

# Broad-scale patterns of the Afro-Palaeartic landbird migration

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## Abstract

**Aim:** Knowledge of broad-scale biogeographical patterns of animal migration is important for understanding ecological drivers of migratory behaviours. Here, we present a flyway-scale assessment of the spatial structure and seasonal dynamics of the Afro-Palaeartic bird migration system and explore how phenology of the environment guides long-distance migration.

**Location:** Europe and Africa.

**Time period:** 2009–2017.

**Major taxa studied:** Birds.

**Methods:** We compiled an individual-based dataset comprising 23 passerine and near-passerine species of 55 European breeding populations, in which a total of 564 individuals were tracked during migration between Europe and sub-Saharan Africa. In addition, we used remotely sensed primary productivity data (the normalized difference vegetation index) to estimate the timing of vegetation green-up in spring and senescence in autumn across Europe. First, we described how individual breeding and non-breeding sites and the migratory flyways link geographically. Second, we examined how the timing of migration along the two major Afro-Palaeartic flyways is tuned with vegetation phenology at the breeding sites.

**Results:** We found the longitudes of individual breeding and non-breeding sites to be related in a strongly positive manner, whereas the latitudes of breeding and non-breeding sites were related negatively. In autumn, migration commenced ahead of vegetation senescence, and the timing of migration was 5–7 days earlier along the Western flyway compared with the Eastern flyway. In spring, the time of arrival at breeding sites was c. 1.5 days later for each degree northwards and 6–7 days later along the Eastern compared with the Western flyway, reflecting the later spring green-up at higher latitudes and more eastern longitudes.

**Main conclusions:** Migration of the Afro-Palaeartic landbirds follows a longitudinally parallel leapfrog migration pattern, whereby migrants track vegetation green-up in spring but depart before vegetation senescence in autumn. The degree of continentality along migration routes and at the breeding sites of the birds influences the timing of migration on a broad scale.

## KEYWORDS

annual cycle, climate change, continentality, geolocator, long-distance migrant, migration speed, NDVI, phenology, spring green-up

## 1 | INTRODUCTION

With >100 species and more than two billion individuals travelling annually, the Afro-Palaeartic bird migration system is the largest landbird migration network in the world (Hahn, Bauer, & Liechti, 2009; Newton, 2008). Songbirds and near-passerine birds make up >80% of all Afro-Palaeartic migrants (Moreau, 1972), but there are considerable gaps in our knowledge about their migration routes and strategies. Generally, long-distance migrants travel between European breeding and sub-Saharan non-breeding grounds via several broad-scale migration corridors and flyways that are channelled through specific geographical locations (Bruderer, 2001; Zalles & Bildstein, 2000; and for the Nearctic–Neotropical migratory system, see La Sorte, Fink, Hochachka, & Kelling, 2016). The flyways that we see today have been formed through the combined effects of geographical bottlenecks and the post-glacial colonization from glacial refugia in the Iberian and Balkan peninsulas (Hewitt, 2000). Despite the growing amount of empirical data from tracking studies (Kays, Crofoot, Jetz, & Wikelski, 2015; McKinnon & Love, 2018), we still lack a continental-scale synthesis of the spatial and temporal patterns of the Afro-Palaeartic landbird migration system. This knowledge is particularly important for understanding the drivers of the ongoing population declines of many migrant species (Dirzo et al., 2014; Gilroy, Gill, Butchart, Jones, & Franco, 2016) and for introducing efficient conservation measures at key sites.

Adopting the concept of migratory flyways can help to summarize the spatial and temporal variation of the diverse migration strategies across species (La Sorte et al., 2014). Historically, two major flyways have been delineated within the Afro-Palaeartic bird migration system, namely the Western and the Eastern flyways that separate approximately at the 19th meridian east of Italy and circumvent the Mediterranean Sea at the western or the eastern side, respectively (Zink, 1973). Although some literature (e.g., Rubolini, Pastor, Pilastro, & Spina, 2002) distinguishes a third flyway, the Central flyway, via the Apennine peninsula and the western Mediterranean islands, the origin and destination of the migrants and species composition on this flyway largely resembles those of the Western flyway. As demonstrated by ring-recovery analyses and recent tracking studies, the use of a particular migratory flyway at individual and population levels is linked to the longitudes of the breeding and non-breeding sites (Hahn, Amrhein, Zehntindijev, & Liechti, 2013; Koleček et al., 2016; Trierweiler et al., 2014; Zink, 1973).

Timing of migration along the flyways should be fine-tuned to local conditions such that individuals can profit from resources in the places they visit and avoid periods of unfavourable or deteriorating conditions (Alerstam, 2011; McNamara, Welham, & Houston, 1998; Thorup et al., 2017). Matching the timing of migration with the local phenology of the environment is important for the survival,

body condition and reproductive success of individuals (Briedis, Hahn, & Adamik, 2017; Brown & Brown, 1998; Marra, Hobson, & Holmes, 1998). Synthesis of observational and ringing data with environmental phenology has considerably improved our knowledge of spring arrival times of birds in relationship to temperature (Marra, Francis, Mulvihill, & Moore, 2005) and latitude (e.g., Sliwinsky, 1938; Southern, 1938). However, little is known about how a longitudinal gradient in environmental conditions across Europe affects the timing of migration. Ring-recovery data have provided some evidence for differences in the timing of migration along the Western and the Eastern flyways (e.g., Bairlein, 2001), but fine-scale quantification of these differences using ring-recovery data is challenging.

The western part of Europe and the Western flyway are generally characterized by oceanic climate with relatively small seasonal temperature fluctuations, whereas the eastern part of Europe, and thus the Eastern flyway, has a noticeably more continental climate with stronger thermal seasonality (Lisovski, Ramenofsky, & Wingfield, 2017; Metzger et al., 2013; Rötzer & Chmielewski, 2001). If the timing of bird migration is fine-tuned to local phenology, such a climatic gradient from west to east can generate broad-scale differences in the timing of bird migration along the flyways (similar to that across latitudes). Migrants might also respond flexibly to the environmental conditions encountered *en route*, depending on the progress of the migratory season (La Sorte & Fink, 2017; Marra et al., 2005; Schmaljohann, Lisovski, & Bairlein, 2017) and their ability to foresee environmental conditions further along the route (Kölzsch et al., 2015). Describing the timing of bird migration on a large spatial scale helps us to understand how phenology of the environment along a migratory route and at the breeding destination influences mass migratory movements and how the life history of migratory species is adapted to seasonality.

