyzed the results of 64 studies made by satellite telemetry showing that in waders, gulls, swifts, and songbirds speeds are significantly higher in spring, while the opposite occurs in waterfowl and owls. The author concluded that seasonal variation in stopover duration is the main biological mechanism regulating seasonal differences in migration speed. Interestingly, species of raptors analyzed in that study migrated faster during spring than during autumn but the difference was not significant. Besides stopover duration and daily migration speed, seasonal differences in route choice are common among migrant birds and greatly affect the total distance, and therefore the duration of migration. In populations that perform such loop migrations, one route might be considered the result of the path of colonization, the other that evolved to shorten the distance and the duration of migration, or to avoid adverse conditions (Newton 2008). Not necessarily all individuals of a population use

a loop migration, and different individuals may use different loop migrations.

The European Honey Buzzard *Pernis apivorus* breeds in the Palearctic region and overwinters mostly in central West Africa (Ferguson-Lees & Christie 2001). This species stores fat before migrating and usually does not feed en route (Panuccio *et al.* 2006). Unlike juveniles, which perform extensive movements within the tropics once reached the wintering ground, adults remain stationary within restricted territories (Hake *et al.* 2003, Strandberg *et al.* 2012, Vansteelant *et al.* 2015). The seasonal route choice of European Honey Buzzards has been studied by satellite and GPS-tracking in various breeding populations. Adults breeding in the Netherlands and wintering in Central West Africa passed via the Strait of Gibraltar during both spring and autumn, and were found to achieve higher travel speed during pre-breeding movements (Vansteelant *et al.* 2015). However, the higher hourly and daily spring migration speed was entirely accounted for by higher wind support in spring (Vansteelant *et al.* 2015) and fine-scale analyses of their thermal-soaring behaviour revealed they alternate between risk averse and time optimal gliding airspeeds in both seasons (Vansteelant *et al.* 2017a). Moreover, the fact that European Honey Buzzards travel faster in spring due to wind assistance is at least partly due to the fact these birds leave West Africa along a westward detour to catch favourable winds for crossing the desert en route to the Strait of Gibraltar (Vansteelant *et al.* 2017). In contrast to the Dutch adults, anecdotal cases from other populations show that at least some European Honey Buzzards take seemingly risky routes directly across the Central Sahara and Mediterranean on spring migration. An adult male breeding in northern Germany and wintering in Nigeria, for example, crossed the Mediterranean at the Strait of Gibraltar in 2004, but in 2005 and 2006 he made longer sea crossings from Algeria to northern Spain via Balearic Islands (Meyburg *et al.* 2010). Another bird showed loop migration at a larger scale, undertaking the crossing of the Central Mediterranean during spring movements (Meyburg *et al.* 2013). As such it seems European Honey Buzzards engage in different loop migrations between different breeding populations, and the causes and consequences of this variation are not well understood. In this picture, it is important to map loop migration patterns across multiple populations to help understand seasonal patterns in migration counts at geographical bottlenecks around the Mediterranean.

In contrast to large soaring birds like eagles and vultures, European Honey Buzzards seem capable of long sea crossings in both seasons thanks to its size and morphology, intermediate between harriers (*Circus* spp.) and true

buzzards (*Buteo* spp.; Agostini *et al.* 2015). Visual observations, however, showed that larger numbers of adult European Honey Buzzards cross the Central Mediterranean during spring rather than during autumn migration, while the opposite occurs at the Strait of Gibraltar (Agostini & Panuccio 2005, 2015, De La Cruz *et al.* 2011, Programa Migres 2009). It has been suggested that thousands of birds, mostly breeding in Central-eastern Europe, regularly use an anticlockwise loop migration on a large scale choosing more direct routes in spring to reach earlier their breeding sites. They would concentrate at the Strait of Gibraltar during post-breeding movements as a result of a risk minimization strategy and would cross the Central Mediterranean during spring performing shorter paths between wintering and breeding grounds but undertaking longer water crossings (Agostini & Panuccio 2005, 2015). In this study we analyze for the first time three autumn and three spring migrations of an adult male breeding in Central-eastern Europe (Hungary) tracked by satellite telemetry, also focusing on how seasonal wind conditions may mediate between risk avoiding and time minimizing route choice in both seasons.

