

Geolocators reveal variation and sex-specific differences in the migratory strategies of a long-distance migrant

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Songbird populations are in decline all over the world, and our understanding of the causal mechanisms remains surprisingly limited. It is important to identify the extent of individual variations in migratory behaviour to better understand species' ability to respond to environmental change. We describe the annual migratory behaviour of British breeding European Pied Flycatchers *Ficedula hypoleuca* by using light-recording geolocators. During both autumn and spring migrations, individuals used previously unknown staging areas on the Iberian Peninsula and northern West Africa. Furthermore, partial sex-specific segregation in the location of non-breeding areas was observed within West Africa, with females located west of males. We also found sex-based phenological differences, with females staying longer in non-breeding areas and undertaking the spring Sahara Desert crossing later than males. Irrespective of sex, multiple use of the two predominant staging regions was identified during both migrations, with 63% of individuals stopping more than once in these regions. We also identified instances of migratory behaviours rarely documented in individually tracked songbirds. These include making day-time landfall during the Sahara crossing, and a case of a temporary retreat migration, with an individual aborting a spring Sahara crossing before making a second successful crossing 14 days later. Together, our results show variability in migratory behaviour both between sexes and between individuals. For Pied Flycatchers, such flexible migratory behaviour may increase their resilience to environmental change.

Keywords: desert grounding, *Ficedula hypoleuca*, migration, Pied Flycatcher, stopover behaviour, temporary retreat migration.

Within species, migratory behaviour can vary among individuals through a number of mechanisms. Variation within populations, such as differences in migratory route and phenology, are predominantly attributed to individual condition (Schmaljohann & Naef-Daenzer 2011, Smolinsky

et al. 2013), where those in poorer condition may require more frequent or longer stops to allow for increased refuelling opportunities at staging areas (Goymann *et al.* 2010, Hoh *et al.* 2018). Another example is provided by populations on different sides of migratory divides that undertake different migrations (Bensch *et al.* 1999, Procházka *et al.* 2018). Understanding the extent of such variation in migratory behaviour is crucial if we are to forecast the potential effects of environmental change on population trends. Greater within-species

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variation and flexible migration behaviours may facilitate individual and population-level resilience to environmental change compared with relatively fixed schedules and behaviour.

Migratory songbirds commonly have differential migration of sex or age classes, in extreme cases resulting in segregation on a broad geographical scale (Catry *et al.* 2005, Rotics *et al.* 2017). Differences in migratory behaviour between sexes can result from selection on males to arrive earlier to breeding areas to secure high-quality territories, with males departing non-breeding grounds earlier (Ouwehand & Both 2017), migrating faster (Tøttrup & Thorup 2008, Woodworth *et al.* 2016) and refuelling at staging areas for less time (Seewagen *et al.* 2013, Bozó & Heim 2016). Resource competition at the non-breeding grounds could also contribute to sex-specific migration as less dominant females are typically outcompeted, leading to geographical and/or habitat segregation between sexes (Parrish & Sherry 1994, Marra & Holmes 2001, Townsend *et al.* 2012).

Here, we describe migratory patterns and behaviour of British breeding European Pied Flycatchers *Ficedula hypoleuca* (hereafter Pied Flycatcher), a long-distance migrant songbird within the Afro-Palearctic flyway, predominantly breeding across northern Europe, and migrating annually to sub-Saharan West Africa. The UK population has declined by 48% since 1995 (Massimino *et al.* 2019), with the causes poorly understood. Despite being one of the most well-studied migratory songbirds within the Afro-Palearctic flyway, relatively little is known about population-specific migratory behaviour or the location of staging and non-breeding areas. For the British population, tracks from two males in a single year, and locations from only five ringing recoveries (out of 724 095 individuals ringed within the UK to 2019), suggest a non-breeding area in a relatively small region of western Africa (Ouwehand *et al.* 2016). Although work from a population in the Netherlands showed differences in migratory timing between sexes and that all individuals cross the Sahara during both autumn and spring migrations by making a non-stop day and night flight (Ouwehand & Both 2016, Ouwehand *et al.* 2016), the migratory routes, staging and non-breeding locations used by Pied Flycatchers have not been examined in detail. Moreover, the extent of variation between individuals' migratory behaviour remains largely unknown, and as female Pied Flycatchers have not

previously been tracked from Britain, it is not clear how distinct any sexual differences might be.

Using light-level geolocators, we describe the full annual cycle of a British breeding Pied Flycatcher population. We determine the predominant ('typical') migration route and migratory timings, and the location and residency periods of staging and non-breeding areas. Particular interest was given to the identification of any variation from the predominant migratory behaviours found, to evaluate the extent of sex-specific or between-individual variation within this breeding population.

METHODS

Geocator attachment and retrieval

All birds were captured in nestboxes while breeding. We deployed 101 geolocators to adult breeding Pied Flycatchers during 2017 (42 males and 37 females) and 2018 (22 males) at East Dartmoor, southwest England (50°36'N, 3°43'W). We used Intigeo-P30Z11-7-DIP Migrate Technology geolocators with a 7-mm-long light pipe, fitted with a Rappole-Tipton leg loop harness (Rappole & Tipton 1991) made from 0.7-mm-diameter elastane. Harness span was determined based on previous deployments on Pied Flycatchers, with several pre-assembled geolocators and harnesses available at deployment to reduce processing time (harness span range 30–36 mm). The tags and harness together weighed 0.42 g, a mean of 3.3% of body mass (range 2.7–3.8%). To assess potential tag effects, a further 48 males (26 in 2017, 22 in 2018) and 39 females (2017 only) were captured and processed in the same way as tagged birds except that no geocator was fitted. All individuals were marked with a single colour ring, and two different colours were used, indicating whether an individual was tagged or untagged with different colours used each year. The 2017/18 return rate of tagged males was 31% compared with 23% for control males, and 16% for tagged females compared with 33% for control females (14% excluding an individual that lost the geocator during the year). The 2018/19 tagged male return rate was 44% compared with 41% for the control cohort. To determine the effect of tagging on apparent between-year survival, we calculated effect sizes for each year and for both sexes separately using the 'esc_2x2' function in R (CRAN

package: esc). This showed no effect on males from tags in either year of the study, 0.22 in 2017/18 (95% CI -0.40 to 0.84) and -0.01 in 2018/19 (95% CI -0.56 to 0.55). However, there was a weak negative tag effect for females, -0.52 (95% CI -1.13 to 0.08).

