

Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors

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Abstract Satellite-tracking technology has allowed scientists to make a quantum leap in the field of migration ecology. Nowadays, the basic description of migratory routes of many species of birds has been reported. However, the investigation of bird migration at individual level (i.e. repeatability in migratory routes and timing) still remains seldom explored. Here, we investigated repeated migratory trips of a trans-Saharan endangered migratory raptor, the Egyptian Vulture *Neophron percnopterus*, tracked by GPS satellite telemetry. We compared between- and within-individual variation in migratory routes and timing in order to assess the degree of repeatability (or conversely, the flexibility) in migration. To this end, we analysed a dataset of 48 trips (23 springs and 25 autumns) recorded for six adult birds during 2007–2013. Our results showed consistent migration timing at the individual level, both in spring and autumn. Interestingly, there was a high degree of flexibility in the routes followed by the same individual in different years, probably due to variations in meteorological conditions. Contrary to expectations of a faster migration in spring than in autumn owing to a time-minimization strategy for breeding, birds spent less time in autumn migration (13 ± 2 days, range = 9–18 d) than in spring migration (19 ± 3 days, range = 13–26 d), which can be explained by differences in environmental conditions en route. Egyptian vultures showed a consistent clockwise loop migration through western Africa, following more easterly routes in autumn than in spring. Finally, our results provide supporting evidence of low phenotypic plasticity in timing of migration (i.e. strong endogenous control of migration) and high flexibility in routes [*Current Zoology* 60 (5): 642–652, 2014].

Keywords Egyptian vulture, Endogenous control, GPS, Loop migration, *Neophron percnopterus*, Random routes, Satellite tracking, Simulation

Understanding adaptive migratory strategies and navigation capabilities of migrating birds constitutes a central question in migration ecology and consequently in behavioural ecology (Alerstam and Lindström, 1990; Berthold, 2001; Alerstam et al., 2006; Knudsen et al., 2011). To date, most studies about repeatability of timing of bird migration and routes have been conducted by means of visual observations and recaptures of marked animals at breeding and/or wintering grounds (Newton, 2010; e.g. Rees, 1989; Møller, 2001; Bety et al., 2004; Gunnarsson et al., 2006; Battley, 2006; Bell et al., 2009; Conklin et al., 2010; Lourenço et al., 2011). However, our knowledge about migration strategies and specifically, about annual schedules of migration and route fidelity at the individual level, still remains limited and largely skewed towards large animals due to limitations of available tracking devices. Thanks to the fast development of bio-logging technologies, primarily satellite-tracking, and more recently through the use of light-level geolocators and isotope analysis, the number of studies reporting repeated migratory journeys of the

same individual in different years has rapidly increased in recent years (Berthold et al., 2002; Meyburg et al., 2002, 2004a; Alerstam et al., 2006; Bobek et al., 2008; Qian et al., 2009; Quillfeldt et al., 2010; Guilford et al., 2011; Mellone et al., 2011; Vardanis et al., 2011; Stanley et al., 2012; Conklin et al., 2013; Dias et al., 2013).

The information recorded for repeatedly-tracked animals is essential to investigate when and where take place the key events of the annual cycle of long-distance migrants (i.e. breeding, migration and wintering). Hence, this information is crucial for understanding the selective pressures affecting each period. Although bird populations show great variation in the timing of the major events of the annual cycle, there is supporting observational and experimental evidence of endogenous control at genetic and physiological level of the timing at which these events take place (Berthold, 1996; Alerstam, 2006; Newton, 2010; Conklin et al., 2010). However, there is also evidence of a certain degree of variation (i.e. flexibility) at both the population and, to a lesser degree, at the individual level (Sutherland, 1998;

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Gill et al., 2014). Between-individual variation in migratory behaviour can be the result of extrinsic factors such as environmental conditions experienced at breeding/wintering areas or en route (e.g. food availability, daylength, meteorological conditions), and intrinsic factors such as individual characteristics (e.g. genetic program, age, sex) (Gordo, 2007; Both, 2010; Mellone et al., 2011; Studds and Marra, 2011; Ockendon et al., 2013). Therefore, the analysis of repeated tracks and annual schedules of long-distance migratory birds is important to assess the degree of behavioural flexibility at both individual and population level and ultimately, to predict animals' response to climate change (Both, 2010; Knudsen et al., 2011; Jaffré et al., 2013). In addition, the study of the fidelity to both breeding and wintering grounds has important implications for the conservation of long-distance endangered species (Sander-son et al., 2006).

Here, we investigated repeated migratory trips of a trans-Saharan migratory raptor, the Egyptian Vulture *Neophron percnopterus*, tracked by GPS satellite telemetry. The species has experienced severe population decline throughout its range and is endangered worldwide (BirdLife International, 2013). The European continental populations are migratory and travel from their breeding grounds to wintering areas in the sub-Saharan Sahel region (Meyburg et al., 2004b; Ceccolini et al., 2009; García-Ripollés et al., 2010; Gradev et al., 2012). Using a dataset of GPS locations recorded for six individuals tracked during consecutive years (from two to seven), our main goals were: (i) to provide a detailed description of timing of migration and descriptive parameters of spring and autumn migration routes; (ii) to compare between- and within-individual variation in migration routes and timing in order to assess the degree of repeatability (i.e. year-to-year fidelity) in migratory tracks and schedule; and (iii) to provide an alternative method based on simulation of randomized tracks to assess the degree of flexibility of individuals' migratory tracks within each season. According to the existing knowledge about major determinants of long-distance migration, we should expect a faster migration in spring than in autumn owing to a time-minimization strategy for breeding (Nilsson et al., 2013). In addition, if there is strong endogenous control of the timing of migration at the individual level, we should expect lower within-individual than between-individual variation in migration schedules in successive years (Vardanis et al., 2011; Stanley et al., 2012; Conklin et al., 2013).