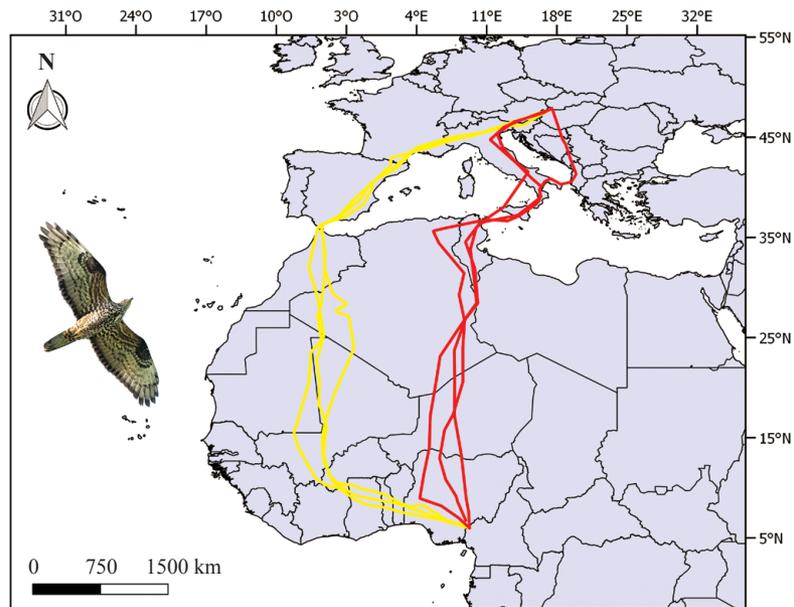
## MATERIAL AND METHODS

### Tagging

The adult male was trapped and tagged first time in 2014, however the logger failed without providing a proper dataset. In 2015 the bird was relocated in the area and successfully trapped again. The logger was replaced, and the new logger was working properly. In both years the bird was trapped during the breeding season close to his nest in northern Hungary (in 2015: Lat 47.8801 N; Long 17.485116 E; Fig. 1). For trapping a realistic Eagle Owl (*Bubo bubo*) model and mist net (mesh size 10x10 cm) were used. In both cases, the bird was tagged with a “DUCK-H” type GPS-GSM logger manufactured by ECOTONE Telemetry and it was attached to the bird with a Teflon harness. The harness was tailor-made fitting the bird’s body and it forms a backpack with the logger (Prommer *et al.* 2012). The solar-powered logger has an in-built GPS unit that can locate the tagged bird with a few metre accuracy. After every 4<sup>th</sup> recorded location the logger transmits the data through GSM network to an online database.

### Tracking data

As mentioned above the dataset included three complete migration cycles, three during autumn (2015, 2016, 2017) and three during spring (2016, 2017, 2018). To calculate migration distances covered by the bird, in each season



**Figure 1.** Migratory routes of the adult European Honey Buzzard in autumn (via Strait of Gibraltar) and spring (via Central Mediterranean).

tracks were divided into daily segments (Limiñana *et al.* 2013), using one location per night included in the interval between 18:00 and 06:00 h of the next day (Klaassen *et al.* 2011).

#### Wind Data

Migration tracks were annotated with ECMWF wind data provided in the Movebank data model (Wikelski & Kays 2018). We thereby extracted east-west (U) and north-south (V) components (m/s) from which we calculated direction (in degrees) and wind speed (in m/s). East-west and north-south components have a spatial resolution of  $2.5 \times 2.5^\circ$  and a temporal resolution of 6 hours, being available at 00:00, 06:00, 12:00 and 18:00 h UTC, so for each daily segment the components were extracted at 06:00, 12:00 and 18:00 h. Data were extracted for a pressure level of 925 hPa, which corresponds to an altitude between 445 and 1145 m (Schmaljohann *et al.* 2012). This pressure level has been used in previous studies of flight behaviour by migrating European Honey Buzzards and other raptors (Klaassen *et al.* 2011, Mellone *et al.* 2012, Vidal Mateo *et al.* 2016).

#### Analysis

As in a previous study (Vidal Mateo *et al.* 2016), we calculated the overall intended direction of migration of the European Honey Buzzard considering different stages; for autumn migration, we calculated the angle between the nest and the location of the crossing of the Mediterranean

Sea, and the angle between this location and the first location at wintering ground. If bird had crossed the Strait of Gibraltar, performing a curvilinear migration, we would have considered two different stages in Europe calculating the angle between the nest and the last location in southern France, and between this location and the Strait of Gibraltar. For the eventual spring migration *via* the Central Mediterranean, we calculated the angle between the last location at wintering ground and the location where the bird started the crossing of the Mediterranean Sea in every year, and between this location and the nest.

#### Forward and perpendicular components of the movement and wind

Segments longer than one day were excluded from the analysis. Segments in which birds' displacement were shorter than 50 km/day were considered stopover days, and for this reason also excluded from the analysis in order to avoid including segments in which birds were not migrating (Klaassen *et al.* 2011, Limiñana *et al.* 2013, Mellone *et al.* 2014, Vidal Mateo *et al.* 2016). For each segment, we established the coordinates (latitude and longitude) of the starting point (coordinates at 06:00), of the ending point (coordinates at 18:00) and the midday point (coordinates at 12:00). Overall, we included 156 daily segments, 94 in autumn and 62 in spring. We calculated the forward and perpendicular components of the movement for each daily segment of migration in km/day in relation to the estimated

intended directions (Klaassen *et al.* 2011, Vidal Mateo *et al.* 2016). Equally, the forward (tailwind) and perpendicular (crosswind) components were calculated with regard to the intended direction. We calculated these components at the beginning of each daily segment (06:00 h), at the midpoint (12:00 h) and at the end point (18:00 h). Finally, to simulate the effect of wind experienced along a whole migration segment, we averaged the overall forward wind and an overall perpendicular wind for every daily segment, giving double weight to the wind estimated at the midpoint of each daily segment (see Klaassen *et al.* 2011, Limiñana *et al.* 2013, Vidal Mateo *et al.* 2016 for a similar approach). Therefore, for the tailwind (TW) calculation we used the formula:  $TW_{segment} = (TW_{onset} + 2 * TW_{midpoint} + TW_{end}) / 4$ , proceeding in the same way for the crosswinds (CW):  $CW_{segment} = (CW_{onset} + 2 * CW_{midpoint} + CW_{end}) / 4$ .