In total, 30 individuals fitted with geolocators were recaptured in the breeding season after deployment, 19 from the 2017 deployment (13 male, six female) and 11 from 2018 (all male). Geolocators were recovered from 29 individuals, as one female tagged in 2017 lost a tag before recapture. Two tags deployed in 2018 failed entirely, and so in total we had usable data for 27 individuals. Of these 27, data for both spring and autumn migrations were recorded for 22 individuals, autumn only for two individuals and three only held data for the non-breeding residency period (Table S1). One male was tracked over two annual cycles from 2017 to 2019.

Ring recovery data from Pied Flycatchers captured during the breeding period (April–July) within the UK, and subsequently recaptured in either Europe or Africa during the autumn (July–September) or spring (March–May) migratory period, were obtained from the British Trust for Ornithology. These data spanned the period 1950–2020.

Geocator analysis

We used the threshold method to derive location estimates from the recorded light data (Lisovski *et al.* 2020). First, we log-transformed light values and defined sunrise and sunset times in the R-package TwGeos (<https://github.com/slisovski/TwGeos>) using a light intensity threshold of 0.8 lux on the log-transformed scale. We distinguished between movement and stationary periods applying the *invChanges* function from the R-package GeoLight v2.0.1 (Lisovski & Hahn 2012). Based on this, twilight events were grouped into either movement or stationary periods; the minimum duration of each period was set to four twilight events, which corresponds to 2 days. We then used *mergeGroups* functions to merge consecutive stationary periods that spatially overlapped by more than 85%.

We used in-habitat calibration as the method of estimating the sun elevation angle (Lisovski & Hahn 2012). Each tag was calibrated for this separately, using the maximum stationary period at the

breeding site after tagging and before departure, or between the end of spring migration and tag retrieval. Finally, we modelled individual migration tracks using the R-package SGAT (<https://github.com/SWotherspoon/SGAT>), which applies a Bayesian framework combining the observed sunrise and sunset data with *a priori* knowledge of bird behaviour to provide location estimates with the associated uncertainty (see Lisovski *et al.* 2020). To this end, we used the group threshold model with the predefined stationary and movement periods described above and allowed the birds to move in any direction, but defined that stationary areas must be located on land. The twilight model was set to follow a log-normal distribution using parameters from the in-habitat sun elevation angle calibration unique to each bird, whereas the behavioural model followed a γ distribution (shape 2.2, scale 0.08), implying relatively few fast movements corresponding to migration between the staging sites. For the initial path, we extrapolated latitudinal positions during the equinox periods by setting the tolerance of solar declination of up to 12°. We initiated the model by drawing 1000 initial samples from a modified Gamma model with relaxed assumptions and then tuned the model five times with all assumptions/priors implemented (Gamma model; 300 iterations each). The model was run for 2000 iterations to ensure convergence. From the resulting 2000 chains, we extracted median location estimates and their 95% credibility intervals of each stationary period and of each twilight during the movement.

Sahara crossing behaviour

For species that continually cross extensive ecological barriers such as deserts in daylight hours, light patterns recorded by geolocators during crossings have a distinctive pattern of high values and low fluctuation resulting from a lack of vegetation shading, and more constant feather and cloud shading. This uninterrupted full light pattern (FLP) method of describing daytime barrier crossings has previously been described by Adamík *et al.* (2016), and has been used in other geolocation studies where it has been verified by differential changes in temperature recorded by the same tags (Jiguet *et al.* 2019, Malmiga *et al.* 2021). FLP data contrast with the light pattern recorded when the bird remains stationary during the day. For each individual, we identified when this pattern of

continuous full light intensity occurred. Although this pattern can be seen visually from plotting the raw light values on a log scale, generating and plotting running mean and running variance on the light data enables the identification of periods of daytime continuous flight with greater confidence. Running mean and variance were applied to log-transformed lux data across a 90-minute time interval around the event of interest (i.e. 45 min before and after). Instances where the running variance was less than 0.001 for a period of 6 h or more during the autumn and spring migratory periods were considered likely to identify bouts of FLP. These periods were cross-referenced to location estimates derived from SGAT, which parameterize the time period in which an individual could be located between the Iberian Peninsula and West Africa, where barrier crossing must occur. Anomalous Sahara crossing behaviours are identifiable when multiple distinct bouts of daytime FLP occurred during this period, which shows that the individual failed to complete the crossing in a single flight.

For all individuals, we assumed that migration over the Sahara commenced immediately after dusk, the start of migratory flights in songbirds (Åkesson *et al.* 1996, Smolinsky *et al.* 2013, Adamík *et al.* 2016). Barrier crossing flights either ended during daylight hours, indicated by an abrupt end to the FLP, or if FLP was not present the following day, we assumed the end was 1 h before sunrise on the day following FLP (Schmaljohann *et al.* 2007, Adamík *et al.* 2016, Jiguet *et al.* 2019, Malmiga *et al.* 2021). We estimated the total duration of flight over the Sahara as the nocturnal period before or after a continuous period of FLP, in addition to the daytime FLP.

Statistical analyses

Outputs from SGAT were used for all aspects of subsequent analysis. Interpretation of SGAT outputs identified the location and timings (arrival at, departure from and duration) of non-breeding residency periods. The resulting data were used to

provide summary statistics and used to test hypotheses. Interpretation of FLP data provided data on the initiation and duration of Sahara crossing events.

