Broad-scale patterns of the Afro-Palearctic landbird migration

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Authors' contributions

MB, SB, and SH conceived the idea and study design. MB, PA, JAA, JSC, TE, LG, JK, MK, FL, CMM, PP, and SH carried out individual tracking projects and provided geolocator data. SL analysed environmental data. MB performed data analyses and wrote the manuscript with inputs from all authors.

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 spatiotemporal viewpoint, links between different annual phases, and interactions between migrants and the environment.

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Running title: Patterns of European-African migration

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-Palearctic 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 where a total of 564 individuals were tracked migrating between Europe and sub-Saharan Africa. In addition, we used remote sensed primary productivity data (NDVI) 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 migration timing along the two major Afro-Palearctic flyways is tuned with vegetation phenology at the breeding sites.

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

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

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

Introduction

87

88   With more than 100 species and more than 2 billion individuals travelling annually, the Afro-

89   Palearctic bird migration system is the world's largest landbird migration network (Newton, 2008;

90   Hahn *et al.*, 2009). Songbirds and near-passerine birds make up more than 80% of all Afro-Palearctic

91   migrants (Moreau, 1972), yet there are considerable gaps in our knowledge about their migration

92   routes and strategies. Generally, long-distance migrants travel between European breeding and sub-

93   Saharan non-breeding grounds via several broad-scale migration corridors and flyways that are

94   channelled through specific geographic locations (Zalles & Bildstein, 2000; Bruderer, 2001; and see La

95   Sorte *et al.* (2016) for the Nearctic-Neotropical migratory system). The flyways that we see today

96   have been formed through the combined effects of geographic bottlenecks and the post-glacial

97   colonisation from glacial refugia in the Iberian and Balkan peninsulas (Hewitt, 2000). Despite the

98   growing amount of empirical data from tracking studies (Kays *et al.*, 2015; McKinnon & Love, 2018),

99   we still lack a continental-scale synthesis of the spatial and temporal patterns of the Afro-Palearctic

100   landbird migration system. This knowledge is particularly important for understanding the drivers of

101   the ongoing population declines of many migrant species (Dirzo *et al.*, 2014; Gilroy *et al.*, 2016) and

102   for introducing efficient conservation measures at key sites.

103   Adopting the concept of migratory flyways can help to summarize the spatial and temporal

104   variation of the diverse migration strategies across species (La Sorte *et al.*, 2014a). Historically, two

105   major flyways have been delineated within the Afro-Palearctic bird migration system, namely the

106   Western and the Eastern flyways that separate approx. at the 19th meridian east of Italy and

107   circumvent the Mediterranean Sea at the western or the eastern side, respectively (Zink, 1973–

108   1985). Although some literature (e.g. Rubolini *et al.*, 2002) distinguish a third, the Central flyway, via

109   the Apennine peninsula and the western Mediterranean islands, the origin and destination of the

110   migrants and species composition on this flyway largely resembles those of the Western flyway. As

111   demonstrated by ring recovery analyses and recent tracking studies, the use of a particular migratory

112   flyway at individual and population levels is linked to the longitudes of breeding and non-breeding

113   sites (Zink, 1973–1985; Hahn *et al.*, 2013; Trierweiler *et al.*, 2014; Koleček *et al.*, 2016).

114   Timing of migration along the flyways should be fine-tuned to local conditions such that

115   individuals can profit from resources in the places they visit and avoid periods of unfavourable or

116   deteriorating conditions (McNamara *et al.*, 1998; Alerstam, 2011; Thorup *et al.*, 2017). Matching the

117   timing of migration with the local phenology of the environment is important for individuals' survival,

118   body condition, and reproductive success (Brown & Brown, 1998; Marra *et al.*, 1998; Briedis *et al.*,

119   2017). Synthesis of observational and ringing data with environmental phenology has considerably

improved our knowledge of spring arrival times of birds in relation to temperature (Marra *et al.*, 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 migration timing 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 while the eastern part of Europe and, thus, the Eastern flyway has a noticeably more continental climate with stronger thermal seasonality (Rötzer & Chmielewski, 2001; Metzger *et al.*, 2013; Lisovski *et al.*, 2017). If bird migration timing is fine-tuned to local phenology, such a climatic gradient from west to east can generate broad-scale differences in bird migration timing along the flyways (similar as across latitudes). Migrants may also flexibly respond to the environmental conditions encountered *en route*, depending on the progress of the migratory season (Marra *et al.*, 2005; La Sorte & Fink, 2017; Schmaljohann *et al.*, 2017) and their ability to foresee environmental conditions further along the route (Kölzsch *et al.*, 2015). Describing timing of bird migration on a large spatial scale helps 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, we first aim to characterize the spatial patterns of songbird migration along the two Afro-Palearctic flyways (i.e. geographic linkage between breeding sites, migratory flyways and non-breeding sites), their seasonal dynamics (i.e. timing of migration), as well as travel speeds and distances. Individual migration strategies should be adapted for maximizing fitness and survival. One way to reduce the mortality risk is to minimize the costs and duration of movement; thus, we expect that longitude of individual breeding and non-breeding sites will be positively correlated to minimize individual migration distances. We also expect spring migration to be faster than autumn migration (Nilsson *et al.*, 2013), due to increased pressure for early (timely) arrival at the breeding grounds (Kokko, 1999; Kokko *et al.*, 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. Because of trade-offs between survival and reproduction (Kokko *et al.*, 2006; Lerche-Jørgensen *et al.*, 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.

Methods

Tracking data

We used individual tracking data from 23 passerine and near-passerine Afro-Palearctic 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°N 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 from and arrival times at the breeding and non-breeding sites, the geographic location of non-breeding sites and assigned it to one of the two flyways. We delineated the Western and the Eastern migratory flyways according to historic convention (Zink, 1973–1985) 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. Since many of the geolocator tracks did not contain exact geographic 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 migration distance (great circle distances between individual breeding and non-breeding sites; km) and travel speeds (km day^{-1}) in each migratory season, i.e. autumn and spring. Since the current tracking technologies do not allow estimating the duration of the pre-departure fuelling period, we defined travel speed as the rate of movement from departure until arrival, including stopovers (but see Lindström *et al.*, 2019). From these calculations we omitted unrealistic values, i.e. those >600 km day^{-1}. Geographic 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 may make *en route*, and recognize that there are limitations to the precision of the calculated migration distances and travel speeds. However, as we aim at comparing migration patterns between the two flyways and 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 systematically affect our results. Furthermore, a recent meta-analysis

185 suggests that biologging devices (geolocators) do not negatively impact on migration timing of the
186 tagged individuals (Brlík *et al.*, 2019).

Phenology of the environment

188 To characterize the phenology of the environment, we used seasonal changes in the normalized
189 difference vegetation index (NDVI). NDVI range from −1 to 1, where negative values indicate lack of
190 vegetation and high values indicate greener vegetation (Pettorelli *et al.*, 2005). Triggered by increase
191 and decrease in primary productivity, seasonal changes in NDVI broadly reflect changes in habitat
192 'greenness' and they can be used to determine the timing of spring green-up and autumn
193 senescence across large spatial scales.

194   To assess annual timing of spring green-up and autumn senescence across the core breeding
195 range of Afro-Palearctic migrants (Europe plus Turkey, Azerbaijan, Armenia, and Georgia) we
196 downloaded weekly composite, noise removed NDVI data with a spatial resolution of 4 x 4 km from
197 the NOAA Centre for satellite applications and research (SMN product from:
198 ftp://ftp.star.nesdis.noaa.gov/pub/corp/scsb/wguo/data/Blended_VH_4km/geo_TIFF/) for 1983 to
199 2017. Each grid-cell was analysed separately as follows: First, a wavelet analysis was used to
200 determine the statistical power of the seasonal dynamics across years (Lisovski *et al.*, 2017). Grid-
201 cells with no seasonality, e.g. desert cells, were not analysed further. For all other cells, the NDVI
202 time series was subdivided into annual cycles of 12 months going from 'winter' to 'winter (W-year)
203 and 'summer' to 'summer' (S-year). An asymmetric double-sigmoid (ADS) curve function was fitted to
204 each W-year and S-year separately (Bradley *et al.*, 2007). The ADS function was computed using the
205 following equation:

$$NDVI(t) = c1 + \frac{1}{2} * (c2 - \tanh(w1 * (t - v)) - \tanh(w2 * (t - \mu)))$$

207   where tanh is the hyperbolic tangent, t is the time (week of the year) and c1, c2, w1, w2, v
208 and μ are the fitting parameters. In this equation, c1 is the baseline and c2 the maximum NDVI value,
209 w1 and w2 define the slope of the annual increase and decrease of the NDVI variation, while v and μ
210 are the dates corresponding to the highest rates of change of NDVI(t). All parameters were fitted
211 with a maximum likelihood routine (mle2 function of R-package bbmle (Bolker & R Development
212 Core Team, 2017), using a Gaussian error distribution. A 'global' ADS curve across years was derived
213 by calculating a smooth linear transition from the fitted W-year curve to the S-year curve for periods
214 with a negative slope of the fitted cosine curve and from S-year to W-year for periods with a positive
215 slope of the fitted cosine curve. The start of the green-up period in spring and senescence in autumn
216 were defined as the date at which the global ADS curve (for each year separately) exceeded 50% of
217 the amplitude (from min value) in spring and fell below 50% of the amplitude (from max value) in

218   autumn. To derive long-term averages of these phenological metrics, we averaged the timing of the

219   spring green-up and autumn senescence for each grid cell across all years (1983–2017).

