Articles

Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*

J. Ouwehand, M. P. Ahola, A. N. M. A. Ausems, E. S. Bridge, M. Burgess, S. Hahn, C. M. Hewson, R. H. G. Klaassen, T. Laaksonen, H. M. Lampe, W. Velmala and C. Both

J. Ouwehand (janneouwehand@gmail.com), A. N. M. A. Ausems, R. H. G. Klaassen and C. Both, Groningen Inst. for Evolutionary Life Sciences, Univ. of Groningen, PO Box 11103, NL-9700 CC Groningen, the Netherlands. RHGK also at: Dutch Montagu's Harrier Foundation, PO Box 46, NL-9679 ZG Scheemda, the Netherlands. – M. P. Ahola, T. Laaksonen and W. Velmala, Section of Ecology, Dept of Biology, FI-20014 Univ. of Turku, Finland. MPA also at: Natural Resources Inst. Finland, Itäinen Pitkäkatu 3, FI-20520 Turku, Finland. – E. S. Bridge, Oklahoma Biological Survey, Univ. of Oklahoma, 111 East Chesapeake Street, Norman, OK 73019, USA. – M. Burgess, Centre for Research in Animal Behaviour, Univ. of Exeter, Exeter, EX4 4QG, UK. – S. Hahn, Swiss Ornithological Inst., Dept of Bird Migration, CH-6204, Sempach, Switzerland. – C. M. Hewson, The Nunnery, British Trust Ornithology, Thetford, IP24 2PU, Norfolk, UK. – H. M. Lampe, Centre for Ecological and Evolutionary Synthesis, Dept of Biosciences, Univ. of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway.

Understanding what drives or prevents long-distance migrants to respond to environmental change requires basic knowledge about the wintering and breeding grounds, and the timing of movements between them. Both strong and weak migratory connectivity have been reported for Palearctic passerines wintering in Africa, but this remains unknown for most species. We investigated whether pied flycatchers *Ficedula hypoleuca* from different breeding populations also differ in wintering locations in west-Africa. Light-level geolocator data revealed that flycatchers from different breeding populations travelled to different wintering sites, despite similarity in routes during most of the autumn migration. We found support for strong migratory connectivity showing an unexpected pattern: individuals breeding in Fennoscandia (S-Finland and S-Norway) wintered further west compared to individuals breeding at more southern latitudes in the Netherlands and SW-United Kingdom. The same pattern was found in ring recovery data from sub-Saharan Africa of individuals with confirmed breeding origin. Furthermore, population-specific migratory connectivity was associated with geographical variation in breeding and migration phenology: birds from populations which breed and migrate earlier wintered further east than birds from 'late' populations. There was no indication that wintering locations were affected by geolocation deployment, as we found high repeatability and consistency in $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios of winter grown feathers of individuals with and without a geolocator. We discuss the potential ecological factors causing such an unexpected pattern of migratory connectivity. We hypothesise that population differences in wintering longitudes of pied flycatchers result from geographical variation in breeding phenology and the timing of fuelling for spring migration at the wintering grounds. Future research should aim at describing how temporal dynamics in food availability across the wintering range affects migration, wintering distribution and populations' capacity to respond to environmental changes.

Every year billions of songbirds migrate thousands of kilometres between Europe and sub-Saharan Africa (Moreau 1972, Hahn et al. 2009). To guide them on their journeys between breeding, staging and wintering sites, long-distance migrants use an endogenous spatiotemporal program, fine-tuned by external cues to time and direct their migrations (Gwinner 1996, Berthold 2001). In many cases, migration between such distant habitats has evolved as a strategy to maximize fitness in seasonal environments: migrants profit from peaks in food abundance at their temperate breeding grounds but avoid harsh conditions in winter (Alerstam et al. 2003). Yet, it is unclear how well these complex migratory life-styles are suited to successfully adapt to ongoing rapid environmental changes that many Afro-Palearctic migrants currently face at different parts of their annual cycle (Knudsen et al. 2011, Vickery et al. 2014).

The pied flycatcher *Ficedula hypoleuca* has become a model species to study annual cycle adjustments to climate change, with a strong emphasis on the ecological conditions at the breeding grounds (Møller et al. 2010). Despite being one of the ten most abundant passerines in the Afro-Palearctic flyway (Hahn et al. 2009), our knowledge on their ecology and distribution outside the breeding season is very limited. It is known that pied flycatchers migrate in autumn primarily through the Iberian Peninsula, regardless of their breeding origin, before flying into west-Africa (Lundberg and Alatalo 1992, Chernetsov et al. 2008). Yet we do not know how pied flycatchers from various breeding areas – with different time schedules – distribute once at their west-African non-breeding grounds, and how these migratory connections affect the rest of their annual cycle or their capacity to respond to environmental changes. Here, we aimed to

determine whether pied flycatchers from different areas in western and northern Europe mix or retain spatial structure at their wintering grounds with respect to their breeding location and breeding phenology.

The links between breeding and non-breeding areas are defined quantitavely by the strength of migratory connectivity. Strong migratory connectivity occurs when birds from different breeding populations show little overlap in their population specific wintering sites, with most individuals within a breeding population migrating to the same non-breeding location. Weak (diffuse) migratory connectivity occurs when individuals within breeding populations spread through several non-breeding grounds and populations show strong overlap in their non-breeding distributions (Webster et al. 2002).

A wide variety of migratory connectivity patterns has already been revealed from ring-recovery data: e.g. year round consistency of east-west distributions (i.e. parallel migrations), funnelling of individuals from a wide breeding range into a small geographical winter range or vice versa (telescopic or fan migration), chain migration and leap-frog migration (Salomonsen 1955, Newton 2008). Although ring-recovery data still gives the most spatially accurate information, advances in tracking techniques have increased the speed by which we can elucidate distribution patterns and reveal migration schedules for populations of small migrants (Bridge et al. 2013, McKinnon et al. 2013). Isotope ratios of winter moulted feathers also have revealed population differences in wintering site use and have proved very helpful in mapping birds to broad isoscapes (examples in *Ficedula* flycatchers: Hjernquist et al. 2009, Hobson et al. 2012, Tonra et al. 2014, Veen et al. 2014). Since the first deployment of light-level geolocators (hereafter 'geolocators') in migratory landbirds in 2007 (Stutchbury et al. 2009), distribution patterns of small landbirds become more widely available (McKinnon et al. 2013). Geolocators have the potential to reveal fine-scale distribution patterns that may not be evident among the broad-scale inferences that are generally yielded by intrinsic geographic markers like stable isotopes and DNA (Irwin et al. 2011, McKinnon et al. 2013). Recent studies reported both strong (Hahn et al. 2013) and weak migratory connectivity (Ambrosini et al. 2009, Kristensen et al. 2013, Lemke et al. 2013), but for most Afro-Palearctic passerines the pattern and strength of migratory connectivity is currently not known.

In a recent review, Cresswell (2014) predicted weak migratory connectivity for populations of Afro-Palearctic passerines, based on the assumption that stochastic processes during orientation of first-time migrants would lead to wide spread of breeding populations over the African wintering grounds. However, actual data on wintering site-selection is often lacking. Pied flycatchers winter over a gradient of habitats and a wide span of longitudes in a highly seasonal environment (Morel and Morel 1992, Salewski et al. 2002b, Dowsett 2010). At least part of these pied flycatchers are faithful to their wintering sites in sub-Saharan Africa, where they fuel for spring migration (Salewski et al. 2000, 2002a). Although pied flycatchers arrive in autumn in lush and green conditions at their wintering sites, these sites become progressively dryer during the season, and fuelling for spring migration takes place at the end of the dry season (Moreau

1972, Salewski et al. 2002c). Hence, wintering site selection can have important implications for other annual cycle routines, for example via differences in migration distance, wintering food sources or spring fuelling conditions. The importance of wintering site-selection will likely increase, given widespread and ongoing habitat change of the Guinea savannah (Brink and Eva 2009) which negatively affects many migrants in winter (Ockendon et al. 2012, Vickery et al. 2014).