Here, our first aim is to characterize the spatial patterns of songbird migration along the two Afro-Palaeartic flyways (i.e., geographical linkage between breeding sites, migratory flyways and non-breeding sites), their seasonal dynamics (i.e., timing of migration), in addition to travel speeds and distances. Individual migration strategies should be adapted for maximizing fitness and survival. One way to reduce the risk of mortality is to minimize the costs and duration of movement; thus, we expect that the longitude of individual breeding and non-breeding sites will be correlated positively to minimize individual migration distances. We also expect spring migration to be faster than autumn migration (Nilsson, Klaassen, & Alerstam, 2013), owing to increased pressure for early (timely) arrival at the breeding grounds (Kokko, 1999; Kokko, Gunnarsson, Morrell, & Gill, 2006). Second, we explore whether the timing of migration along the two flyways is adapted to the phenology of the environment along the flyways and at the breeding destinations. As a result of trade-offs between survival and reproduction

(Kokko et al., 2006; Lerche-Jørgensen, Korner-Nievergelt, Tøttrup, Willemoes, & Thorup, 2018), we expect spring migration along the flyways to happen in accordance with the vegetation green-up, but autumn migration to elapse ahead of vegetation senescence.

## 2 | METHODS

### 2.1 | Tracking data

We used individual tracking data from 23 passerine and near-passerine Afro-Palaeartic long-distance migrant species (body mass range of the species: 12–160 g) from 55 European breeding populations that had been tracked using light-level geolocators or solar-powered Platform Transmitter Terminal tags (PTT tags) between 2009 and 2017 (a list of the data sources is given in the Appendix). The total number of tracks was 564 (average per species = 24.5; range = 1–91).

The breeding (and tagging) sites spanned across Europe from 37 to 60° N latitude and from 8° W to 28° E longitude (Figure 1). For each individual track, we determined migration timing (i.e., departure and arrival times at the breeding and non-breeding sites) and the geographical location of non-breeding sites, and assigned the individual to one of the two flyways. We delineated the Western and the Eastern migratory flyways according to historical convention (Zink, 1973) and known Quaternary glacial refugia (Hewitt, 2000). Hence, individuals whose migration paths crossed the Iberian and Apennine peninsulas were assigned to the Western flyway and individuals travelling via the Balkan Peninsula and the Middle East to the Eastern flyway. Given that many of the geocator tracks did not contain exact geographical information on stopover sites or full migratory pathways, we relied on the available information (e.g., longitude estimates or description of stopover behaviour) when assigning individuals to the flyways. Some individuals changed their migration routes between the seasons (i.e., performed loop migration) and thus were assigned to different flyways in autumn and spring. If an individual resided at multiple non-breeding sites in Africa, we considered the first site as the arrival site in autumn and the last site as the departure site in spring.

For all individuals, we calculated the migration distance (great circle distances between individual breeding and non-breeding sites; in kilometres) and speed of travel (in kilometres per day) in each migratory season, that is, autumn and spring. Given that the current tracking technologies do not allow estimation of the duration of the predeparture fuelling period, we defined the speed of travel as the rate of movement from departure until arrival, including stopovers (but see Lindström, Alerstam, & Hedenström, 2019). From these calculations, we omitted unrealistic values, that is, those > 600 km/day. Geographical positioning using light-level geolocators inherently contains a positional error of up to a few hundreds of kilometres (Lisovski et al., 2012); therefore, we cannot account for detours that migrants might make *en route*, and we recognize that there are limitations to the precision of the calculated migration distances and travel speeds. However, given that our aim was to compare migration

patterns between the two flyways and that it is unlikely that there is a trend in positional errors between the flyways or a difference in its magnitude (Lisovski et al., 2012), these limitations should not affect our results systematically. Furthermore, a recent meta-analysis suggests that biologging devices (geolocators) do not negatively impact the timing of migration of the tagged individuals (Brlik et al., 2019).