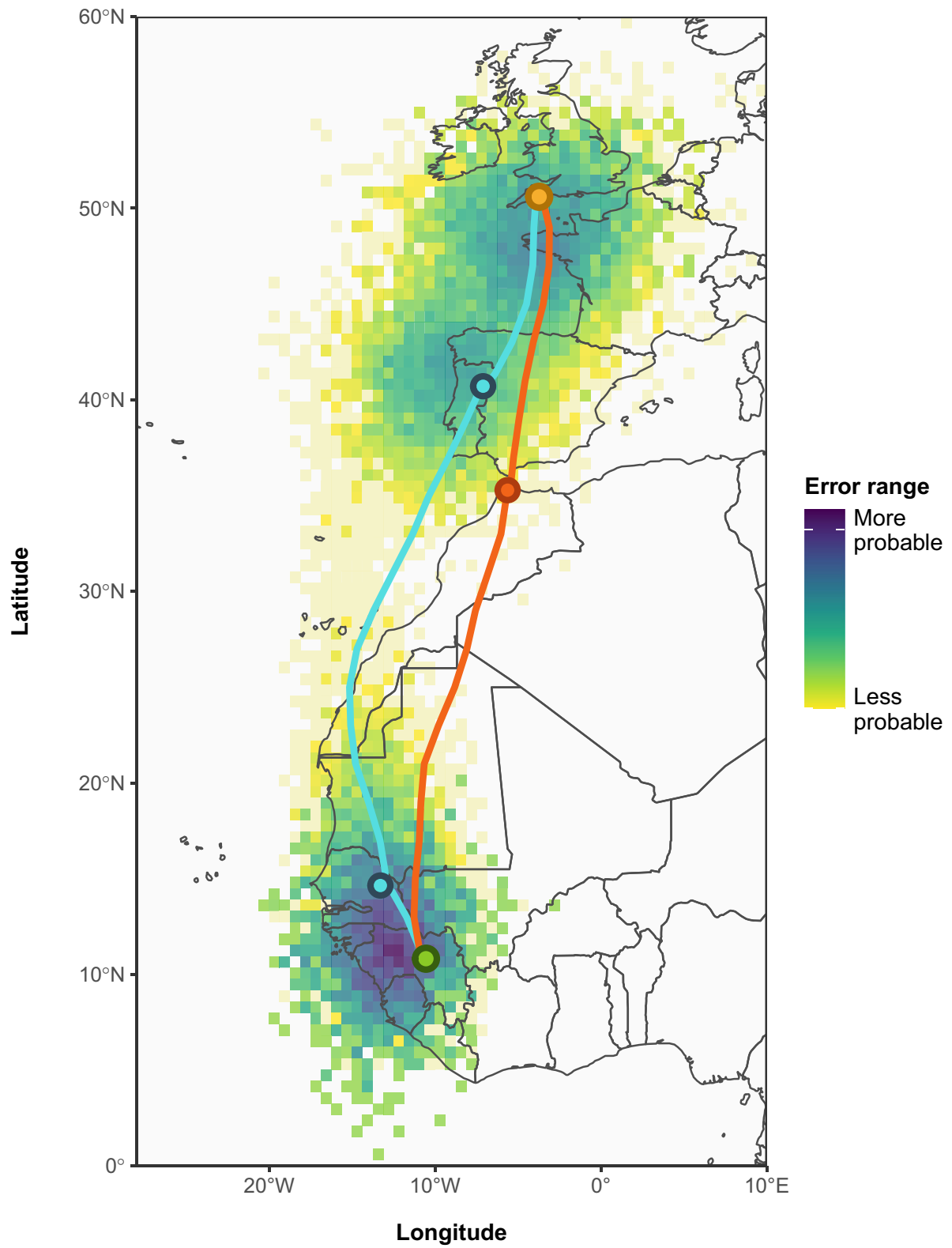
General linear models (GLMs) were used to assess individual and sex-specific differences in autumn and spring migrations (CRAN package: stats). GLMs determined seasonal differences within four separate models to investigate the number of staging sites used, the duration of the entire migration, the duration of the Sahara crossing and the stationary duration at staging sites as response variables, fitted against season as the explanatory term. Subsequent GLMs determined sex-specific differences within five separate models to investigate the effect of duration of stationary period residency, date of departure from non-breeding areas, arrival at breeding site, spring Sahara crossing commencement and longitude of non-breeding area as response variables, fitted against sex as the explanatory term. Log transformations ($\ln$) improved model fit in some instances, and Poisson errors were used where non-normality was observed. Year was included as an additional explanatory variable in GLMs to account for annual effects, as was individual identity in separate models to account for the single individual that was repeat tracked for two migrations. Wilcoxon t tests for unequal variance were used to account for homoscedastic errors relating to use of staging sites (either seasonal differences in duration, or annual differences in numbers used). All analyses were conducted in R 3.6.2 (R Core Team 2019).

RESULTS

Predominant migration route, staging site use and timings

The typical migratory route is shown in Figure 1 (comprising the average route and average locations of main non-breeding and staging areas which were used by >80% of individuals). In autumn, breeding individuals departed Britain over a 35-day period commencing in mid-July (average 2 August, range

Figure 1. The average migratory route derived from all tracked Pied Flycatchers, from breeding grounds in the UK (yellow circle) to non-breeding grounds in West Africa (green circle). Blue and orange lines represent the average estimated route of all birds combined, during autumn and spring migrations respectively, with major staging areas (used by > 80% of the population) indicated by blue circles. The 50% probability distributions of location estimates are provided based upon the mean error produced for each individual.