In addition to conditions within the wintering range, wintering-site selection may be strongly influenced by an individuals' time schedule. In the case of Afro-Palearctic migrants, several studies highlighted the importance of accounting for such differences in individual migration schedules when trying to explain responses to environmental conditions during winter or migration (pied flycatchers: Both et al. 2006, Both and te Marvelde 2007, Both 2010; multiple species: Robson and Barriocanal 2011, Ockendon et al. 2012). If we aim to understand wintering distributions of migrants, it might therefore be important also to consider individual differences as well as population-level variation in migration phenology.

In the present study, we investigated whether adult pied flycatchers from different breeding sites – with different breeding and migration phenology but converging autumn migration routes – show spatial separation in their west-African wintering locations. We discuss these results mainly within the framework of Afro-Palaearctic migration, given that differences between flyways may yield very different patterns of migratory connectivity due to a variety of landscape level differences (e.g. range studied, habitat available, barriers and ecological dynamics; Cresswell 2014). In 2011 and 2012, we equipped breeding birds with geolocators to estimate timing of migration as well as non-breeding locations of birds from four sites in Europe: S-Finland, S-Norway, the Netherlands and SW-United Kingdom. Geolocators rely on accurate measurements of light levels to infer the timing of sunrise and sunset, which in turn allows for estimates of longitude and latitude (Lisovski et al. 2012b). Latitude cannot be reliably estimated close to the spring and autumn equinoxes. Moreover, for woodland birds like pied flycatchers, (variable) shading in the habitat can compromise location estimates, especially with regard to latitude (Lisovski et al. 2012b). Fortunately, estimates for longitude are relatively accurate and are particularly meaningful within the known wintering range of pied flycatchers, which spans ~ 4000 km from east to west (while covering only a narrow latitudinal band; Fig. 1). Longitude estimates can also provide a proxy for migration routes if the migrations are not solely in N-S direction but also include an E-W component. The emphasis of this study was to describe the wintering longitude distribution in relation to the breeding longitude and latitude, breeding phenology, and migration phenology of the individual and its breeding population.

Since deployment of geolocators can sometimes affect the normal behaviour of birds tracked by geolocation (Costantini and Møller 2013, Scandolara et al. 2014) it is important to assess potential negative effects and, if possible, the reliability of the geolocation data. Therefore we also describe the wintering distribution by an independent
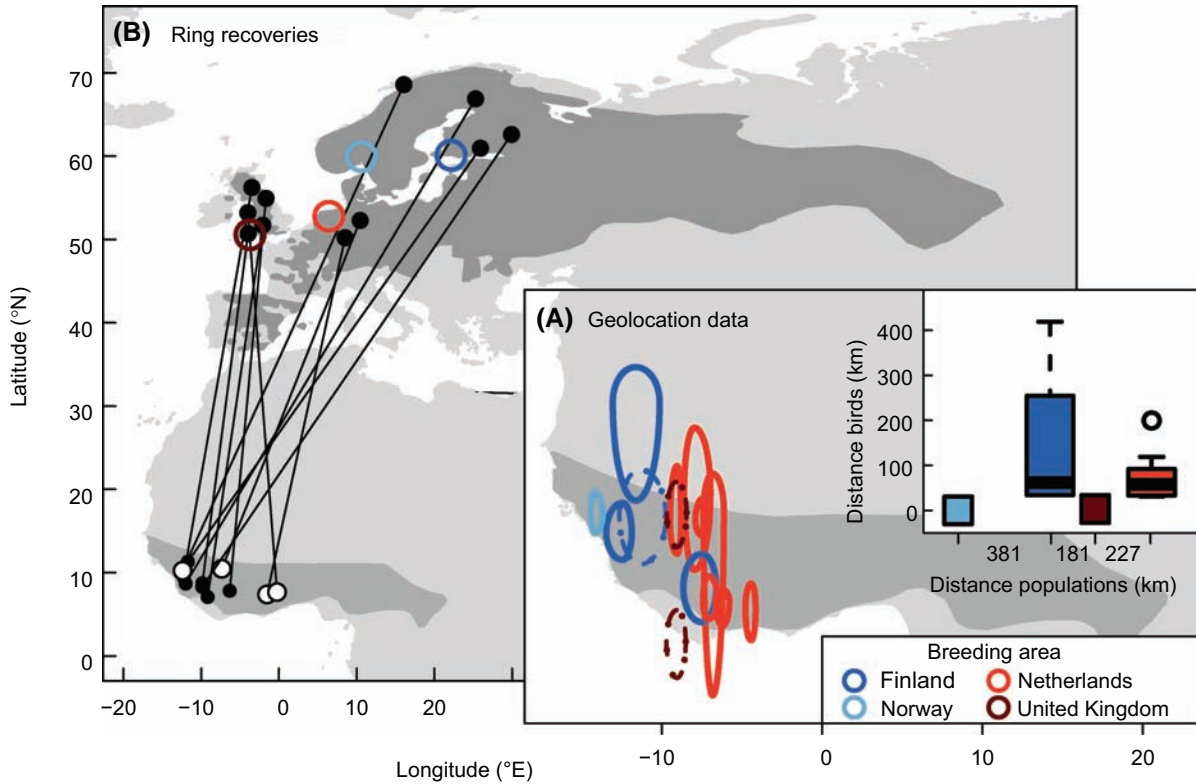
Figure 1. Wintering locations of pied flycatchers were inferred from (A) geolocators deployed in four breeding areas, and (B) ring recoveries south of the Sahara of birds with confirmed breeding origins. In (A), polygons indicate 25–75% quartile ranges around the filtered median geolocation position from 15 November to 15 February (n = 11) or from winter arrival until the geolocator stopped working (n = 3). Dashed polygons indicate that the estimate for latitude is very uncertain (i.e. the Hill–Ekstrom calibration procedure during winter was not successful). The inset in (A) describes the strength of migratory connectivity by the wintering distances between populations in relation to the wintering distances between individuals within a particular population (box plots with median and quartiles, in km). For Norway no within population distance could be calculated (as n = 1). In (B), filled dots mark the natal or breeding location, and the recovery location of birds found 'freshly dead' in December–early March. Open symbols indicate wintering recoveries during September–October, April, or unknown exact date. Dark grey areas show the wintering range (after Dowsett 2010) and the breeding range of pied flycatchers (nb atlas flycatcher *Ficedula speculigera* is not shown).

data set of ring recoveries from the non-breeding season in sub-Saharan Africa from pied flycatchers with a known breeding origin (1971–2008). Furthermore, we assessed geolocator impact on wintering site use (e.g. location, habitat) within individuals by comparing stable isotope ratios of winter moulted feathers in the year before and during geolocator deployment. Pied flycatchers undergo pre-breeding moult by the end of the winter, including tertial feathers (hereafter 'tertials') (Jenni and Winkler 1994, Salewski et al. 2004). Although the relative differences of isotope ratios of carbon and nitrogen (hereafter respectively, $\delta^{13}C$ and $\delta^{15}N$) in these tertials do not provide a direct measure of the spatial wintering location, they do carry an inert isotopic fingerprint that reflects the isotopic composition of the conditions during moult (Hobson and Wassenaar 2008). Pied flycatchers are known to have high winter-site fidelity (Salewski et al. 2000, 2002a), and an earlier explorative analysis showed high repeatability in wintering ground feather isotope ratios between years (JO unpubl.). We reason that if carrying a geolocator affects wintering site selection or use, then we should observe lower repeatability in feather-isotope ratios within tracked individuals compared to control individuals.

This assessment of geolocator impact on wintering isotopic ratios also allowed us to explore (as a post-hoc analysis) whether variation in wintering longitudes described by geolocation data is reflected in $\delta^{13}C$ and $\delta^{15}N$ values of winter moulted tertials. However, we only expect this if birds spread out in winter over a gradient of isotopically distinct locations (Craine et al. 2009, Hobson et al. 2012).