1 Materials and Methods

1.1 Bird trapping and marking

We tracked the spring and autumn repeated migrations of six adult Egyptian vultures (EV) between 2007 and 2013. One bird was repeatedly tracked during two consecutive years, another bird during three years, two birds during four years, one during five years, and one individual was tracked during seven consecutive years. Overall, the complete dataset included 48 complete migratory trips (23 spring and 25 autumn journeys). Egyptian vultures were captured at the end of the breeding season at two vulture restaurants (i.e. places where farmers drop carcasses of dead cattle) located in Castellón and Guadalajara provinces (Spain) and artificial feeding stations located within breeding territories (López-López et al., 2013). All birds were territorial breeders and showed consistent high fidelity to the same territories in different years (López-López et al., 2014). Birds were equipped with a 45-gram solar-powered GPS tag (Microwave Telemetry Inc., Columbia, USA) mounted in a backpack configuration designed to ensure that the harness would fall off at the end of the tag's life. The mass of the equipment, including the harness, metal ring and tag, was below 3% of the bird's body mass, which is within recommended limits (Kenward, 2001). The GPS-tags were programmed to obtain GPS fixes (nominal accuracy ± 18 m) every two hours on a 24 hours ON duty cycle during the migratory periods (February–March and late August–October). Data were retrieved and managed using the Satellite Tracking and Analysis Tool (Coyne and Godley, 2005). Only locations recorded during complete migratory journeys were included in this study. According to molecular sexing, four birds were females (EV#1, EV#2, EV#3 and EV#5) and two birds were males (EV #4 and EV#6) (Fridolfsson and Ellegren, 1999). For further details on birds trapping methods and approved ethics required for this study see García-Ripollés et al. (2010) and López-López et al. (2013).

1.2 Description of migration routes

For each bird and migratory season we recorded departure and arrival dates (Julian day, i.e. January 1st = 1), the duration and a set of descriptive parameters including the linear distance from breeding areas to wintering grounds, the cumulative distance of the route and the average migration speed (calculated as the cumulative distance/duration; cf. “total migration speed” *sensu* Nilsson et al., 2013). Egyptian vultures depart abruptly from breeding and wintering areas (García-Ripollés et

al., 2010). Hence, the onset and end of migration were directly recorded by means of a visual inspection of raw data in Google Earth (Google Inc.). Data were projected in Universal Transverse Mercator (UTM) coordinates and plotted in a Geographic Information System (ArcMap 10.0; ESRI Inc. www.esri.com). Cumulative distance (i.e. the track length) was computed in Geospatial Modelling Environment software (Beyer, 2012) as the total sum of step lengths recorded between two consecutive locations (i.e. the Euclidean linear distance). We also calculated the straightness index (Batschelet, 1981) computed as the ratio between the linear distance from breeding to wintering areas and the cumulative distance. This simple index ranges between 0, which corresponds to a route infinitely crooked, to 1, a perfectly straight track, and has proven to be a rough estimate of the orientation efficiency of animals (Benhamou, 2004). Results are reported as averages \pm standard deviation and range (minimum-maximum).

1.3 Route flexibility

In order to test the degree of repeatability of migratory routes we determined for each bird and migratory season the longitudes at which two latitudes (30°N and 24°N) were crossed. These two latitudes were considered to represent independent measures of the crossing of the Sahara desert, a major ecological barrier that Egyptian vultures must overcome to reach their final destination during autumn and spring migration. We did not analyse individual consistency in route at other latitudes (i.e. in Spain and the crossing of the Strait of Gibraltar) because a direct inspection of migration maps showed that all birds were funnelled through this narrow corridor to cross between Europe and Africa.

Furthermore, using data of each individual, we propose an alternative method in order to assess the degree of flexibility of individuals' migratory tracks within each season. This method is based on a comparison between observed routes and a set of randomized routes produced by Monte Carlo simulations that generate random samples from a probability distribution based on real data (Gotelli and Ellison, 2004). In comparison with standard parametric analyses, Monte Carlo simulations have the advantage of not relying on the assumption that the data are sampled from a specific theoretical probability distribution (Gotelli and Ellison, 2004; Manly, 2006). To this end, observed routes were compared with 1000 simulated routes obtained by rearranging the different segments (i.e. the steps recorded between two consecutive positions) of the real routes for each combination of individual-season-year. Each seg-

ment was moved so that it started at the end of the previous segment resulting in a new simulated route that started and ended at the same place of the real route. Simulated routes were automatically generated using the "Randomize route segments" option of Alternate Animal Movement Routes extension for ArcView 3.2 (Jenness, 2005). Then, we recorded for each track (i.e. the observed and 1,000 simulated routes), the longitudes at which latitudes between 36°N and 18°N (each 3° of latitude) were crossed. Significant deviation of the original route from simulated ones was obtained by sorting the 1000 longitude values at each latitude value and calculating the ranking of the observed longitude within the simulated routes. Thereby, if the longitude of the real route was above or below the percentiles 2.5% and 97.5% of the distribution (i.e. equivalent of a two-tailed test with $\alpha = 0.05$) we considered that the observed routes deviated significantly from simulated random routes. Significance probability values, equivalent to traditional *P*-values, were obtained by counting the number of randomized cases that resulted in an equal or larger/smaller value than the observed value of longitude at each latitude of analysis, and then divided by the total number of randomizations (i.e. 1,000 in our case). Since all Egyptian vultures crossed through the Strait of Gibraltar en route to Africa and moved more or less following a straight line from breeding areas to this major migratory bottleneck, the analysis of route flexibility was only conducted for the African stretch of migration, from the parallel 36°N, which corresponds with the Strait of Gibraltar, to the parallel 18°N. Importantly, this analysis of simulated routes was not aimed at comparing different tracks between individuals or between different seasons.

