'Same procedure as last year?' Repeatedly tracked swifts show individual consistency in migration pattern in successive years

A. H. J. Wellbrock, C. Bauch, J. Rozman and K. Witte

A. H. J. Wellbrock (wellbrock@biologie.uni-siegen.de), J. Rozman and K. Witte, Research Group of Ecology and Behavioral Biology, Inst. of Biology, Dept of Chemistry and Biology, Univ. of Siegen, Siegen, Germany. – C. Bauch, Behavioural and Physiological Ecology, Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, Groningen, the Netherlands.

Individual migration pattern during non-breeding season is still a black box in many migratory birds. However, knowledge on both individual level and population level in migration and overwintering is fundamental to understand the life cycle of these birds and the constraints affecting them. We showed in a highly aerial migrant, the common swift *Apus apus*, that repeatedly tracked birds breeding at one site in Germany used the same individual-specific migration routes and wintering areas in subsequent years. In contrast, different individuals from the same breeding colony showed diverse movement patterns during non-breeding season suggesting that several suitable areas for overwintering coexist. We found lower variation in timing of autumn and spring migration within than between individuals. Our findings provide first indication of individual consistency but between-individual variation in migration pattern in a small non-passerine bird revealed by geolocators. This supports that swifts have diverse but individual-specific 'step-by-step' migration patterns revealing high flexibility through individual strategies.

Long-distance migratory birds travel between different areas of the world as part of their annual life cycle (Newton 2008, Rappole 2013). Research on movements during the non-breeding season, the major part of this cycle, needs more attention because an ongoing decline in breeding populations of many Palaearctic-African migrants has been observed (Vickery et al. 2014, Gilroy et al. 2016) and carry-over effects from the non-breeding season on reproduction and survival have been described in numerous studies (Walther et al. 2002, Both et al. 2006, Gilroy et al. 2016). Therefore, we need detailed information on migration patterns not only at the population level but even more importantly at the individual level of a species (Marra et al. 2015). Furthermore, repeated tracks of the same individual are necessary to understand the flexibility in migration route and overwintering in a species (Stanley et al. 2012). Especially for small birds, data of repeatedly tracked individuals are rare (Newton 2008, Cresswell 2014), and light-level geolocators are the only devices by now that allow long-term tracking of birds below 100 g of body mass (Kays et al. 2015). To our knowledge, there is only one geolocator study with repeated tracking in a small passerine migrant, the Nearctic wood thrush *Hylocichla mustelina* (Stanley et al. 2012).

Here, we present geolocator data of repeatedly tracked individuals in a small non-passerine Palaearctic-African migrant, the common swift *Apus apus* (hereafter called swift). Swifts are highly aerial, long-distance and long-living migrants (Lack 1956). They spend the entire non-breeding season, up to ten months, non-stop on the wing (Hedenström et al. 2016). So far, migration routes and exact wintering areas of swifts are poorly defined due to limited recoveries of identification rings in Africa (Weitnauer 1980, Perrins 2002, Åkesson et al. 2012, Bairlein et al. 2014). Two geolocator studies of swifts breeding in Sweden suggested wintering areas in the Congo basin and in west Africa (Åkesson et al. 2012, 2016). However, swifts breeding in the Netherlands, Belgium or UK migrated farther to wintering areas in eastern and southern and South Africa (Appleton 2012, Genton and Jacquat 2014, Klaassen et al. 2014).

In this study, we investigated whether swifts from the same breeding colony were faithful to their individual-specific migration routes, stopover sites, and wintering areas in two successive years. Thus, we assessed individual consistency and between-individual variation in migration pattern.

Methods

Geolocator deployment

We equipped adult swifts with archival light-level geolocators in a breeding colony (about 45 pairs) inside a road bridge near Olpe (51°02′28″N, 7°49′36″E), Germany, in two subsequent years (2012 and 2013). In total, we attached twenty geolocators (ten per year) from Biotrack (Wareham, UK) to swifts with a full body harness (Åkesson et al. 2012).