Material and methods

Study sites, geolocator deployment and recovery

Adult breeding pied flycatchers were equipped with light-level geolocators during 2011 and 2012 in four European nest box populations that vary in geography and breeding phenology (Fig. 1, Table 1): east Dartmoor in SW-United Kingdom (UK: 50.6°N, 3.7°W), Drenthe in the Netherlands (NL: 52.8°N, 6.4°E), Oslo in S-Norway (NO: 60.0°N, 10.6°E) and Ruissalo in S-Finland (FI: 60.2°N, 22.2°E). Birds were tracked using different types of geolocators: MK6540C (BAS, Dorset, UK) in UK, OU-Cornell

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Table 1. Information on the breeding locations of pied flycatchers equipped with geolocators and their return rates compared to birds without geolocators (i.e. controls). Numbers and return percentages are shown per group (geolocator, control). Control birds existed of same sexed individuals marked with one or more colour rings with return rates calculated over the years of geolocation. For populations where these controls were absent or return rates of controls were presumed abnormal, we report also return rates (in italics) of same sexed birds without geolocators or colour rings in the years of geolocation (UK) or an average over 2005–2010 (FI).

Country	Area	Latitude, Longitude, Altitude	Mean egg laying date[1]	Habitat	Geolocator type	Harness type, material	Years	Sex	Returns geolocator	Returns control
Finland	Ruissalo	60.2° 22.2° 16 m	27 May	Coniferious, deciduous	SOI-GDL2	Leg-loop, silicon 1.0 mm	2011–2012	male	11–13/100 (11–13%)[2]	*124/483 (26%)*
Norway	Oslo	60.0° 10.6° 180 m	25 May	Coniferious, deciduous non-oak	Intigeo-W50B1	Leg-loop, silicon 1.0 mm	2012–2013	male	1/23 (4%)	
Netherlands	Drenthe	52.8° 6.4° 3 m	8 May	Oak, coniferious, mixed	OU-Cornell	Leg-loop, elastan 0.7 mm	2011–2012	female	2/22 (9%)	6/21 (28%)
Netherlands	Drenthe	52.8° 6.4° 3 m	8 May	Oak, coniferious, mixed	OU-Cornell	Leg-loop, elastan 0.7 mm	2011–2012	male	16/38 (42%)	10/63 (16%)
Netherlands	Drenthe	52.8° 6.4° 3 m	8 May	Oak, coniferious, mixed	OU-Cornell	Leg-loop, elastan 0.7 mm	2012–2013	male	10/60 (17%)	31/125 (25%)
England	East Dartmoor	50.6° -3.7° 200 m	5 May	Oak	MK6540C	Leg-loop, elastan 0.7 mm	2012–2013	male	2/20 (10%)	49/87 (56%) *3/29 (10%)*

[1]Populations mean egg laying date over 2011–2014.
[2]Highest values indicate returns including birds that lost their geolocator.

(Univ. of Oklahoma, Cornell Univ., US) in NL, Intigeo-W50B1 (Migrate Technology, Cambridge, UK) in NO and SOI-GDL2 (Swiss Ornithological Inst., Sempach, CH) in FI. The SOI-GDL2 geolocator was the only one with a 5 mm long light-stalk. Geolocators weighed between 0.55–0.65 g including harness. A leg-loop harness was used to attach the device to the bird's back (Rappole and Tipton 1991). Geolocators were attached to adult birds prior to chick fledging (chick age 6–15 d), by capturing them in the nest box during chick feeding. Upon capture, individuals were ringed with an aluminium ring (if unringed), anodised coloured ring or additionally fitted with one or two colour-rings to allow recognition of individuals upon return in the next year. For all birds we recorded first egg laying date, body mass, age and sex. In most study sites, only males were equipped with geolocators because males show more breeding site-fidelity than females (Lundberg and Alatalo 1992). Body mass of the birds at the time of geolocator deployment varied between 11.2–13.5 g. Geolocator mass corresponded to an average of 4.9% of the individuals' body mass (Table 2). To retrieve geolocators, we searched for and recaptured birds within the study populations at the start of the breeding seasons 2012 and 2013. In total 44 birds returned that were equipped with geolocators (two females and 42 males of which two lost their device), but only 14 geolocators (35%) contained enough data to estimate wintering locations (Table 1–2).

Geolocator analysis

Clock-drift correction, filtering of twilight data
Data from geolocators were downloaded and linearly corrected for clock-drift if the drift exceeded one minute. Post-hoc inspection of geolocation data for signs of continuous longitudinal drift in one direction during stationary periods did not reveal clock drift problems (for details on clock drift in geolocation data, see Supplementary material Appendix 1). The light threshold was set slightly above the baseline value (i.e. just above darkness) using TransEdit (BAS) to define sunset and sunrise times from light-intensity data. Threshold values varied between geolocators (range 1–16) due to differences in geolocator type (i.e. light sensors and scales to record light intensity differed among device types) and variation in shading. Aberrant twilight events were removed by manual and standardized filtering procedures (Supplementary material Appendix 1). We further filtered transition data by removing all twilight events during the wintering phase that led to day lengths outside the 50–99% distribution of day lengths (i.e. removing days with severe shading). Since (minor) seasonal changes in day length occur in the wintering areas, we performed filtering on a monthly basis for each geolocator separately.

The corrected and filtered transition data (i.e. sunset and sunrise times) were used to estimate timing of migration and positions (longitude, latitude).

Timing of migration
The annual cycle was divided into four phases: breeding, autumn migration, wintering and spring migration. The breeding phase lasted until the bird started its autumn migration, and included breeding and post-breeding moult. For geolocators that were still working upon retrieval (n = 8 out

Table 2. Individual characteristics of pied flycatchers equipped with geolocators in four European breeding populations, including information on body mass (g), tag mass (g, % of body mass), tag deployment, timing and duration of annual cycle events as inferred from field observations and (with headers in italics) geolocation data. Empty cells refer to missing values, e.g. in case geolocators stopped working before birds were recaptured.

ID	Sex	Body mass (g)	Tag mass (g), % of body mass	Egg laying	Hatching	Tagged	Autumn departure	Arrival wintering site	Spring departure	Arrival breeding site	Observed arrival breeding site	Autumn migration duration (days)	Spring migration duration (days)	Winter duration (days)
Finland														
3gs	male	13.5	0.59, 4.4%	22-5-2011	17-6-2011	23-6-2011	17-8-2011	3-10-2011	10-4-2012	27-4-2012		47	17	190
3ox	male	12.4	0.63, 5.1%	23-5-2011	18-6-2011	24-6-2011	25-8-2011	17-10-2011				53		
3pg	male	12.1	0.60, 5.0%	25-5-2011	21-6-2011	28-6-2011	28-8-2011	5-10-2011				38		
3je	male		0.60	25-5-2011	13-6-2011	19-6-2011	28-8-2011	4-10-2011	14-4-2012	3-5-2012		37	19	193
Norway														
2935	male	11.2	0.55, 4.9%	24-5-2012	11-6-2012	20-6-2012	16-8-2012	14-10-2012	15-4-2013		14-5-2013	59	29[2]	183
Netherlands														
30	male	11.5	0.60, 5.2%	6-5-2011[1]	1-6-2011	14-6-2011	2-8-2011	31-8-2011			22-4-2012	29		
36	male	13.2	0.60, 4.5%	5-5-2011	31-5-2011	15-6-2011	13-8-2011	22-9-2011	6-4-2012	30-4-2012	30-4-2012	40	24	197
40	male	12.7	0.60, 4.7%	9-5-2011	4-6-2011	18-6-2011	14-8-2011	29-10-2011	5-4-2012	20-4-2012	19-4-2012	76	15	159
b17	male	13.0	0.55, 4.2%	26-4-2011	23-5-2011	6-6-2011	5-8-2011	3-9-2011			16-4-2012	29		
201	male	12.0	0.65, 5.4%	2-5-2012	21-5-2012	2-6-2012	8-8-2012	4-9-2012			17-4-2013	27		
207	male	12.5	0.65, 5.2%	29-4-2012	21-5-2012	2-6-2012	27-7-2012	2-9-2012	31-3-2013	16-4-2013	18-4-2013	37	16	210
233	male	12.8	0.65, 5.1%	24-5-2012	8-6-2012	14-6-2012	13-8-2012	17-9-2012	3-4-2013	15-4-2013	17-4-2013	35	12	198
England														
8	male	12.2	0.60, 4.9%	12-5-2012	31-5-2012	10-6-2012	19-8-2012	21-9-2012	26-3-2013	13-4-2013	17-4-2013	33	18	186
15	male	11.6	0.57, 4.9%	11-5-2012	28-5-2012	9-6-2012	20-8-2012	24-9-2012	29-3-2013	14-4-2013	20-4-2013	35	16	186

[1]This date refers to the latest clutch of this male. The first clutch with a different female was started on 23-4-2011.
[2]Since the geolocator stopped working during spring migration, the duration of spring migration is inferred from the difference between the observed arrival at the breeding ground and the spring departure from the wintering site.