220   The same NDVI dataset was used to assess the relationship between timing of bird arrival at,

221   and departure from, the breeding site and NDVI measures. To this end, we extracted NDVI values

222   from the breeding sites of all tracked birds for the week and year of individual autumn departure and

223   spring arrival.

Statistical analyses

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

226   information on individual departure and arrival times from breeding and non-breeding sites but

227   lacked more detailed information on migration timing in between. To at least partially resolve this,

228   we calculated the time of crossing 30°N latitude, considering a constant travel speed (individual-

229   specific speed as calculated by the tracking data) along a great circle route between the individual

230   breeding and non-breeding sites. This latitude roughly borders the northern edge of the Sahara

231   Desert – a major ecological barrier that separates temperate breeding and subtropical non-breeding

232   grounds of trans-Saharan migratory birds.

233   To test a relationship between latitude and longitude of individual breeding and non-

234   breeding sites, we used linear mixed-effects models (LMM) with species as a random effect. We used

235   LMMs to further compare migration distances, travel speeds, and migration timing between the two

236   flyways, and to account for the non-independence of hierarchical data, we included species, breeding

237   latitude (nested within species), and year (nested within species and breeding latitude) as random

238   factors in the models. Because the species included in our study may differ in their migration timing,

239   we standardized all individual values across each timing event (departure, arrival, crossing 30°N

240   latitude) to zero-mean before including them in LMMs. Accordingly, individual values <0 denoted

241   relatively earlier migration while values >0 denoted relatively later migration timing. If an individual

242   was tracked over multiple years, we included only one track per individual in the models (n repeat

243   tracks = 24). The same model structure was further used to test for differences between the two

244   flyways in breeding site NDVI values at individual departure times in autumn and arrival times in

245   spring. All data analyses were done in R (R Core Team, 2018). LMMs were run with the R-package

246   'lme4' (Bates *et al.*, 2014) and estimates of parameters whose 95% CI did not overlap zero were

247   considered significant. Marginal and conditional R^2 values for model fit were obtained using the R-

248   package 'MuMIn' (Barton, 2019).

249

Results

Spatial structure of the migratory system

Overall, we found a strong positive relationship between the longitudes of individual breeding and non-breeding sites (β = 1.12, 95% CI = 1.02 to 1.21, conditional R^2 = 0.87; Figure 1), i.e. birds breeding further west in Europe over-wintered further west in Africa, and birds breeding further east in Europe over-wintered further east in Africa. Consequently, birds with more easterly breeding and non-breeding sites predominately used the Eastern flyway while birds with more westerly breeding and non-breeding sites predominately used the Western flyway (breeding longitude: $β_{eastern\ flyway}$ = 11.56, 95% CI = 10.31 to 12.79, conditional R^2 = 0.69; non-breeding longitude: $β_{eastern\ flyway}$ = 18.53, 95% CI = 16.44 to 20.65, conditional R^2 = 0.73).

We found a negative relationship between the latitudes of breeding and non-breeding sites (β = −0.47, 95% CI = −0.62 to −0.31, conditional R^2 = 0.79) with northern breeders leap-frogging southern breeders at the non-breeding sites. Moreover, using the Eastern flyway was strongly associated with more southerly non-breeding latitudes compared to the Western flyway ($β_{eastern\ flyway}$ = −3.97, 95% CI = −2.19 to −5.77, conditional R^2 = 0.74), while there was no association between breeding latitude and flyway use ($β_{eastern\ flyway}$ = −0.34, 95% CI = −1.29 to 0.60, conditional R^2 = 0.60). 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% (50/564) 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%; 29/163; 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%; 21/401; Great Reed Warbler (1), Collared Flycatcher (20)).

Migration distance and travel speed

Although the migration distances were generally longer along the Eastern flyway (median and IQR; Western flyway = 4531 km (2154–5412), Eastern flyway = 5167 km (3937–8114); 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 = 4491 km (3937–6286), spring = 4636 km (4053–6188); Figure 2a) but again, this difference was not significant (Table 1a). Travel speeds were significantly higher in spring compared to autumn (autumn

283 = 117 km day^{-1} (83–178), spring = 153 km day^{-1} (113–201); Figure 2b) but there were no differences

284 between the flyways (Table 1b).

Seasonal dynamics of the migratory system

286 We found both latitude of the breeding sites and flyway to be significant predictors for the timing of

287 various phases of the autumn migration. Although birds from different breeding latitudes started the

288 autumn migration at similar time, breeders from higher latitudes crossed the 30°N latitude and

289 arrived at the non-breeding sites later (Figure 3a, Table 1c-e). Our model results revealed that

290 individuals using the Western flyway migrated on average 5–7 days earlier than individuals using the

291 Eastern flyway at all stages of autumn migration (Table 1c-e).

292   In spring, migration started at similar times on both flyways, but birds travelling along the

293 Eastern flyway crossed the 30°N latitude and arrived at their European breeding sites later compared

294 to the birds travelling along the Western flyway (Figure 3b). Our model estimates accounting for

295 breeding latitude revealed a ca. 6.5-day difference between the two flyways for crossing 30°N

296 latitude and arrival at the breeding sites (Table 1gh). We found a positive relationship between

297 latitude of the breeding sites and spring arrival times, with each additional 1° latitude delaying

298 migration by ca. 1.5 days (Table 1h).

299   The migration period (migration window) was overall longer on the Eastern flyway in both

300 seasons (difference between the average start and end time of migration: autumn Western flyway =

301 42.4 days (95% CI = 39.6–45.3), autumn Eastern flyway = 59.5 days (53.2–65.9), spring Western

302 flyway = 32.9 days (30.4–35.5), spring Eastern flyway = 44.7 days (40.3–49.2); Figure 3).

303   The timing of spring green-up and autumn senescence revealed a SW-NE gradient with later

304 spring green-up and earlier autumn senescence in north-eastern Europe and, consequently, along

305 the Eastern flyway compared to the south-western Europe and the Western flyway (Figure 4).

306 Comparing the NDVI values from the breeding sites measured at the time of individual autumn

307 departures revealed that birds migrating along the Eastern flyway left their respective breeding sites

308 when the environment was more depleted compared to departure NDVI values for the birds

309 migrating along the Western flyway (Figure 5ab, Table 1i). Upon spring arrival, however, NDVI

310 measures were similar for birds migrating along both flyways (Figure 5cd, Table 1j).

311

Discussion

313 Migration routes of Afro-Palearctic migrants can be organized in two broadly defined flyways which

314 roughly converge between 10–20°E in Central Europe. The birds mainly follow a longitudinally

315 parallel migration pattern and northern breeders surpass southern breeders at the sub-Saharan non-

316 breeding sites, i.e. performing leapfrog migration. Our comparison of the migration timing revealed
317 generally later migration along the Eastern compared to the Western flyway in both autumn and
318 spring, which probably results from phenological differences between Western and Eastern Europe.
319 Indeed, the NDVI data showed a longitudinal gradient with later spring green-up and earlier autumn
320 vegetation senescence further east in Europe. In spring, irrespective of which flyway the birds used,
321 they matched arrival time at breeding sites with timing of local vegetation green-up, suggesting that
322 spring arrival time is fine-tuned in accordance with phenology of the breeding site. Furthermore,
323 birds breeding at higher latitudes arrived at their non-breeding sites in Africa and breeding sites in
324 Europe increasingly later at a rate of ca. 1.5 days delay per 1° increase in breeding latitude.