Birds were recaptured one year or two years later, and geolocators were removed (for further details on recaptured birds and geolocator types see Supplementary material Appendix 1 Table A1). Overall, we were able to recover eleven geolocators from ten different individuals for data download (six loggers deployed in 2012 and five loggers deployed in 2013). Male (ID '5907') was fitted with a logger in 2012 and again in 2013. Two males carried the same geolocator for two years (ID '6000' and ID '2930'). In total, this equalled six tracks of repeatedly tracked males and seven data sets of individuals (five females and two males) which were tracked for only one non-breeding season. Among the ten individuals, we tracked a breeding pair in 2012/2013 (results are given in Supplementary material Appendix 2).

Analysis of geolocation data

We processed light data downloaded from the geolocators with the R-package 'GeoLight' (Lisovski and Hahn 2012; for further analysis details see Supplementary material Appendix 1). The function 'changeLight' of the R-package 'GeoLight' was applied to determine stationary periods (i.e. wintering areas and stopover sites) entering the options 'quantiles = 0.9' and 'days = 4' as minimal stationary period at stopover sites (Lisovski and Hahn 2012) and 'days = 14' for wintering areas, respectively. Each individual track was divided into three seasons: autumn migration, wintering period and spring migration. We defined the date on which an individual swift arrived at a sub-Saharan site for a calculated stationary period of at least 14 d as the end of the autumn migration. Accordingly, we rated the date when a swift left the last site at which it stayed for at least 14 d before crossing the Sahara as the start of spring migration (Trierweiler et al. 2014). Stationary periods of 4 to 13 d in sub-Saharan western Africa, northern Africa and Europe were ranked as stopover sites where swifts stayed in an airspace within a definable area. We determined the total duration as travel duration plus days at stopover sites for autumn and spring migration, respectively. The sum of all days between autumn and spring migrations was defined as the duration of the wintering period. We considered only stationary periods within the wintering period that lasted at least 14 d as wintering areas.

Statistical analyses

We analysed separately the within- and between-individual variation in migration routes and wintering movements with a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) using the function 'adonis' of the R-package 'vegan' (Oksanen et al. 2010). Geographic position was used as dependent bivariate variable (latitude combined with longitude). Each geographic position of a track could be treated as an independent data point because permutations remove spatial and temporal autocorrelation (Anderson 2005). Two data sets were examined: 1) one data set for the analysis of within-individual variation and 2) another data set for the analysis of between-individual variation. The 'within'-data set consisted of the six tracks of the three repeatedly tracked individuals. Each first track of the two males '5907' and '6000' was shortened

to the length of the second ending at the same Julian date because the second track of these males was not repeated completely. The 'between'-data set included the tracks of the seven singly tracked individuals plus the first entire track of the three repeatedly tracked individuals (n = 10). For the 'within'-analysis, we used 'track' (coded as first or second) as explanatory variable in the test and 'individual' as cofactor. In the 'between'-analysis, we applied 'individual' as explanatory variable. We entered 'season' and 'date' (as Julian date) as covariates in the PERMANOVA of both data sets. To constrain permutations for the F-tests within the different non-breeding seasons, we used 'non-breeding season' in the argument 'strata'. Analysis of both data sets was repeated with data subsets including data of each season separately.

An ANOVA-based method was used to calculate repeatability for each of the seven following parameters in the three repeatedly tracked individuals (Lessells and Boag 1987): departure date from the breeding site, travel duration, stopover duration, number of stopover sites, and total duration of autumn migration, arrival date at the first wintering area and arrival at the breeding site. To test for consistency in timing and route (spatial position) during autumn migration in the repeatedly tracked individuals, we calculated the repeatability of longitude coordinates and dates a birds' migratory route crossed selected latitudes representing different regions along the migration routes. Following Vardanis et al. (2016), we chose three latitudes: 46°N – Europe, 36°N – Mediterranean Sea and 26°N – Sahara Desert. Since our swifts went farther south, we added 16°N representing the Sahelian zone as a fourth latitude. We applied the function 'rpt' from the R-package 'rptR' for calculating confidence intervals and p-values (Nakagawa and Schielzeth 2010). Differences in timing and duration between years or migration seasons were analysed with non-parametric tests (see Supplementary material Appendix 1, non-parametric tests). All data analyses were performed in R, ver. 3.0.3 (R Development Core Team).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.p17r6 > (Wellbrock et al. 2017).

