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Across their ranges, different populations of migratory species often use separate routes to migrate between breeding and non-breeding grounds. Recent changes in climate and land-use have led to breeding range expansions in many species but it is unclear whether these populations also establish new migratory routes, non-breeding sites and migration phenology. Thus, we compared the migration patterns of European Bee-eaters *Merops apiaster* from two established western ( $n = 5$ ) and eastern ( $n = 6$ ) breeding populations in Europe, with those from a newly founded northern population ( $n = 19$ ). We aimed to relate the breeding populations to the two known non-breeding clusters in Africa, and to test for similarities of migration routes and timing between the old and new populations. Western Bee-eaters used the western flyway to destinations in West Africa; the eastern birds uniformly headed south to southern African non-breeding sites, confirming a complete separation in time and space between these long-established populations. The recently founded northern population, however, also used a western corridor, but crossed the Mediterranean further east than the western population and overwintered mainly in a new non-breeding area in southern Congo/northern Angola. The migration routes and the new non-breeding range overlapped only slightly with the western, but not with the eastern, population. In contrast, migration phenology appeared to differ between the western and both the northern and the eastern populations, with tracked birds from the western population migrating 2–4 weeks earlier. The northern population thus shares some spatial traits with western Bee-eaters, but similar phenology only with eastern population. This divergence highlights the adjustments in the timing of migration to local environmental conditions in newly founded populations, and a parallel establishment of new breeding and non-breeding sites.

**Keywords:** annual cycle, flyway, Meropidae, migratory connectivity, range expansion, timing of migration.

Many long-distance migratory species have broad breeding distributions. As a result, various

populations within the same species may use separate migratory routes to migrate between their breeding and non-breeding grounds: for example, Great Reed Warblers *Acrocephalus arundinaceus* and Common Reed Warblers *Acrocephalus*

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*scirpaceus* (Koleček *et al.* 2016, Procházka *et al.* 2018), Nightingales *Luscinia megarhynchos* (Hahn *et al.* 2013) or European Rollers *Coracias garrulus* (Finch *et al.* 2015) migrating between Europe and Africa, Swainson's Thrush *Catharus ustulatus* (Delmore *et al.* 2012) and Ovenbirds *Seiurus aurocapilla* (Hallworth *et al.* 2015) migrating between North and Central/South America, and Pintails *Anas acuta* (Hupp *et al.* 2011) and Bar-tailed Godwits *Limosa lapponica* (Battley *et al.* 2012) migrating between northeast Asia and Australasia. Some of these migration corridors and non-breeding sites can be hundreds if not thousands of kilometres apart, with little or no overlap between populations.

Differences in migratory pathways in Holarctic species are likely to have arisen as relicts from the last glaciation, when species ranges contracted into refugia, before expanding again when the climate warmed (Newton 2008). Range expansions still remain common in birds today; prominent recent examples include Barn Swallows *Hirundo rustica* in the Nearctic/Neotropic (Winkler *et al.* 2017) and Scarlet Rosefinches *Carpodacus erythrinus* (Stjernberg 1985), Marsh Warblers *Acrocephalus palustris* (Leisler & Schulze-Hagen 2011) and Black-tailed Godwits *Limosa limosa* (Gunnarsson *et al.* 2012) in parts of the Palaearctic. Models on the impact of current climate change on bird distribution predict range shifts in many species, and range expansion in some species (Huntley 2007). For migratory birds, it is often unclear how migratory behaviour might change during this process – will birds establish a new migratory corridor, or will they continue to fly along the same ‘ancient’ migratory routes? Furthermore, how quickly might they adapt their phenology to local conditions at new sites?

Migrating along different routes does not necessarily imply that the population is separated in their non-breeding ranges, which would result in low migratory connectivity (Webster *et al.* 2002). Conversely, a spatial overlap in migratory routes does not necessarily mean that individuals from different populations will meet each other, as final destinations and/or passage times can differ between populations, making encounters unlikely (Bauer *et al.* 2016). Studying the level of spatiotemporal overlap in breeding, staging and non-breeding sites within and across populations can be used to understand the associated degree of migratory connectivity between populations to

inform conservation planning (Dhanjal-Adams *et al.* 2017, Kramer *et al.* 2018).