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of 14), a second, short breeding phase was defined from arrival upon return (defined from geolocation data) until birds were recaptured at the breeding grounds. Timing of arrival at the breeding site derived from geolocation was often very similar to field observations of arrival date (Table 2). The wintering phase refers to non-breeding residency in sub-Saharan Africa in the boreal winter (hereafter 'wintering'): from arrival at the wintering grounds until birds started spring migration. The autumn and spring migration (including stopovers) were defined as phases associated with major changes in twilight times that refer to south-westward movements during summer and autumn, and northward migration in spring. These major changes in sunset-rise times were extracted using the changeLight-function in the R-package GeoLight (Lisovski et al. 2012a), setting the minimal stopover period to three days and the quantile probability threshold (Q) to 0.95. The output from these analyses was used to decide which periods needed to be pooled into one of four annual cycle phases. In addition, we manually checked whether autumn migration was recognized by changeLight for each tracked bird. If movements were not recognized by change-Light (mainly gradual autumn migration), we defined end and start dates of movement phases based on visual inspection of changes in twilight times, latitude and longitude.

Geolocation positions, reliability of estimates

Wintering locations of 14 male pied flycatchers were estimated from geolocation transition data: 2 from UK, 7 from NL, 1 from NO, 4 from FI (Supplementary material Appendix 2, Table A2). Longitudes are estimated using the noon and midnight time from the geolocator relative to Coordinated Universal Time (UTC). Latitudes were inferred via various calibration procedures that describe the relation between the measured day length in the transition data and latitude by finding the correct sun elevation angle (SEA).

For each bird we calculated the median (Q2) wintering location and the 25–75% quartiles (Q1–Q3) of geolocation estimates (i.e. which are depicted as wintering ellipses). The precision of geolocation was described by the lower and upper quartile differences in degrees relative to the median (ΔQ2–Q1, ΔQ3–Q2). Moreover, we calculated geolocation accuracy over two breeding seasons, since differences between years may also give rise to biases in longitude associated with geolocator type or clock drift. More details on the geolocator analyses, calibration procedures and an overview of accuracy and precision over different periods during breeding and wintering (with and without day-length filtering) can be found in the Supplementary material Appendix 2, Table A1–A2.

Unfortunately, wintering latitude estimates were, on average, imprecise. The known core wintering range of pied flycatchers (Dowsett 2010) with respect to latitude is roughly 6° wide (at maximum), while the latitude precision during the whole winter was on average 3.22° for ΔQ2–Q1 (358 km) and 2.76° for ΔQ3–Q2 (308 km) when excluding 15 d either side of equinoxes (n = 11, if Hill–Ekstrom (i.e. HE) calibration could be performed). Since HE calibration procedures were not always successful, we could not obtain reliable latitude estimates for all geolocators in our dataset in a way that estimates were unbiased towards breeding ground conditions (see Supplementary material Appendix 1, 2 for

details on geolocator analyses). Even for birds where HE calibrations were performed, the resulting median wintering latitudes ranged between 4.4–16.9°N (n = 11), which clearly exceeded the latitude range shown for ring recovery data (this study) as well as the main wintering range known for pied flycatchers (Fig. 1: wintering range after Dowsett 2010). Latitude estimates can be inaccurate and imprecise if shading is common and variable (Lisovski et al. 2012b), as in our study. The severity of shading differed over the year, between individuals and among types of geolocators used (thus populations). Restricting analyses to the highest quality data sets was not a viable option given the overall sample size and uneven representation of the study sites. Hence, we relied solely on geolocation estimates of longitude to approximate migratory routes and to infer migratory connectivity.

The precision of longitude was on average 0.80°/87 km (ΔQ2–Q1) and 0.76°/84 km (ΔQ3–Q2), using day-length filtered data over the whole wintering phase (n = 14). Although the longitude precision was influenced by severe shading we are confident that our median estimates of wintering longitude were not impaired by shading events, given that median wintering longitudes changed little with or without day-length filtering (whereas latitude medians shifted substantially; Supplementary material Appendix 2, Table A2). The geolocation accuracy of longitude was on average 71 km (range 4–325 km): i.e. average differences of the known position (nest box) to the median position in the breeding phase. Geolocation accuracy fluctuated within populations, but not consistently between populations (Supplementary material Appendix 2, Table A1), which implies that the reliability of geolocation estimates of longitudes are not dependent on the type of device used or the amount of clock drift corrected for. Also the estimated accuracy upon return (year $t + 1$) differed on average only 59 km (range 14–111 km, n = 8) from the accuracy in year t (Supplementary material Appendix 2, Table A1), even though this second breeding phase is only very short (Fig. 4). Hence we are confident that the longitude estimates among different populations are comparable and not impaired by the use of different devices between populations. To improve the precision of wintering longitude we used a core period in winter from 15 Nov to 15 Feb, if geolocators worked at least until 15 Feb (n = 11). If geolocators stopped working before 15 Feb (n = 3), we used the whole available wintering period. During the core period in winter the (variation in) shading was less pronounced compared to the start of the wintering phase, likely because of trees shedding their leaves in late winter. Using the core rather than the whole wintering period thus improved the precision of longitude estimates (Supplementary material Appendix 2, Table A2).

For all calculations on migratory connectivity in geolocation data we used the median longitudes of day-length filtered data of the core wintering phase, or day-length filtered data of the whole available wintering period for geolocators that stopped working before 15 Feb.

Ring recovery data

In addition to geolocation longitudes, we described wintering distributions and migratory connectivity using ring recovery data. Pied flycatcher ring recoveries (1971–2008) from the African wintering grounds of birds ringed at

breeding locations were obtained from the EURING database (< www.euring.org >). We additionally included a Norwegian bird ringed as nestling and recovered in south-west Guinea (coordinates inferred from Bakken et al. 2006). The core wintering range of pied flycatchers ranges from Cameroon to west Sierra Leone (Dowsett 2010), while there are very few confirmed records of pied flycatchers in east Africa (Pearson 1998, Dowsett 2010) where they can easily be mistaken for other *Ficedula* flycatchers or hybrids. Hence, we excluded one record of a Swedish bird recovered in Uganda as being an outlier. We restricted our dataset to recoveries of birds found in winter south of 20°N for which the natal or breeding origin (ringed as nestling, nesting or breeding) was confirmed. This meant exclusion of several birds: one from the UK recovered in the Central Africa Republic (Wernham et al. 2002), one from France recovered in Nigeria, and all recoveries with EURING status 'P' (i.e. passing through). The remaining 11 birds are depicted by two different symbols in graphs, since the certainty of wintering status is higher for the six birds recovered 'freshly dead' in December to early March than for five birds recovered in late April, late September or October (n = 3 from UK and Germany), or if exact recovery dates were unknown (n = 2). We treated all 11 birds as 'wintering', since the recovery locations were within the pied flycatcher wintering range and their status and body condition (e.g. fat score, if available) did not suggest these birds to be transients.