Spatial structure

326 Century-long efforts of bird ringing have revealed general migration directions and often also non-
327 breeding areas of most long-distance migrants breeding in Europe (e.g., Zink, 1973–1985; Bairlein,
328 2001; Wernham *et al.*, 2002; Bønløkke *et al.*, 2006; Cepák *et al.*, 2008; Valkama *et al.*, 2014). Our
329 findings add to this knowledge by identifying a strong relationship between the longitudes of
330 breeding and non-breeding sites such that individuals with eastern (European) breeding sites also
331 typically have eastern (African) non-breeding sites. Irrespective of whether it is a cause or a
332 consequence, this relationship extends to the use of a particular flyway. As a result, the parallel
333 migration system that links Europe and sub-Saharan Africa generates a certain degree of community
334 and ecosystem connectivity between Western Europe and West Africa, and Eastern Europe and
335 Central/East Africa (Bauer & Hoye, 2014). The presence of east-west oriented ecological barriers, i.e.
336 the Sahara Desert and the Mediterranean Sea, further facilitates migration pathways that flow
337 through the western and eastern edges of the barriers where the projected flight distance over
338 inhospitable areas are shorter when compared to the central part of the Sahara (Adamík *et al.*,
339 2016).

340   In some species, extending their breeding ranges while maintaining the genetically imprinted
341 migration direction and non-breeding areas has led to more complex migratory networks with longer
342 migration distances and, hence, higher costs of migration. For example, Aquatic Warbler
343 *Acrocephalus paludicola* has gone extinct in Western Europe, and the entire world population is now
344 breeding in eastern Europe yet maintaining the species' historic migration route along the Western
345 flyway to their non-breeding areas in West Africa (Salewski *et al.*, 2019). Similarly, the breeding range
346 of Pied Flycatcher *Ficedula hypoleuca* extends to 93°E and virtually the entire Palearctic population
347 migrates through the Iberian Peninsula along the Western flyway (Lundberg & Alatalo, 1992). On the
348 contrary, Red-backed Shrikes *Lanius collurio* breeding on the Iberian Peninsula migrate exclusively
349 along the Eastern flyway and overwinter in southern Africa (Tøttrup *et al.*, 2017).

350   The negative correlation between the latitudes of individual breeding and non-breeding sites

351   suggests leapfrog migration to be the prevailing pattern among long-distance migrants in the Afro-

352   Palearctic bird migration system. Leapfrog migration is thought to have arisen from competition at

353   the non-breeding sites during the post-glacial expansion of the breeding areas (Newton, 2008). As

354   the species increased in abundance and colonised new breeding sites further north, the competition

355   for resources at the non-breeding sites increased, forcing northern breeders to migrate further south

356   and leapfrog their conspecifics. Therefore, individuals from more northern breeding populations

357   typically migrate longer distances than their southern conspecifics.

Seasonal dynamics

359   Our results indicate that the timing of migration differs between the two flyways by approx. 5–7 days

360   at all annual migration stages, except for start of spring migration. The differences in spring arrival

361   times are likely driven by differences in phenology of the environment (spring green-up) along the

362   two flyways. We found a strong SW-NE gradient in the timing of spring green-up and autumn

363   senescence across Europe (Figure 4; Menzel *et al.*, 2005) that is likely resulting from the degree of

364   continentality, i.e. by how much a region's climate is influenced by the advection of air masses from

365   the ocean and from the landmass (Franzén, 1991).

366   Analyses of ring recovery data have already suggested such flyway-scale differences in annual

367   migration timing in, e.g. White Stork *Ciconia ciconia* (Bairlein, 2001), but quantifying these

368   differences for other annual stages than spring arrival remains often elusive with ring-recovery data.

369   Earlier tracking studies of long-distance migrants have shown population specific timing of annual

370   migration routines which are linked to spring phenology at various breeding latitudes (Conklin *et al.*,

371   2010; Briedis *et al.*, 2016; Gow *et al.*, 2019). Moreover, the northward progression of migrants in

372   spring was found to be tuned with vegetation phenology in the Nearctic-Neotropical migration

373   system (Marra *et al.*, 2005; La Sorte *et al.*, 2014b), where atmospheric and environmental conditions

374   *en route* played an important role in shaping seasonal and flyway scale differences in migrations

375   strategies (La Sorte *et al.*, 2014a,b, 2016; La Sorte & Fink, 2017). This finding is supported by scarce

376   evidence from tracking studies. For example, Barn Swallows breeding at the same location in the

377   Czech Republic differed in spring arrival dates depending on flyway with birds following the Eastern

378   flyway arriving on average five days later than birds following the Western flyway (Klvaňa *et al.*,

379   2018) – a difference that coincides with our estimates (Table 1h). To avoid adverse conditions *en*

380   *route* in early spring, long-distance migrants travelling along the Eastern flyway should be adapted to

381   cross the Sahara later compared to migrants on the Western flyway. Selection pressure against

382   premature arrival is likely high as early arriving individuals have been shown to suffer increased

383   mortality (Lerche-Jørgensen *et al.*, 2018), particularly in years with delayed spring green-up (Briedis

384   *et al.*, 2017).

385   In autumn, birds travelling along the Eastern flyway departed from their breeding sites later

386   compared to the birds travelling along the Western flyway despite an earlier vegetation senescence

387   in the Eastern Europe. Long-distance migrants generally depart from their breeding sites well ahead

388   of senescence of the environment in autumn (Briedis *et al.*, 2016), suggesting that departure timing

389   in autumn is probably controlled by mechanisms other than deteriorating habitat conditions.

390   Experimental studies on Stonechats *Saxicola torquatus* revealed that migratory restlessness

391   (*Zugunruhe*) starts significantly earlier in Irish birds compared to their continental counterparts (Van

392   Doren *et al.*, 2017) suggesting endogenous control for the start of autumn migration (Pedersen *et al.*,

393   2018).

394   *Zugunruhe* data also demonstrate seasonal differences in the length and intensity of

395   migratory activity (Van Doren *et al.*, 2017). We found that the migration window was shorter (and,

396   thus the migration traffic was more synchronized) and travel speed was faster in spring compared to

397   autumn on both flyways. Theoretical models predict faster and more synchronized spring migration

398   due to high importance for early arrival at the breeding grounds (Kokko, 1999; Kokko *et al.*, 2006)

399   that is counterbalanced by increased costs of premature arrival (Lerche-Jørgensen *et al.*, 2018). The

400   ratio of average travel speeds in spring and autumn that we found in our study falls within the range

401   of values reported earlier for the Afro-Palearctic migratory system (Karlsson *et al.*, 2012; Nilsson *et*

402   *al.*, 2013, 2014).

403   To summarize, our findings indicate important differences in seasonal dynamics between the

404   western and the eastern parts of the Afro-Palearctic migration system. Long-distance migrants track

405   vegetation green-up when arriving at the breeding sites in spring but depart ahead of vegetation

406   senescence in autumn. Consequently, the degree of continentality along migration routes and at the

407   birds' breeding sites influences the timing of migration on a broad scale.

Conclusion

408

409   Scaling up from individual tracking and adopting the concept of migratory flyways helps to identify

410   broad-scale spatiotemporal movement patterns of migratory birds (La Sorte *et al.*, 2014a). This

411   knowledge is fundamental for understanding the main drivers that shape migration strategies of

412   birds. Since a parallel migration pattern exists between Europe and Africa with distinct differences in

413   timing, this must be an adaptation to the prevailing environmental settings along each flyway.

414   To uncover the potential effects of global change on migratory systems, continued effort in

415   monitoring migrants and synthesising datasets are necessary. To this end, citizen science data (e.g.

416   EuroBirdPortal.org) offer a great potential to study the timing of bird migration across Europe, and

417   the continent-wide weather radar network can provide the rate of migration (Nussbaumer *et al.*,

418   2019), while individual-based tracking still present the best opportunities to link breeding, stopover

419   and non-breeding sites on individual and population level.

References

Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti, F., Procházka, P., Salewski, V. & Hahn, S. (2016) Barrier crossing in small avian migrants: Individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*, **6**, 21560.