Here, we investigate the migratory behaviour of three breeding populations of European Bee-eater *Merops apiaster* (henceforth ‘Bee-eater’) along a West–North–East gradient in Europe. Bee-eaters are common in warm-temperate climates and their historical breeding distribution has mainly encompassed Southern Europe delimited by the July 21 °C isotherm in the north (Fry 1984). In recent decades, the species has expanded its range northwards and successfully (re)colonized regions north of 47°N in central Europe, presumably benefiting from recent climatic niche expansions and land-use changes (Kinzelbach *et al.* 1997, Huntley 2007). Currently, Bee-eaters form a viable breeding population with more than 1000 breeding pairs at about 51°N in central-eastern Germany (Schönbrodt & Schulze 2017). The origin(s) of founder individuals is unknown and the very few ring recoveries suggests an ongoing immigration from, or an exchange with, the southern-central European populations (Arbeiter *et al.* 2012).

Bee-eaters in the northern hemisphere are obligate long-distance migrants and are thought to overwinter in two distinct regions: West Africa and southern Africa (Fry 1984). Surprisingly, population-specific non-breeding sites and individual migration routes remain almost unknown for the species. Recent studies on population genetics have revealed little differentiation between many European populations, pointing to historical and current exchange between populations (Ramos *et al.* 2016, Carneiro de Melo Moura *et al.* 2019). In contrast, the few ring recoveries (Ramos *et al.* 2016) and observations of Bee-eaters of unknown provenance point towards a classical migratory divide in European breeding populations, which migrate either along a western route via Iberia to west Africa or along an eastern route around the Mediterranean Sea and along the rift valley to south-eastern Africa (Fry 1984), although recent genetic analyses also highlight panmixia (Carneiro de Melo Moura *et al.* 2019). The migratory divide is expected to occur in central Europe, with birds breeding in the Pannonian basin taking the easterly route and birds from France taking the westerly route. The breeding origin of the birds spending the non-breeding period in West Africa and southern Africa has not been identified yet, but probably follows these suggested western and eastern migration corridors.

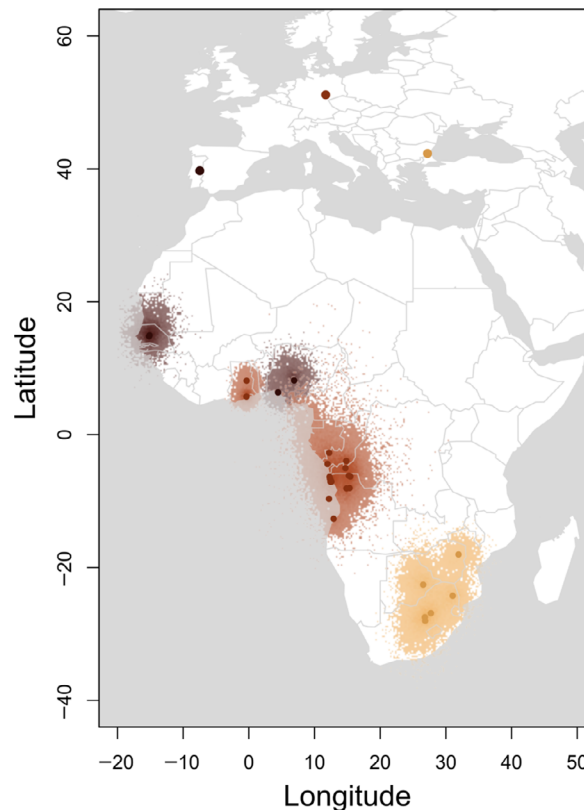
In our study, we used geolocation to unravel the divergent migration corridors and the resultant disjunct non-breeding ranges of Bee-eaters from western and eastern European breeding populations (Fry 1984). Moreover, we compared migration patterns of these long-established populations with the migration corridor and non-breeding range of the recently founded northern population. We expected spatially divergent migration routes and non-breeding sites between the westernmost and the eastern European breeding populations, with no overlap and little within-population variation at continental scale (Fry 1984). Based on the currently known distant non-breeding clusters, we expected the newly established northern population to overwinter in western Africa if these birds take the western flyway, and in south-eastern Africa if they migrate along the eastern flyway. Additionally, we expected the timing of migration (i.e. departure from and arrival at residence sites) to be influenced by climatic seasonality and migratory distance, rather than by the migration corridor used (e.g. van Wijk *et al.* 2018). Thus, we expected the arrival and departure to differ between breeding regions (and thus study populations) but to be similar between populations in the same non-breeding region.

## METHODS

We used geolocation by light to track adult Bee-eaters from three distant and distinct breeding populations across the species' breeding range in Europe: a western breeding population in Portugal (PT; two colonies at about 39.9 and 38.1°N, 7.15°W, less than 200 km apart;  $n = 5$ ); an eastern population in Bulgaria (BG; 42.4°N, 27.4°E;  $n = 6$ ) which is *c.* 2900 km from the western population; and a recently established northern

population in Germany (DE; 51.3°N, 12.0°E;  $n = 19$ ) which is situated *c.* 2000 km and *c.* 1500 km from the western and the eastern populations, respectively (Table 1, Fig. 1).