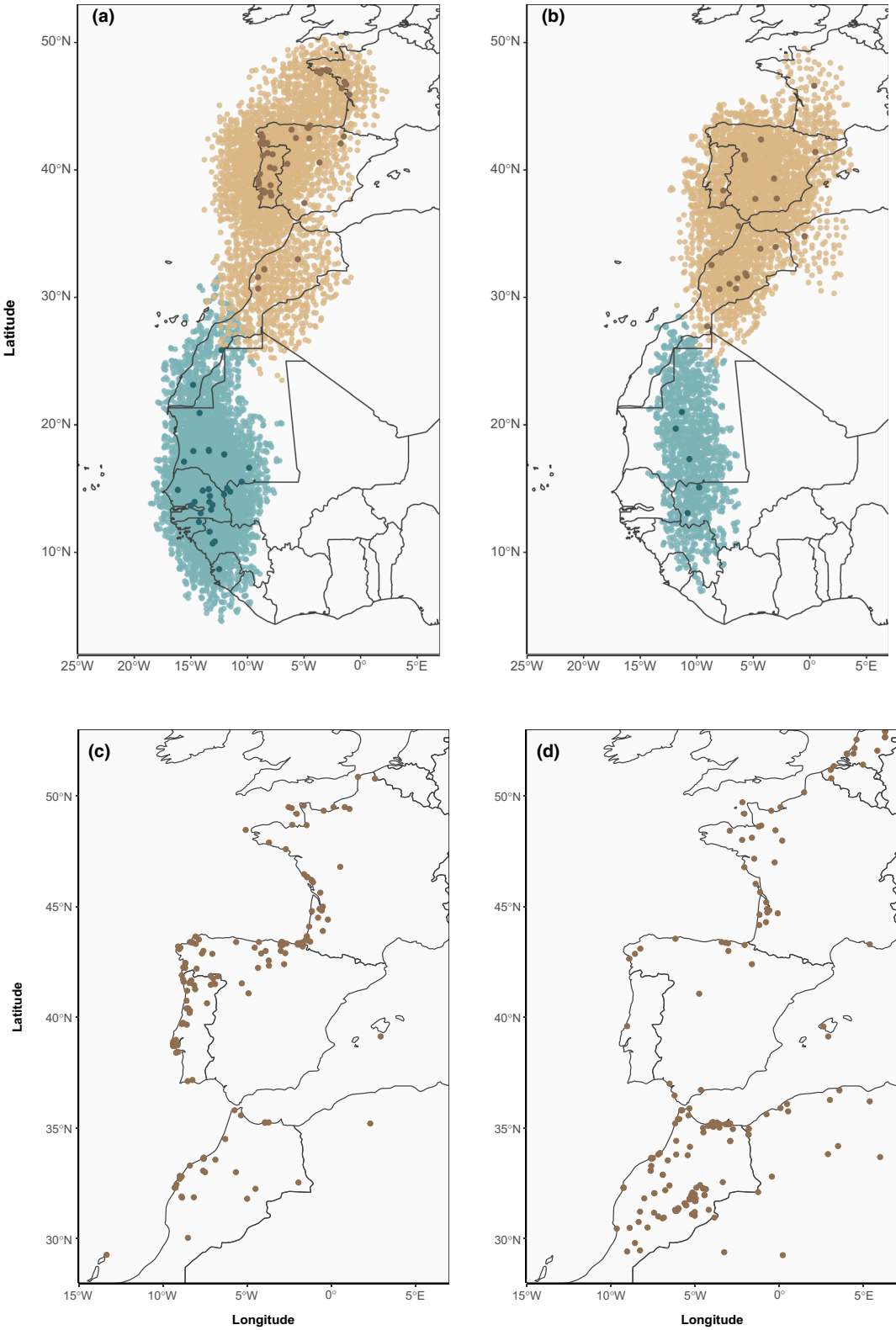


Figure 2. Staging areas of tracked Pied Flycatchers during autumn (a) and spring (b) migrations, indicating stops typically made on the Iberian Peninsula (orange: autumn $n = 46$, spring $n = 23$) and northern West Africa (blue: autumn $n = 22$, spring $n = 5$). Darker circles represent median positions derived from SGAT analysis, and coloured regions represent 25% probability distributions of location estimates. The bottom row shows ring recovery data from UK breeding Pied Flycatchers, which were recovered in autumn (c) and spring (d). Ten per cent of spring recovery data are located outside the graphics limits, but are not shown to aid visual comparison. These occur in central Europe, predominantly Germany.

15 July to 19 August; Table S2), migrating south along the western coast of France. All individuals used staging sites on the Iberian Peninsula (Fig. 2a) for a mean $\pm$ sd of 10.8 ± 6.2 days (range 2.4–28.4 days). After staging, individuals followed the western coast of North Africa, and undertook non-stop flights to cross the Sahara at its western edge (longitudinal average 14.8°W , range 9.6°W to 17.8°W). After the Sahara crossing, most individuals (89%) stopped at a second staging area in northwest West Africa, the majority (64%) located in Senegal or Mauritania (longitudinal average 13.3°W , range 9.8°W to 16.2°W), for an average 12.6 ± 6.8 days (range 3.5–32.5 days) before making a flight to the main non-breeding area.

Most individuals were stationary at the main non-breeding areas between mid-September (average 19 September, range 31 August to 3 November) until late March (average 25 March, range 27 February to 25 April). These were located in Western Africa, centred on Guinea but encompassing Sierra Leone, Liberia, Ivory Coast and southern Mali (Table S2), although one individual was located further north in southern Mauritania.

Migration duration was shorter for all individuals between West Africa and Britain in spring compared with autumn (8.7 days in spring, 16.9 days in autumn; Poisson GLM $\chi^2_{1,20} = 9.37$, $r^2 = 0.78$, $P = 0.002$), excluding time spent stationary at staging areas. Spring migration distance was shorter compared with autumn, with individuals crossing the Sahara at longitudes further east (longitudinal range 7.1°W to 13.2°W). However, the desert crossing duration was not significantly different to autumn (1.7 ± 0.2 days, range 1.5–2.5 days in autumn, 1.8 ± 0.3 days, range 1.5–2.5 days in spring, GLM $F_{1,48} = 1.35$, $r^2 = 0.03$, $P = 0.25$).

Uninterrupted crossings over the Sahara in both autumn and spring consisted of non-stop daytime flight (defined as typical behaviour as observed in 90% of individuals). After crossing the Sahara in spring, most individuals (86% of tags still recording at this stage) stopped at staging areas in either

northwest Africa or, more frequently, on the Iberian peninsula, for 6.9 ± 4.3 days (range 1.9–14.8 days), the same region used for staging during the autumn migration (Fig. 2b; Table S3). This spatial pattern was matched by ring recovery data from all capture records of UK breeding Pied Flycatchers, which were subsequently recovered in the autumn (July–September, $n = 158$, Fig. 2c), or in the spring (March–May, $n = 213$, Fig. 2d).

Variation in staging site use and timings

The majority of individuals (82%) made three distinct stops at staging areas during their migrations, two stops during the autumn migration, first on the Iberian Peninsula and second in northern West Africa, and one stop during the spring migration, again on the Iberian Peninsula, suggesting a typical staging ecology (Fig. 2; Table 1). Four individuals additionally stopped in the northern West African staging region on spring migration before crossing the Sahara. These four birds departed non-breeding areas earlier (Poisson GLM run for males only, to account for sex-specific differences in departure from non-breeding area, $\chi^2_{1,15} = 17$, $r^2 = 0.7$, $P < 0.001$), then were stationary for an extended period of time (average 20 days, 471.1 h). Multiple use of the two predominant staging regions (Iberian Peninsula and northern West Africa) was common (Fig. 2), with 63% of individuals stopping within these regions during both autumn and spring migration. Additional stops were more frequent during autumn compared with spring (2.7 in autumn, 1.3 in spring, Poisson GLM $\chi^2_{1,47} = 13.16$, $r^2 = 0.49$, $P < 0.001$), and were for a longer duration (301.6 h in autumn, 28.5 h in spring, Wilcoxon test $t_{46} = 6.74$, $P < 0.001$, Table 1), though sites in northern West Africa were used for an overall longer duration than those in Iberia (GLM $F_{1,99} = 9.38$, $r^2 = 0.09$, $P = 0.003$). Staging areas were also identified along the west coast of France, where eight individuals stopped for an average of 10 days (240 h).

Table 1. Staging behaviour of tracked Pied Flycatchers. The absolute number of stops is identified, with the corresponding proportion of the tracked individuals. Staging behaviour is separated into typical stops – those which are used in the majority of instances by >80% of the tracked individuals, and those which are made in addition to the typical behaviour, which were only made by a subset of individuals.