We also calculated the width of the migration corridor in order to provide an additional measure of route flexibility (Alerstam et al., 2006). The width of the migration corridor was measured by computing the linear distance of the maximum longitudinal separation (i.e. East-West) of repeated tracks of each individual at 3° latitude intervals from 18°N to 36°N. The width of migration corridors was computed separately for spring and autumn seasons.

1.4 Statistical analysis

We compared between- and within-individual variation in migration timing and migration parameters by means of a one-way ANOVA with "individual" as a categorical factor. Basic assumptions of the ANOVA were checked and homogeneity of variances was tested by means of the Levene's test. Repeatability values (i.e.

in our case the intra-class correlation coefficient of the variable “individual”) were based on variance components derived from the previous ANOVA and were computed following the cautions of Lessells and Boag (1987). Repeatability provides a measure of how consistently individuals differ from each other and is thus becoming a popular metric in migration studies (Nakagawa and Schielzeth, 2010; Conklin et al., 2013). Relationships between migration parameters were tested by means of Spearman rank order correlations. The Mann-Whitney test was used to compare migration parameters between migratory seasons. All statistical analyses were performed using STATISTICA version 10.0 (StatSoft Inc., www.statsoft.com). Statistical significance was set at $P < 0.05$.

2 Results

Overall, 185 ± 34 locations per individual were recorded during spring and 122 ± 41 locations/individual were recorded during autumn migration ($n = 6$ individuals). No significant differences in the number of locations among individuals were recorded either during spring migration (One-Way ANOVA: $F_{5,17} = 2.10$, $P = 0.12$; Levene test: $F_{5,17} = 1.02$, $P = 0.44$) or during autumn migration (One-Way ANOVA: $F_{5,19} = 0.88$, $P = 0.51$; Levene test: $F_{5,19} = 1.34$, $P = 0.29$).

2.1 Route description and timing of migration

All Egyptian vultures migrated from their breeding grounds in Spain to their wintering areas in the Sahel region (Fig. 1). As expected, all birds crossed the Strait of Gibraltar during autumn and spring migrations. Importantly, no stopovers were detected during migration.

A summary of values of migration timing and descriptive parameters of migration are shown in Table 1. Significant seasonal differences were found in descriptive parameters of the migration journeys (duration, linear distance, cumulative distance, speed and straightness) with all Mann-Whitney comparisons between spring and autumn values showing $P < 0.01$ (detailed results not shown).

Considering all data, departure dates of spring migration spanned 22 days, whereas autumn departures occurred during a total span of 44 days. Arrival dates spanned 25 days in spring and 47 days in autumn. Departure and arrival dates, both during spring and autumn migration, were different among individuals and highly consistent across repeated tracks within individuals, particularly during autumn (repeatability values: $r > 0.7$ in both cases) (Table 2). In both seasons, departure and arrival dates were highly correlated (Spearman correla-

tions: $r_{\text{spring}} = 0.80$, $P < 0.001$; $r_{\text{autumn}} = 0.93$, $P < 0.001$). However, no significant correlations were found between departure dates and duration of migration ($r_{\text{spring}} = -0.19$, $P = 0.38$; $r_{\text{autumn}} = 0.22$, $P = 0.30$).

Birds spent less time in autumn migration (13 ± 2 days, range = 9–18) than in spring migration (19 ± 3 days, range = 13–26) (Table 1). Both linear and cumulative distances were lower in autumn than spring migration (Table 1), because local movements during winter made that the arrival locations in autumn and departure locations in spring were different (Fig. 1). We also observed significant differences between individuals in linear distances and high consistency within them (r -values: 0.71–0.87) (Table 2). Egyptian vultures showed high fidelity to both breeding and wintering areas (Fig. 1). Individual differences in cumulative distances were only observed during spring migration, although with a low repeatability ($r = 0.33$) (Table 2).

In relation to average migration speed, birds migrated faster during autumn than during spring and also covered longer distances in autumn (maximum = 352 km/day) than in spring (maximum = 275 km/day) (Table 1). Logically, speed was negatively correlated with duration of both spring (Spearman correlation: $r_{\text{spring}} = -0.86$, $P < 0.001$) and autumn migration ($r_{\text{autumn}} = -0.89$, $P < 0.001$). However, no significant correlations were found between speed and departure or arrival dates in both seasons (all $P > 0.05$). Individual differences in average migration speed were only found in autumn ($r = 0.35$), but not in spring (Table 2).

2.2 Route flexibility and migration corridors

On average, Egyptian vultures followed more easterly routes in autumn migration than in spring (Fig. 1). Moreover, autumn routes were more direct than spring routes (mean straightness_{autumn} > mean straightness_{spring}; Table 1). Individual differences in straightness were obtained in spring ($r = 0.43$), but not in autumn migration (Table 2).

All individuals' migration tracks practically followed a straight line in the Iberian Peninsula in their outward and backward migrations. Once in Africa, routes fanned out, especially when individuals entered into the Sahara desert (approximately at 33°N) (Fig. 1). Similar divergence in migratory journeys across the Sahara was observed during spring migration.