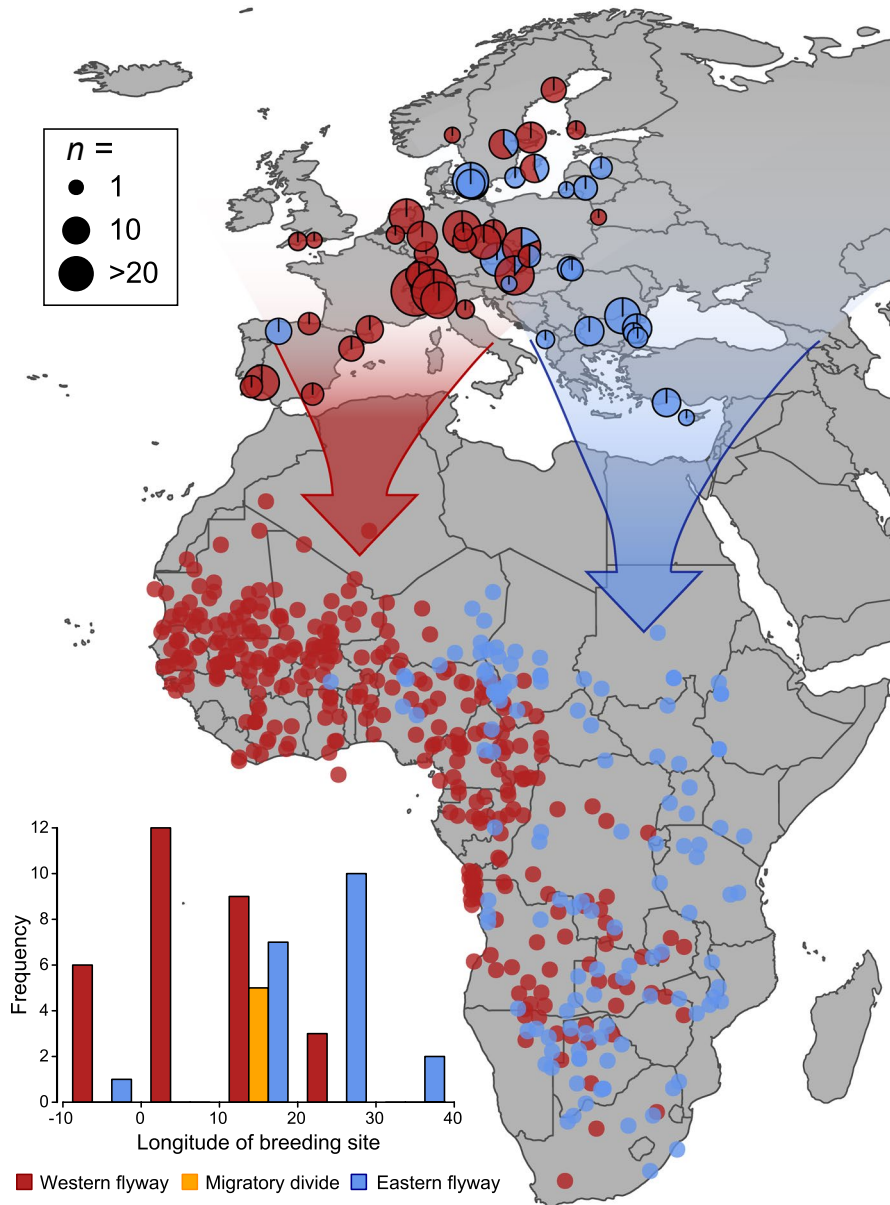
### 2.2 | Phenology of the environment

To characterize the phenology of the environment, we used seasonal changes in the normalized difference vegetation index (NDVI), which ranges from minus one to plus one, where negative values indicate lack of vegetation and high values indicate greener vegetation (Pettorelli et al., 2005). Triggered by the increase and decrease in primary productivity, seasonal changes in NDVI broadly reflect changes in habitat “greenness”, and they can be used to determine the timing of spring green-up and autumn vegetation senescence across large spatial scales.

To assess the annual timing of spring green-up and autumn senescence across the core breeding range of Afro-Palaeartic migrants (Europe plus Turkey, Azerbaijan, Armenia and Georgia), we downloaded weekly composite, noise-removed NDVI data with a spatial resolution of 4 km × 4 km from the NOAA Centre for satellite applications and research (SMN product from: [ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blended\\_VH\\_4km/geo\\_TIFF/](ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blended_VH_4km/geo_TIFF/)) for 1983–2017. Each grid cell was analysed separately as follows: First, a wavelet analysis was used to determine the statistical power of the seasonal dynamics across years (Lisovski et al., 2017). Grid cells with no seasonality (e.g., desert cells) were not analysed further. For all other cells, the NDVI time series was subdivided into annual cycles of 12 months, going from “winter” to “winter” (W-year) and “summer” to “summer” (S-year). An asymmetric double-sigmoid (ADS) curve function was fitted to each W-year and S-year separately (Bradley, Jacob, Hermance, & Mustard, 2007). The ADS function was computed using the following equation:

$$\text{NDVI}(t) = c_1 + \frac{1}{2} \times \{c_2 - \tan h [w_1 \times (t - \nu)] - \tan h [w_2 \times (t - \mu)]\},$$

where  $\tan h$  is the hyperbolic tangent,  $t$  is the time (week of the year) and  $c_1$ ,  $c_2$ ,  $w_1$ ,  $w_2$ ,  $\nu$  and  $\mu$  are the fitting parameters. In this equation,  $c_1$  is the baseline and  $c_2$  the maximum NDVI value,  $w_1$  and  $w_2$  define the slope of the annual increase and decrease of the NDVI variation, and  $\nu$  and  $\mu$  are the dates corresponding to the highest rates of change of NDVI( $t$ ). All parameters were fitted with a maximum likelihood routine (mle2 function of R package bbmle; Bolker & R Development Core Team, 2017), using a Gaussian error distribution. A ‘global’ ADS curve across years was derived by calculating a smooth linear transition from the fitted W-year curve to the S-year curve for periods with a negative slope of the fitted cosine curve and from S-year to W-year for periods with a positive slope of the fitted cosine curve. The start of the green-up period in spring and senescence in autumn was defined



**FIGURE 1** Flyway use of Afro-Palaeartic long-distance migrants (red = Western flyway; blue = Eastern flyway). Pie charts mark the breeding site locations [diameter indicates sample size ( $n$ )] and show the proportions of individuals that use either of the flyways within each population. Individual non-breeding sites are marked with dots. The inset shows the frequency distribution of flyway use according to breeding site longitude (values are binned into 10° longitudinal bands). The orange bar indicates populations that use both flyways (i.e., populations with a migratory divide)

as the date at which the global ADS curve (for each year separately) exceeded 50% of the amplitude (from minimum value) in spring and fell below 50% of the amplitude (from maximum value) in autumn. To derive long-term averages of these phenological metrics, we averaged the timing of the spring green-up and autumn senescence for each grid cell across all years (1983–2017).

The same NDVI dataset was used to assess the relationship between the timing of bird arrival at, and departure from, the breeding site and NDVI measures. To this end, we extracted NDVI values from the breeding sites of all tracked birds for the week and year of individual autumn departure and spring arrival.

### 2.3 | Statistical analyses

The individual tracking data in this study were compiled from the literature and often provided information only on individual departure

and arrival times from breeding and non-breeding sites but lacked more detailed information on migration timing in between. To resolve this, in part, we calculated the time of crossing 30° N latitude, considering a constant speed of travel (individual-specific speed as calculated by the tracking data) along a great circle route between the individual breeding and non-breeding sites. This latitude roughly borders the northern edge of the Sahara Desert, which is a major ecological barrier that separates temperate breeding and subtropical non-breeding grounds of trans-Saharan migratory birds.