Results

Effects of track, individual and date

We found no significant differences within individuals between first and second tracks in successive years, neither within the entire track nor within the subsets for autumn migration and wintering period (Table 1, Fig. 1, 2). However, there was a highly significant effect of individual on the geographic position, both in the 'within'- and 'between'-data sets regarding the entire track as well as the seasons' sub sets (Table 1). Julian date predicted the geographic position during the migration seasons but neither during the wintering period nor in the entire track (see only results from the single tracks, Table 1).

Table 1. Separate analyses of variation within a) and between b) individuals in entire tracks including 'season' and 'date' as covariates. Within-individual variation was tested with the factor 'track', between-individual variation with the factor 'individual'. Data subsets according to season (autumn migration, wintering period and spring migration) were tested separately. Given are F-ratios with degrees of freedom in parenthesis and permutational p-values from the PERMANOVA. Significant effects of explanatory factors or variables are shown in bold.

Data set	Factor/ variable	a) within (n = 6)		b) between (n = 10)	
		F	p	F	p
Entire	track	$7.2_{(1,1841)}$	0.408		
track	individual	$\mathbf{13.7_{(2,1841)}}$	**0.003**	$\mathbf{320.9_{(9,3993)}}$	**0.001**
	season	$\mathbf{1729.3_{(2,1841)}}$	**0.001**	$\mathbf{3259.4_{(2,3993)}}$	**0.001**
	date	$\mathbf{36.9_{(1,1841)}}$	**0.001**	$0.9_{(1,3993)}$	0.352
Autumn	track	$3.8_{(1,340)}$	0.118		
	individual	$\mathbf{12.7_{(2,340)}}$	**0.001**	$\mathbf{26.5_{(9,638)}}$	**0.001**
	date	$\mathbf{292.2_{(1,340)}}$	**0.001**	$\mathbf{510.1_{(1,638)}}$	**0.001**
Winter	track	$1.1_{(1,1445)}$	0.196		
	individual	$\mathbf{87.1_{(2,1445)}}$	**0.001**	$\mathbf{828.5_{(9,2993)}}$	**0.001**
	date	$\mathbf{35.8_{(1,1445)}}$	**0.001**	$3.1_{(1,2993)}$	0.083
Spring	individual			$\mathbf{22.9_{(9,342)}}$	**0.001**
	date			$\mathbf{436.7_{(1,342)}}$	**0.001**