Interestingly, no differences among individuals were found in the longitudes at which latitudes 30°N and 24°N were crossed (Table 2). In both seasons, repeatability values were low ($r < 0.3$ in all cases), with spring values being higher than in autumn (Table 2). In both

seasons, within-individual variation was much higher than between-individual variation. These results showed consistent low route fidelity within individuals in both spring and autumn migration.

According to the analysis of simulated routes, significant deviations of observed routes from random routes were observed (Fig. 2). In general, spring tracks showed more consistent deviation than autumn routes (percentage of routes that deviated from random routes

ranging from 22% to 70% between 18°N and 33°N). Autumn tracks deviated significantly at the end of migration, especially between 24°N and 18°N (percentages ranging from 56% to 84%). The significant deviations in the simulation analyses reflected that the birds followed a consistent loop pattern with deviations both in spring and autumn from flight paths with random variation along the direct flight route between the Strait of Gibraltar and the overwintering areas.

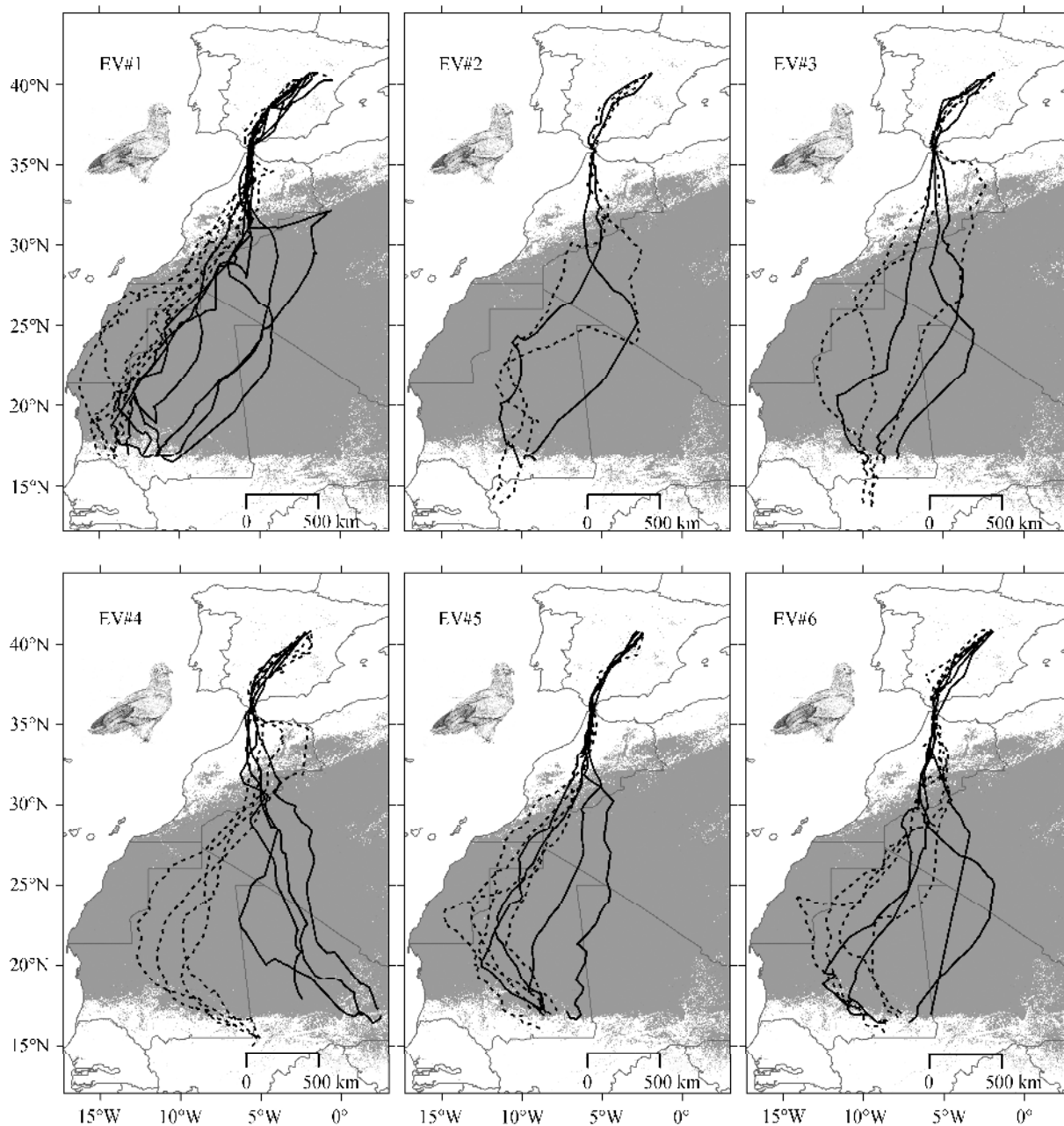


Fig. 1 Repeated migratory tracks of six adult Egyptian vultures breeding in Spain and tracked by means of GPS satellite telemetry during 2007–2013

Solid lines indicate autumn routes and dashed lines indicate spring routes. Background grey shows bare and desert areas. Overall, 48 complete migratory routes (25 autumn and 23 spring) were recorded.