We analysed the variation of Forward and Perpendicular movements (dependent variables) during migration by using linear models (two for each season) to test the effect of the following covariates: tailwind TW (numerical), crosswind CW (numerical), year (categorical), area (categorical: Europe, Africa), Julian date (numerical). The Generalized Variance Inflation Factor (GVIF) was measured for the model with a threshold of 2 to test for collinearity among variables (Fox & Monette 1992, Zuur *et al.* 2010). We applied an ANCOVA to each linear model to test for the significance of the covariates. Finally, we compared the mean daily distances covered during travelling days in the two seasons using a Welch two sample t-test. The normality distribution of variables was tested with Shapiro-Wilk tests. All statistical analyses were made using R (R Core Development Team 2015).

### Types of behaviour

Daily segments between 06:00 and 18:00 were classified into three different behavioural categories depending on the relationship between perpendicular movement component and crosswinds (Klaassen *et al.* 2011, Limiñana *et al.* 2013, Vidal Mateo *et al.* 2016): (a) drift segments, when the perpendicular movement component was higher than 50 km/day or lower than -50 km/day with equal sign than for perpendicular winds; (b) compensation segments: when the perpendicular movement component was between 50 km/day and -50 km/day; and (c) overcompensation segments: when the perpendicular movement component was higher than 50 km/day or lower than -50 km/day (as for the drift segments) with opposite sign between this component and the perpendicular wind. We considered the distance of 50 km/day as a substantial variation from the intended direction, according to their normal daily travel

rates (mean daily distance for travelling days recorded in this study:  $216 \pm 88$  (SD) km/day and  $265 \pm 98.5$  (SD) km/day during autumn and spring, respectively). We evaluated the behavioural response to wind conditions among seasons and regions using chi-square tests in contingency tables (Limiñana *et al.* 2013). To this end, journeys were divided into two different regions (Europe and Africa), thus building two sub-samples to make comparisons among the first and final segments of the migration itself.

## RESULTS

### Migration flyways

The male European Honey Buzzard showed an anticlockwise loop migration, heading towards the Strait of Gibraltar in autumn and crossing the Mediterranean 1500 km to the east via the Cap Bon Peninsula (Tunisia) during spring (Fig. 1). The bird wintered always in the same, restricted area, located in northern Cameroon about 4720 km SSW from the nest (Lat. 5.990366 N, Long. 9.262583 E; Fig. 1). The autumn migration lasted on average 43 days; In this period the bird covered on average 7046 km (149% of the beeline between the nest and the wintering ground), moving at an average speed of 166 km/day and showing a total of 37 days of stop-over (on average 12.3 days per autumn season). A total of 18 days of stopover occurred at the end of migration, south of Sahara, the longest lasting 9 days (20-28 September 2016) and performed close to the border between Burkina Faso and Ivory Coast. The spring migration lasted on average 23 days, the bird covered on average 5598 km (119% of the beeline) at an average speed of 245 km/day showing a total of only six days of stopover. As mentioned above, the average speed in each season considering only travelling days (> 50 km covered per day) was  $216 \pm 88$  (SD) km/day and  $265 \pm 98.5$  (SD) km/day during autumn and spring, respectively ( $t = -3.2$ , d.f. = 121.8,  $P < 0.01$ ). As regards flexibility of routes within each season, the bird showed the greater plasticity during spring when crossing the Central Mediterranean region. In particular, in 2016 the buzzard crossed the Channel of Sicily, between the Cap Bon Peninsula (Tunisia) and western Sicily and, after then, the Tyrrhenian Sea, between north-western Sicily (where the bird roosted) and Central Italy, flying about 400 km over water in two days. Once reached the Italian Peninsula the bird did not choose to fly directly towards the breeding area by crossing the Adriatic Sea, but followed the eastern coast of the Italian Peninsula and passed through northeastern Italy. Conversely, during both spring 2017 and 2018, the bird crossed the southern side of the Channel of Sicily and reached Southern Sicily after a long

**Table 1.** Results of Linear Models explaining the variation of Forward and Perpendicular movements during autumn.

Dependent variable	Covariates		Estimate $\pm$ SE	DF	F	P
a. Forward movement	Julian date		-4.1 $\pm$ 0.9	1	21.7	< 0.001*
	Year	2016	32.5 $\pm$ 18.1	2	1.6	> 0.05
		2017	15.0 $\pm$ 16.9			
	Region	Europe	-9.6 $\pm$ 26.2	1	0.1	> 0.05
	TW		13.8 $\pm$ 3.2	1	18.7	< 0.001*
	CW		1.2 $\pm$ 3.8	1	0.1	> 0.05
b. Perpendicular movement	Julian date		-8.7 $\pm$ 1.1	1	63.3	< 0.001*
	Year	2016	70.9 $\pm$ 22.7	2	5.7	< 0.01*
		2017	8.9 $\pm$ 21.2			
	Region	Europe	-147.1 $\pm$ 32.8	1	20.2	< 0.001*
	TW		12.9 $\pm$ 3.9	1	10.6	< 0.01*
	CW		4.3 $\pm$ 4.8	1	0.8	> 0.5