To examine the relationship between the latitude and longitude of individual breeding and non-breeding sites, we used linear mixed-effects models (LMMs), with species as a random effect. We also used LMMs to compare migration distances, speeds of travel and timing of migration between the two flyways, and to account for the non-independence of hierarchical data, we included species, breeding latitude (nested within species) and year (nested within species and breeding latitude) as random factors

in the models. Given that the species included in our study may differ in their timing of migration, we standardized all individual values across each timing event (departure, arrival and crossing 30° N latitude) to zero-mean before including them in LMMs. Accordingly, individual values less than zero denoted relatively earlier migration, whereas values greater than zero denoted relatively later timing of migration. If an individual was tracked over multiple years, we included only one track per individual in the models ( $n$  repeat tracks = 24). The same model structure was also used to test for differences between the two flyways in breeding site NDVI values at individual departure times in autumn and arrival times in spring. All data analyses were done in R (R Core Team, 2018). The LMMs were run with the R package lme4 (Bates, Mächler, Bolker, & Walker, 2014), and estimates of parameters whose 95% confidence interval (CI) did not overlap zero were considered significant. Marginal and conditional  $R^2$  values for model fit were obtained using the R package MuMIn (Barton, 2019).

### 3 | RESULTS

#### 3.1 | Spatial structure of the migratory system

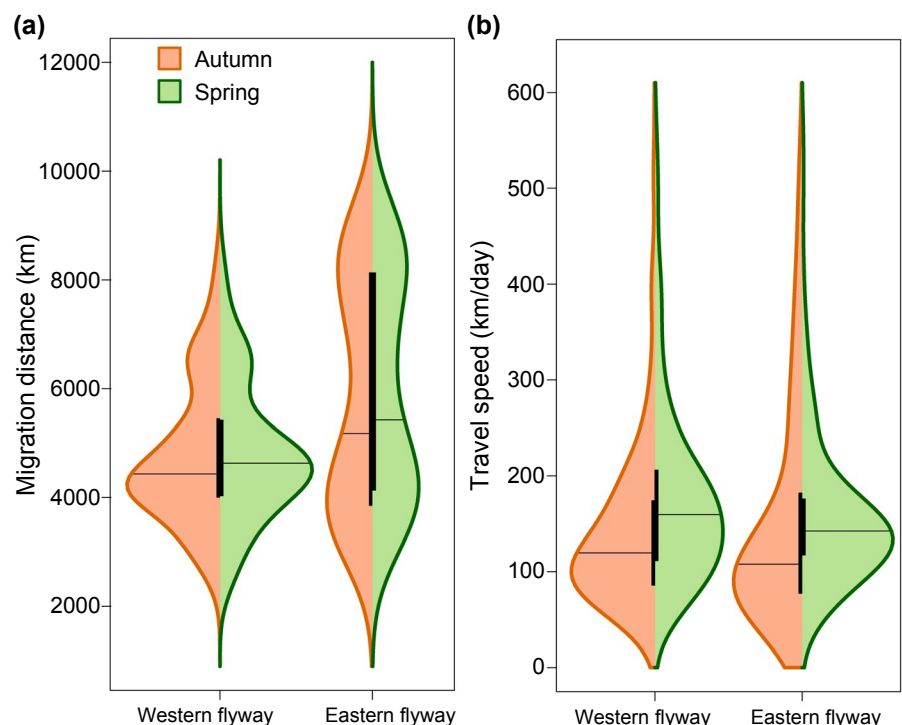
Overall, we found a strong positive relationship between the longitudes of individual breeding and non-breeding sites ( $\beta = 1.12$ , 95% CI = 1.02 to 1.21, conditional  $R^2 = .87$ ; Figure 1), that is, birds breeding further west in Europe overwintered further west in Africa, and birds breeding further east in Europe overwintered further east in Africa. Consequently, birds with more easterly breeding and non-breeding sites predominately used the Eastern flyway, whereas birds with more westerly breeding and non-breeding sites predominately

used the Western flyway (breeding longitude:  $\beta_{\text{Eastern flyway}} = 11.56$ , 95% CI = 10.31 to 12.79, conditional  $R^2 = .69$ ; non-breeding longitude:  $\beta_{\text{Eastern flyway}} = 18.53$ , 95% CI = 16.44 to 20.65, conditional  $R^2 = .73$ ).

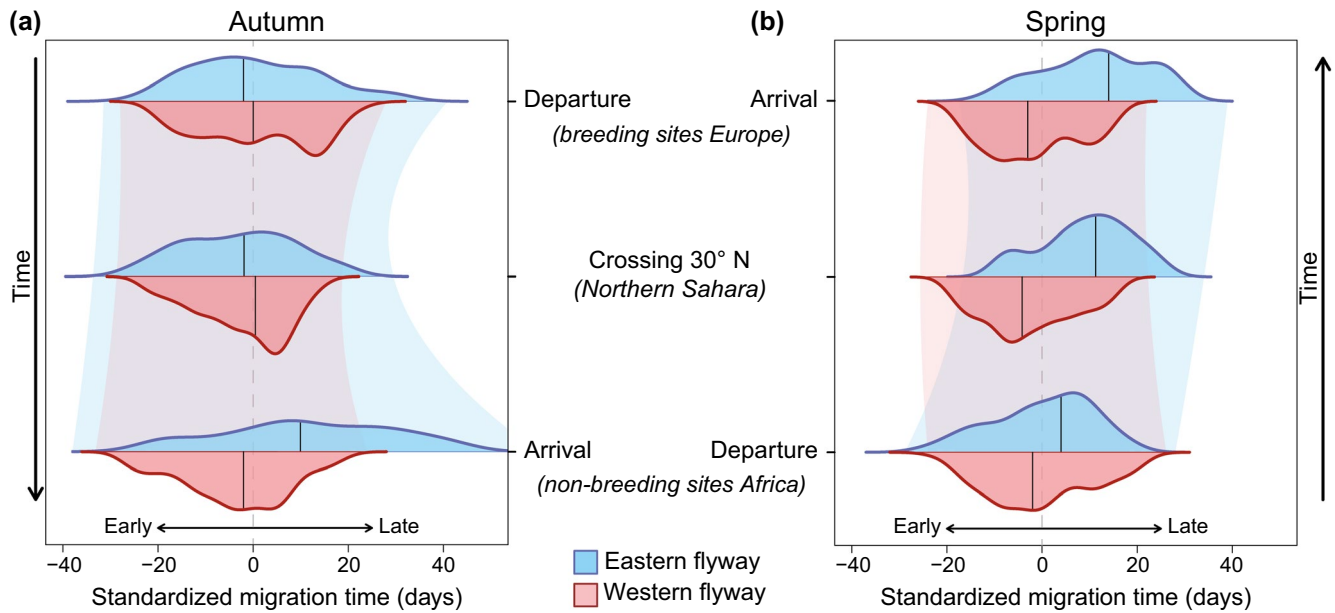
We found a negative relationship between the latitudes of breeding and non-breeding sites ( $\beta = -0.47$ , 95% CI =  $-0.62$  to  $-0.31$ , conditional  $R^2 = .79$ ), with northern breeders leapfrogging southern breeders at the non-breeding sites. Moreover, use of the Eastern flyway was strongly associated with more southerly non-breeding latitudes compared with the Western flyway ( $\beta_{\text{Eastern flyway}} = -3.97$ , 95% CI =  $-2.19$  to  $-5.77$ , conditional  $R^2 = .74$ ), whereas there was no association between breeding latitude and flyway use ( $\beta_{\text{Eastern flyway}} = -0.34$ , 95% CI =  $-1.29$  to 0.60, conditional  $R^2 = .60$ ). Migratory divides (i.e., areas occupied by populations where individuals exhibit divergent migration directions) were identified between a narrow range of 10–20° E longitude (Figure 1 inset). Less than 9% (50 of 564) of individuals changed their flyway between the seasons, with proportionally more individuals switching from the Eastern flyway in autumn to the Western flyway in spring [17.8%; 29 of 163 individuals; species: great reed warbler, *Acrocephalus arundinaceus* ( $n = 8$ ); European roller, *Coracias garrulus* (1); common cuckoo, *Cuculus canorus* (9 = all individuals); house martin, *Delichon urbicum* (2); collared flycatcher, *Ficedula albicollis* (1); barn swallow, *Hirundo rustica* (7); sand martin, *Riparia riparia* (1)] than vice versa [5.2%; 21 of 401 individuals; great reed warbler (1); collared flycatcher (20)].