Table 1 Migration schedules of six adult Egyptian vultures *Neophron percnopterus* breeding in Spain tracked by GPS satellite telemetry during 2007–2013

Bird	Number of tracks	Spring migration						
		Departure	Arrival	Duration (days)	Linear distance (km)	Cumulative distance (km)	Speed (distance/day)	Straightness
EV#1	6	27 Feb (23 Feb – 4 Mar)	19 Mar (15 Mar – 23 Mar)	20 ± 5 (13 – 26)	2903 ± 31 (2865 – 2941)	3471 ± 80 (3366 – 3569)	184 ± 51 (131 – 275)	0.84 ± 0.01 (0.82 – 0.86)
EV#2	2	27 Feb (25 Feb – 28 Feb)	19 Mar (18 Mar – 19 Mar)	20 ± 1 (19 – 21)	3047 ± 105 (2972 – 3121)	4023 ± 533 (3647 – 4400)	203 ± 41 (174 – 232)	0.76 ± 0.07 (0.71 – 0.81)
EV#3	3	16 Feb (13 Feb – 18 Feb)	5 Mar (1 Mar – 9 Mar)	18 ± 3 (16 – 21)	3084 ± 13 (3073 – 3098)	3564 ± 103 (3457 – 3663)	206 ± 36 (165 – 229)	0.87 ± 0.03 (0.84 – 0.89)
EV#4	4	22 Feb (18 Feb – 26 Feb)	15 Mar (10 Mar – 18 Mar)	21 ± 2 (18 – 23)	2814 ± 47 (2765 – 2872)	3758 ± 260 (3485 – 4038)	184 ± 16 (166 – 200)	0.75 ± 0.06 (0.68 – 0.80)
EV#5	4	26 Feb (21 Feb – 7 Mar)	17 Mar (13 Mar – 26 Mar)	19 ± 2 (17 – 21)	2711 ± 61 (2664 – 2800)	3340 ± 173 (3119 – 3494)	175 ± 24 (149 – 206)	0.81 ± 0.03 (0.77 – 0.85)
EV#6	4	23 Feb (20 Feb – 27 Feb)	13 Mar (10 Mar – 14 Mar)	18 ± 3 (15 – 21)	2762 ± 64 (2696 – 2847)	3599 ± 339 (3278 – 3965)	198 ± 15 (186 – 219)	0.77 ± 0.06 (0.70 – 0.83)
All	23	24 Feb ± 5 days	15 Mar ± 6 days	19 ± 3	2866 ± 137	3580 ± 286	190 ± 32	0.80 ± 0.06

Bird	Number of tracks	Autumn migration						
		Departure	Arrival	Duration (days)	Linear distance (km)	Cumulative distance (km)	Speed (distance/day)	Straightness
EV#1	7	7 Sept (1 Sept – 15 Sept)	19 Sept (12 Sept – 28 Sept)	12 ± 2 (9 – 16)	2818 ± 26 (2790 – 2864)	3458 ± 240 (3172 – 3958)	298 ± 41 (247 – 352)	0.82 ± 0.06 (0.71 – 0.89)
EV#2	2	8 Sept (7 Sept – 8 Sept)	23 Sept (21 Sept – 24 Sept)	15 ± 1 (14 – 16)	2799 ± 67 (2751 – 2846)	3308 ± 50 (3272 – 3343)	221 ± 18 (209 – 234)	0.85 ± 0.01 (0.84 – 0.85)
EV#3	3	11 Sept (4 Sept – 20 Sept)	27 Sept (19 Sept – 4 Oct)	16 ± 2 (14 – 18)	2781 ± 32 (2745 – 2804)	3203 ± 105 (3097 – 3307)	206 ± 23 (184 – 229)	0.87 ± 0.02 (0.85 – 0.89)
EV#4	5	4 Sept (2 Sept – 8 Sept)	17 Sept (13 Sept – 21 Sept)	13 ± 2 (10 – 15)	2650 ± 66 (2542 – 2709)	3122 ± 331 (2803 – 3678)	253 ± 45 (205 – 309)	0.85 ± 0.07 (0.73 – 0.91)
EV#5	4	17 Aug (7 Aug – 28 Aug)	30 Aug (18 Aug – 9 Sept)	13 ± 3 (11 – 17)	2689 ± 26 (2653 – 2710)	3139 ± 117 (2974 – 3251)	253 ± 43 (191 – 287)	0.86 ± 0.03 (0.83 – 0.90)
EV#6	4	8 Sept (5 Sept – 13 Sept)	21 Sept (19 Sept – 25 Sept)	13 ± 2 (12 – 16)	2739 ± 45 (2676 – 2774)	3200 ± 281 (2829 – 3511)	244 ± 29 (218 – 271)	0.86 ± 0.07 (0.79 – 0.95)
All	25	4 Sept ± 10 days	17 Sept ± 10 days	13 ± 2	2745 ± 77	3256 ± 254	256 ± 46	0.85 ± 0.05

Descriptive parameters of migration routes are reported as average values, standard deviations and range (minimum – maximum).

Table 2 One-Way ANOVA testing the effects of “individual” on migration parameters. Repeatability (r) values (i.e. the intra-class correlation coefficient of the variable “individual”) are shown

Season	Variable	df	F	P	r
Spring	Departure date	5,17	3.877	0.016*	0.434
	Arrival date	5,17	5.832	0.003**	0.563
	Duration	5,17	0.438	0.816	-0.176
	Linear distance	5,17	26.865	0.000***	0.873
	Cumulative distance	5,17	2.874	0.047*	0.333
	Speed	5,17	0.420	0.829	-0.183
	Straightness	5,17	3.872	0.016*	0.433
	Latitude 30°N	5,17	2.584	0.065	0.297
Latitude 24°N	5,17	1.719	0.184	0.161	
Autumn	Departure date	5,19	10.651	0.000***	0.705
	Arrival date	5,19	10.636	0.000***	0.704
	Duration	5,19	1.564	0.218	0.122
	Linear distance	5,19	11.083	0.000***	0.714
	Cumulative distance	5,19	1.593	0.210	0.128
	Speed	5,19	3.186	0.030*	0.351
	Straightness	5,19	0.584	0.712	-0.115
	Latitude 30°n	5,19	1.002	0.443	0.001
Latitude 24°n	5,19	1.131	0.378	0.033	