Birds were captured in their nest burrows using walk-in traps (PT, DE) and mist-nets (BG) during the chick-rearing periods. Adult Bee-eaters were



**Figure 1.** Non-breeding ranges of tracked Bee-eaters from the western (Portugal, brown,  $n = 5$ ), northern (Germany, red,  $n = 18$ ) and eastern (Bulgaria, orange,  $n = 6$ ) populations. Circles represent median positions of the main non-breeding site derived from geolocators using SGAT and coloured regions represent the 99% probability distributions of location estimates.

**Table 1.** Number of birds per study site equipped with geolocators (#geoloc), recovered with device ( $N$ -total (males/females)) and the resultant records for autumn and spring migration and non-breeding site location.

Population (country)	Year	#geoloc	$N$ -total (males/females)	$N$ -autumn	$N$ -non-breeding site	$N$ -spring
Western (PT)	2015/2016	60 <sup>a</sup>	6 (3/3)	2-3	5	2-3
Northern (DE)	2010/2011	40 <sup>a</sup>	1 (1/0)	1	1	–
	2011/2012	40 <sup>a</sup>	2 (2/0)	2	2	1
	2014/2015	75 <sup>a,c</sup>	6 (2/4)	5	5	5
	2015/2016	80 <sup>c</sup>	10 (6/4)	9	10	7
Eastern (BG)	2015/2016	80 <sup>b,c</sup>	6 (–/–)	6	6	3

<sup>a</sup>SOI-GDL1 (*c.* 1.38 g). <sup>b</sup>SOI-GDL2 (*c.* 0.85 g). <sup>c</sup>SOI-GDL3 (*c.* 1.45 g).

sexed and aged based on plumage characteristics (only for PT, DE; [https://aulaenred.ibercaja.es/wp-content/uploads/284\\_Bee-eaterMapiaster.pdf](https://aulaenred.ibercaja.es/wp-content/uploads/284_Bee-eaterMapiaster.pdf)). We equipped Bee-eaters with geolocators (SOI-GDL1/GDL2/GDL3; all Swiss Ornithological Institute) using a leg-loop harnesses made from Silicone or cord material. Geolocators including harnesses weighed 0.84–1.56 g on average, representing 1.6–3.0% of adult body mass. Additionally, we established a control group, ringed-only birds, to check for geocator effects on local site fidelity (PT and DE only). Local recapture rates of tagged birds varied largely between sites and years potentially according to site-specific capture effort (PT: 10%, DE: 8–14%, BG: 7%); recapture rates of controls were higher (PT: 28%, DE: 24–32%). The lower local recapture rates for tagged birds include breeding site dispersal to an unknown extent (Arbeiter *et al.* 2012). Birds from all three populations (PT, DE and BG) were successfully tracked in 2015/2016, resulting in 18 tracks and 21 non-breeding sites. We considered a longer time series to check for potential large variation in non-breeding locations in the northern population by including eight additional tracks from 2010/2011, 2011/2012 and 2014/2015 (DE only, Table 1).

### Geolocation analysis

We used SGAT (<https://github.com/SWother spoon/SGAT>) and GeoLight (Lisovski & Hahn 2012) to analyse the light data from these tagged birds using a threshold method. We started by identifying sunrise and sunset events from log-transformed light intensity data (using a threshold of  $-8$ , which is the lowest light value consistently above any noise in the night-time light levels), within the R package *TwGeos* (<https://github.com/slisovski/TwGeos>). Because the estimate of twilight events from the geocator differs from the theoretical twilight events by a few minutes, we used the period where the birds were still in the breeding grounds (after tagging but before migration), and therefore in a known location, for calibration (i.e. to fit an error distribution to the data which is later used by SGAT as parameter alpha – see below). This period varied from bird to bird and was used to quantify the inherent measurement error of individual geolocators caused by shading from behaviour and feathers.