Alerstam, T. (2011) Optimal bird migration revisited. *Journal of Ornithology*, **152**, 5–23.

Bairlein, F. (2001) Results of bird ringing in the study of migration routes. *Ardea*, **89**, 7–19.

Barton, K. (2019) MuMIn: Multi-Model Inference. R package version 1.43.6.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bauer, S. & Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, **344**, 1242552.

Bolker, B. & R Development Core Team (2017) bbmle: Tools for General Maximum Likelihood Estimation.

Bønløkke, J., Madsen, J.J., Thorup, K., Pedersen, K.T., Bjerrum, M. & Rahbek, C. (2006) *Dansk Trækfugleatlas*, Rhodos, Humlebæk.

Bradley, B.A., Jacob, R.W., Hermance, J.F. & Mustard, J.F. (2007) A curve fitting procedure to derive inter-annual phenologies from time series of noisy satellite NDVI data. *Remote Sensing of Environment*, **106**, 137–145.

Briedis, M., Bauer, S., Adamík, P., Alves, J.A., Costa, J.S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C.M., Procházka, P., Hahn, S. (2020) Data from: Broad-scale patterns of the Afro-Palearctic landbird migration. *Dryad Digital Repository*. (https://doi.org/10.5061/dryad.hdr7sqvdc)

Briedis, M., Hahn, S. & Adamík, P. (2017) Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology*, **17**, 11.

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. & Adamík, P. (2016) Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology*, **47**, 743–748.

Brlík, V., Koleček, J., Burgess, M., Hahn, S., Humple, D., Krist, M., Ouwehand, J., Weiser, E.L., Adamík, P., Alves, J.A., Arlt, D., Barišić, S., Becker, D., Belda, E.J., Beran, V., Both, C., Bravo, S.P., Briedis, M., Chutný, B., Ćiković, D., Cooper, N.W., Costa, J.S., Cueto, V.R., Emmenegger, T., Fraser, K., Gilg, O., Guerrero, M., Hallworth, M.T., Hewson, C., Jiguet, F., Johnson, J.A., Kelly, T., Kishkinev, D., Leconte, M., Lislevand, T., Lisovski, S., López, C., McFarland, K.P., Marra, P.P., Matsuoka, S.M., Matyjasiak, P., Meier, C.M., Metzger, B., Monrós, J.S., Neumann, R., Newman, A., Norris, R., Pärt, T., Pavel, V., Perlut, N., Piha, M., Reneerkens, J., Rimmer, C.C., Roberto-Charron, A., Scandolara, C., Sokolova, N., Takenaka, M., Tolkmitt, D., van Oosten, H., Wellbrock, A.H.J., Wheeler, H., van der Winden, J., Witte, K., Woodworth, B.K. & Procházka, P. (2019) Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias. *Journal of Animal Ecology*, **00**, 0–14.

Brown, C.R. & Brown, M.B. (1998) Intense natural selection on body size and wing and tailsymmetry in Cliff Swallows during severe weather. *Evolution*, **52**, 1461–1475.

Bruderer, B. (2001) Recent studies modifying current views of nocturnal bird migration in the Mediterranean. *Avian Ecol Behav*, **7**, 11–25.

15

463 Cepák, J., Klvaňa, P., Škopek, L., Schröpfer, L., Jelínek, M., Horák, D., Formánek, J. & Zárybnický, J.
464   (2008) *Atlas migrace ptáku Ceské a Slovenské Republiky*, Aventinum, Prague.

465 Conklin, J.R., Battley, P.F., Potter, M.A. & Fox, J.W. (2010) Breeding latitude drives individual
466   schedules in a trans-hemispheric migrant bird. *Nature Communications*, **1**, 67.

467 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the
468   Antrhopocene. *Science*, **401**, 401–406.

469 Van Doren, B.M., Liedvogel, M. & Helm, B. (2017) Programmed and flexible: long-term Zugunruhe
470   data highlight the many axes of variation in avian migratory behaviour. *Journal of Avian Biology*,
471   **48**, 155–172.

472 Franzén, L.G. (1991) The changing frequency of gales on the swedish west coast and its possible
473   relation to the increased damage to coniferous forests of Southern Sweden. *International
474   Journal of Climatology*, **11**, 769–793.

475 Gilroy, J.J., Gill, J.A., Butchart, S.H.M., Jones, V.R. & Franco, A.M.A. (2016) Migratory diversity predicts
476   population declines in birds. *Ecology Letters*, **19**, 308–317.

477 Gow, E.A., Burke, L., Winkler, D.W., Knight, S.M., Berzins, L.L., Bradley, D.W., Clark, R.G., Be, M.,
478   Blake, T., Bridge, E.S., Dawson, R.D., Dunn, P.O., Garant, D., Holroyd, G., Horn, A.G., Hussell,
479   D.J.T., Lansdorp, O., Laughlin, A.J., Leonard, M.L., Pelletier, F., Shutler, D., Siefferman, L., Taylor,
480   C.M., Trefry, H., Vleck, C.M., Vleck, D., Whittingham, L.A., Norris, D.R. & Gow, E.A. (2019) A
481   range-wide domino effect and resetting of the annual cycle in a migratory songbird. *Proceeding
482   of the Royal Society B: Biological Sciences*, **286**, 20181916.

483 Hahn, S., Amrhein, V., Zehtindijev, P. & Liechti, F. (2013) Strong migratory connectivity and seasonally
484   shifting isotopic niches in geographically separated populations of a long-distance migrating
485   songbird. *Oecologia*, **173**, 1217–1225.

486 Hahn, S., Bauer, S. & Liechti, F. (2009) The natural link between Europe and Africa - 2.1 billion birds
487   on migration. *Oikos*, **118**, 624–626.

488 Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.

489 Karlsson, H., Nilsson, C., Bäckman, J. & Alerstam, T. (2012) Nocturnal passerine migrants fly faster in
490   spring than in autumn: A test of the time minimization hypothesis. *Animal Behaviour*, **83**, 87–
491   93.

492 Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and
493   planet. *Science*, **348**, 1222–1232.

494 Klvaňa, P., Cepák, J., Munclinger, P., Michálková, R., Tomášek, O. & Albrecht, T. (2018) Around the
495   Mediterranean: an extreme example of loop migration in a long-distance migratory passerine.
496   *Journal of Avian Biology*, **49**, jav-01595.

497 Kokko, H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–
498   950.

499 Kokko, H., Gunnarsson, T.G., Morrell, L.J. & Gill, J.A. (2006) Why do female migratory birds arrive
500   later than males? *Journal of Animal Ecology*, **75**, 1293–1303.

501 Koleček, J., Procházka, P., El-Arabany, N., Tarka, M., Ilieva, M., Hahn, S., Honza, M., de la Puente, J.,
502   Bermejo, A., Gürsoy, A., Bensch, S., Zehtindjiev, P., Hasselquist, D. & Hansson, B. (2016) Cross-
503   continental migratory connectivity and spatiotemporal migratory patterns in the great reed
504   warbler. *Journal of Avian Biology*, **47**, 756–767.

505 Kölzsch, A., Bauer, S., de Boer, R., Griffin, L., Cabot, D., Exo, K.M., van der Jeugd, H.P. & Nolet, B.A.

506   (2015) Forecasting spring from afar? Timing of migration and predictability of phenology along
507   different migration routes of an avian herbivore. *Journal of Animal Ecology*, **84**, 272–283.

508   Lerche-Jørgensen, M., Korner-Nievergelt, F., Tøttrup, A.P., Willemoes, M. & Thorup, K. (2018) Early
509   returning long-distance migrant males do pay a survival cost. *Ecology and Evolution*, **8**, 11434–
510   11449.

511   Lindström, Å., Alerstam, T. & Hedenström, A. (2019) Faster fuelling is the key to faster migration.
512   *Nature Climate Change*, **9**, 288–289.

513   Lisovski, S., Hewson, C.M., Klaassen, R.H.G.G., Korner-Nievergelt, F., Kristensen, M.W., Hahn, S., W.,
514   K.M. & Hahn, S. (2012) Geolocation by light: accuracy and precision affected by environmental
515   factors. *Methods in Ecology and Evolution*, **3**, 603–612.