	Expected 'typical' staging events			Additional staging use				
	Autumn		Spring Iberia	Autumn			Spring	
	Iberia	NW Africa		France	Iberia	NW Africa	NW Africa	Iberia
2017/18	18 (100%)	17 (94%)	14 (82%)	8 (39%)	6 (28%)	3 (17%)	5 (29%)	4 (24%)
2018/19	9 (100%)	8 (89%)	5 (100%)	1 (11%)	4 (33%)	0	0	0

Sample size varied due to battery failure, with five tags (one from 2017/18, four from 2018/19) not recording the spring migration.

The number of staging sites used was variable between years as well as among individuals, with fewer stops made in 2018 (2017: 4.2, 2018: 3, Wilcoxon test $t_{16} = 3.54$, $P = 0.003$). In both seasons, frequency of staging site use was similar irrespective of sex (in autumn males stopped 2.8 times, females 2.6 times, Poisson GLM $\chi^2_{1,25} = 0.21$, $r^2 = 0.07$, $P = 0.83$, and in spring males 1.4 times, females 0.8 times, Poisson GLM $\chi^2_{1,20} = 1.05$, $r^2 = 0.48$, $P = 0.26$), with the exception that in spring, only males used northern West African staging areas again, and females only stopped after successfully crossing the Sahara and reaching the Iberian Peninsula. Duration of use of main staging areas similarly did not differ by sex, although in both seasons, females tended to spend less time at staging areas. In autumn, staging areas on the Iberian Peninsula or northern West Africa were used by males for 32.6 days, and by females for 24.7 days (GLM_{ln} $F_{1,25} = 1.26$, $r^2 = 0.06$, $P = 0.22$). In spring, staging areas on the Iberian Peninsula were used by males for 7.5 days and by females for 4.8 days (Poisson GLM $\chi^2_{1,25} = 1.26$, $r^2 = 0.06$, $P = 0.21$).

One male was tracked over two successive years, providing data on two migrations. This male showed apparent repeatability in non-breeding longitude (9.3°W in 2017/18, 9.7°W in 2018/19) with the estimated main non-breeding locations 120 km apart (within the range of geolocation error), but stopped at six staging areas in 2017/18 compared with three in 2018/19.

Variation in migratory behaviour

We found no evidence suggesting within-population variation of migratory route. However,

we observed alternative patterns for crossing the Sahara, with five out of 50 desert crossings showing an interrupted pattern. In contrast to the constant FLP characteristic of uninterrupted crossings (Fig. 3a), differences in Sahara crossing patterns were observed in five instances where FLP was separated into two distinct flights (Table S4). Three interrupted crossings were in autumn, and one in spring (Fig. 3b, all were in 2018). The times between the two subsequent crossing flights were 1.2, 0.6 and 0.6 days in autumn, and 0.6 in spring, assuming that migration over the Sahara commenced immediately after dusk, and ended with the end of the FLP, or 1 h before sunrise on the day following FLP. The total duration of the entire desert crossing was consequently longer compared with uninterrupted non-stop crossings (uninterrupted Sahara crossing duration in autumn 1.7 ± 0.2 days, range 1.5–2.5 days, and spring 1.8 ± 0.3 days, range 1.5–2.5 days, interrupted crossings in autumn 2.7, 3.5 and 2.7 days, and 2.7 days in spring). Excluding the time between crossing flights (when we assume individuals were stationary), the total duration of FLP for each full crossing provides an estimate of the time taken to cross the Sahara (2.1, 1.5 and 2.9 days in autumn, and 2.1 days in spring).

Two periods of FLP were identified from one individual during a spring desert crossing, indicating an aborted crossing followed by a complete crossing 14 days later. This individual initially attempted to cross the Sahara on 21 March, and fully crossed on 4–5 April (Fig. 3c). The initial Sahara crossing attempt lasted 1.4 days, approximately 0.6 days less than expected for a complete spring crossing (2 days average, range 1.5–2.5 days). The second crossing attempt was