flight over water (approx 270 km) probably via the Island of Pantelleria. Once reached the area of the Strait of Messina, between Eastern Sicily and Southern Continental Italy, in 2017 crossed the Adriatic Sea via the Channel of Otranto, the shorter water crossing between Italy and Albania (approx. 80 km), reaching the nest via the Balkan Peninsula. In 2018, after crossing the Strait of Messina, he again travelled over land via the Italian Peninsula, reaching the breeding ground via northeastern Italy as in 2016 (Fig. 1).

#### Variation of forward and perpendicular component

During autumn migration the main elements explaining the variation of the forward component were the Julian date and the tailwind (Table 1a). In particular, a negative effect occurred with Julian date while, as expected, tailwind had a positive effect. As regards the variation of the perpendicular

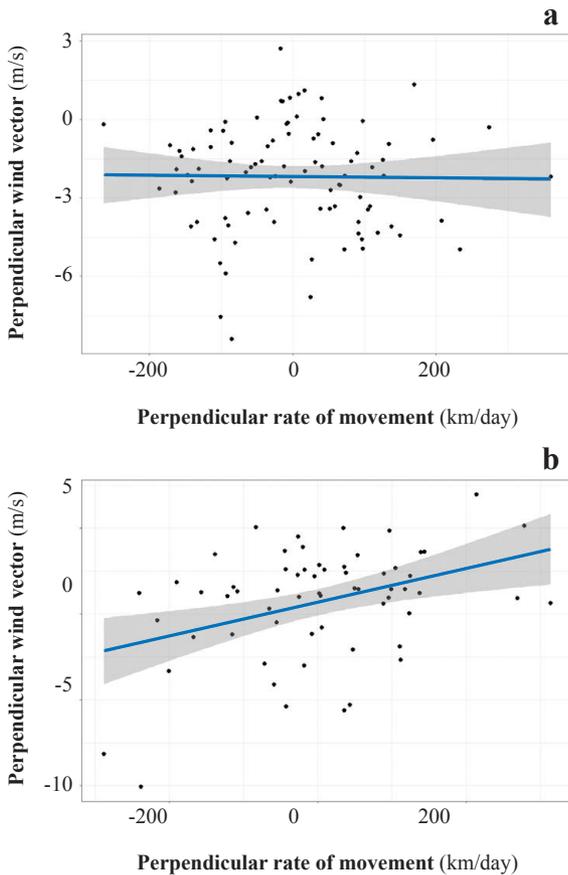
component it was negatively affected by Julian date and region (Europe), positively by the year (in particular during 2016) and by tailwind (Table 1b). During spring migration the forward component was slightly negatively affected by region (Europe) and slightly positively affected by tailwind (Table 2a). Conversely, the perpendicular component was positively affected by the year (2018) and, as expected, by crosswind (Table 2b). As a general statement, the relationship between perpendicular movement and crosswinds and forward movement and tailwinds reached higher values in spring than in autumn (Fig. 2, 3).

#### Types of behaviour: drift, compensation and overcompensation

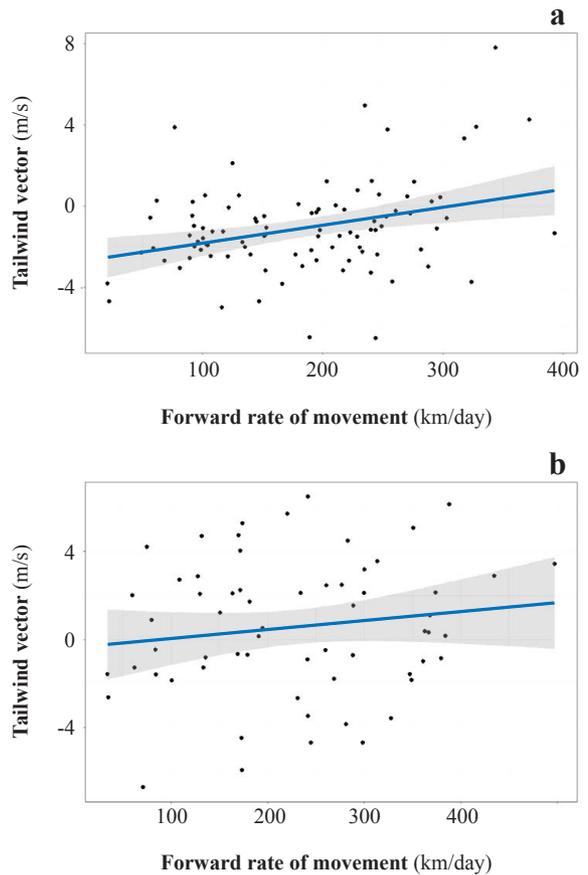
There were no differences in the frequencies of drift, compensation and overcompensation segments between the