Because Bee-eaters breed in burrows, sunrise and sunset times can be missed by a few minutes, and the calibration data can provide an inaccurate sun elevation angle for latitude estimation. For this reason, we used a Hill–Ekstrom calibration to correct the estimated sun elevation angle (Lisovski *et al.* 2012). We then used the *changeLight* function in GeoLight (Lisovski & Hahn 2012) to identify short stopover periods (stationary periods ranging from 1 to 3 days, with a change in light probability  $q$  of 0.5–0.9 depending on data quality). The *changeLight* function uses the difference in day length to estimate movement periods given a change in probability  $q$ . The function is therefore sensitive to data quality and is geocator-specific (Lisovski & Hahn 2012). We used *changeLight* in combination with the *mergeSites* function to compare all stationary periods and to determine what their spatial overlap was, and whether they could be merged as a single stationary period. We always started with a high  $q$  in *changeLight*, reducing it if the stationary periods caused SGAT to crash. Indeed, shading can cause two distinct stopover sites to be falsely classified as one by *changeLight*, preventing SGAT from converging (it is impossible to estimate one location if the sunrises and sunsets are too different). Lowering  $q$ , however, often overestimates movement periods, but does not create incorrect stopover periods.

Identifying correct stationary sites enabled us to use a grouped model in SGAT. This method estimates one location from multiple sunrise and sunset events, thus finding the best possible fit to the data during the identified stationary periods and importantly, increasing the precision of the estimated location. SGAT uses a Bayesian framework to incorporate prior information including stopover periods, twilight error distribution (parameter alpha from the calibration), speed distribution (parameter beta) and a land mask (so that when the bird stops over, it is less likely to do so in the sea). Markov chain Monte Carlo simulations then model the geographical probability distribution of each location where the bird is known to have stopped. We fixed the first and last location to the known capture and recapture locations where appropriate (if the sensor stopped logging light before the recapture date, the last point was not fixed). We first ran a modified Gamma model (relaxed assumptions) for 1000 iterations to initiate the model, before tuning the model with final assumptions/priors (three runs with 300 iterations).

Finally, the model was run for 2000 iterations to ensure convergence. For two incomplete datasets (from Portugal and Germany), we ran SGAT only during the period where light was recorded – primarily during the non-breeding residence period (but still using the breeding site for calibration).

To calculate consistent stopovers between all birds for timing and resident period comparisons, we again used the *changeLight* function, this time with a stationary period of at least 3 days and a probability  $q$  of 0.8 (this avoided the aforementioned overestimation of movement periods). Once stopover periods were identified, we calculated the median location of birds during these stationary periods based on the geolocation estimates. In further analyses (e.g. Table 2), we considered only stopover/residence sites within the sub-Saharan non-breeding range with a spatially variable northern limit  $< 18^{\circ}\text{N}$  in West Africa and  $< 12^{\circ}\text{N}$  in Central and East Africa due to the longitudinally different southern edge of the Sahara desert. Furthermore, we distinguished between non-breeding residence periods/sites with minimum durations of  $> 14$  days and non-breeding stopover periods/sites with durations of up to 14 days.

Tracking data are available upon request from the Movebank online database (<https://www.movebank.org/>, project IDs: 725039955 (PT), 759031657 (DE) and 753257610 (BG)).

### Migration distance and migration speeds

We calculated migration distances as the orthodromic (great circle) distance between the breeding and non-breeding residence sites (in km, rounded to the nearest 10 km). Furthermore, we determined the annual cumulative travel distance

(sum km/year) based on occupied sites and the movements between sites within each modelled track.

We calculated the total migration speed (km/day) between departure from breeding/non-breeding sites and arrival at the final destination. The available data on seasonal changes in body masses (Cramp 1986) indicate that European Bee-eaters do not appear to fuel before departure on migration (Fry 1984) as they are aerial foragers and thus are able to feed during migration. Hence, pre-departure fattening periods do not compromise our calculation of migration duration and migration speed.

## RESULTS

### Non-breeding residences

All birds from the western population (Portugal) spent the non-breeding period in West Africa between the Gambia/Senegal and Nigeria (Fig. 1), with main residence sites occurring 3730 km (median) away from the breeding colony (25–75% = 2670–3790 km,  $n = 5$ ). Two of four birds (with complete non-breeding period records) used more than a single site of residence. Sojourn time at the main sites ranged between 116 and 154 days; total residence times averaged 186 days.