Geolocator impact, feather collection

Carrying a geolocator has been shown to affect local return rates (Costantini and Møller 2013), and may also result in aberrant behaviour and wintering site choice. Comparing return rates in this study is problematic because different geolocators types were used (device type was confounded with population) and because of methodological differences in field data collection (e.g. recapture effort, selection of control and geolocator birds). Table 1 shows return rates of birds with and without a geolocator (i.e. controls) in each population. Control birds existed of birds marked with one or more colour rings that were selected based on similarity to birds with geolocators (sex in all cases; for timing of breeding and age in UK; for subarea in NL). If proper controls were lacking for the year of geolocation (FI) or return rates of controls were considered abnormal for that population and year (UK), we reported the return rates of same sexed 'ringed only' individuals during the years of geolocation (UK) or during a wider time interval (FI: 2005–2010). The heterogeneity in device use and data collection mainly occurred because the field data were not collected with the purpose of performing a comparative study.

If geolocators affect wintering site choice, then there may be differences in stable isotope ratios of winter grown feathers within birds which that indicate that they used different wintering sites from one year to the next. Individual flycatchers have been shown to have high winter site philopatry (Salewski et al. 2000, 2002a), and this phylopatry is associated with high repeatability of stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) in the winter-grown feathers of individuals without geolocators (Hjernquist et al. 2009, JO unpubl.). If carrying a geolocator influences wintering site selection,

we would expect the isotope ratios of the feathers grown during the winter with the geolocator to differ from feather isotope ratios associated with the previous winter (i.e. lowering the repeatability and individual consistency). Hence, we analysed winter-moulted mid-tertial feathers both in the year of geolocator deployment (year *t*), and upon recovery in the next year (year *t* + 1) for $\delta^{13}C$ and $\delta^{15}N$. We compared 21 birds with geolocators (also including some that failed to record data) to 17 control birds for which feathers were available from the same years and that were similar to tracked birds in sex and breeding origin (and age, if known). For Norwegian birds, feathers were not collected in both years.

Stable isotope analysis

Tertial feathers were cleaned of organic contaminants using hexane and were then air dried. The feather tip was cut into small fragments using scissors and loaded into tin cups. Samples (350–700 μg) were analysed for their stable carbon ($^{13}C/^{12}C$) and stable nitrogen isotope ratio ($^{15}N/^{14}N$) at the NIOZ Royal Netherlands Inst. for Sea Research, the Netherlands. The stable isotope ratios were determined with a Thermo Scientific Flash 2000 Elemental Analyser coupled to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. Results were expressed in standard δ-notation relative to Pee Dee Belemnite (v PDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$ values. The maximum recorded deviations as determined using laboratory standards calibrated by certified international reference samples were in all cases < 0.2‰ for $\delta^{13}C$ and < 0.3‰ for $\delta^{15}N$ values.

Statistical analysis

We evaluated migratory connectivity using geolocation data (n = 14) and ring recovery data (n = 11). For ring recoveries both wintering longitude and latitude were used; whereas for geolocation data only wintering longitudes could be used to study migratory connectivity. For recovery data wintering longitude and latitude were studied using linear models (LM), because breeding origins of ring-recovered birds were spread in time and space (and hence assumed to be independent). For geolocation data, birds tagged in the same breeding populations lack independence, so we tested for breeding site 'dependence' among birds' wintering longitudes using likelihood ratio tests performed on linear-mixed-effect models (LMM) with and without breeding population as a random intercept.

Although the number of birds per population tracked by geolocation is small and variable, we attempted to quantify the strength of migratory connectivity using a novel method that compared the average estimated nearest-neighbour distances (NND) among birds from the same breeding population during the non-breeding period to the average distances among populations on the wintering grounds (Hahn et al. 2013). To conduct these distance calculations without depending on unreliable latitude estimates (also see Supplementary material Appendix 1–2) we calculated means and NND from individuals' median longitudes while setting all population mean wintering latitudes to 9°N (i.e. the middle

latitude of the ring recovery wintering range). All distances were calculated as great-circle distances.

Because breeding populations differ in many aspects, such as breeding latitude, longitude and breeding phenology, we next explored which geographical components contribute most to the observed migratory connectivity. To do so, we conducted separate analyses relating the population wintering locations in relation to breeding population longitude, latitude and breeding phenology (phenology information was available only for geolocation data). We characterized large-scale population differences in breeding phenology based on population mean egg laying dates over a four-year period (2011–2014). We used a four-year annual mean because this metric is less sensitive to annual differences in local conditions than year-specific mean dates, and not depending on the timing of specific individuals in our small set of geolocator fitted birds.

Although breeding phenology in pied flycatchers covaries with population breeding latitude, longitude and altitude (Both and te Marvelde 2007), breeding and migration phenology also vary considerably between individuals within populations. Therefore, we tested whether observed variation in wintering longitudes was also associated with five components of the annual cycle for individual birds: 1) egg laying date, 2) start of autumn migration, 3) arrival at the wintering site, 4) start of spring migration, 5) arrival at the breeding site (2–5 derived from geolocator data) using LMs. We explored the explanatory power of the between- and within-population variation in the association between wintering longitudes and timing components by comparing models with (LMM) and without breeding population (LM) as a random intercept included, by using likelihood ratio tests to test for significant improvements to linear models. For each LMM, the contribution of the fixed factor (e.g. a timing component) was expressed by the marginal R^2 that describes the proportion of variance explained by the fixed effect alone in the LMM. The conditional R^2 includes also variance explained by the fixed and random effects in the LMM.

We tested for repeatability in $\delta^{13}C$ and $\delta^{15}N$ values of winter-moulted feathers from the winter prior to and after geolocators were deployed. Repeatability (i.e. R value) is defined as the proportion of the total variance accounted for by differences among individuals. Linear mixed-effect (LMM) repeatability analyses were performed separately for birds with and without geolocators, using a LMM repeatability analysis with a MCMC function from the R-package 'rptR' (Nakagawa and Schielzeth 2010). To test if the repeatability differed significantly between groups (geolocator vs control) we calculated the mean over the differences from the MCMC chain estimates between both groups which describes the approximate confidence interval. All results for repeatability calculations were obtained using δ values expressed relative to the population mean (both years combined), since populations mean δ values were not always independent ($\delta^{13}C$: $X_1^2 = 2.41$, p = 0.12; $\delta^{15}N$: $X_1^2 = 7.58$, p = 0.006). However, in Fig. 5 the raw data are shown, since absolute δ values are more informative than relative δ values.

Similarity among R values do not necessarily indicate high consistency, because R values are made up of both inter-and intra-individual variation (discussed in Conklin et al. 2013). Therefore we also described inter-and intra-individual variation separately. For the inter-individual variation in δ values among birds in each group (geolocator, control) we pooled all observed values across the two annual cycles (two per bird) and calculated the range (i.e. the difference between the lowest and highest δ values). To describe intra-individual variation in δ values within birds in each group we used the difference between the first and the second year for each individual and calculated the mean and SD across all individuals in each group (geolocator, control).

Furthermore, we explored whether longitudes obtained from geolocation were related to $\delta^{13}C$ and $\delta^{15}N$ values in the corresponding winter. For this analysis we ran separate models with $\delta^{13}C$ and $\delta^{15}N$ as fixed effects and compared models with and without breeding population as a random intercept included (by likelihood ratio tests). All statistical analyses were performed in R, ver. 3.0.1 (R Development Core Team).

Results

Return rates of geolocator birds ranged between 0.04–0.42 and were in most cases lower than the control group or, if proper controls were lacking, the expectation from population specific return rates (Table 1). But for males in Drenthe the return rate over 2011–2012 was higher for birds with a geolocator than for control birds.

Wintering sites, migratory connectivity

All 14 males tracked by geolocation spent the European winter in the western part of the pied flycatchers' wintering range in west-Africa (Fig. 1A) between 4.4–14.2°W. Ring recovery data south of the Sahara were congruent with this pattern (Fig. 1B): pied flycatchers from west or north-west European breeding populations were recovered during winter (December–March, 1971–2008, n = 11) between Guinea and Ghana (0.3–12.4°W), in a narrow latitudinal band (7.1–11.3°N).