**Table 2.** Results of Linear Models explaining the variation of Forward and Perpendicular movements during spring.

Dependent variable	Covariates		Estimate $\pm$ SE	DF	F	P
a. Forward movement	Julian date		4.1 $\pm$ 3.7	1	1.2	> 0.05
	Year	2017	-56.2 $\pm$ 36.1	2	2.1	> 0.05
		2018	-85.9 $\pm$ 45.4			
	Region	Europe	-112.3 $\pm$ 50.5	1	4.9	< 0.05*
	TW		9.9 $\pm$ 4.6	1	4.7	< 0.05*
	CW		0.7 $\pm$ 6.0	1	0.01	> 0.05
b. Perpendicular movement	Julian date		3.8 $\pm$ 3.9	1	0.9	> 0.05
	Year	2017	-3.0 $\pm$ 37.5	2	7.6	< 0.01*
		2018	161.2 $\pm$ 47.1			
	Region	Europe	-37.1 $\pm$ 52.5	1	0.5	> 0.05
	TW		0.2 $\pm$ 4.8	1	0.003	> 0.05
	CW		32.9 $\pm$ 6.3	1	27.6	< 0.001*



**Figure 2.** Regression analysis between perpendicular rate of movement and perpendicular wind during autumn (a) and spring migration (b).



**Figure 3.** Regression analysis between forward rate of movement and forward wind during autumn (a) and spring migration (b).

two seasons ( $\chi^2 = 2.58$ , d.f. =2,  $P > 0.05$ ,  $N = 156$ ). However, considering the frequencies of segments shown in the different regions (Europe and Africa), during autumn migration the adult European Honey Buzzard showed higher proportion of compensation segments in Europe ( $\chi^2 = 41.5$ , d.f. =2,  $P < 0.001$ ,  $N = 94$ ), while this strategy was adopted mostly in Africa during spring migration ( $\chi^2 = 6.09$ , d.f. = 2,  $P < 0.05$ ,  $N = 62$ ). During both seasons he showed higher frequency of drift segments during the final stage of migration (Fig. 4). As regards the flights through the Central Mediterranean region, the bird showed drift during the crossings of the Channel of Sicily and of the Channel of Otranto, compensation when flying through the Tyrrhenian Sea. In particular, the bird flew in south-westerly winds when passing through the northern side of the Channel of Sicily and through the Tyrrhenian Sea in spring 2016, in north-westerly winds when flying through the southern side of the Channel of Sicily in 2017 and 2018, and in westerly winds when crossing the Channel of Otranto in 2017.

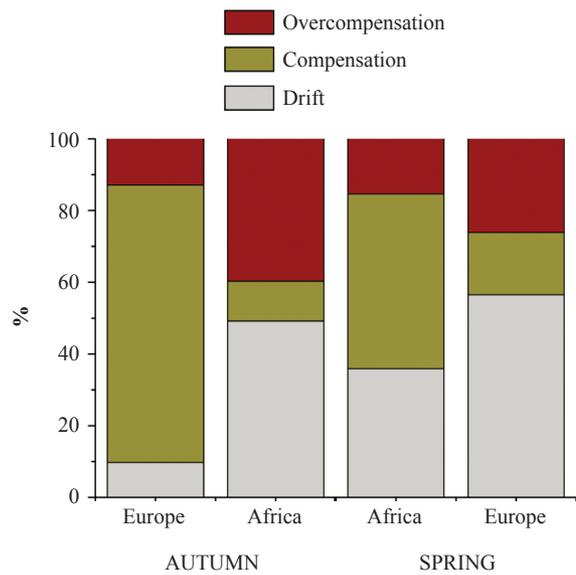
## DISCUSSION

The adult male European Honey Buzzard breeding in Hungary performed an anticlockwise loop migration, detouring the Mediterranean Sea via the Strait of Gibraltar in autumn, while performing a more direct return migration through the Central Mediterranean flyway in spring. This required the bird to make long sea-crossings in spring, which are similar to those performed by juvenile European Honey Buzzards in autumn (Agostini *et al.* 2002, 2004, Hake *et al.* 2003, Agostini 2004, Panuccio *et al.* 2013, Vansteelant *et al.* 2017b).

During their first migration juvenile European Honey Buzzards migrate later than adults (Kjellén 1992, Agostini & Logozzo 1995) and, for this reason, they cannot learn the safer routes around the Mediterranean by following elders (i.e. via the Bosphorus or the Strait of Gibraltar). They orientate along an inherited direction of migration moving along a NNE-SSW axis, flying on a broad front and

starting the Mediterranean crossing as soon as they hit the coast rather than extending their flights over land as long as possible (Agostini *et al.* 2002, Hake *et al.* 2003, Agostini 2004, Vansteelant *et al.* 2017b). In so doing, they are subject to substantial wind drift (Thorup *et al.* 2003), to such an extent that stochastic wind drift has a greater effect than individual differences in orientation on the routes they follow on their first migration and the location at which they settle individual wintering sites in sub-Saharan Africa (Vansteelant *et al.* 2017b). If individual early life experiences determined life-long route choice of European Honey Buzzards we would expect substantial numbers of birds born in central-eastern Europe to cross the Mediterranean Sea heading SSW. The bird we studied here, however, followed an autumn route that is unlikely to emerge due to stochastic wind influences in early life. We suggest it probably learnt the detour via Gibraltar later in life by following experienced conspecifics. Given that European Honey Buzzards tend to travel in flocks also when migrating across water bodies (Agostini *et al.* 2016) suggesting social interaction was also key for this individual to find its way across the Sahara to the Cap Bon Peninsula, after which it learnt to cross the Mediterranean Sea in a flexible direction according to prevailing winds.