The non-breeding range of the northern breeding population (eastern Germany) stretched from eastern parts of West Africa (two birds in Ghana/Togo, one bird in Nigeria) to northern Angola, Gabon and the Republic of Congo, where 82% of the birds overwintered. Thus, the non-breeding range of the northern population overlapped occasionally (11% of 18 non-breeding residences) with those of the western population between  $2^{\circ}\text{W}$  and  $5^{\circ}\text{E}$  in eastern West Africa. The non-breeding sites

**Table 2.** Seasonal migration speed of Bee-eaters from western, northern and eastern populations in 2015/2016.

Migration section	Season	Median migration speed (range, km/day)						$P$
		Western population	$n$	Northern population	$n$	Eastern population	$n$	
Breeding site – first sub-Saharan site	Autumn	159 (106/212)	2	206 (189–224)	9	317 (193–465)	6	0.26
	Spring	76.5 (66/87)	2	164 (131–165)	7	147 (116–245)	3	0.99
Breeding site – main non-breeding site	Autumn	46 (37/55)	2	195 (150–207)	9	201 (157–249)	6	0.44
	Spring	50.5 (35/66)	2	133 (123–165)	7	105 (98–110)	3	0.12

Speeds are given for autumn and spring as median speed (km/day) and its range,  $n$  gives sample size; the last column gives  $P$ -values for Mann–Whitney  $U$  comparisons between northern and eastern populations.

were 6360 km (median) away from the breeding colony (for all years, 25–75% = 6060–6660 km,  $n = 18$ ; for the year 2015, median = 6410 km, 25–75% = 6120–6760 km). About 53% of birds used more than one residence (complete non-breeding records only). Sojourn time on the main residence site averaged 140 days (for multiple site birds) and 183 days (for single site birds); the total non-breeding residence period averaged 185 days.

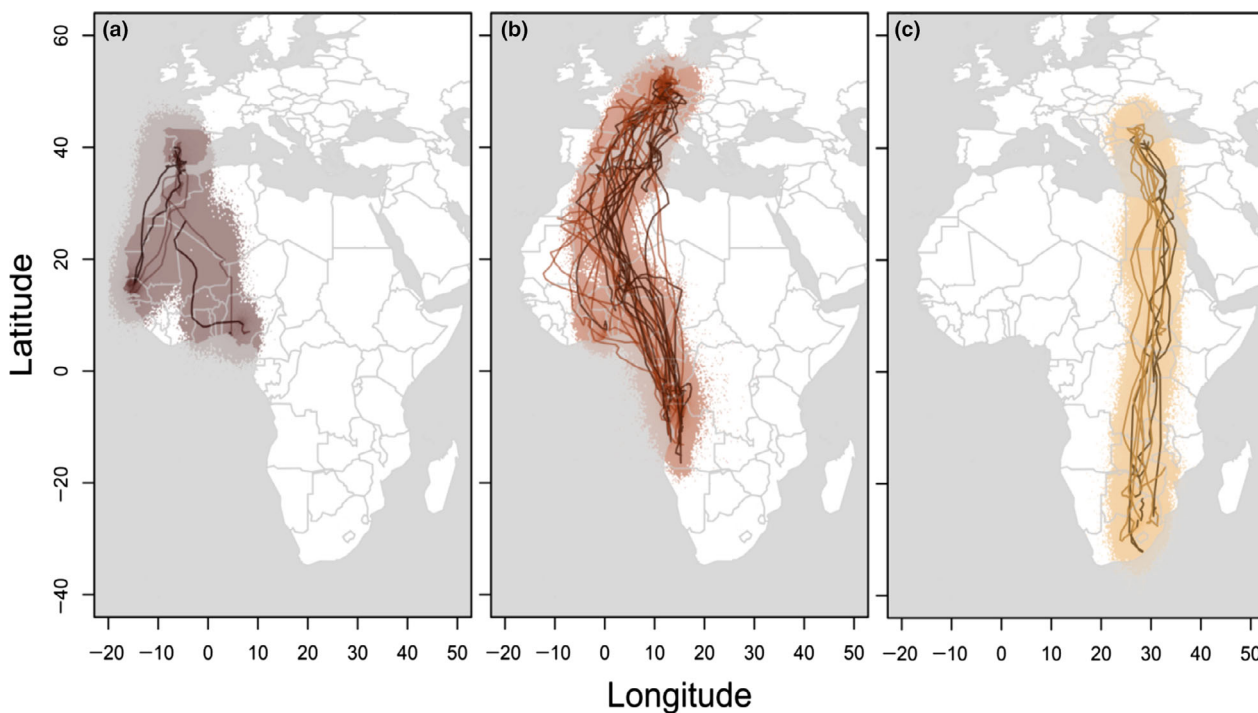
Birds from the eastern European population (Bulgaria) were geographically separated, with their non-breeding range being situated in southern Africa (South Africa, Botswana and Zimbabwe) and not overlapping with the western or the northern populations. The median great circle distance between the main residence site and the breeding colony was 7550 km (25–75% = 7070–7792 km). Five birds with complete non-breeding tracks used more than a single residence site with average duration of 154 days for the main site, and a total duration of 194 days.