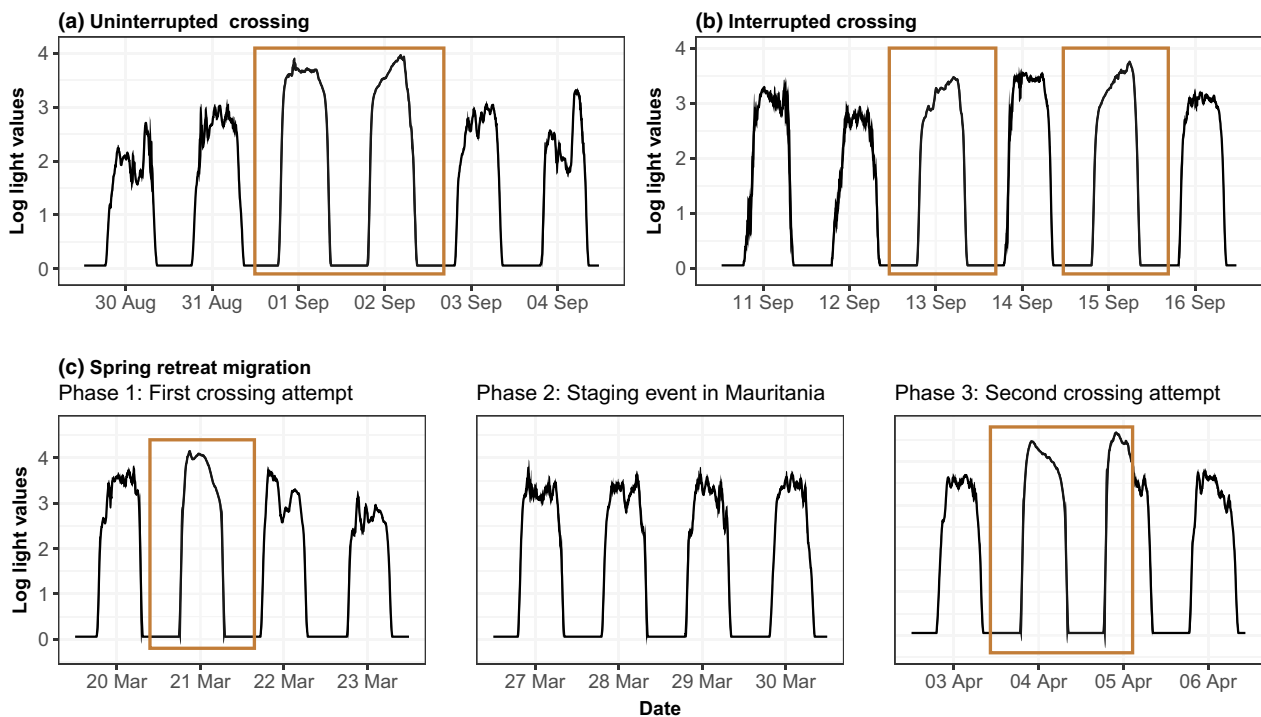


Figure 3. Barrier crossing behaviour in Pied Flycatchers, showing both uninterrupted Sahara crossings and all interrupted Sahara crossing behaviours. Log-transformed light (lux) values are provided over time during the period of interest, and light data are shown as a running mean with variance (10 fixes equivalent to 45 min, either side of each data point). All full light pattern (FLP) data are identified within a box, which are indicative of Sahara crossings. Uninterrupted successful migration across the Sahara Desert is illustrated in (a). Light values with large fluctuations (from shading) depict typical movement data shown for 2 days either side of the FLP crossing, whereas the crossing is characterized by little fluctuation around a high running mean. Grounding events, which occur during an interrupted crossing, are similar to typical daily data, but are also characterized by higher light values, as illustrated in (b). (c) Chronology of events for a temporary retreat migration: an initial aborted Sahara crossing attempt, subsequent movement data typically associated with a staging event in Mauritania, and finally a successful crossing attempt 2 weeks later.

completed in 1.8 days, closer to the average time taken to complete the spring crossing. Over the spring equinox, when estimation of latitude is impossible, geolocation analysis of longitude supports this event, as after departure from the non-breeding location, daily longitude estimates indicated a movement east, and a subsequent movement west to a staging area, rather than a constant and direct movement as observed in all other spring migration tracks. Geolocation analysis suggested that the bird was stationary for at least 8 days (93 h, Table S2) south of the desert (Mauritania) between 25 March and 2 April.

Sex-specific migration

There were sex-specific differences in location of the main non-breeding period, with females

spending the non-breeding period located west of males (average female longitude $12.00^{\circ}\text{W} \pm 0.63^{\circ}\text{W}$; male $10.18^{\circ}\text{W} \pm 1.2^{\circ}\text{W}$, Fig. 4a, GLM $F_{1,23} = 12.53$, $r^2 = 0.35$, $P < 0.002$). Sex-specific migration duration and phenological patterns were evident (Fig. 4b; Table S5 and Fig. S1). Females were stationary in main non-breeding areas for longer than males (females 205 ± 10.8 days, range 191–217 days, males 181 ± 21 days, range 123–204 days, Poisson GLM $\chi^2_{1,20} = 11.7$, $r^2 = 0.23$, $P < 0.001$), departed later (female 7 April, range 29 March to 25 April; male 21 March, range 27 February to 4 April; GLM $F_{1,20} = 9.77$, $r^2 = 0.33$, $P = 0.005$), and commenced the spring Sahara crossing later than males (female 8 April, range 28 March to 25 April; male 28 March, range 11 March to 5 April; Poisson GLM $\chi^2_{1,20} = 4.84$, $r^2 = 0.3$, $P = 0.02$). All individuals arrived at

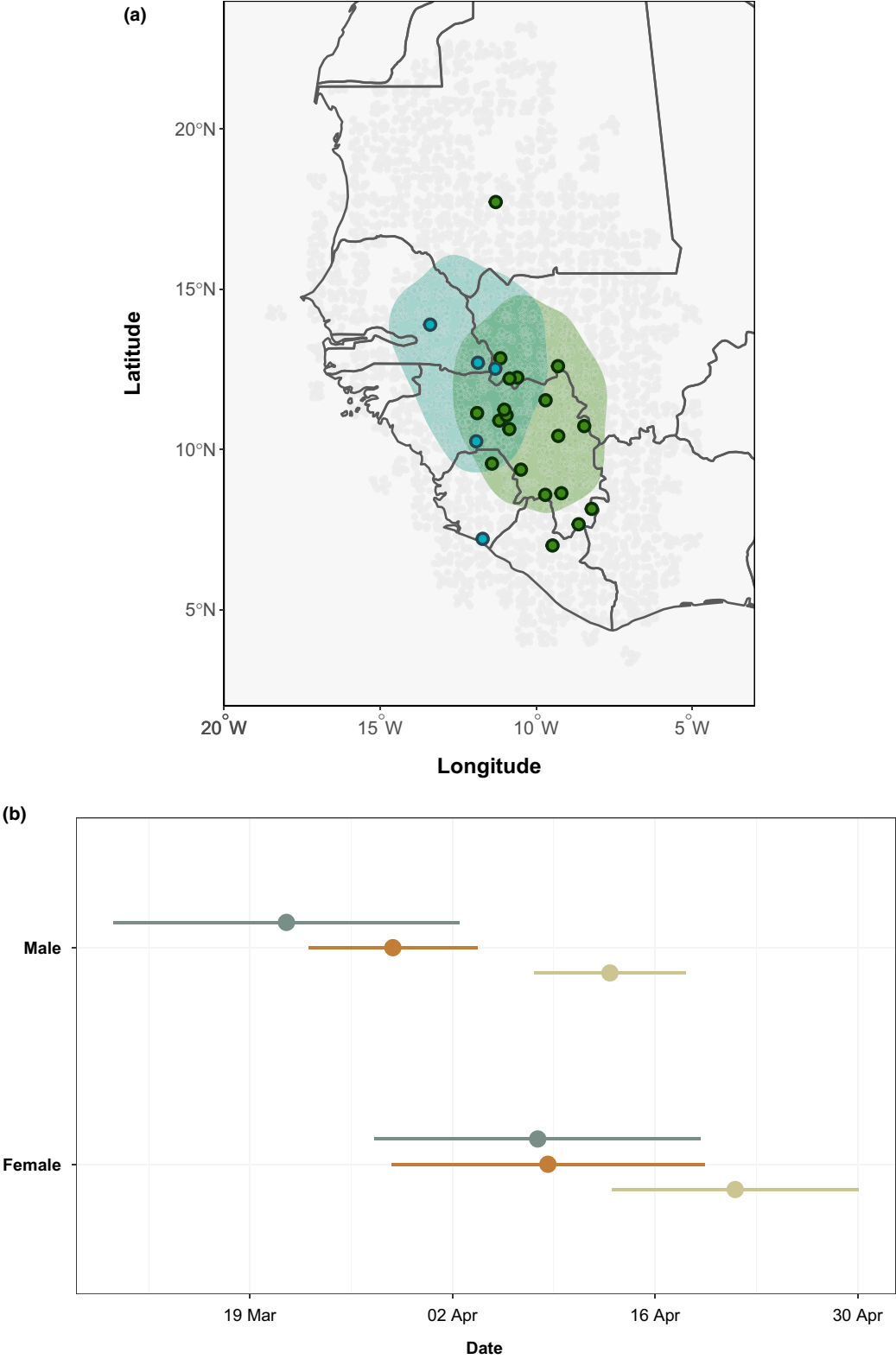


Figure 4. Sex-specific location and phenology. (a) Sex-specific locations of main non-breeding grounds. Points indicate median positions estimated during the non-breeding period by SGAT analysis with females (blue $n = 5$) west of males (green $n = 19$). Coloured regions display 10% probability distribution of location estimates separated by sex, and the shaded area represents the average 25% probability distribution of all location estimates. (b) Sex-specific phenological differences identified within spring migration of departure from non-breeding grounds (grey), commencement of spring Sahara crossing (orange) and spring arrival into breeding grounds (cream). Average dates are shown as a point, with range whiskers indicating error.