516   Lisovski, S., Ramenofsky, M. & Wingfield, J.C. (2017) Defining the degree of seasonality and its
517   significance for future research. *Integrative and Comparative Biology*, **57**, 934–942.

518   Lundberg, A. & Alatalo, R. V (1992) *The Pied Flycatcher*, Poyser, London.

519   Marra, P.P., Francis, C.M., Mulvihill, R.S. & Moore, F.R. (2005) The influence of climate on the timing
520   and rate of spring bird migration. *Oecologia*, **142**, 307–315.

521   Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory
522   bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.

523   McKinnon, E.A. & Love, O.P. (2018) Ten years tracking the migrations of small landbirds: Lessons
524   learned in the golden age of bio-logging. *The Auk*, **135**, 834–856.

525   McNamara, J.M., Welham, R.K. & Houston, A.I. (1998) The timing of migration within the context of
526   an annual routine. *Journal of Avian Biology*, **29**, 416–423.

527   Menzel, A., Sparks, T.H., Estrella, N. & Eckhardt, S. (2005) "SSW to NNE" - North Atlantic Oscillation
528   affects the progress of seasons across Europe. *Global Change Biology*, **11**, 909–918.

529   Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Sayre, R., Trabucco, A. & Zomer, R. (2013) A high-
530   resolution bioclimate map of the world: A unifying framework for global biodiversity research
531   and monitoring. *Global Ecology and Biogeography*, **22**, 630–638.

532   Moreau, R.E. (1972) *The Palearctic African Bird Migration Systems*, Academic Press, London.

533   Newton, I. (2008) *The migration ecology of birds*, Academic Press, London, UK.

534   Nilsson, C., Bäckman, J. & Alerstam, T. (2014) Seasonal modulation of flight speed among nocturnal
535   passerine migrants: differences between short- and long-distance migrants. *Behavioral Ecology*
536   *and Sociobiology*, **68**, 1799–1807.

537   Nilsson, C., Klaassen, R.H.G. & Alerstam, T. (2013) Differences in speed and duration of bird migration
538   between spring and autumn. *The American Naturalist*, **181**, 837–45.

539   Nussbaumer, R., Benoit, L., Mariethoz, G., Liechti, F., Bauer, S. & Schmid, B. (2019) A geostatistical
540   approach to estimate high resolution nocturnal bird migration densities from a weather radar
541   network. *Remote Sensing*, **11**, 2233.

542   Pedersen, L., Jackson, K., Thorup, K. & Tøttrup, A.P. (2018) Full-year tracking suggests endogenous
543   control of migration timing in a long-distance migratory songbird. *Behavioral Ecology and*
544   *Sociobiology*, **72**.

545   Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. (2005) Using the
546   satellite-derived NDVI to assess ecological responses to environmental change. *Trends in*
547   *Ecology and Evolution*, **20**, 503–510.

548   R Core Team (2018) R: A language and environment for statistical computing.

549   Rötzer, T. & Chmielewski, F. (2001) Phenological maps of Europe. *Climate Research*, **18**, 249–257.

550   Rubolini, D., Pastor, A.G., Pilastro, A. & Spina, F. (2002) Ecological barriers shaping fuel stores in barn
551   swallows Hirundo rustica following the central and western Mediterranean flyways. *Journal of*
552   *Avian Biology*, **33**, 15–22.

553   Salewski, V., Flade, M., Lisovski, S., Poluda, A., Iliukha, O., Kiljan, G., Malashevich, U. & Hahn, S. (2019)
554   Identifying migration routes and non-breeding staging sites of adult males of the globally
555   threatened Aquatic Warbler *Acrocephalus paludicola*. *Bird Conservation International*, 1–12.

556   Schmaljohann, H., Lisovski, S. & Bairlein, F. (2017) Flexible reaction norms to environmental variables
557   along the migration route and the significance of stopover duration for total speed of migration
558   in a songbird migrant. *Frontiers in Zoology*, **14**, 1–16.

559   Sliwinsky, U. (1938) Isopiptesen einiger Vogelarten in Europa. *Zoologica Poloniae*, **2**, 249–287.

560   La Sorte, F. a., Fink, D., Hochachka, W.M., Farnsworth, A., Rodewald, A.D., Rosenberg, K. V., Sullivan,
561   B.L., Winkler, D.W., Wood, C. & Kelling, S. (2014a) The role of atmospheric conditions in the
562   seasonal dynamics of North American migration flyways. *Journal of Biogeography*, **41**, 1685–
563   1696.

564   La Sorte, F.A. & Fink, D. (2017) Migration distance, ecological barriers and en-route variation in the
565   migratory behaviour of terrestrial bird populations. *Global Ecology and Biogeography*, **26**, 216–
566   227.

567   La Sorte, F.A., Fink, D., Hochachka, W.M., Delong, J.P. & Kelling, S. (2014b) Spring phenology of
568   ecological productivity contributes to the use of looped migration strategies by birds.
569   *Proceedings of the Royal Society Series B*, **281**, 20140984.

570   La Sorte, F.A., Fink, D., Hochachka, W.M. & Kelling, S. (2016) Convergence of broad-scale migration
571   strategies in terrestrial birds. *Proceedings of the Royal Society B: Biological Sciences*, **283**,
572   20152588.

573   Southern, H.N. (1938) The spring migration of the Swallow over Europe. *Brittish Birds*, **32**, 4–7.

574   Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., Dasari, H.P.,
575   Araújo, M.B., Wikelski, M. & Rahbek, C. (2017) Resource tracking within and across continents
576   in long-distance bird migrants. *Science Advances*, **3**, E1601360.

577   Tøttrup, A.P., Pedersen, L., Onrubia, A., Klaassen, R.H.G. & Thorup, K. (2017) Migration of red-backed
578   shrikes from the Iberian Peninsula: optimal or sub-optimal detour? *Journal of Avian Biology*, **48**,
579   149–154.

580   Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K., Komdeur, J., Bairlein, F. & Koks, B.J. (2014)
581   Migratory connectivity and population-specific migration routes in a long-distance migratory
582   bird. *Proceedings of the Royal Society B*, **281**, 20132897.

583   Valkama, J., Saurola, P., Lehikoinen, A., Lehikoinen, E., Piha, M., Sola, P. & Velmala, W. (2014) *The*
584   *Finnish Bird Ringing Atlas. Vol. II*, Finnish Museum of Natural History and Ministry of
585   Environment, Helsinki.

586   Wernham, C.V., M.P., T., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds). (2002) *The*
587   *Migration Atlas: movements of the birds of Britain and Ireland*, T. & A. D. Poyser, London.

588   Zalles, J.I. & Bildstein, K.L. eds. (2000) *Raptor watch a global directory of raptor migration sites*,
589   BirdLife International & Hawk Mountain Sanctuary, Cambridge & Kempton.

590   Zink, G. (1973) *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel*, Vols. 1-3.
591   AULA-Verlag, Wiesbaden, Germany.
592

Data accessibility

593

594   Data are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.hdr7sqvdc

595   (Briedis et al. 2020).