#### 3.2 | Migration distance and travel speed

Although the migration distances were generally longer along the Eastern flyway [median and interquartile range; Western flyway = 4,531 (2,154–5,412) km, Eastern



**FIGURE 2** Season- and flyway-specific individual: (a) migration distances; and (b) travel speeds. The shape of the violins illustrates the density distribution of data; horizontal black lines indicate median values, and vertical black bars denote interquartile ranges



**FIGURE 3** Standardized migration timing on the Western (red) and Eastern (blue) flyways in: (a) autumn; and (b) spring. Density plots show the distribution of individual migration timing at three migration stages: departure (start of migration); crossing of the 30° N parallel; and arrival (end of migration). Black lines indicate medians, and the shaded area shows the 95% confidence interval of the migration window

flyway = 5,167 (3,937–8,114) km; Figure 2a], we did not find significant differences in migration distances between the two flyways (Table 1a). Some species (particularly Alpine swift, *Tachymarptis melba*, and great reed warbler) showed intra-tropical movements, during which individuals typically moved farther away from their breeding sites. Therefore, the median migration distance in spring was somewhat longer than in autumn [autumn = 4,491 (3,937–6,286) km, spring = 4,636 (4,053–6,188) km; Figure 2a] but again, this difference was not significant (Table 1a). Speed of travel was significantly higher in spring compared with autumn [autumn = 117 (83–178) km/day, spring = 153 (113–201) km/day; Figure 2b], but there were no differences between the flyways (Table 1b).

### 3.3 | Seasonal dynamics of the migratory system

We found both latitude of the breeding sites and flyway to be significant predictors for the timing of various phases of the autumn migration. Although birds from different breeding latitudes started the autumn migration at a similar time, breeders from higher latitudes crossed the 30° N latitude and arrived at the non-breeding sites later (Figure 3a; Table 1c–e). Our model results revealed that individuals using the Western flyway migrated on average 5–7 days earlier than individuals using the Eastern flyway at all stages of autumn migration (Table 1c–e).

In spring, migration started at a similar time on both flyways, but birds travelling along the Eastern flyway crossed the 30° N latitude and arrived at their European breeding sites later compared with the birds travelling along the Western flyway (Figure 3b). Our model estimates accounting for breeding latitude revealed a difference

of c. 6.5 days between the two flyways for crossing 30° N latitude and arrival at the breeding sites (Table 1g,h). We found a positive relationship between the latitude of the breeding sites and spring arrival times, with each additional 1° latitude delaying migration by c. 1.5 days (Table 1h).

The overall migration period (migration window) was longer on the Eastern flyway in both seasons [difference between the average start and end time of migration: autumn Western flyway = 42.4 days (95% CI = 39.6 to 45.3 days), autumn Eastern flyway = 59.5 days (53.2–65.9 days), spring Western flyway = 32.9 days (30.4–35.5 days), spring Eastern flyway = 44.7 days (40.3–49.2 days); Figure 3].

The timing of spring green-up and autumn senescence revealed a SW–NE gradient, with later spring green-up and earlier autumn senescence in north-eastern Europe and, consequently, along the Eastern flyway compared with south-western Europe and the Western flyway (Figure 4). Comparison of the NDVI values from the breeding sites measured at the time of individual autumn departures revealed that birds migrating along the Eastern flyway left their respective breeding sites when the environment was more depleted compared with departure NDVI values for the birds migrating along the Western flyway (Figure 5a,b; Table 1i). In spring, despite the c. 6.5 day later arrival of the birds migrating along the Eastern flyway, NDVI measures were similar for birds migrating along both flyways (Figure 5c,d; Table 1j).