The migration distances from breeding to main non-breeding sites differed significantly between all

populations (ANOVA,  $F_{2,20} = 131.48$ ,  $P < 0.001$ ; pairwise *post hoc* tests, all  $P < 0.05$ ). The cumulative distance travelled within the entire year was smallest for the western population (about 5700 km) and about 2.3 times longer in both the northern and the eastern population (ANOVA,  $F_{2,12} = 5.99$ ,  $P = 0.02$ ; *post hoc* comparison North vs. West,  $P = 0.80$ ; Fig. S1).

### Migration routes

Bee-eaters from the Western population initially headed south, crossing the Strait of Gibraltar and the desert at its western rim in West Sahara, Mauritania and western Algeria (Fig. 2a). Birds from the northern population headed southwest first, then crossed the Mediterranean Sea further east between 2°W and Corsica/Sardinia, before crossing the Sahara, from Algeria heading south to Mali and western Niger (Fig. 2b). Although migration routes spatially overlapped at about 0–2°E in some individuals from the northern and western populations (Fig. 2a,b), we found little simultaneous



**Figure 2.** Modelled tracks of birds with complete tracking records per season from (a) the western population (Portugal,  $n = 3$ ), (b) the northern population (Germany,  $n = 9$ ) and (c) the eastern population (Bulgaria,  $n = 6$ ). Shading represents the average estimate of all tracks with 99% confidence interval (CI). Coloured tracks represent autumn migration and black tracks represent spring migration.

passage in this area (Fig. S2). On the other side of the range, birds from the eastern population headed mainly south–southeast to cross the eastern Mediterranean Sea at about 20°E to Egypt. None of the tracked BG birds made a detour across the Levant. After reaching the North African coast, the birds followed the Nile river area and the Albertine rift to their non-breeding destination (Fig. 2c). Thus, the overlap in the migration corridors of the western and the northern populations was minimal. Only the eastern-most migrants from the western population overlapped with the northern population during autumn migration. The corridor used by the eastern population did not overlap with either the western or the northern populations.

### Timing of migration and speed

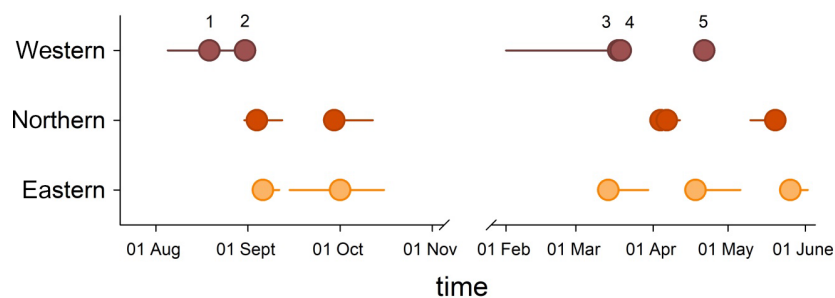
Birds from the western population departed from the breeding grounds about 2.4 weeks earlier than those from the northern and eastern populations (ANOVA,  $F_{2,18} = 6.04$ ,  $P = 0.01$ , Fig. 3) and arrived at the first sub-Saharan non-breeding site about 4.4 weeks earlier compared with Bee-eaters from the northern ( $t$ -test,  $t_9 = -5.98$ ,  $P < 0.001$ ) and eastern populations ( $t$ -test,  $t_6 = -2.48$ ,  $P = 0.05$ ). Additionally, departures from the last sub-Saharan non-breeding site and the arrival at breeding sites were about 1 month earlier compared with the northern and eastern populations (for details and sample sizes, see Table S1). The timing of autumn migration of the northern and eastern populations was similar (difference in breeding site departure: Mann–Whitney  $U$ ,  $t_{15} = 0.41$ ,  $P = 0.74$ ; and arrival at the first sub-

Saharan non-breeding site: Mann–Whitney  $U$ ,  $t_{14} = 47.0$ ,  $P = 0.95$ ), but differed for spring migration, with eastern birds departing 1 week later from their last sub-Saharan non-breeding site, and arriving later at the breeding sites (departure:  $t_9 = 2.12$ ,  $P = 0.01$ ; arrival:  $t_8 = 2.36$ ,  $P = 0.05$ ). Interestingly, eastern breeding birds started to move northwards from the South African non-breeding sites by about 1 month before final departure from the sub-Saharan region in spring (Fig. 3).