Tables

Table 1

598 Results of linear mixed-effects models. Interactions where 95% CI does not overlap zero are
599 highlighted in bold.

600

601

	Marginal R²	Conditional R²	Fixed effects			Random effects		
				Estimate	95% CI		Variance	SD
(a) Migration distance (km)	<0.01	0.89	Intercept	5303	4664 – 5942	Year:(BS* latitude:Species)	61359	247.7
			Flyway(western)	42.05	−177.8 – 260.2	BS latitude:Species	640134	800.1
			Season(spring)	69.64	−0.3 – 139.5	Species	1796471	1340.3
						Residual	299379	547.2
(b) Travel speed (km day⁻¹)	0.03	0.25	Intercept	131.2	107.0 – 155.2	Year:(BS latitude:Species)	26.7	5.2
			Flyway(western)	−4.48	−21.9 – 13.1	BS latitude:Species	136.6	11.7
			Season(spring)	**28.51**	**17.6 – 39.4**	Species	1870.3	43.3
						Residual	7301.7	85.5
(c) BS departure	0.02	0.76	Intercept	242.3	225.8 – 258.8	Year:Species	24.4	4.9
			Flyway(western)	**−6.65**	**−9.89 – −3.38**	Species	374.6	19.4
			BS latitude	−0.20	−0.49 – 0.09	Residual	131.8	11.5
(d) Crossing 30°N autumn	0.08	0.72	Intercept	221.0	206.4 – 235.7	Year:Species	16.7	4.1
			Flyway(western)	**−5.60**	**−8.47 – −2.68**	Species	204.7	14.3
			BS latitude	**0.77**	**0.51 – 1.04**	Residual	96.8	9.8
(e) non-BS arrival	0.09	0.75	Intercept	219.9	200.5 – 239.3	Year:Species	42.3	6.5
			Flyway(western)	**−7.36**	**−11.4 – −3.4**	Species	457.3	21.4
			BS latitude	**1.42**	**1.08 – 1.76**	Residual	189.8	13.8
(f) non-BS departure	0.06	0.69	Intercept	33.3	16.7 – 49.8	Year:Species	16.4	4.0
			Flyway(western)	−2.30	−5.76 – 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	0.15	0.68	Intercept	54.9	40.9 – 69.0	Year:Species	8.7	2.9
			Flyway(western)	**−6.42**	**−9.41 – −3.45**	Species	159.0	12.6
			BS latitude	**1.07**	**0.81 – 1.33**	Residual	101.8	10.1
(h) BS arrival	0.20	0.71	Intercept	52.8	39.6 – 66.0	Year:Species	9.1	3.0
			Flyway(western)	**−6.52**	**−9.33 – −3.71**	Species	172.8	13.1
			BS latitude	**1.47**	**1.23 – 1.71**	Residual	104.5	10.2
(i) NDVI at BS departure	0.04	0.73	Intercept	0.205	0.107 – 0.304	Year:Species	0.342	0.059
			Flyway(western)	**0.047**	**0.026 – 0.068**	Species	0.688	0.083
			BS latitude	**0.003**	**0.001 – 0.005**	Residual	0.409	0.064
(j) NDVI at BS arrival	0.03	0.68	Intercept	0.178	0.095 – 0.262	Year:Species	0.216	0.046
			Flyway(western)	0.017	−0.001 – 0.003	Species	0.488	0.070
			BS latitude	**0.003**	**0.002 – 0.005**	Residual	0.340	0.058

* BS = breeding site

602

Figures

Figure 1

605 Flyway use of Afro-Palearctic long-distance migrants (red – Western flyway, blue – Eastern flyway).
606 Pie charts mark the breeding site locations (diameter indicates sample size [n]) and show the
607 proportions of individuals that use either of the flyways within each population. Individual non-
608 breeding sites are marked with dots. *inset* Frequency distribution of flyway use according to breeding
609 site longitude (values are binned into 10° longitudinal bands). The orange bar indicates populations
610 that use both flyways, i.e. populations with a migratory divide.
611

612
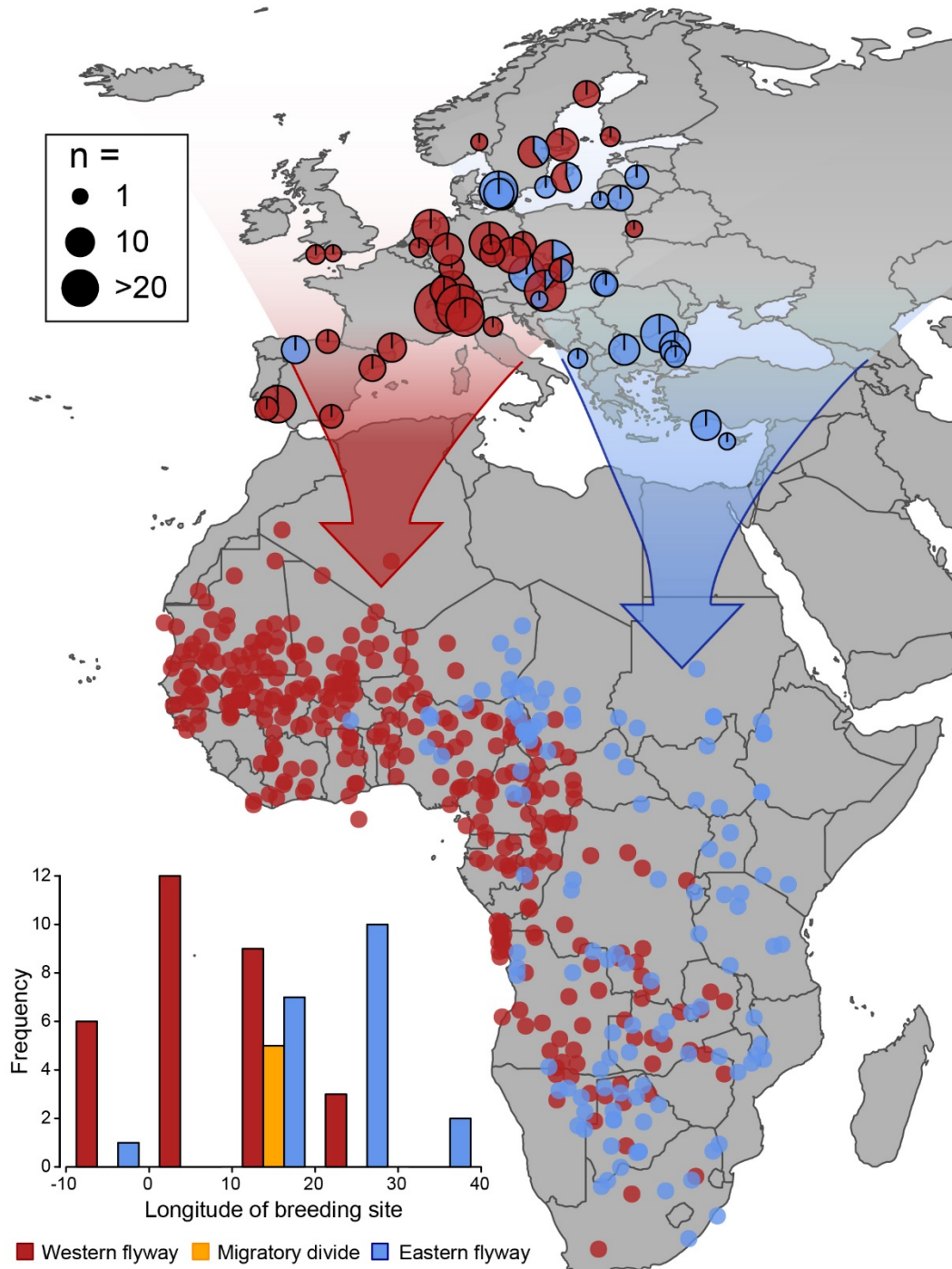
Figure 2

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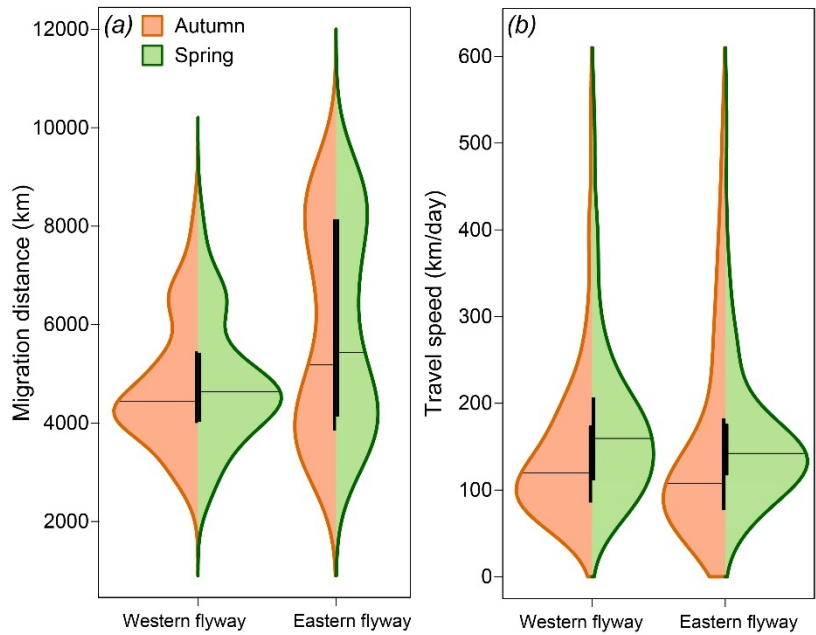