Significance level indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The mean width of migration corridors ranged from 18 ± 5 km and 15 ± 8 km at 36°N to 541 ± 197 km and 569 ± 123 at 24°N , in spring and autumn, respectively (Fig. 3). The maximum East-West separation of repeated routes was 786 km in spring (at 24°N) and 844 km in autumn (21°N), in both cases corresponding to the same individual (EV#6). Seasonal differences in the width of migration corridors were observed at 21°N (Mann-Whitney test: $U = 2.00$, $Z = 2.56$, $P = 0.01$) and at 18°N ($U = 3.00$, $Z = 2.40$, $P = 0.02$). No significant differences in the width of migration corridors were observed at other latitudes.

3 Discussion

Repeated tracking of the same individuals during consecutive years can improve our understanding about the spatial and temporal variability and the role of flexibility in animals' migratory behaviour (Vardanis et al., 2011). As a consequence, this is opening new avenues of research in the field of migration ecology, which will ultimately provide important advances in our comprehension of the role of individual behaviour in determining overall emergent properties of complex systems (i.e.

when the properties of an upper level of organization are not equal to the sum of the properties of the components of a lower level but the results of their asymmetric interactions; Novikoff, 1945; Salt, 1979). The results of Gill et al. (2014), which have observed an advance of arrival dates of Icelandic black-tailed godwit *Limosa limosa islandica* at the population level but not at individual level is a good example of these emergent properties in migratory behaviour. Therefore, the behavioural response at the individual level is necessary for a better understanding of the response at the population level.

Our results, based on repeated tracking of Egyptian vultures, provide supporting evidence of low phenotypic plasticity in timing of migration (i.e. strong endogenous control of migration) and high flexibility in routes (Vardanis et al., 2011; Stanley et al., 2012; Dias et al., 2013). Although anecdotal, one of the individuals of this study was tracked for seven consecutive years (EV#1) and was quite close to the world record for longest continued bird migration with the same trans-

mitter (the bird was shoot down in southern Mauritania and stopped transmitting in December 2013). To the best of our knowledge, this record is held by a female Greater Spotted Eagle *Aquila clanga* that was tracked for at least ten years (Meyburg and Meyburg, 2009). Other birds, such as White Storks *Ciconia ciconia* have also been tracked for similar lengths of time, but the satellite-tracking devices have been exchanged during the period (Meyburg and Meyburg, 2009). Leaving anecdotes aside, repeated tracking in successive years of free-living animals is key to assess the degree of behavioural consistency (or conversely flexibility) in migration, as highlighted in this study.

Our results showed consistent migration timing at the individual level, both in spring and autumn. However, in contrast to other studies (Vardanis et al., 2011; Stanley et al., 2012), we found higher repeatability in departure and arrival dates for autumn migration than spring migration (Table 2). It might be explained by higher predictability of environmental conditions in Europe at the