The shorter path during spring along with a higher overall migration speed suggest a time minimization strategy. In particular, his migration speed along the two seasons was affected not only by the length of the path (shorter during spring) and by the stopover duration (longer during autumn), but also by his daily travel speed, significantly higher during spring migration also when considering only travelling days. In addition, his behaviour in relation to wind greatly changed in the two seasons. The use of the tail wind component was more efficient during spring probably to increase the migration speed. As regards the crosswind component, he compensated its effect during the onset of autumn migration en route to the Strait of Gibraltar as a result of a risk-minimization strategy; conversely, he showed higher frequency of drift (even in tailwind and especially in 2016) and overcompensation segments in Africa perhaps to save energy. During spring, he flew northwards to reach the Cap Bon Peninsula showing higher frequency of compensation segments, while showed higher frequency of drift when passing through the Central Mediterranean region flying in different wind conditions with a stronger overall drift effect in 2018. Interestingly, our results partially agree with that of a previous study on adult Egyptian Vultures *Neophron percnopterus* and Booted Eagles *Hieraetus pennatus* breeding in Spain and wintering in the Sahel region via the Strait of Gibraltar (Vidal Mateo *et al.* 2016). In that study, both species compensated more



**Figure 4.** Percentage of drift, compensation and overcompensation segments in different seasons (autumn, spring) and regions (Europe, Africa) shown by the adult European Honey Buzzard (autumn: Europe N = 31, Africa N = 63; spring: Africa N = 39, Europe N = 23).

frequently at the onset of autumn migration and showed a higher proportion of drift segments at the end of the season when reaching their wintering areas. However, in contrast to the European Honey Buzzard of this study, those species showed a higher drift at the onset of spring migration and a higher compensation at the end. Exploitation of favourable winds and passive wind drift have both been suggested as a possible explanation of these loop migration patterns during migration over the Sahara Desert, exhibited also by other raptor species (Klaassen *et al.* 2010, Limiñana *et al.* 2012a, 2012b). However, the fact that our study bird compensated for crosswinds en route to the Central Mediterranean region confirms that this bird intended to actively follow a direct route back to its breeding grounds, even if that required additional energy expenditure through compensation for side winds.

The complex paths performed during the crossings of the Central Mediterranean confirm the great plasticity of the strategy of the European Honey Buzzard during this critical phase of the migration cycle, as suggested by studies based on visual observations that revealed wind conditions strongly affect inter-annual variation in migration counts at bottleneck sites in this region (Agostini *et al.* 2016). After reaching the Cap Bon Peninsula, European Honey Buzzards seem to choose between alternative routes, moving through the northern side of the Channel of Sicily and through the Tyrrhenian Sea only when southerly

winds allow them to do so, whereas they more commonly encounter northwesterly winds forcing them to fly through the southern side of the Channel of Sicily, and to converge through the Strait of Messina. Finally, reached the Italian Peninsula, the bird tracked in this study used two different paths en route to the breeding ground, flying around the Gulf of Taranto in 2017 to cross the Adriatic Sea at its narrowest point (the Channel of Otranto), but following the Peninsula during the other two springs.

Unlike the paths used by European Honey Buzzards breeding in Netherlands, which migrated via the Strait of Gibraltar during both spring and autumn, our study confirms the existence of a large-scale, anticlockwise loop migration between Central-eastern Europe and Central West Africa. We suggest this route allows birds breeding in Central-eastern Europe to minimize the time spent travelling in spring, although we note that such birds may need to stock more fat deposits in their wintering quarters to be able to compensate for adverse wind conditions along this flyway. As such our study confirms high behavioural plasticity of this species in relation to wind conditions when migrating through large bodies of water. Future research should verify how widespread this loop migration pattern is in this species, such as the existence of a loop migration performed by adults moving through the Central-eastern Mediterranean region (Agostini *et al.* 2012) and migratory divides among subpopulations migrating through different flyways.