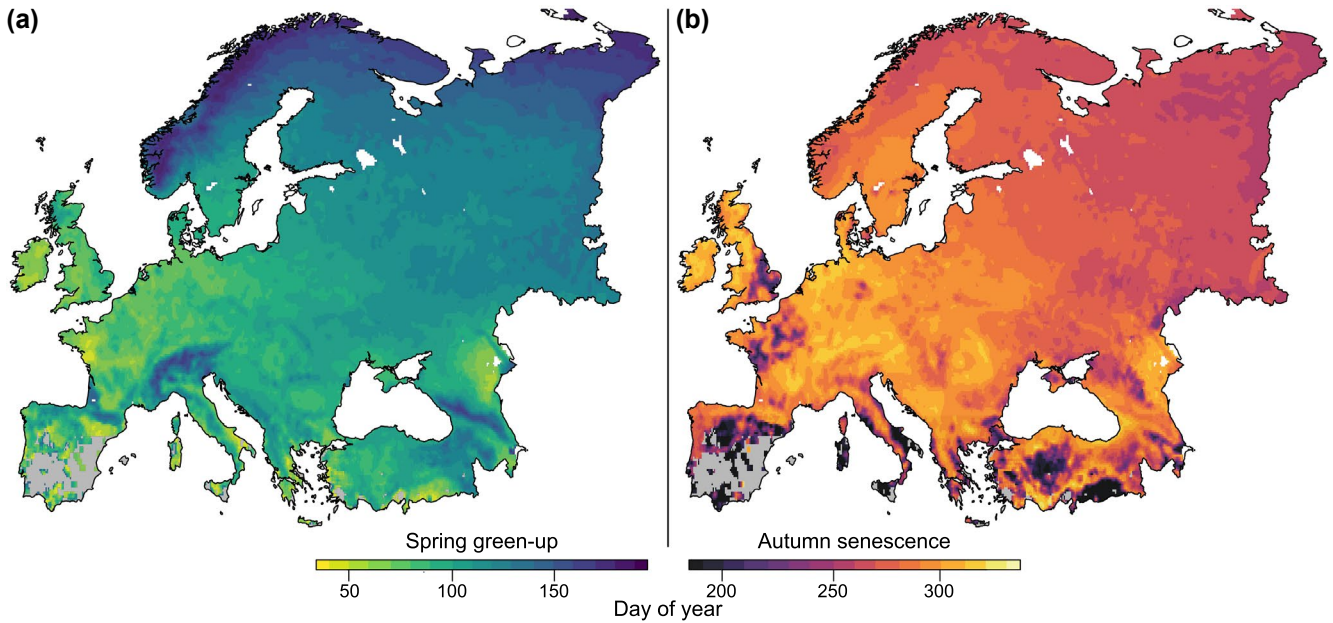
## 4 | DISCUSSION

Migration routes of Afro-Palaeartic migrants can be organized in two broadly defined flyways, which converge between c. 10 and

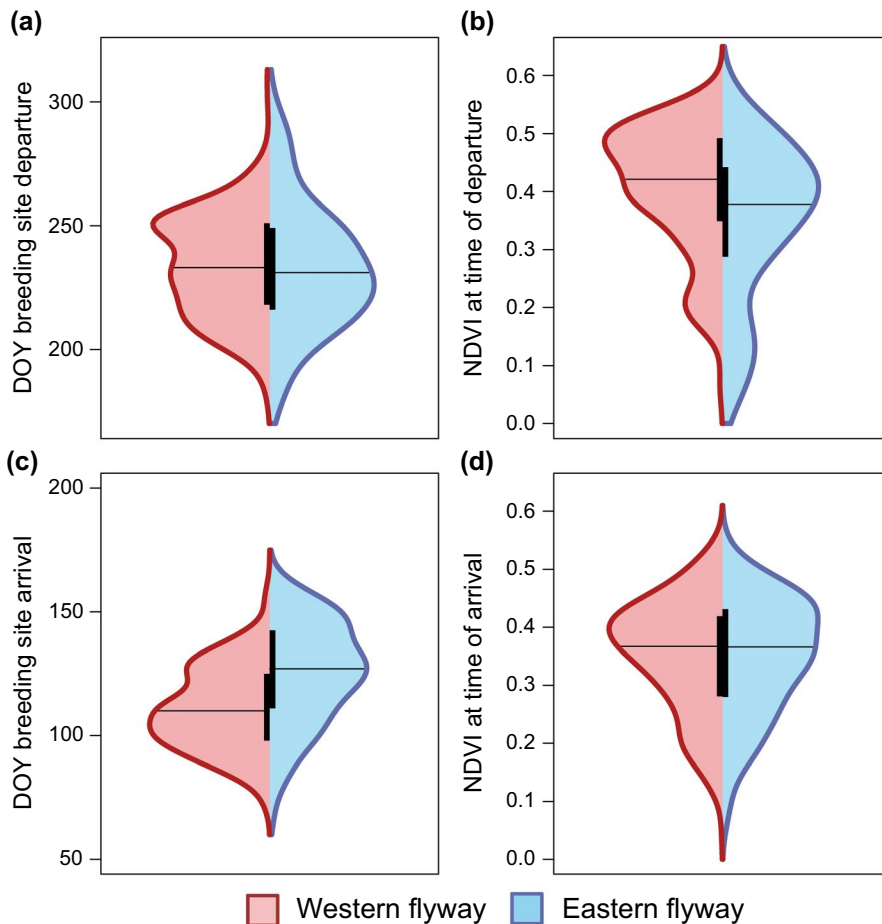
TABLE 1 Results of linear mixed-effects models