Figure 3

Standardized migration timing on the Western (red) and Eastern (blue) flyways in (a) autumn and (b) spring. Density plots show 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, shaded area shows 95% CI of migration window.
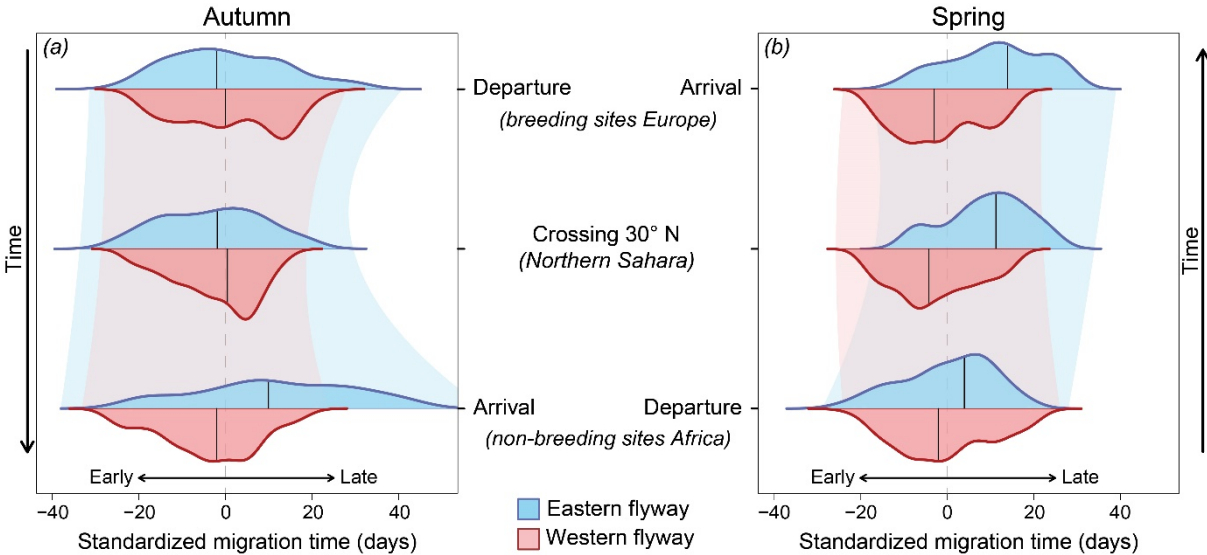
Figure 4

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 likely driven by agricultural practices that might also result in the early autumn senescence patterns at various parts of southwestern Europe, e.g. western France and eastern England). Estimates are smoothed values across neighbouring cells (mean values across nine cells) based on a 4 x 4 km grid-cell.
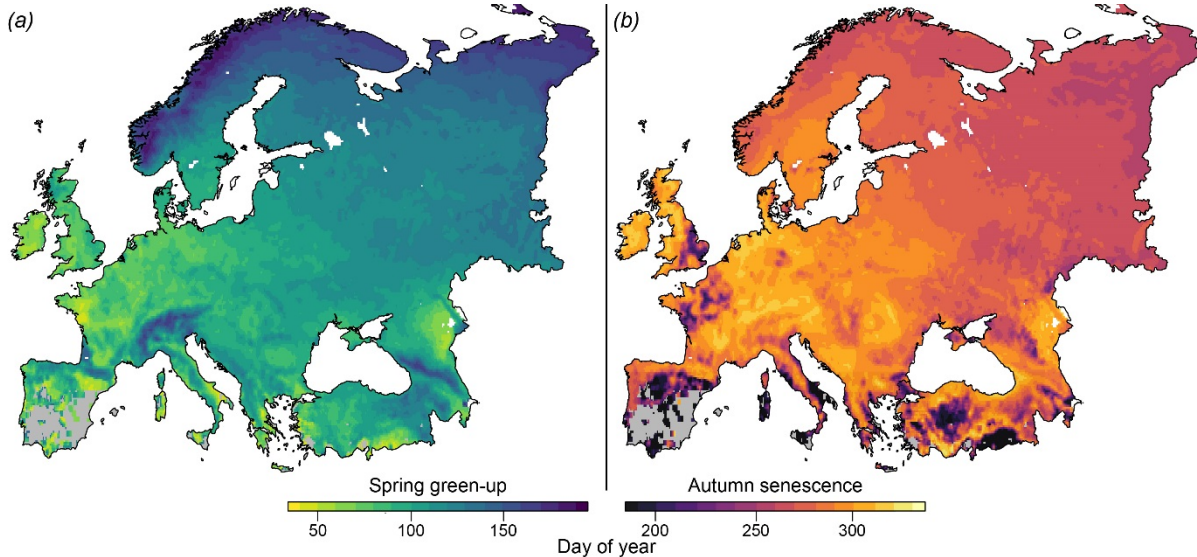

Figure 5

Individual breeding site departure and arrival times (day of the year – DOY) and corresponding NDVI values at the breeding sites according to the individual flyway use (red – Western flyway, blue – Eastern flyway). (a) individual departure from the breeding site times in autumn, (b) NDVI measures at the breeding sites at the time of departure, (c) individual breeding site arrival time in spring, and (d) NDVI measure at the breeding sites at the time of arrival. The shape of the violins illustrates density distribution of data; horizontal black lines indicate median values; vertical black bars denote interquartile ranges.
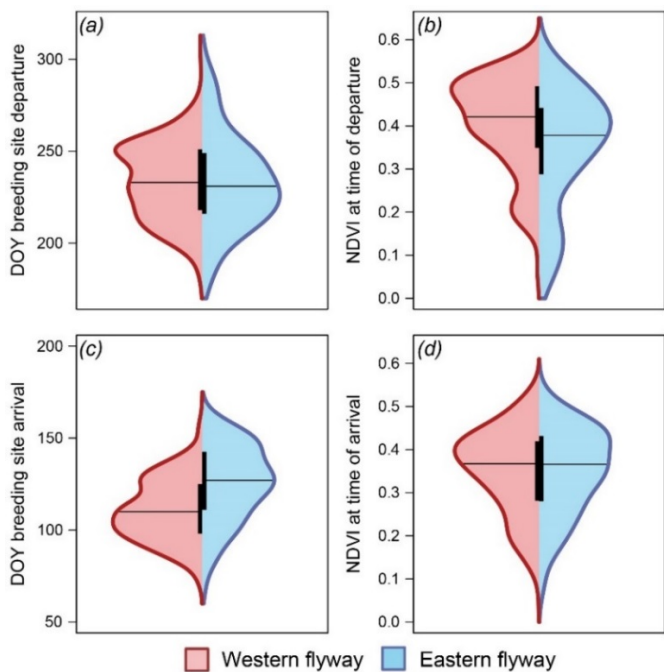
Appendix

Data sources

Arizaga, J., Willemoes, M., Unamuno, E., Unamuno, J.M. & Thorup, K. (2015) Following year-round movements in Barn Swallows using geolocators: Could breeding pairs remain together during the winter? *Bird Study*, **62**, 141–145.

Arlt, D., Olsson, P., Fox, J.W., Low, M. & Pärt, T. (2015) Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. *Animal Migration*, **2**, 47–62.

Bäckman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjöberg, S., Thorup, K. & Tøttrup, A.P. (2017) Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study. Journal of Avian Biology, **48**, 309–319.

Briedis, M., Beran, V., Hahn, S. & Adamík, P. (2016a) Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators. *Journal of Ornithology*, **157**, 619–626.

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. & Adamík, P. (2016b) Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology*, **47**, 743–748.

Briedis, M., Kurlavičius, P., Mackevičienė, R., Vaišvilienė, R. & Hahn, S. (2018a) Loop migration, induced by seasonally different flyway use, in Northern European Barn Swallows. *Journal of Ornithology*, **159**, 885–891.

Briedis, M., Krist, M., Král, M., Voigt, C.C. & Adamík, P. (2018b) Linking events throughout the annual cycle in a migratory bird - wintering period buffers accumulation of carry-over effects. *Behavioral Ecology and Sociobiology*, **72**, 93.

Briedis, M., Träff, J., Hahn, S., Ilieva, M., Král, M., Peev, S. & Adamík, P. (2016c) Year-round spatiotemporal distribution of the enigmatic Semi-collared Flycatcher *Ficedula semitorquata*. *Journal of Ornithology*, **157**, 895–900.

Catry, I., Catry, T., Granadeiro, J.P., Franco, A.M.A. & Moreira, F. (2014) Unravelling migration routes and wintering grounds of European rollers using light-level geolocators. *Journal of Ornithology*, **155**, 1071–1075.