Migration duration, timing and route

In repeatedly tracked swifts, the repeatability estimates were higher than 0.5 (although not significant) in travel duration, stopover duration (but not in total duration) during autumn migration and in arrival date at the first wintering area (Table 2). There are indications for consistency in travel duration and stopover duration during autumn and spring, in departure from the wintering area, in total duration during spring, and in arrival at first wintering area in repeatedly tracked individuals in two successive years (Supplementary material Appendix 2 Table A2). Variation in departure date from breeding site was higher within individuals than between them (negative repeatability estimate) while within- and between-individual variation was about the same size in arrival at the breeding site (estimate close to zero, Table 2). In repeatedly tracked individuals, there were high but non-significant repeatability estimates of more than 0.7 for timing of the passage at latitudes 36°N, 26°N and 16°N (Table 3). In contrast, within-individual variation was higher than between-individual variation (negative estimate)
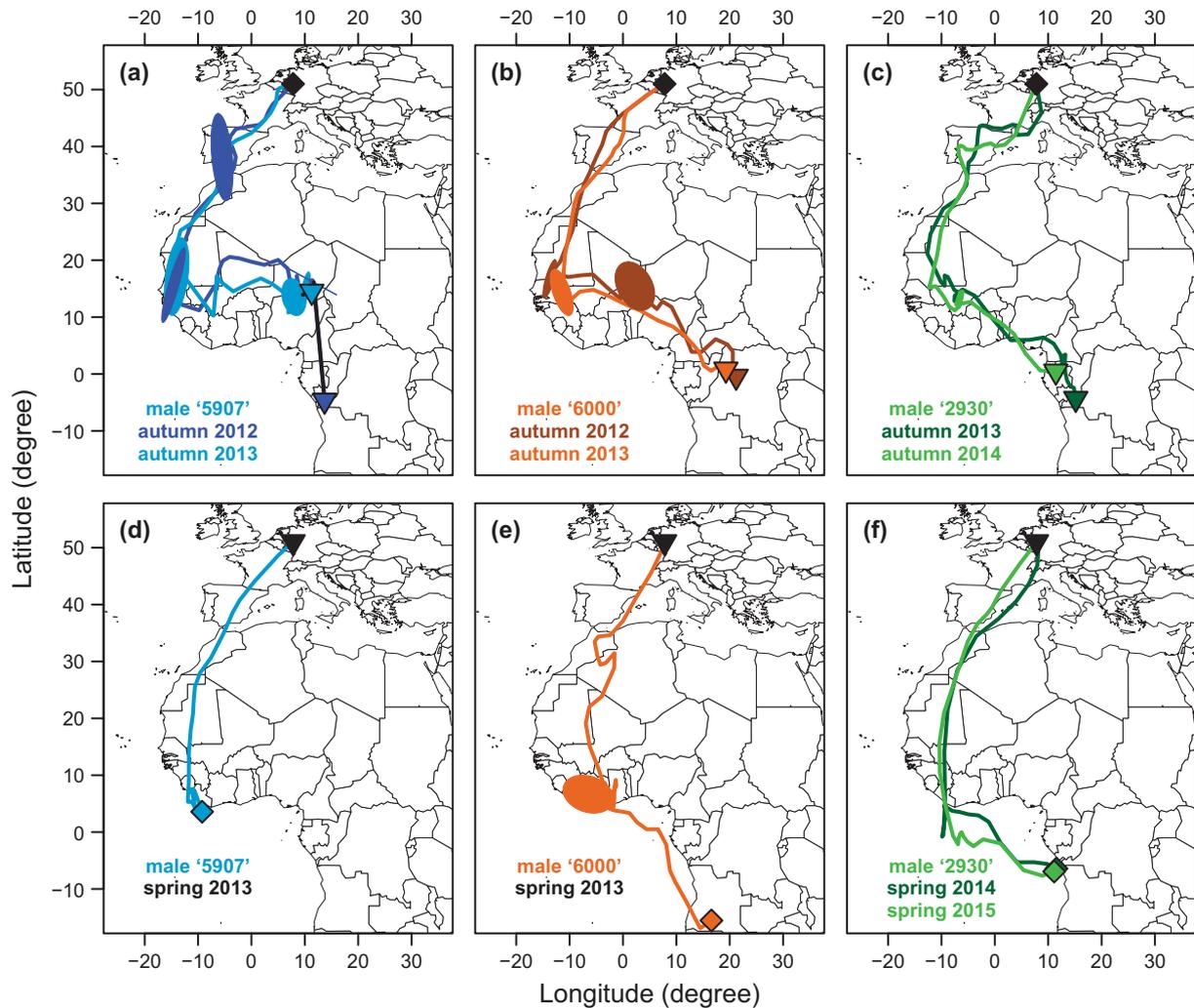