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## REFERENCES

- Agostini N., 2004. Additional observations of age-dependent migration behaviour in western honey buzzards *Pernis apivorus*. *J. Avian Biol.* 35: 469–470.
- Agostini N., Coleiro C., Corbi F., Di Lieto G., Pinos F. & Panuccio M., 2002. Water-crossing tendency of juvenile honey buzzards during migration. *Avocetta* 26: 41–43.
- Agostini N., Coleiro C. & Panuccio M. 2004. Analysis of the autumn migration of juvenile Honey Buzzards (*Pernis apivorus*) across the central Mediterranean. *J. Raptor Res.* 38: 283–286.
- Agostini N. & Logozzo D., 1995. Autumn migration of honey buzzards in southern Italy. *J. Raptor Res.* 29: 275–277.
- Agostini N., Gustin M., von Hardenberg J. & Panuccio M., 2016. Wind patterns affect migration flyways and flock size of a soaring bird over sea. *Avian Biol. Res.* 9: 159–166.
- Agostini N., Lucia G., Mellone U., Panuccio M., von Hardenberg J., Evangelidis A. & Kominos T., 2012. Loop migration of adult European Honey Buzzards *Pernis apivorus* through the central-eastern Mediterranean. *Italian J. Zool.* 79: 280–286.
- Agostini N. & Panuccio M., 2005. Analysis of the spatial migration patterns of adult Honey Buzzards (*Pernis apivorus*) during spring and autumn in the Central Mediterranean. *Ring* 27: 215–220.
- Agostini N. & Panuccio M., 2015. Is the water-crossing tendency of adult European Honey Buzzards influenced by a time minimization strategy during spring migration? *Riv. ital. Orn.* 85: 67–72.
- Agostini N., Panuccio M. & Pasquaretta C. 2015. Morphology, flight performance, and water crossing tendencies of Afro-Paleartic raptors during migration. *Current Zoology* 61: 951–958.
- Alves J.A., Dias M.P., Méndez V., Katrínardóttir B. & Gunnarsson T.G., 2016. Very rapid long-distance sea crossing by a migratory bird. *Sci. Rep.*, doi: 10.1038/srep38154.
- Bustnes J.O., Moe B., Helberg M. & Phillips R.A., 2013. Rapid long-distance migration in Norwegian Lesser Black-backed Gulls *Larus fuscus fuscus* along their eastern flyway. *Ibis* 155: 402–406.
- De La Cruz A., Onrubia A., Pérez B., Torralvo C., Arroyo G.M., Elorriaga J., Ramírez J., González M. & Benjumea R., 2011. Seguimiento de la migración de las aves en el estrecho de Gibraltar: resultados del Programa Migres 2009. *Migres* 2: 79–88.
- De Luca W.V., Woodworth B.K., Rimmer C.C., Marra P.P., Taylor P.D., McFarland K.P., Mackenzie S.A., Ryan D. & Norris D.R., 2015. Transoceanic migration by a 12 g songbird. *Biol. Lett.* 11, doi: 10.1098/rsbl.2014.1045.
- Ferguson-Lees J. & Christie D., 2001. *Raptors of the World*. Helm, London.
- Fox J. & Monette G., 1992. Generalized collinearity diagnostics. *J. Am. Statist. Assoc.* 87: 178–183.
- Fransson T., 1995. Timing and speed of migration in north and west European populations of *Sylvia* warblers. *J. Avian Biol.* 26: 39–48.
- Hake M., Kjellén N. & Alerstam T., 2003. Age dependent migration strategy in Honey buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103: 385–396.
- Kölsch A., Müskens G., Kruckenberg H., Glazov P., Weinzierl R., Nolet B.A. & Wikelski M., 2016. Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos* 125: 1496–1507.
- Karlsson H., Nilsson C., Bäckman J. & Alerstam T., 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Anim. Behav.* 83: 87–93.
- Kjellén N., 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scand.* 23: 420–434.
- Klaassen R.H.G., Strandberg R., Hake M., Olofsson P., Tøttrup A.P. & Alerstam T., 2010. Loop migration in adult marsh harriers *Circus aeruginosus* as revealed by satellite telemetry. *J. Avian Biol.* 41: 200–207.
- Klaassen R.H.G., Hake M., Strandberg R. & Alerstam T., 2011. Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proc. R. Soc. Lond. B.* 278: 1339–1346.
- Kokko H., 2006. Competition for early arrival in birds. *J. Anim. Ecol.* 68: 940–950.
- Limiñana R., Romero M., Mellone U. & Urios V., 2012a. Mapping the migratory routes and wintering areas of Lesser Kestrels *Falco naumanni*: new insights from satellite telemetry. *Ibis* 154: 389–399.
- Limiñana R., Soutullo A., Urios V. & Reig-Ferrer A., 2012b. Migration and wintering areas of adult Montagu's harriers *Circus pygargus* breeding in Spain. *J. Ornithol.* 153: 85–93.