Based on different timing and migration distance, migration speed was consistently lower for western compared with northern and eastern populations, although sample sizes were too low for statistical comparison in the western population. There was no significant difference between northern and eastern populations (Table 2).

### DISCUSSION

Here, we have provided important first insights into migration patterns of European Bee-eaters and, in doing so, we have tested some of the long-standing assumptions surrounding the natural history of this iconic species. Although sample sizes were often small, as is typical for such exploratory studies (see Brlík *et al.* 2019 for an overview), we nonetheless have contributed significantly to the knowledge of migration routes and timing in this species. First, we have confirmed that western European breeders migrate on a western route to non-breeding regions in West Africa, and that eastern European birds migrate on an eastern route to southern Africa. Secondly, we have discovered that birds from the recently established northern-



**Figure 3.** Timing of migration of Bee-eaters from western (Portugal, brown), northern (Germany, red) and eastern (Bulgaria, orange) populations during the 2015/2016 season. Symbols are medians with whiskers corresponding to 25/75 percentiles; the events are: 1 – departure from the breeding site; 2 – arrival at the first sub-Saharan non-breeding site; 3 – departure from the main non-breeding site; 4 – departure from the last sub-Saharan non-breeding site; 5 – arrival at the breeding site.

central European population use the western migration corridor to reach a new core non-breeding range, located between northern Angola and the southern parts of Congo. Finally, we have provided some evidence for earlier timing of migration in the western population than in the northern and eastern populations.

### Migration direction, migratory divide and non-breeding ranges

The newly established northern breeding population from eastern Germany uniformly headed westwards from their breeding sites and used a western migration corridor, similar to, but not overlapping with, birds from the western population in Portugal. Because passage times differ (see below), northern birds are unlikely to encounter western birds during migration, despite using similar regions. There is no information on migration direction or flight corridor for birds from south-western Germany; the nearest population is about 4–5° west of our study site, but it seems very likely that these birds also use a western migration corridor like birds from France, which are considered typical western migrants (Cramp 1986). Further east, Bee-eaters breeding in the Czech Republic and Slovakia, which is about 5–10° east of the colonies in eastern Germany, are eastern migrants, as confirmed by ring recoveries of adult birds in the Balkan peninsula (Cepak *et al.* 2008). They might use the same corridor as the tracked eastern birds from Bulgaria, which crossed the southern Balkan Peninsula and the Mediterranean Sea but did not detour via the Levant (Fig. 2). Thus, the migratory divide of the European Bee-eater in central Europe north of the Alps must be situated east of 12°E, separating the East German and the Czech/Slovakian populations, which also resembles the postglacial divide and their associated hybrid zones in many species in central Europe (Hewitt 2000). The location of the divide in southern-central Europe, i.e. south of the Alps, remains open, as the small number of ring recoveries in Italy (Spina & Volponi 2008) and missing data from the western Balkan peninsula do not yet allow for firm conclusions to be drawn.

Our tracking data suggested that western populations, namely from Portugal, overwinter in West Africa and do not move further, either to the main non-breeding range of the northern population in northern Angola or to the second main non-

breeding region of the species in south-eastern Africa (Fry 1984). Thus, western and eastern populations are also geographically isolated from each other during the non-breeding period, with the latter being more than 3800 km away in south-eastern Africa. Frequent exchanges between the two populations during the non-breeding period seem therefore implausible (see also Cramp 1986), which is in line with a slight west–east differentiation in population genetic structure using microsatellites (Ramos *et al.* 2016, Carneiro de Melo Moura *et al.* 2019). In contrast to this rather strict ecological separation, the non-breeding range of the northern population overlapped at its western edge, from Ghana to Nigeria, with the non-breeding range of the western populations (Fig. 1). Moreover, migration routes of the birds from both populations which crossed the Sahara desert in western Algeria and Mali were very similar (Fig. 2a,b). The fact that migration routes and non-breeding areas of the northern population were more similar to the western than to the eastern populations suggests exchanges of individuals between those two populations. Considering the genetic similarity, such dispersal events might not be exceptional (Carneiro de Melo Moura *et al.* 2019).

We located the main non-breeding range of the northern population south of the Congo basin rainforest belt in southern Congo and northern Angola (Fig. 1). However, the population did stop over between Ghana and Nigeria, with some birds overwintering in the region (11% of the tracked birds) and others continuing further southeast. Because the western population already occupies this region and arrives earlier (Fig. 3), most birds from the later arriving northern population may be continuing southward to the Congo basin, thus establishing a kind of leapfrog migration system (Bell 2005). Interestingly, this area has not been described as a non-breeding range for European breeding birds (Fry 1984, Fry *et al.* 1988), although there is some suggestion that South African breeding birds may migrate to the region during their non-breeding season (Brooke & Herroelen 1988).