We found clear indications for migratory connectivity in pied flycatcher populations, since 'breeding population' as a random intercept explained considerable variance in wintering longitude (LMM: $X_1^2 = 6.40$, p = 0.011, $R^2 = 0.38$). The Norwegian bird wintered in west Guinea (or possibly Guinea-Bisseau) about 381 km west of the mean longitude of all Finnish birds (or 263 km when excluding one Finnish bird wintering in Ivory Coast). The two birds from the UK wintered in Liberia or south-east Guinea and overlapped somewhat with the Dutch birds (that concentrate around west Ivory Coast), wintering on average at a distance of, respectively, 562 and 789 km east of the Norwegian bird. Furthermore, the distance within populations (measured from nearest-neighbour distances of individuals within populations) was considerably less than the average distance between populations (boxplot inset in Fig. 1A), implying strong migratory connectivity.

The observed wintering longitude distribution of pied flycatchers tracked by geolocation tended to associate with breeding latitude of the population (LMM: $\beta = -0.45$,
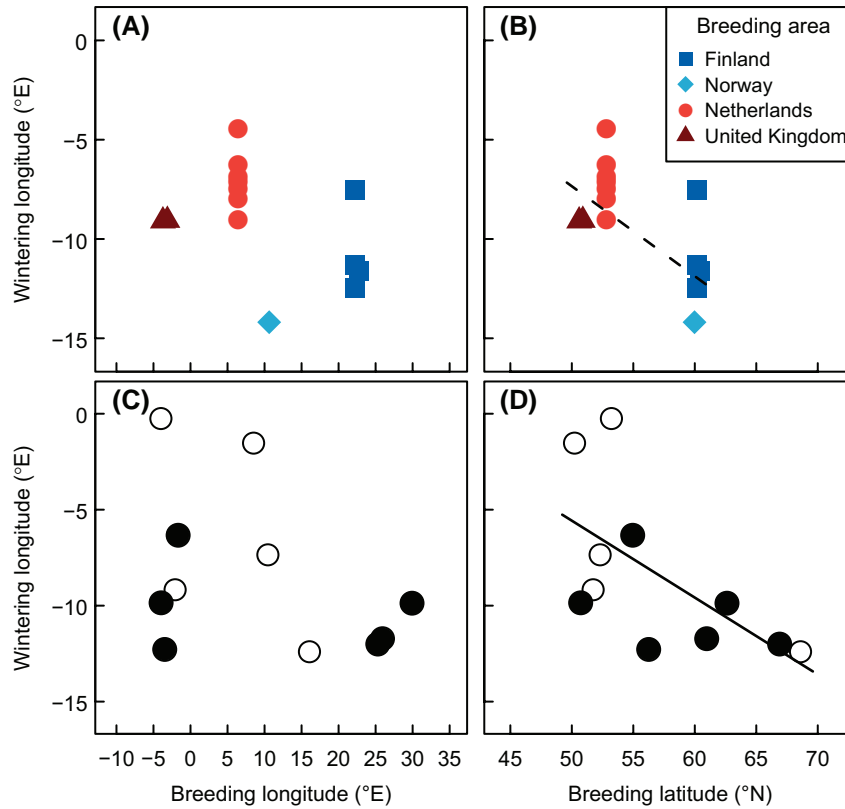
Figure 2. Breeding area longitude and latitude in relation to wintering longitude based on geolocation positioning (A, B) and ring recoveries (C, D). Black dots mark recoveries south of the Sahara of pied flycatchers with a confirmed breeding origin that were reported 'freshly dead' in December–early March. Open symbols indicate recoveries in September–October, April, or exact date unknown. Lines indicate a trend (p < 0.1; dashed line) or significant effect (p < 0.05; solid line) in the linear mixed model (B) or linear model (D). For visibility, overlapping data points (in A, B) are slightly shifted along the x-axis.

$X_1^2 = 3.59$, p = 0.058, marginal $R^2 = 0.32$), rather than with breeding longitude (LMM: $\beta = -0.10$, $X_1^2 = 0.67$, p = 0.41, marginal $R^2 = 0.06$; Fig. 2A). Figure 2B shows that birds from more northern breeding latitudes (FI, NO) wintered further west than birds from more southern breeding latitudes (NL, UK). Further support for a breeding latitudinal gradient on migratory connectivity came from ring recoveries; the recovery longitude of pied flycatchers in sub-Saharan Africa was negatively correlated with breeding latitude (LM: $\beta = -0.41$, $t_9 = -2.40$, p = 0.040; Fig. 2D), but not with breeding longitude (LM: $\beta = -0.13$, $t_9 = -1.33$, p = 0.22; Fig. 2C). The recovery latitudes of pied flycatchers in winter did not show an association with the latitude or longitude of the breeding population (LM, respectively: $\beta = 0.10$, p = 0.15; $\beta = 0.05$, p = 0.15). We cannot perform a comparable analysis with geolocator data as we lack accurate latitudinal estimates.

Timing of migration and breeding

The breeding populations we sampled differ in breeding phenology (Table 1). These timing differences were also found in individuals tracked by geolocation and extended to other phases of the annual cycle (Table 2). On average, flycatchers from UK and NL had laid their eggs 17 d earlier, started autumn migration 13 d earlier, and arrived 22 d earlier at their wintering grounds than the more northerly breeding

populations from Fennoscandia (FI, NO). Within these populations there was also considerable variance in timing of egg laying, autumn migration and especially wintering arrival (SD of pooled data: respectively 8.3, 7.9, 18.5 d in UK/NL; 1.3, 5.9, 6.4 d in FI/NO).