	Marginal $R^2$		Conditional $R^2$	Fixed effects			Random effects		
		< .01		Estimate	95% CI	Variance	SD		
(a) Migration distance (km)	.89		Intercept	5.303	4,664–5,942	Year:(BS × latitude:species)	61,359	247.7	
			Flyway <sub>(western)</sub>	42.05	–177.8 to 260.2	BS latitude:species	640,134	800.1	
			Season <sub>(spring)</sub>	69.64	–0.3 to 139.5	Species	1,796,471	1,340.3	
						Residual	299,379	547.2	
(b) Travel speed (km/day)	.25		Intercept	131.2	107.0–155.2	Year:(BS latitude:species)	26.7	5.2	
			Flyway <sub>(western)</sub>	–4.48	–21.9 to 13.1	BS latitude:species	136.6	11.7	
			Season <sub>(spring)</sub>	<b>28.51</b>	<b>17.6–39.4</b>	Species	1,870.3	43.3	
						Residual	7,301.7	85.5	
(c) BS departure	.76		Intercept	242.3	225.8–258.8	Year:species	24.4	4.9	
			Flyway <sub>(western)</sub>	<b>–6.65</b>	<b>–9.89 to –3.38</b>	Species	374.6	19.4	
			BS latitude	–0.20	–0.49 to 0.09	Residual	131.8	11.5	
(d) Crossing 30° N autumn	.72		Intercept	221.0	206.4–235.7	Year:species	16.7	4.1	
			Flyway <sub>(western)</sub>	<b>–5.60</b>	<b>–8.47 to –2.68</b>	Species	204.7	14.3	
			BS latitude	0.77	0.51–1.04	Residual	96.8	9.8	
(e) Non-BS arrival	.75		Intercept	219.9	200.5–239.3	Year:species	42.3	6.5	
			Flyway <sub>(western)</sub>	<b>–7.36</b>	<b>–11.4 to –3.4</b>	Species	457.3	21.4	
			BS latitude	1.42	1.08–1.76	Residual	189.8	13.8	
(f) Non-BS departure	.69		Intercept	33.3	16.7–49.8	Year:species	16.4	4.0	
			Flyway <sub>(western)</sub>	–2.30	–5.76 to 1.17	Species	302.3	17.4	
			BS latitude	0.98	0.68–1.28	Residual	154.9	12.4	
(g) Crossing 30° N spring	.68		Intercept	54.9	40.9–69.0	Year:species	8.7	2.9	
			Flyway <sub>(western)</sub>	<b>–6.42</b>	<b>–9.41 to –3.45</b>	Species	159.0	12.6	
			BS latitude	1.07	0.81–1.33	Residual	101.8	10.1	
(h) BS arrival	.71		Intercept	52.8	39.6–66.0	Year:species	9.1	3.0	
			Flyway <sub>(western)</sub>	<b>–6.52</b>	<b>–9.33 to –3.71</b>	Species	172.8	13.1	
			BS latitude	1.47	1.23–1.71	Residual	104.5	10.2	
(i) NDVI at BS departure	.73		Intercept	0.205	0.107–0.304	Year:species	0.342	0.059	
			Flyway <sub>(western)</sub>	<b>0.047</b>	<b>0.026–0.068</b>	Species	0.688	0.083	
			BS latitude	<b>0.003</b>	<b>0.001–0.005</b>	Residual	0.409	0.064	
(j) NDVI at BS arrival	.68		Intercept	0.178	0.095–0.262	Year:species	0.216	0.046	
			Flyway <sub>(western)</sub>	0.017	–0.001 to 0.003	Species	0.488	0.070	
			BS latitude	<b>0.003</b>	<b>0.002–0.005</b>	Residual	0.340	0.058	

Abbreviations: BS = breeding site; NDVI = normalized difference vegetation index. Interactions where 95% confidence interval (CI) does not overlap zero are indicated in bold.



**FIGURE 4** Timing of: (a) spring green-up; and (b) autumn vegetation senescence across Europe, averaged for the period between 1983 and 2017. Grey areas indicate lack of seasonality in primary productivity (e.g., no vegetation or constant productivity, probably driven by agricultural practices that might also result in the early autumn senescence patterns at various parts of southwestern Europe, such as western France and eastern England). Estimates are smoothed values across neighbouring cells (mean values across nine cells) based on a 4 km × 4 km grid cell



**FIGURE 5** Individual breeding site departure and arrival times (DOY = day of the year) and corresponding normalized difference vegetation index (NDVI) values at the breeding sites according to the individual flyway use (red = Western flyway; blue = Eastern flyway). (a) Individual breeding site departure times in autumn. (b) NDVI measured at the breeding sites at the time of departure. (c) Individual breeding site arrival times in spring. (d) NDVI measured at the breeding sites at the time of arrival. The shape of the violins illustrates the density distribution of data. Horizontal black lines indicate median values, and vertical black bars denote interquartile ranges



20° E in Central Europe. The birds mainly follow a longitudinally parallel migration pattern, and northern breeders surpass southern breeders at the sub-Saharan non-breeding sites (i.e., they perform leapfrog migration). Our comparison of the timing of migration revealed generally later migration along the Eastern compared with the Western flyway in both autumn and spring, which probably results from phenological differences between Western and Eastern Europe. Indeed, the NDVI data showed a longitudinal gradient, with later spring green-up and earlier autumn vegetation senescence further east in Europe. In spring, irrespective of which flyway the birds used, they matched their time of arrival at breeding sites with the timing of local vegetation green-up, suggesting that spring arrival time is fine-tuned in accordance with the phenology of the breeding site. Furthermore, birds breeding at higher latitudes arrived at their non-breeding sites in Africa and breeding sites in Europe increasingly later, at a rate of c. 1.5 days delay per 1° increase in breeding latitude.

#### 4.1 | Spatial structure

Century-long efforts of bird ringing have revealed general migration directions and often also the non-breeding areas of most long-distance migrants breeding in Europe (e.g., Bairlein, 2001; Bønløkke et al., 2006; Cepák et al., 2008; Valkama et al., 2014; Wernham et al., 2002; Zink, 1973). Our findings add to this knowledge by identifying a strong relationship between the longitudes of breeding and non-breeding sites such that individuals with eastern (European) breeding sites also typically have eastern (African) non-breeding sites. Irrespective of whether it is a cause or a consequence, this relationship extends to the use of a particular flyway. As a result, the parallel migration system that links Europe and sub-Saharan Africa generates a certain degree of community and ecosystem connectivity between Western Europe and West Africa and between Eastern Europe and Central/East Africa (Bauer & Høye, 2014). The presence of east-west-oriented ecological barriers (i.e., the Sahara Desert and the Mediterranean Sea) also facilitates migration pathways that flow through the western and eastern edges of the barriers, where the projected flight distances over inhospitable areas are shorter when compared with the central part of the Sahara (Adamík et al., 2016).

In some species, extension of their breeding ranges while maintaining the genetically imprinted direction of migration and non-breeding areas has led to more complex migratory networks with longer migration distances, hence higher costs of migration. For example, the aquatic warbler, *Acrocephalus paludicola*, has gone extinct in Western Europe, and the entire world population is now breeding in eastern Europe but maintaining the historical migration route for the species along the Western flyway to their non-breeding areas in West Africa (Salewski et al., 2019). Likewise, the breeding range of the pied flycatcher, *Ficedula hypoleuca*, extends to 93° E, and virtually the entire Palearctic population migrates through the Iberian Peninsula along the Western flyway (Lundberg & Alatalo,

1992). On the contrary, red-backed shrikes, *Lanius collurio*, breeding on the Iberian Peninsula migrate exclusively along the Eastern flyway and overwinter in southern Africa (Tøttrup, Pedersen, Onrubia, Klaassen, & Thorup, 2017).