Figure 1. Migration routes and stopover sites of three repeatedly tracked swifts, male '5907' (a and d), male '6000' (b and e) and male '2930' (c and f). Autumn migration are shown in the upper row and spring migration in the lower row (only repeated in male '2930'). Darker colour shade indicates movements and stopover sites in the first year, lighter shade in the subsequent year. Rhombuses mark start points of tracks, triangles represent end points. Stopover sites are given as ellipses (covering 90% of positions). Black symbols mark the position of the breeding site. In (a), some movements occurred during or close to autumnal equinox (black line).
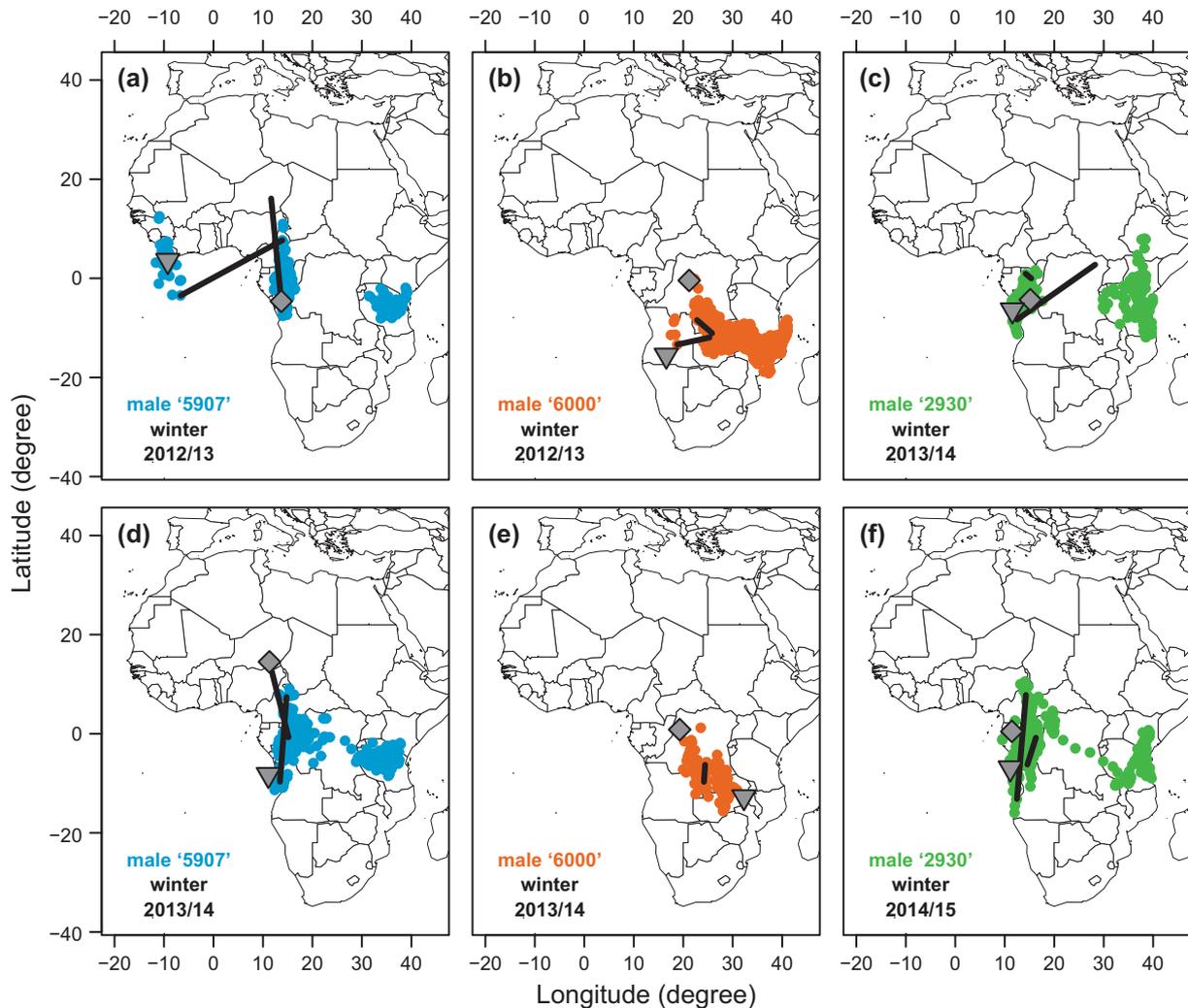
Figure 2. Wintering areas of repeatedly tracked swifts. Maps show up to two daily positions of three individuals, male '5907' (a and d), male '6000' (b and e) and male '2930' (c and f) during two subsequent wintering periods. The upper row gives positions during the first recorded wintering period, the lower row shows positions during the second recorded wintering period (not fully completely repeated in males '5907' and '6000'). Rhombuses indicate start points of tracks, triangles represent end points. Black lines connect first and last position three weeks before and after autumnal or vernal equinox.