Wintering longitudes correlated with large-scale differences in breeding phenology (LMM: $\beta = -0.21$, $X_1^2 = 6.08$, p = 0.014, marginal $R^2 = 0.48$, conditional $R^2 = 0.72$) in which earlier breeding populations wintered further east (Fig. 3A). Similarly, individual birds that wintered further west laid eggs later (LM: $\beta = -0.14$ d^{-1}, $t_{12} = -2.78$, p = 0.017) and started autumn migration later (LM: $\beta = -0.18$, $t_{12} = -2.76$, p = 0.017) than birds wintering at more easterly longitudes (Fig. 3A–B). Later in the annual cycle the association between timing and wintering longitude faded (LM: winter arrival $\beta = -0.07$, $t_{12} = -1.88$, p = 0.08, Fig. 3C; breeding arrival $\beta = -0.02$, $t_6 = -0.15$, p = 0.89, Fig. 3E), but note that sample sizes shrank as well. Although non-significant, we found a similar slope of wintering longitude on spring departure, again suggesting that individuals that departed earlier from the wintering grounds wintered at more easterly longitudes (LM: spring departure $\beta = -0.21$, $t_7 = -1.51$, p = 0.18, Fig. 3D). Including breeding population as a random factor reduced the fit between timing and wintering longitude for most events (LMM: egg laying $\beta = -0.05$, $X_1^2 = 1.82$, marginal $R^2 = 0.05$, p = 0.18; autumn departure $\beta = -0.10$, $X_1^2 = 1.77$ marginal $R^2 = 0.10$,
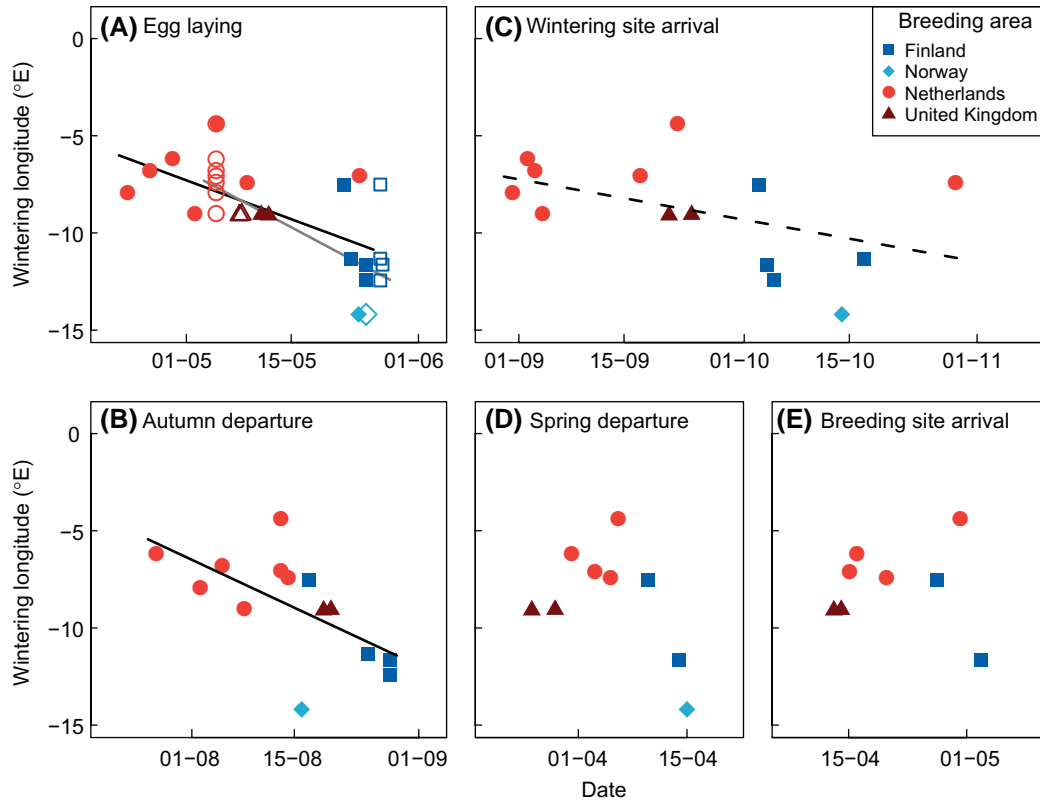
Figure 3. Timing differences in the annual cycle of pied flycatchers in relation to wintering longitude. Variation in wintering longitude is shown in relation to differential timing of (A) egg laying date, (B) start of autumn migration, (C) arrival at the wintering grounds, (D) departure from the wintering grounds, (E) arrival at the breeding grounds. Solid symbols represent annual cycle events on an individual level, as inferred from field observations (A) or geolocation (B–E). The associated lines indicate a trend (p < 0.1; dashed line) or significant effect (p < 0.05; solid line) in the linear model. Open symbols (and short line) in (A) refer to the population mean egg laying date over 2011–2014. The short dark grey line in (A) indicates a significant effect (p < 0.05) in the linear mixed model. For visibility, overlapping data points (in A) are slightly shifted along the x-axis.

p = 0.18; spring departure β = –0.21, X_1^2 = 2.20, marginal R^2 = 0.19, p = 0.14; other events: p > 0.5, marginal R^2 < 0.005). Although these results may suggest that timing of the annual cycle is mostly associated with the non-breeding longitude on a population level, our small and variable sample sizes reduced the power to allow a good assessment within populations.

Migration direction, duration

After the breeding phase all tagged birds showed clear westward heading values during southbound autumn migration, regardless of their breeding origin (Fig. 4). Although our ability to precisely define longitudes varied somewhat among birds (Fig. 4) the data suggest that each individual headed as far west as 14–17°W at some point during autumn migration, which could indicate they follow the coast of west-Africa during part of their journey. After this south and west-ward migration, some (especially UK, NL) birds changed longitude direction to the east to arrive at their wintering sites, while others (mostly FI, NO) remained at these western longitudes for the rest of the winter. During northbound spring migration, most birds gradually headed eastwards and none clearly headed west-ward (Fig. 4).

The total duration of autumn migration took 41 d (± 14 SD; n = 14) about twice as long as spring migration (18 ± 5

d, n = 9). Birds spent on average 189 (± 14 SD) days at their wintering grounds (range 159–210, n = 9; Table 2).

Wintering isotope ratios, geolocator impact

Repeatability of wintering δ values of pied flycatchers was high for $\delta^{13}C$ (geolocator: R = 0.80 ± 0.10; control: R = 0.56 ± 0.17) and $\delta^{15}N$ (geolocator: R = 0.82 ± 0.09; control: R = 0.88 ± 0.07) suggesting similarity in wintering conditions across the two years. Birds with and without geolocators did not differ significantly in wintering repeatability in $\delta^{13}C$ (p = 0.21) or $\delta^{15}N$ (p = 0.53) (Fig. 5). The range in δ values (i.e. inter-individual component of R) in birds with a geolocator (span: $\delta^{13}C$ = –23.3‰ to –19.6‰; $\delta^{15}N$ = + 6.3‰ to + 11.9‰) was very similar compared to birds without a geolocator (range: $\delta^{13}C$ = –23.3‰ to –19.8‰; $\delta^{15}N$ = + 6.5‰ to + 12.4‰). Furthermore, individual consistency was similar for birds with geolocators (Δ $\delta^{13}C$: –0.35 ± 0.45‰; Δ $\delta^{15}N$: –0.11 ± 0.45‰) and birds without (Δ$\delta^{13}C$: –0.23 ± 0.63‰; Δ$\delta^{15}N$: –0.13 ± 0.70‰), as measured from the shift (mean Δ ± SD) in an individuals δ value from one year to the next. This suggests similar among and within individual variation in wintering conditions for birds with and without a geolocator.

Median wintering longitude of an individual was not correlated to δ values in tertials that had been moulted in
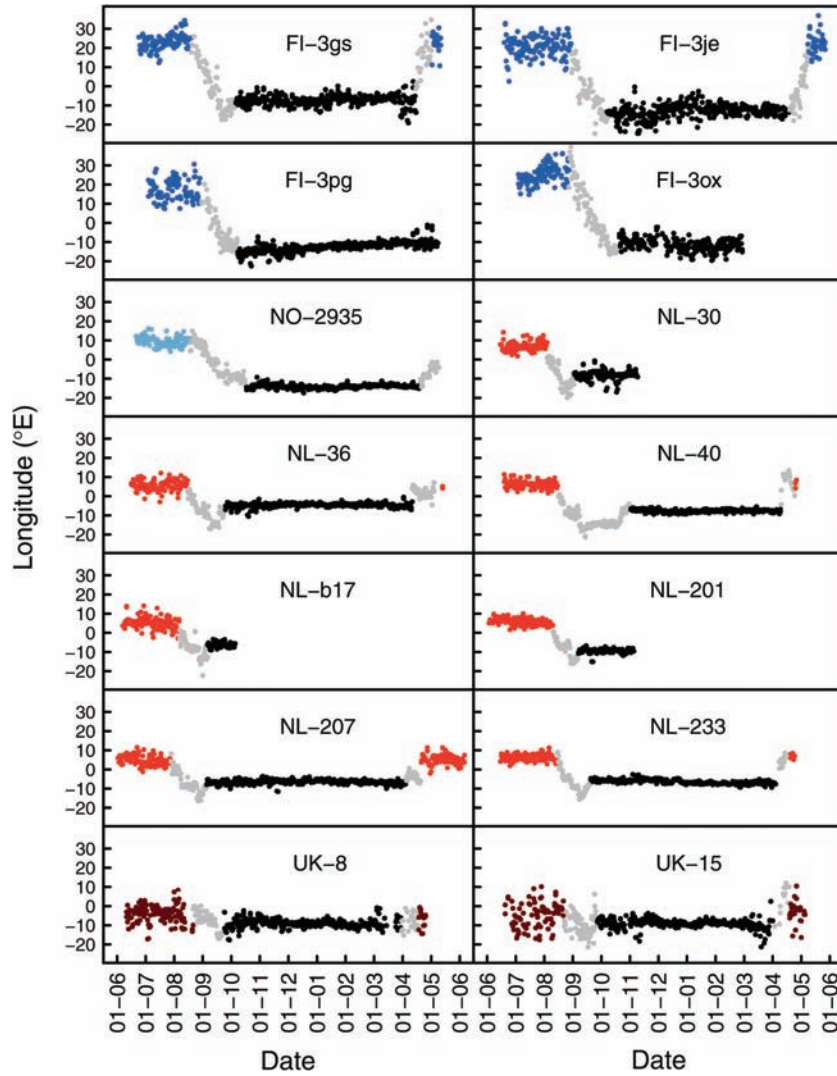
Figure 4. Estimated longitudes obtained by geolocation for male pied flycatchers. Migration periods are shown in grey. Black dots refer to the wintering phase, while the breeding phase is shown with population specific colours (FI = dark blue; NO = light blue, NL = bright red, UK = dark red).
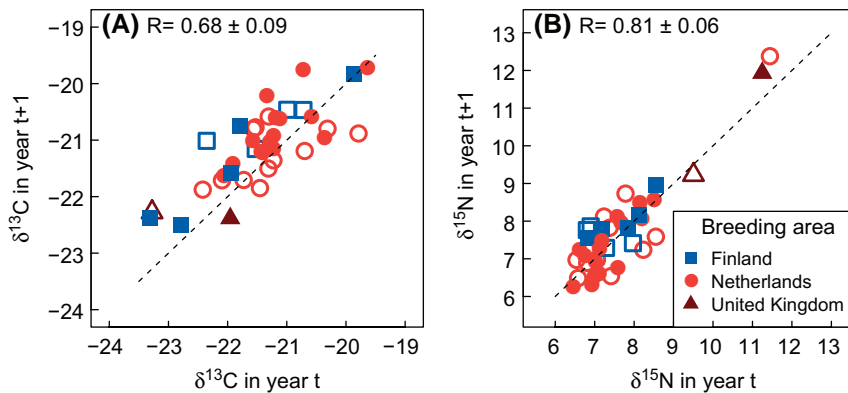