British breeding grounds in April (Table S2), with males arriving on average 9 days earlier than females (12 and 21 April respectively, GLM_{ln} $F_{1,20} = 6.91$, $r^2 = 0.26$, $P = 0.02$).

DISCUSSION

Our results show variations in Pied Flycatcher migration behaviour, with individuals using multiple staging sites and a variation in the frequency and duration of use between years. We provide evidence of interruption and retreat migration of the normally continuous flight made over the Sahara. We found differences in migratory timings between males and females, and a suggestion of a previously undocumented sex-specific difference in the main non-breeding area. The variation we found within 26 individuals (one tracked over two annual cycles) indicates flexibilities in migratory behaviour that may optimize individual survival and enable the adaptation of populations to changing environments.

Predominant migration route, staging site use and timings

The autumn migration route of British breeding Pied Flycatchers was first southwest, then after crossing the Sahara at the western edge, southeast to reach the final non-breeding areas in West Africa. This autumn route has been observed in the migrations of many other western European breeding songbird populations (Lerche-Jørgensen *et al.* 2017, Burgess *et al.* 2020). Spring migration was comparatively direct, being shorter in both distance and duration. The main non-breeding area was located in the dry savannah zone centred on Guinea, confirming the estimated locations of two males tracked from the same British breeding population in 2012/13 and non-breeding ringing recoveries of UK breeding flycatchers (Ouweland *et al.* 2016). Estimated longitudes from an

individual tracked over two successive years suggest site fidelity to the main non-breeding area (although the low precision of geolocation prevents certainty), as observed in some other Afro-Palaearctic migrants including Pied Flycatchers (Salewski *et al.* 2000, Blackburn & Cresswell 2016).

Typically, British breeding Pied Flycatchers used the same two staging regions during both spring and autumn migration, suggesting that a stop was required shortly after crossing the Sahara similar to other migratory songbirds (Tøttrup *et al.* 2012, Blackburn *et al.* 2019, Jiguet *et al.* 2019). An area predominantly on the Iberian Peninsula was used for a prolonged duration in autumn, and similarly in spring. However, this area was more southern and centred on northern Morocco. Long-term ring recovery data closely matched these locations, indicating that this region is an obligatory staging area for the British breeding population, as previously proposed (Hope Jones *et al.* 1977). Low fidelity to staging sites was expected (Veiga 1986), but our data suggest possible fidelity to areas on the Iberian Peninsula in both autumn and spring.

We identified a second staging area for British breeding Pied Flycatchers in northern West Africa, previously unknown because of the near absence of ring recovery data outside Europe. Little is known about the ecology and resource requirements of Pied Flycatchers at these staging locations, but it seems likely that individuals are taking advantage of ephemeral resources as their arrival into, and departure from, West Africa coincides with the more productive wet season associated with higher invertebrate and fruit densities (Seghieri *et al.* 2012, Kishimoto-Yamada & Itioka 2015).

Variation in staging site use and timing

We found no distinct variation between years or sexes in migration route, but identified variation between individuals in the frequency of use of

staging areas (with 63% of individuals stopping more often). A staging area in northern West Africa was used by most individuals in the autumn (92%), but by few in spring (29%). In spring, four individuals departed the main West African non-breeding areas an average of 24 days earlier than other individuals, using staging sites in Mauritania, Mali or Burkina Faso for an extended time before crossing the Sahara on a similar schedule to other individuals. This movement coincides with the onset of the wet season (early March), when habitats north of the main non-breeding areas become suitable staging sites for Pied Flycatchers to exploit seasonally abundant resources. Coinciding with the onset of the wet season and the rapid greening of arid environments, ambient light levels, which remain relatively constant with little shading from vegetation during the dry season (November–February), may become more variable in the wet season. As such, it is possible that these apparent early spring staging events in northern West Africa may be an analytical artefact of an individual changing habitat, rather than location. However, such a habitat shift would be associated with an increase in tag shading, shortening recorded day length and resulting in geolocation that would have indicated a southwards movement, whereas our results indicate relocation north of the main non-breeding areas.

Variation in migratory behaviour

We identified variation in Sahara crossing behaviour compared with the predominant pattern. Five instances of alternative Sahara crossing behaviours were observed, where individuals undertook two distinct flights to complete a single desert crossing, remaining stationary between flights. We consider this behaviour unusual in Pied Flycatchers, which normally cross the Sahara in a non-stop night and day flight (Adamík *et al.* 2016, Ouwehand *et al.* 2016), and rarely stop within the desert (Jenni-Eiermann *et al.* 2011). However, we found four individuals were stationary for around half a day, indicating a land-grounding within the desert. Our data also suggested that one individual undertook a temporary retreat migration, aborting an initial desert crossing to return to the southern edge of the desert before making a complete crossing 14 days later.

Temporary groundings in deserts, and retreat migration behaviours, are associated with a higher

risk of mortality and delayed phenology (Komenda-Zehnder *et al.* 2002, Strandberg *et al.* 2010). Such behaviours are documented infrequently (Salewski *et al.* 2010, Jenni-Eiermann *et al.* 2011, Nilsson & Sjöberg 2016), and to our knowledge we provide the first evidence of detecting these in songbirds from geolocators. Within light-level geocator studies, alternative crossing strategies will rarely be documented because they can only be identified during daylight hours whereas an individual is continually migrating over sea or desert (when FLP pattern data are evident). Multi-sensor loggers that record activity or air pressure and enable the identification of migration behaviours night and day (Emmenegger *et al.* 2020), including the kinds of alternative barrier crossing behaviour that we observed, are becoming miniaturized and will further advance such research.