- Limiñana R., Romero M., Mellone U. & Urios V., 2013. 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. *Behav. Ecol. Sociobiol.* 67: 823–835.
- López-López P., García-Ripollés C. & Urios V., 2014. Individual repeatability in timing and spatial flexibility of migration routes of trans Saharan migratory raptors. *Curr. Zool.* 60: 642–652.
- McNamara J.M., Welham R.K. & Houston A.I., 1998. The timing of migration within the context of an annual routine. *Oikos* 29: 416–423.
- Meyburg B.U., Meyburg C., Ziesemer F. & Martens H., 2013. Migration and wintering strategies of adult Honey Buzzards *Pernis apivorus* from Germany revealed by satellite telemetry. 9th Conf. Eur. Orn. Union: 150.
- Meyburg B.U., Ziesemer F., Martens H.D. & Meyburg C., 2010. On the biology of Honey Buzzards (*Pernis apivorus*). Results of satellite tracking. 7th Int. Symp. "Population Ecology of Raptors and Owls", 21–24.
- Mellone U., Klaassen R.H.G., García-Ripollés C., Limiñana R., López-López P., Pavón D., Strandberg R., Urios V., Vardakis M. & Alerstam T., 2012. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS One* 7: e39833.
- Mellone U., De la Puente J., López-López P., Limiñana R., Bermejo A. & Urios V., 2014. Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: A multi-scale approach. *Behav. Ecol. Sociobiol.*, doi: 10.1007/s00265-014-1818-4.
- Moore F. R., Smith R. & Sandberg R., 2005. Stopover ecology of intercontinental migrants: en route problems and consequences for reproductive performance. Pp. 251–261 in: Greenberg R. & Marra P. (eds.), *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins Press, Baltimore.
- Mosbech A., Gilchrist G., Merkel F., Sonne C., Flagstad A. & Nyegaard H., 2006. Year-round movements of Northern Common Eiders *Somateria mollissima borealis* breeding in Arctic Canada and West Greenland followed by satellite telemetry. *Ardea* 94: 651–665.
- Newton I., 2008. *The Migration Ecology of Birds*. Elsevier, Oxford.
- Nilsson C., Klaassen R.H.G. & Alerstam T., 2013. Differences in speed and duration of bird migration between spring and autumn. *Am. Nat.* 181: 837–845.
- Nuijten R.J.M., Kölzsch A., Van Gils J.A., Hoyer B.J., Oosterbeek K., De Vries P.P., Klaassen M., & Nolet B.A., 2014. The exception to the rule: retreating ice front makes Bewick's swans *Cygnus columbianus bewickii* migrate slower in spring than in autumn. *J. Avian Biol.* 45: 113–122.
- Panuccio M., Agostini N., Wilson S., Lucia G., Ashton-Booth J., Chiatante G., Mellone U. & Todisco S., 2006. Does the Honey-buzzard feed during migration? *Br. Birds* 99: 367–368.
- Panuccio M., Chiatante G. & Tarini D., 2013. Two different migration strategies in response to an ecological barrier: Western Marsh Harriers and juvenile European Honey Buzzards crossing the central-eastern Mediterranean in autumn. *J. Biol. Res.* 19: 10–18.
- Programa Migres, 2009. Seguimiento de la migración de las aves en el estrecho de Gibraltar: resultados del Programa Migres 2008. *Migres* 1: 83–101.
- Prommer M., Bagyura J., Chavko J. & Uhrin M., 2012. Migratory movements of Central and Eastern European Saker Falcons (*Falco cherrug*) from juvenile dispersal to adulthood. *Aquila* 119: 111–134.
- R Development Core Team, 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Schmaljohann H., Fox J.W. & Bairlein F., 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Anim. Behav.* 84: 623–640.
- Schmaljohann H., 2018. Proximate mechanisms affecting seasonal differences in migration speed of avian species. *Scientific Reports* 8: 4106, doi:10.1038/s41598-018-22421-7.
- Sergio F., Tanferna A., De Stephanis R., López Jiménez L., Tavecchia G., Preatoni D., & Hiraldo F., 2014. Individual improvements and selective mortality shape lifelong migratory performance. *Nature* 515: 410–413.
- Shamoun-Baranes J., Baharad A., Alpert P., Berthold P., Yom-Tov Y., Dvir Y. & Leshem Y., 2003. The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. *J. Avian Biol.* 34: 97–104.
- Strandberg R., Hake M., Klaassen R.H.G. & Alerstam T., 2012. Movements of immature European Honey Buzzards *Pernis apivorus* in tropical Africa. *Ardea* 100: 157–162.
- Thorup K., Alerstam T., Hake M. & Kjellén N., 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. R. Soc. B.* 270: S8–S11, doi:10.1098/rsbl.2003.0014.
- van Noordwijk A.J., McCleery R.H. & Perrins C.M., 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J. Animal Ecol.* 64: 451–458.
- Vansteelant W.M., Bouten W., Klaassen R.H.G., Koks B., Schlaich A., van Diermen J., van Loon E.E. & Shamoun-Baranes J., 2015. Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. *J. Avian Biol.* 46: 25–39.
- Vansteelant W.M.G., Shamoun-Baranes J., van Manen W., van Diermen J. & Bouten W., 2017a. Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic flyway. *J. Animal Eco.* 86: 179–191.
- Vansteelant W.M.G., Kekkonen J. & Byholm P., 2017b. Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. *Proc. R. Soc. B.* 284, 20170387.
- Vidal Mateo J., Mellone U., Lopez-Lopez P., De La Puente J.D., Garcia-Ripollés C., Bermejo A. & Urios V., 2016. Wind effects on the migration routes of trans-Saharan soaring raptors: geographical, seasonal and interspecific variation. *Current Zool.* 62: 89–97.
- Yohannes E., Biebach H., Nikolaus G. & Pearson D.J., 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *J. Avian Biol.* 40: 126–134.
- Wikelski M. & Kays R., 2018. Movebank: archive, analysis and sharing of animal movement data. Hosted by the Max Planck Institute for Ornithology. [www.movebank.org](http://www.movebank.org).
- Zuur A.F., Ieno E.N. & Elphick C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1: 3–14.

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