Cresswell, B. & Edwards, D. (2013) Geolocators reveal wintering areas of European Nightjar (*Caprimulgus europaeus*). *Bird Study*, **60**, 77–86.

Dhanjal-Adams, K.L., Bauer, S., Emmenegger, T., Hahn, S., Lisovski, S. & Liechti, F. (2018) Spatiotemporal group dynamics in a long-distance migratory bird. *Current Biology*, **28**, 2824–2830.e3.

Emmenegger, T., Mayet, P., Duriez, O. & Hahn, S. (2014) Directional shifts in migration pattern of rollers (*Coracias garrulus*) from a western European population. *Journal of Ornithology*, **155**, 427–433.

Evens, R., Beenaerts, N., Witters, N. & Artois, T. (2017) Repeated migration of a juvenile European Nightjar *Caprimulgus europaeus*. *Journal of Ornithology*, **158**, 881–886.

Finch, T., Saunders, P., Avilés, J.M., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., Račinskis, E., Rodríguez-Ruiz, J., Sackl, P., Schwartz, T., Tiefenbach, M., Valera, F., Hewson, C., Franco, A. & Butler, S.J. (2015) A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. *Diversity and Distributions*, **21**, 1051–1062.

Gersten, A. & Hahn, S. (2016) Timing of migration in Common Redstarts (*Phoenicurus phoenicurus*) in relation to the vegetation phenology at residence sites. *Journal of Ornithology*, **157**, 1029–1036.

Hahn, S., Amrhein, V., Zehtindjiev, P. & Liechti, F. (2013) Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. *Oecologia*, **173**, 1217–1225.

Hahn, S., Alves, J. A., Bedev, K., Costa, J. S., Emmenegger, T., Schulze, M., Tamm, P., Zehtindjiev, P. and Dhanjal-Adams, K. L. (in press). Range wide migration corridors and non-breeding areas of a northward expanding Afro-Palaearctic migrant, the European Bee-eater *Merops apiaster*. Ibis.

Hasselquist, D., Montràs-Janer, T., Tarka, M. & Hansson, B. (2017) Individual consistency of long-distance migration in a songbird: significant repeatability of autumn route, stopovers and wintering sites but not in timing of migration. Journal of Avian Biology, **48**, 91–102.

Klvaňa, P., Cepák, J., Munclinger, P., Michálková, R., Tomášek, O. & Albrecht, T. (2018) Around the Mediterranean: an extreme example of loop migration in a long-distance migratory passerine. Journal of Avian Biology, **49**, jav-01595.

Koleček, J., Hahn, S., Emmenegger, T. & Procházka, P. (2018) Intra-tropical movements as a beneficial strategy for Palearctic migratory birds. *Royal Society Open Science*, **5**, 171675.

Koleček, J., Procházka, P., El-Arabany, N., Tarka, M., Ilieva, M., Hahn, S., Honza, M., de la Puente, J., Bermejo, A., Gürsoy, A., Bensch, S., Zehtindjiev, P., Hasselquist, D. & Hansson, B. (2016) Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology*, **47**, 756–767.

Lemke, H.W., Tarka, M., Klaassen, R.H.G., Åkesson, M., Bensch, S., Hasselquist, D. & Hansson, B. (2013) Annual cycle and migration strategies of a trans-Saharan migratory songbird: A geolocator study in the Great Reed Warbler. *PLoS ONE*, **8**, e79209.

Liechti, F., Scandolara, C., Rubolini, D., Ambrosini, R., Korner-Nievergelt, F., Hahn, S., Lardelli, R., Romano, M., Caprioli, M., Romano, A., Sicurella, B. & Saino, N. (2015) Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. *Journal of Avian Biology*, **46**, 254–265.

Meier, C.M., Karaardıç, H., Aymí, R., Peev, S.G., Bächler, E., Weber, R., Witvliet, W. & Liechti, F. (2018) What makes Alpine swift ascend at twilight? Novel geolocators reveal year-round flight behaviour. *Behavioral Ecology and Sociobiology*, **72**, 45.

Ouwehand, J., Ahola, M.P., Ausems, A.N.M.A., Bridge, E.S., Burgess, M., Hahn, S., Hewson, C., Klaassen, R.H.G., Laaksonen, T., Lampe, H.M., Velmala, W. & Both, C. (2016) Light-level geolocators reveal migratory connectivity in European

705   populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, **47**, 69–83.
706   Ouwehand, J. & Both, C. (2017) African departure rather than migration speed determines variation in spring arrival in pied
707   flycatchers. *Journal of Animal Ecology*, **86**, 88–97.
708   Procházka, P., Brlík, V., Yohannes, E., Meister, B., Auerswald, J., Ilieva, M. & Hahn, S. (2018) Across a migratory divide:
709   divergent migration directions and non-breeding grounds of Eurasian reed warblers revealed by geolocators and
710   stable isotopes. *Journal of Avian Biology*, **49**, e01769.
711   Rodríguez-Ruiz, J., De La Puente, J., Parejo, D., Valera, F., Calero-Torralbo, M.A., Reyes-González, J.M., Zajková, Z., Bermejo,
712   A. & Avilés, J.M. (2014) Disentangling migratory routes and wintering grounds of Iberian near-threatened European
713   rollers *Coracias garrulus*. *PLoS ONE*, **9**, e115615.
714   Salewski, V., Flade, M., Lisovski, S., Poluda, A., Iliukha, O., Kiljan, G., Malashevich, U. & Hahn, S. (in press) Identifying
715   migration routes and non-breeding staging sites of adult males of the globally threatened Aquatic Warbler
716   *Acrocephalus paludicola*. *Bird Conservation International*.
717   Schmaljohann, H., Buchmann, M., Fox, J.W. & Bairlein, F. (2012) Tracking migration routes and the annual cycle of a trans-
718   Sahara songbird migrant. *Behavioral Ecology and Sociobiology*, **66**, 915–922.
719   Selstam, G., Sondell, J. & Olsson, P. (2015) Wintering area and migration routes for Ortolan Buntings *Emberiza hortulana*
720   from Sweden determined with light-geologgers. *Ornis Svecica*, **25**, 3–14.
721   Szép, T., Liechti, F., Nagy, K., Nagy, Z. & Hahn, S. (2017) Discovering the migration and non-breeding areas of sand martins
722   and house martins breeding in the Pannonian basin (central-eastern Europe). *Journal of Avian Biology*, **48**, 114–122.
723   Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L., Dasari, H.P., Araújo, M.B., Wikelski, M.
724   & Rahbek, C. (2017) Resource tracking within and across continents in long-distance bird migrants. *Science Advances*,
725   **3**, E1601360.
726   Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jørgensen, P.S., Fox, J., Afanasyev, V., Rahbek,
727   C. & Alerstam, T. (2012) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-
728   temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences*, **279**,
729   1008–16.
730   Tøttrup, A.P., Pedersen, L., Onrubia, A., Klaassen, R.H.G. & Thorup, K. (2017) Migration of red-backed shrikes from the
731   Iberian Peninsula: optimal or sub-optimal detour? *Journal of Avian Biology*, **48**, 149–154.
732   Wellbrock, A.H.J., Bauch, C., Rozman, J. & Witte, K. (2017) 'Same procedure as last year?' Repeatedly tracked swifts show
733   individual consistency in migration pattern in successive years. *Journal of Avian Biology*, **48**, 897–903.
734   van Wijk, R.E., Schaub, M. & Bauer, S. (2017) Dependencies in the timing of activities weaken over the annual cycle in a
735   long-distance migratory bird. *Behavioral Ecology and Sociobiology*, **71**, 73.
736   van Wijk, R.E., Schaub, M., Hahn, S., Juárez-García-Pelayo, N., Schäfer, B., Viktora, L., Martín-Vivaldi, M., Zischewski, M. &
737   Bauer S. (2018) Diverse migration strategies in hoopoes (*Upupa epops*) lead to weak spatial but strong temporal
738   connectivity. *The Science of Nature*, **105**, 42.
739   Willemoes, M., Strandberg, R., Klaassen, R.H.G., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M. &
740   Alerstam, T. (2014) Narrow-front loop migration in a population of the Common Cuckoo Cuculus canorus, as revealed
741   by satellite telemetry. PLoS ONE, 9, e83515.