We observed a flexible response to a context-dependent event as the single individual tracked over two successive years undertook additional staging site use and an atypical Sahara crossing behaviour in one year only. There is previous evidence of similar flexibility within songbird migration associated with weather events, such as in response to drought or low temperatures, with changes documented in migratory phenology (Tøttrup *et al.* 2012) and survival (Briedis *et al.* 2017). Within a population, individually variable migratory strategies may provide population resilience to unfavourable conditions; in contrast, relatively fixed strategies by individuals may reduce population resilience and slow adaptation to change.

It is important to note that our study was conducted using archival tags that require recapture of tagged birds the following year to retrieve the tag and data, so providing information only for individuals that survived both an autumn and a spring migration (Bridge *et al.* 2013). Although we provide evidence of retreat migration and desert groundings, and show that individuals can survive these events, they are likely to be a cause of mortality, so archival devices are unable to truly reveal how frequent these behaviours are, and they may be more common than we are able to show. It is also possible that other routes or behaviours are used in direct response to conditions met on migration that are not survivable and so are not detectable with archival devices.

Sources of variation between individuals

Temporary grounding and additional staging behaviours interrupt migration. Such strategies are expected in response to a weather event (Barriocanal *et al.* 2002), or to minimize the risk of encountering adverse environmental conditions (Åkesson *et al.* 2016). They may also be attributable to individual condition, with individuals in poorer condition stopping more frequently, or for longer (McKinnon *et al.* 2014), with the latter observed in Pied Flycatchers visiting European staging sites (Veiga 1986). These strategies may be adaptive and used flexibly in certain conditions, for example to await favourable winds, to seek foraging opportunity or to rest during the hottest hours to reduce water loss (Nilsson *et al.* 2013, Deppe *et al.* 2015). Conversely, adaptive shortening of a migration may occur when individuals shorten or miss a staging event to use conditions that aid migration (Liechti & Bruderer 1998). For example, in this study, fewer staging events were made in the second year. Such behaviour may buffer against delays (i.e. from late departure) and readjust migration schedules (Briedis *et al.* 2018).

Sex-specific migration

Between sexes, we found variation in migration timings and the location of the main non-breeding areas, but no difference in migration route or staging behaviour. Males departed the main non-breeding sites on average 17 days earlier than females, crossing the Sahara 11 days earlier in spring and arriving at breeding sites 9 days earlier. Earlier male migration phenology is a pattern common in migratory songbirds (Briedis *et al.* 2019) due to selection for earlier arrival to breeding sites to secure higher quality territories and mates, and to maximize opportunities to breed earlier (Morbey *et al.* 2012). Females may delay departure from non-breeding areas due to slower fattening rates than males (Seewagen *et al.* 2013), so an increased duration in the main non-breeding site may be to gain fat.

Our results suggest sex-biased segregation of Pied Flycatchers at non-breeding areas, with females located an average of 215 km west of males, and therefore migrating a shorter distance. This pattern may not be representative of all breeding populations as it was not evident in Pied

Flycatchers tracked from a breeding area in the Netherlands (Ouwehand & Both 2017). Sex-specific segregation of non-breeding location from the same breeding population is currently only documented for two short-distance migrant songbirds in the Afro-Palaearctic flyway – the European Robin *Erithacus rubecula* (Catry *et al.* 2004) and the Chiffchaff *Phylloscopus collybita* (Catry *et al.* 2005, Arizaga *et al.* 2015) – with examples of sex-specific habitat segregation similarly few (Nisbet & Medway 1972, Herremans 1997). In contrast, sex-specific segregation on non-breeding grounds is described from the Neotropical flyway, relating to location (Marra & Holmes 2001, Townsend *et al.* 2012, de Zwaan *et al.* 2019) and habitat (Parrish & Sherry 1994, Murphy *et al.* 2001), with competition for high-quality habitats resulting in the less dominant sex occupying less suitable habitats (Marra & Holmes 2001). Such segregation may result in a population-level demographic-specific vulnerability, if one sex is more likely to be affected by environmental drivers (Briedis & Bauer 2018). Further exploration is required from a larger sample size and from multiple years.

Previous assessment from the same population showed no effects of tagging male Pied Flycatchers on breeding behaviour, breeding success or apparent between-year survival (Bell *et al.* 2017). However, in this study, tagging female Pied Flycatchers suggested a weak negative impact on return rate. Therefore, tagging may have caused higher mortality or lower site fidelity affecting females and not males in the single year when females were tagged. Females may be more susceptible to less favourable environmental conditions than males, or to differential conditions compared with males as a result of non-breeding locations differing from those of males as our data suggest, and breeding dispersal is much more frequent in female compared with male Pied Flycatchers (Eeva *et al.* 2008).

CONCLUSION

We identified previously unknown staging areas in Iberia and northern sub-Saharan Africa, areas from which little is known about Pied Flycatcher ecology and resource requirements, especially in Africa. Further research is necessary to understand staging ecology, including habitat use, re-fuelling rates, diet, competition and phenology to identify potential constraints and threats to populations

using these regions during migration, such as from degradation of Pied Flycatcher habitats on the Iberian peninsula caused by agriculture (Hernández 2009, Arosa *et al.* 2017). This, combined with a greater understanding of Pied Flycatcher ecology across non-breeding areas, and the weather and climatic drivers of variations in migration behaviour, will greatly improve understanding of the factors influencing the population trends of Pied Flycatchers and other migrant songbirds.

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AUTHOR CONTRIBUTION

Fraser Bell: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Resources (supporting); Software (supporting); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Stuart Bearhop:** Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (lead); Validation (supporting); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal). **Martins Briedis:** Formal analysis (lead); Methodology (equal); Software (lead); Validation (supporting); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Myriam El Harouchi:** Data

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Data Availability Statement

The datasets generated during and/or analysed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.1732qn7j> (Bell *et al.*, 2021).

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SUPPORTING INFORMATION

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

Table S1. Summary of sample sizes for major phenological events, across the complete tracked annual cycle.

Table S2. Summary of individual pied flycatcher tracking results, with phenological dates and coordinates corresponding to the major events during the annual cycle shown.

Table S3. Detailed staging behaviour of pied flycatchers including the phenology and location of all staging areas used throughout the entire tracked annual cycle.

Table S4. Abnormal Sahara spring and autumn desert crossing behaviours identified throughout the study.

Table S5. Sex-specific phenological differences identified during the non-breeding period, and during spring migration.

Figure S1. Phenological and sex-specific change in estimated longitude of all tracked Pied Flycatchers during a single annual cycle, for males (green) and females (blue).