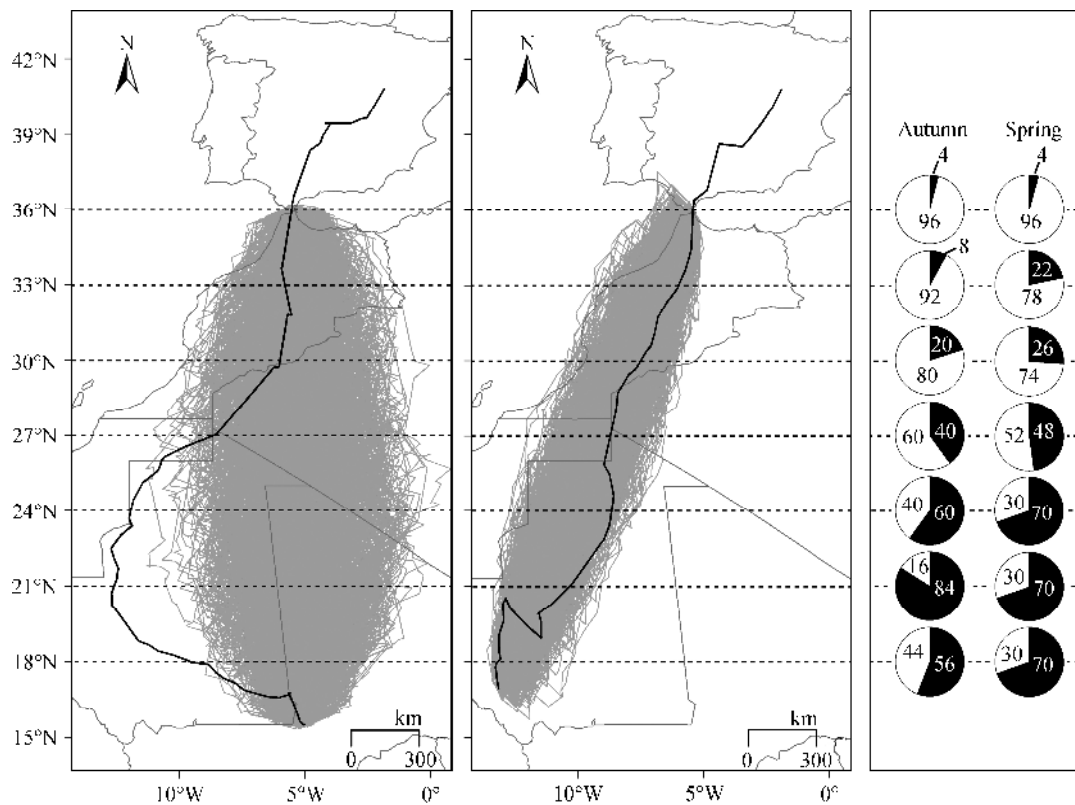


Fig. 2 Analysis of simulated routes

Individual flexibility in migration routes was tested by comparing observed routes (black line) with 1000 simulated routes (grey lines) obtained by rearranging the different segments of the real routes for each combination of individual-season-year (further details in Methods). Left: example of a spring route that deviated significantly at 18°N, 21°N, 24°N and 27°N. Centre: example of an autumn route that did not deviate significantly between 36°N and 21°N. Right: pie charts showing the number of observed routes (expressed as percentage) that deviated significantly from simulated routes (black area with numbers in white) and that did not deviate from simulated routes (white area with numbers in black) at each 3° of latitude during autumn and spring.

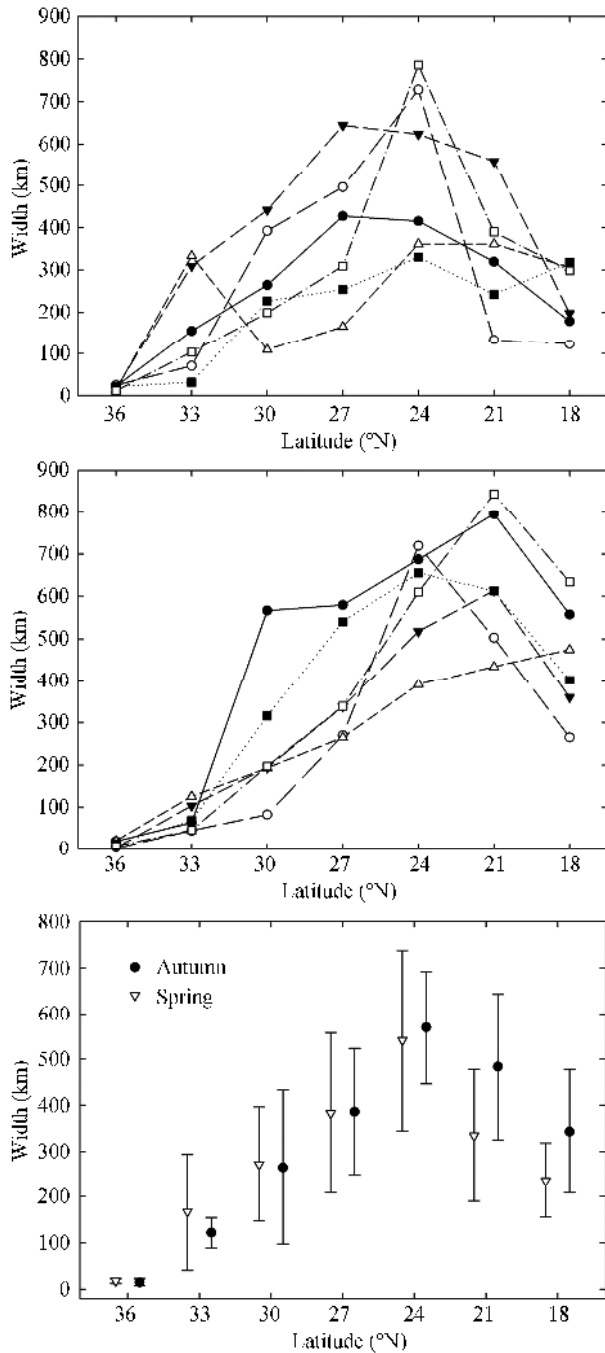


Fig. 3 Width of the migration corridor (km) at different latitudes for six adult Egyptian vultures tracked on repeated journeys between breeding sites in Spain and wintering areas in the Sahel region between 2007 and 2013

Different lines represent each individual. Note the differences in the width of the migration corridor during spring migration (upper panel) and autumn migration (central panel). For comparison, the average values of the width of the migration corridor in spring and autumn are shown in the lower panel. Vertical bars indicate standard deviation.

end of the summer season than in the Sahel region just before the onset of spring migration (U. Mellone, com. pers.). In agreement with this, predictability of environmental cues has been argued to explain consistent

timing of migration and flexibility in routes in other raptors (Vardanis et al., 2011).

Overall, we observed low within-individual variation in departure and arrival dates which, in combination with significant differences among individuals, suggests a rigid endogenous control of migration timing (Tables 1 and 2). High repeatability values in autumn migration were a consequence of a larger variation in the onset and end of migration between-individuals than within-individuals. The repeatability values obtained in spring (around 0.5) were the result of similar values of within- and between-individual variation. The high consistency of these results provide supporting evidence of a stronger influence of endogenous schedules than local environmental conditions, similarly to observed in other species (Alerstam et al., 2006; Battley, 2006; Vardanis et al., 2011; Stanley et al., 2012). It should be highlighted the “extreme” cases of one individual (EV#5), which began the spring migration in the same day in different years (2011 and 2013) or the case of one bird (EV#4) that started autumn migration in the same day in two different years (2009 and 2012). Other individuals showed similar results, with observed onset of spring and autumn migration within a time-window of one day in different non-consecutive years. The observed high repeatability in the timing of both spring and autumn migration supports the existence of individually optimized migration schedules (Battley, 2006; Bell et al., 2009; Vardanis et al., 2011).