in date at latitude 46°N. However, repeatability index was significant in the spatial position of the route for latitude 46°N during autumn migration (Table 3). An index of more than 0.5 (although not significant) was also determined in

route for the latitude 26°N, but not in latitudes 36°N and 16°N.

Stopover sites

Repeatedly tracked swifts had the same number (± 1) of stopover sites in both non-breeding seasons (Fig. 1,

Table 2. Repeatability estimates (r) from repeated tracks (n = 6) for departure date from the breeding site, travel duration, stopover duration, total duration and number of stopover sites (log-transformed) during autumn migration, arrival date at the first wintering area and arrival at the breeding site. Given are 95% confidence intervals (CI) and significance levels (p). The estimate in bold is significant.

Season	Parameter	r	CI	p
Autumn	Departure date	−0.45	−2.66, 1.76	0.714
	Travel duration	0.51	−1.56, 2.57	0.189
	Stopover duration	0.70	−0.70, 2.11	0.095
	Total duration	0.43	−1.84, 2.69	0.229
	No. stopover sites	**0.95**	**0.65, 1.24**	**0.008**
Winter	Arrival date	0.67	−0.85, 2.19	0.108
Spring	Arrival date	−0.07	−2.84, 2.69	0.506

Table 3. Repeatability estimates (r) from repeated tracks (n = 6) for route (longitude) and timing (date) at four different latitudes, representing different regions/barriers along the autumn migration route: Europe (46°N), Mediterranean Sea (36°N), Sahara Desert (26°N) and Sahel zone (16°N). Given are 95% confidence intervals (CI) and significance levels (p). The significant estimate is highlighted in bold.

	Longitude			Date		
Latitude	r	CI	p	r	CI	p
46°N	**0.87**	**0.19, 1.55**	**0.029**	−0.40	−2.74, 1.94	0.685
36°N	−0.07	−2.83, 2.70	0.501	0.70	−0.70, 2.11	0.095
26°N	0.59	−1.22, 2.40	0.148	0.77	−0.38, 1.91	0.067
16°N	0.33	−2.13, 2.80	0.280	0.74	−0.53, 2.01	0.080

Supplementary material Appendix 2 Table A2). This consistency is further supported by a significant repeatability estimate for number of stopover sites during autumn migration (Table 2). Individual number of stopover sites in all ten individuals ranged from 0 to 6 sites per year during entire migration (autumn and spring), with on average 1–2 stopover sites less in spring than in autumn (Fig. 1, Supplementary material Appendix 2 Table A2, Fig. A1). Stopover duration varied between 0 up to 37 d in all ten individuals during autumn migration and from 0 to 32 d during spring migration. On average, stopover duration lasted longer than travel duration in autumn 2012 and vice versa in spring 2013 (ratio 1:0.8 in autumn and 1:1.3 in spring, n = 6, Supplementary material Appendix 2 Table A2). In 2013/2014, stopover duration was shorter than travel duration in both migration seasons (ratio 1:1.4 in autumn and 1:3.3 in spring, n = 4).

Movement patterns at wintering areas

Winter positions of the three repeatedly tracked males were almost coextensive within individuals in two subsequent years (Fig. 2), whereas the winter movement patterns differed clearly between all ten individuals (Table 1, Supplementary material Appendix 2 Fig. A2). Overall, wintering areas of swifts covered mainly central, southern and south-eastern parts of Africa leaving out both the dry southwest (Namib and Kalahari) and the eastern highland regions (Fig. 2, Supplementary material Appendix 2 Fig. A2). Different sub-regions of the Congo basin (e.g. estuary, central lowlands, Lake Mweru) represented a central hub for nine individuals, mainly at the beginning and at the end of the wintering period. Furthermore, five individuals visited sites along the Niger River basin, in Guinea and in Liberia during their wintering period (Fig. 2a, Supplementary material Appendix 2 Fig. A2a, d–f).