The tracked northern breeding population in eastern Germany has grown exponentially in the last two decades since it was established in 1990 (Schönbrodt & Schulze 2017). We assume that the recent non-breeding range might have been established in parallel, having been occupied in the



last 10–15 years. There are no recent monitoring data from the non-breeding region, but the presence of non-breeding Bee-eaters in northern Namibia during the boreal winter (Harrison *et al.* 1997; <http://sabap2.adu.org.za/>) points towards a regular occurrence in countries of south-western Africa.

### Migration timing and speed

Routes, timing and non-breeding destinations differed largely between the western and the eastern breeding populations. Interestingly, the northern populations shared geographical features (migration direction and corridor) with the western population, including some overlap, but the migration timing and notably departure dates (Fig. 3) and speeds (Table 2) were more similar to the eastern population. Indeed, the northern and eastern populations breed in pronounced seasonal climates, i.e. Köppen climate classifications Cfa and Cfb, in contrast to the less seasonal climate Csa for the western population (Peel *et al.* 2007), and thus they probably share similar environmental cues that trigger migration.

We therefore anticipated that the northern and eastern breeders would depart at similar times but arrive in the non-breeding grounds at different times if travel distances differed. However, we found that the mean arrival times for the northern and eastern populations in the non-breeding grounds overlapped. In fact, even though the distances between the breeding and non-breeding grounds at first glance appear shorter for the northern than the eastern population (6360 and 7550 km, respectively), the cumulative distance travelled (Fig. S2) during migration was on average similar (*c.* 7500 km; Fig. S1), and was in some cases greater for the northern population (up to *c.* 10 000 km; Fig. S1). Indeed, the eastern birds followed the rift valley along the Nile in an almost straight fashion but the migratory route of the northern birds was less direct (Fig. 2). The less straight flight routes probably allowed birds to reduce the energetically demanding crossing of geographical barriers such as the Gulf of Guinea and the Mediterranean, with little thermal lift, or the Sahara, with unpredictable aerial food availability.

Peak departure dates from the breeding and the non-breeding grounds, and the corresponding arrival dates were sequential from west to east, which points towards a general and slightly shifted annual

programme (Gwinner 1996) across the studied populations. However, eastern birds (which spend the non-breeding period further south) departed the main non-breeding site early to 'pre'-migrate northwards towards Lake Victoria, before continuing towards the breeding grounds (Fig. 3). The sequential arrival at breeding regions is consistent across the last 19 years: first observations are on average in the 4th week of March/1st week of April for Portugal, in the last week of April/1st week of May for Bulgaria, and 1st to 2nd week of May in Germany (<https://ebird.org>, period: 2000–2018, accessed 9 November 2018).

### CONCLUSIONS

In the two last decades, European Bee-eaters have established not only new breeding sites in northern central Europe, but also new migratory routes and non-breeding sites in the Congo basin and northern Angola, in an intermediate area between the non-breeding ranges of western and eastern populations in West Africa and southern Africa, respectively. There is, however, a small proportion of northern birds that spend the non-breeding period in western Africa, suggesting that non-breeders in western Africa may come from breeding sites anywhere between Portugal and Germany. Thus, these populations may display lower migratory connectivity (by covering a wider nonbreeding range) than the easterly population, which additionally did not overlap either spatially or temporally with the other two populations. Despite these differences in migratory pathways, there was an indication that populations have distinct migration timing. This highlights the importance of population-specific or colony-specific behaviour (Dhanjal-Adams *et al.* 2018) and local adaptations to environmental conditions, particularly seasonality, in shaping Bee-eaters' annual cycles. Hence, we expect a gradual change in migration patterns, similar to population genetic structures (Ramos *et al.* 2016, Carneiro de Melo Moura *et al.* 2019) from western to eastern populations. However, the position of intermediate breeding populations, i.e. from France, Italy or the western Balkans, remains to be confirmed.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Timing of main migration stages of Bee-eaters from western (PT), northern (DE) and eastern (BG) breeding populations in Europe.

**Figure S1.** Cumulative distance travelled over time, by (a) two birds from the western population, (b) nine birds from the northern population, and (c) six birds from the eastern population, all between July 2015 and July 2016.

**Figure S2.** Estimated longitudes (upper panel) and latitudes (lower panel) of European Bee-eaters over the entire annual cycle of 2015/16.