Egyptian vultures migrated at higher average speed during autumn than during spring migration. This result is apparently contradictory to the general observed pattern of higher speeds reported during spring migration, which has been primarily interpreted as a consequence of a time-minimization strategy because of competition for early arrival at breeding grounds (Nilsson et al., 2013). However, a detailed analysis of migration speed, both at hourly and daily scale, showed that tailwind support is the most important factor explaining variation in daily distance covered by Egyptian vultures during both spring and autumn (Mellone et al., 2012). In that study, using the same individuals included here, we analysed hourly and daily speed of Egyptian vultures across the Sahara desert, observing seasonal differences and faster hourly ground speeds (i.e. the horizontal speed of the bird relative to the ground) in autumn than in spring (Mellone et al., 2012). However, controlling for external factors (mainly tailwind), we observed that daily distance was higher in spring than during autumn migration. Furthermore, our comparison of the migra-

tory performance of four raptor species showed that the Egyptian vulture was the only species experiencing more favourable factors simultaneously (tailwind and day length) in the same season (autumn), thus explaining the lower duration of migration during this season (Mellone et al., 2012). Therefore, our results would not contradict the time-minimization hypothesis, at least during the crossing of the Sahara desert, which is in agreement with previous results that indicate that birds try to maximize migration speed during spring rather than during autumn (Nilsson et al., 2013). Similar results, in which wind regimes could explain faster autumn migration ground speeds have been reported in the case of the Levant Sparrowhawk *Accipiter brevipes* (Spaar et al., 1998) and the Great Snipe *Gallinago media* (Klaassen et al., 2011) (for a complete review see Nilsson et al., 2013).

In contrast to migration timing, there was a high degree of flexibility in the routes followed by the same individual in different years, maybe due to different meteorological conditions experienced en route (Mellone et al., 2011). Our results of univariate analysis showed that there was higher within-individual variation than between-individual variation in migratory routes, thus supporting high route flexibility (or conversely, low route fidelity). As a consequence, repeatability values were very low in both spring and autumn migration ($r < 0.3$) (Table 2). Furthermore, our method to analyse within-individual route flexibility for each season by means of simulation of randomized tracks also supported these results. This method is based on a modification of the method proposed by Strandberg et al. (2009) and later used by López-López et al. (2010) to analyse the existence of converging migration routes. In contrast to other methods based on the univariate comparison of longitudinal scatter at different latitudes (e.g. Vardanis et al., 2011; Stanley et al., 2012), our method has the advantage that it makes clear and explicit the underlying assumptions and the structure of the null hypothesis (Gotelli and Ellison, 2004), an important issue that is not always guaranteed using one-way ANOVAs. In fact, in most cases it is difficult to accept that the basic assumptions of the ANOVA, principally the independence of observations and homogeneity of variances, are met when data of repeated tracks of the same individuals are analysed (see for example some words of caution about this issue in Alerstam et al., 2006).

Finally, Egyptian vultures showed a consistent clockwise loop migration through western Africa, following

more easterly routes in autumn than in spring. Seasonal differences in the geometry of migratory routes could be explained by different environmental or meteorological conditions experienced en route (Kemp et al., 2010; Klaassen et al., 2010; Mellone et al., 2013). It should be further explored in detail if the main direction of prevailing winds at the altitude of migration is the main determinant of the observed deviation from a straight line, particularly in autumn. The effect of adverse conditions such as crosswinds and sand storms on migratory performance is particularly important when birds try to overcome ecological barriers (López-López et al., 2010; Strandberg et al., 2010). Similar seasonal differences in prevailing wind conditions causing differential detour in migratory journeys have been reported for other long-distance migrants crossing the same regions of the Egyptian vultures, such as the Marsh harrier *Circus aeruginosus* (Klaassen et al., 2010) and the Montagu's harrier *Circus pygargus* and Lesser Kestrel *Falco naumanni* (Limiñana et al., 2013).

In conclusion, the high flexibility observed in both spring and autumn routes suggests that migratory birds employ a complex interaction of compass mechanisms (Alerstam, 2006). It is plausible that birds could use mechanisms based on landmark recognition or map-based navigation at least to reach intermediary goal areas during migration such as the Strait of Gibraltar. However, it is challenging how the same individuals are able to reach the same African wintering areas in different years with the striking degree of flexibility exhibited in their journeys (likewise the Strait of Gibraltar during spring). Our results showed that flight paths from repeated journeys by the same individual were up to 786 and 844 km apart during the Sahara crossing in spring and autumn, respectively. These distances exceed the expected normal range of vision of diurnal raptors and thus it suggests that landmark recognition is not of primary importance for navigation, as reported for other species such as the Osprey *Pandion haliaetus* (Alerstam et al., 2006). Path-integration in combination with experience may thus play a key role in optimizing individual migration routes and schedule (Alerstam et al., 2006). In fact, our results have demonstrated that Egyptian vultures are able to show important flexibility not only in their migratory behaviour, but also in their foraging behaviour all over the annual cycle (López-López et al., 2013, 2014). This suggests that not only environmental conditions explain individuals' behaviour but also individuals' cognitive abilities (fundamentally memory effects) could play an important role in their behav-

our. Future studies comparing the geometry of repeated migratory journeys of individuals of different age (juvenile naïve birds versus adults) will be key to disentangle the role of experience in determining the behaviour of migratory birds. Ultimately, the degree of behavioural flexibility exhibited by long-distance migratory birds will be a key factor to regulate their response to environmental changes.

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