The negative correlation between the latitudes of individual breeding and non-breeding sites suggests leapfrog migration to be the prevailing pattern among long-distance migrants in the Afro-Palearctic bird migration system. Leapfrog migration is thought to have arisen from competition at the non-breeding sites during the post-glacial expansion of the breeding areas (Newton, 2008). As the species increased in abundance and colonized new breeding sites further north, the competition for resources at the non-breeding sites increased, forcing northern breeders to migrate further south and leapfrog their conspecifics. Therefore, individuals from more northern breeding populations typically migrate longer distances than their southern conspecifics.

#### 4.2 | Seasonal dynamics

Our results indicate that the timing of migration differs between the two flyways by c. 5–7 days at all annual migration stages, except for the start of spring migration. The differences in spring arrival times are probably driven by differences in phenology of the environment (spring green-up) along the two flyways. We found a strong SW–NE gradient in the timing of spring green-up and autumn vegetation senescence across Europe (Figure 4; Menzel, Sparks, Estrella, & Eckhardt, 2005) that is likely to result from the degree of continentality, that is, by how much the climate of a region is influenced by the advection of air masses from the ocean and from the landmass (Franzén, 1991).

Analyses of ring-recovery data have already suggested such flyway-scale differences in the timing of annual migration in, for example, white stork, *Ciconia ciconia* (Bairlein, 2001), but quantifying these differences for annual stages other than spring arrival often remains elusive with ring-recovery data. Earlier tracking studies of long-distance migrants have shown population-specific timing of annual migration routines, which are linked to spring phenology at various breeding latitudes (Briedis et al., 2016; Conklin, Battley, Potter, & Fox, 2010; Gow et al., 2019). Moreover, the northward progression of migrants in spring was found to be aligned with vegetation phenology in the Nearctic–Neotropical migration system (La Sorte, Fink, Hochachka, Delong, & Kelling, 2014; Marra et al., 2005), where atmospheric and environmental conditions *en route* played an important role in shaping seasonal and flyway-scale differences in migration strategies (La Sorte, et al., 2014, 2016; La Sorte & Fink, 2017). This finding is supported by scarce evidence from tracking studies. For example, barn swallows breeding at the same location in the Czech Republic differed in spring arrival dates depending on flyway, with birds following the Eastern flyway arriving on average 5 days later than birds following the Western flyway (Klvaňa et al., 2018); a difference that coincides with our estimates (Table 1h). To avoid adverse conditions *en route* in early spring, long-distance migrants travelling along the Eastern flyway should be adapted to cross

the Sahara later compared with migrants on the Western flyway. Selection pressure against premature arrival is likely to be high, because individuals arriving early have been shown to suffer increased mortality (Lerche-Jørgensen et al., 2018), particularly in years with delayed spring green-up (Briedis et al., 2017).

In autumn, birds travelling along the Eastern flyway departed from their breeding sites later compared with the birds travelling along the Western flyway despite an earlier vegetation senescence in the Eastern Europe. Long-distance migrants generally depart from their breeding sites well ahead of senescence of the environment in autumn (Briedis et al., 2016), suggesting that the timing of departure in autumn is probably controlled by mechanisms other than deteriorating habitat conditions. Experimental studies on stonechats, *Saxicola torquatus*, revealed that migratory restlessness (*Zugunruhe*) starts significantly earlier in Irish birds compared with their continental counterparts (Van Doren, Liedvogel, & Helm, 2017), suggesting endogenous control for the start of autumn migration (Pedersen, Jackson, Thorup, & Tøttrup, 2018).

*Zugunruhe* data also demonstrate seasonal differences in the length and intensity of migratory activity (Van Doren et al., 2017). We found that the migration window was shorter (therefore, the migration traffic was more synchronized) and the speed of travel faster in spring compared with autumn on both flyways. Theoretical models predict faster and more synchronized spring migration owing to high importance for early arrival at the breeding grounds (Kokko, 1999; Kokko et al., 2006), which is counterbalanced by increased costs of premature arrival (Lerche-Jørgensen et al., 2018). The ratio of average travel speeds in spring and autumn that we found in our study falls within the range of values reported earlier for the Afro-Palaeartic migratory system (Karlsson, Nilsson, Bäckman, & Alerstam, 2012; Nilsson, Bäckman, & Alerstam, 2014; Nilsson et al., 2013).

To summarize, our findings indicate important differences in seasonal dynamics between the western and the eastern parts of the Afro-Palaeartic migration system. Long-distance migrants track vegetation green-up when arriving at the breeding sites in spring but depart ahead of vegetation senescence in autumn. Consequently, the degree of continentality along migration routes and at the breeding sites of the birds influences the timing of migration on a broad scale.

## 5 | CONCLUSION

Scaling up from individual tracking and adopting the concept of migratory flyways helps to identify broad-scale spatio-temporal movement patterns of migratory birds (La Sorte et al., 2014). This knowledge is fundamental for understanding the main drivers that shape migration strategies of birds. Given that a parallel migration pattern exists between Europe and Africa with distinct differences in timing, this must be an adaptation to the prevailing environmental settings along each flyway.

To uncover the potential effects of global change on migratory systems, continued effort in monitoring migrants and synthesizing datasets is necessary. To this end, citizen science data (e.g., EuroBirdPortal.org) offer great potential to study the timing of bird

migration across Europe, and the continent-wide weather radar network can provide the rate of migration (Nussbaumer et al., 2019), whereas individual-based tracking still presents the best opportunity to link breeding, stopover and non-breeding sites at the individual and population levels.

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## AUTHOR CONTRIBUTIONS

M.B., S.B. and S.H. conceived the idea and study design. M.B., P.A., J.A.A., J.S.C., T.E., L.G., J.K., M.K., F.L., C.M.M., P.P. and S.H. carried out individual tracking projects and provided geolocator data. S.L. analysed environmental data. M.B. performed data analyses and wrote the manuscript with inputs from all authors.

## DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hdr7sqvdc> (Briedis et al., 2020).

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## BIOSKETCH

**Martins Briedis** is a wildlife biologist with a main research focus on avian migration ecology in the context of the full annual cycles. He is particularly interested in the concept of migratory connectivity from a spatio-temporal viewpoint, links between different annual phases, and interactions between migrants and the environment.

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## APPENDIX

## DATA SOURCES

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