Discussion

We found that repeatedly tracked swifts showed consistent and individual-specific migration behaviour in two successive years, but different individuals of the same breeding colony varied in migration routes, timing of migration, and wintering areas. Due to our small sample size, statistical analyses are tentative, but indicate a tendency that variation in migration is lower within than between individuals. Besides, our data give the first insight into migration and overwintering of swifts breeding in Germany for which limited ring recoveries suggested a wintering area in the Congo basin (Bairlein et al. 2014).

In contrast to other repeatedly tracked bird species (Vardanis et al. 2011, Stanley et al. 2012, Dias et al. 2013, López-López et al. 2014), swifts in our study were comparatively faithful to their migration routes like the osprey *Pandion haliaetus* (Vardanis et al. 2016). Routes of the same individual were more similar to each other than those of different ones. Despite the small sample size, within-individual variation was lower than between-individual variation in spatial position (longitude) of the autumn migration route at latitudes 46°N, 26°N and 16°N. At the Mediterranean

Sea (36°N), routes of repeatedly tracked swifts were not distinguishable between individuals, possibly because the Gulf of Gibraltar provides a small favourable region for passage. However, same individuals were almost consistent in timing of crossing the Mediterranean Sea and the Sahara Desert as well as arrival in the Sahelian zone, which supports the idea that swifts are individual migrants.

Several migratory bird species head repeatedly for specific stopover sites (Newton 2008, Cresswell 2014). Based on the data collected so far, our repeatedly tracked swifts were consistent in the number of stopovers. Swifts are said to combine a 'fly-and-forage' strategy with stopovers, similar to the osprey (Strandberg and Alerstam 2007, Åkesson et al. 2012, Vardanis et al. 2016). This mixed strategy makes them potentially less dependent on specific stopover sites in general (like pelagic seabirds, Dias et al. 2013) and thus probably less vulnerable to unpredictable weather conditions and limited food supply (but see Åkesson et al. 2016).

We found that stopover duration lasted longer than travel duration in autumn migration but shorter in spring migration in the first study year (2012/2013). This is in accordance with the Swedish study in which the ratio of stopover duration to travel duration was on average 1:0.8 during autumn and 1:2.6 during spring migration (Åkesson et al. 2012). In the Dutch study (Klaassen et al. 2014), the ratio amounted to 1:1.0 in autumn and 1:0.7 in spring migration which is contrary to our results from the second study year (2013/2014). Since our tracks and those of the two other studies were recorded in different years (our study: 2012/2013, 2013/2014; Sweden: 2009/2010; the Netherlands: 2010/2011 and 2011/2012), the duration of stopover might be influenced by annual effects (e.g. differences in wind support, Åkesson et al. 2016).

Our repeatedly tracked swifts were surprisingly faithful to their wintering areas as previously shown in large migratory birds like raptors, seabirds, waders, waterfowl (Newton 2008, Raine et al. 2013, Cresswell 2014, Grist et al. 2014, Yamamoto et al. 2014) and in the small North American wood thrush (Stanley et al. 2012). Winter site fidelity was not necessarily expected in swifts because their food source, aerial insects, should be more evenly distributed in space than food sources on terrestrial patches (Hockey 2000). Moreover, costs of changing sites are expected to be rather low in swifts since they are adapted to fast flying (Lentink et al. 2007). Additionally, the between-individual variation in movement patterns in our study indicates that several suitable wintering areas for swifts exist coincidently in separate regions of Africa as they have rainy season within the Intertropical Convergence Zone (ITCZ) and, hence, mass-occurrence of insects at the same time. Individual swifts may be faithful to their wintering areas in subsequent years because they experienced profitable foraging conditions. By this, individuals reduce costs sampling suitable wintering areas and diminish uncertainty from successive migrations (Cresswell 2014).

In summary, our findings indicate for the first time consistent individual-specific migration patterns in swifts between successive years. These swifts showed individual consistency but between-individual variation in timing of migration, migration routes and wintering areas. This reveals

a high degree of plasticity in migration pattern in individual swifts from the same breeding colony.

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