Figure 5. The $\delta^{13}C$ (A) and $\delta^{15}N$ values (B) indicate wintering conditions of individual birds in the year before (year t) and the year of geolocator deployment (year $t + 1$), as measured from winter-moulted tertials. Filled symbols refer to birds with geolocators (incl. devices that contained no data). Open symbols refer to control birds of similar sex, age (if known) breeding location and years. The dashed line shows the x = y-line. For Norwegian birds, no feathers were collected. R-values refer to absolute repeatability and standard error of pooled data (with and without geolocator) calculated from the relative isotopic δ-values around the overall population mean.

the winter of geolocation, year t + 1 (LM: $\delta^{13}C$: $\beta = 0.52$, $t_9 = 0.64$, $p = 0.54$; $\delta^{15}N$: $\beta = -0.01$, $t_9 = 0.02$, $p = 0.98$, Supplementary material Appendix 2, Fig. A1). When breeding population was included as a random intercept again no clear correlation was found between wintering longitude and δ-values in winter-moulted tertial feathers: $\delta^{13}C$ (LMM: $\beta = 0.01$, $X_1^2 = 0.01$, marginal $R^2 < 0.001$, $p = 0.92$) and $\delta^{15}N$ (LMM: $\beta = 1.61$, $X_1^2 = 2.30$, marginal $R^2 = 0.19$, $p = 0.13$).

Discussion

Our study describes how pied flycatchers from different European breeding sites distribute themselves across their west-African wintering grounds. The longitudes at which pied flycatchers spent the winter were associated with the latitude of their breeding site, but not with breeding site longitude. Geolocator data and ring recoveries showed a similar pattern in which Fennoscandian populations settled in the westerly part of the species' wintering range, and western European populations more to the east. Although local return rates of birds with geolocators were generally lower than controls (see also Costantini and Møller 2013, Gómez et al. 2014), we are confident that the general migratory connectivity pattern is not an artefact of carrying a geolocator because of the consistency with ring recoveries. Moreover, $\delta^{13}C$ and $\delta^{15}N$ values were highly repeatable and consistent in geolocator and control birds during the winter, indicating that birds (with and without geolocators) tend to reencounter similar conditions in subsequent winters. This high repeatability and consistency of δ values in winter fit well with previous findings from stable isotope studies (Yohannes et al. 2007, Hjernquist et al. 2009) and more direct descriptions of wintering site-fidelity in pied flycatchers (Salewski et al. 2000, 2002a) and many other long-distance migrants (Curry-Lindahl 1981, Zwarts et al. 2009, Cresswell 2014).

We did not expect strong migratory connectivity because all pied flycatcher populations are assumed to travel through the Iberian Peninsula in autumn (Bibby and Green 1980, Lundberg and Alatalo 1992, Chernetsov et al. 2008). All tracked birds headed far west (approx. 14–17°W) after which some changed heading direction to the east, while others stayed at westerly longitudes. As inferred from these longitude patterns pied flycatchers probably diverge only fairly late during autumn migration. Radar and catching data corroborate this pattern and show that pied flycatchers continue in a south-western direction until reaching the southwestern border of the Sahara, where they shift direction ('Zugknick') to the south or east-south-east (Salewski and Schaub 2007, Liechti et al. 2012). In spring, birds changed their longitudes more gradually (no clear shifts) suggesting that they migrated more directly towards the breeding grounds (implying counter-clock wise loop migration).

The strong migratory connectivity found in pied flycatchers contrasts with weak migratory connectivity described for several Afro-Palearctic passerines such as common redstarts *Phoenicurus phoenicurus* (Kristensen et al. 2013), great reed warblers *Acrocephalus arundinaceus* (Lemke et al. 2013) and barn swallows *Hirundo rustica* (Ambrosini et al. 2009, Liechti et al. 2014). Moreover, the distribution pattern was notably different from other Afro-Palearctic landbirds where parallel migratory connectivity (e.g. in common nightingales *Luscinia megarhynchos* (Hahn et al. 2013) and Montagu's harriers *Circus pygargus* (Trierweiler et al. 2014)), but also leap-frog migration patterns have been found (yellow wagtails *Motacilla flava* (Bell 1996)). The only study that we are aware of that showed a similar pattern – with more northern populations wintering more westward than southern breeding populations – demonstrated this pattern in a neotropical migrant (black-throated blue warblers *Setophaga caerulescens*) using stable isotopes (Rubenstein et al. 2002).

The birds in our study all had a north-western breeding origin, whereas no data were available for birds with a southern or eastern breeding origin. Furthermore, many pied flycatchers winter east of the longitudes observed in our study (in Ghana, Nigeria and Central African Republic: Dowsett 2010). A recent stable-hydrogen assignment study revealed that pied flycatchers wintering in Ghana most likely originate from breeding locations in the central part of the breeding range with respect to latitude (Tonra et al. 2014). Another stable-isotope assignment study on *Ficedula* flycatchers from south Sweden found a high likelihood that Swedish pied flycatchers wintered in the western part of west-Africa (across Liberia and Sierra Leone) or in the southeastern part (Cameroon, Equatorial Guinea, Gabon and northern Congo) (Veen et al. 2014). However, this second region shows very limited overlap with the narrow wintering range described by Dowsett (2010). Since direct evidence is lacking, it remains therefore to be tested whether the migratory connectivity pattern as described in our study persists across the species range.

In our study, wintering longitudes correlated with population specific timing of breeding and autumn departure (Fig. 3A–B). This observation may not be surprising as breeding and migration phenology covaries with population breeding latitude, longitude and altitude (Both and te Marvelde 2007). Yet, migratory connectivity may also arise because of population differences in phenology, depending on processes such as timing of arrival, competition for wintering sites, time and energy constraints (reviewed by Newton 2008), or fluctuations in environmental constraints (Cresswell 2014). Since pied flycatchers occur over a wide wintering range and occupy various habitats (Morel and Morel 1992, Salewski et al. 2002b), wintering sites probably differ in quality. Is it possible that early populations occupy different wintering sites, since they probably arrive first at the wintering grounds? We found a weak trend between wintering longitude and arrival at wintering grounds (Fig. 3C), but there was relatively large variation in arrival dates within populations compared to other timing events. Although the latter seem to suggest little direct pressure on adults to arrive first at their wintering grounds, prior occupancy advantage might have been important in their recent (e.g. first winter) or evolutionary history. Furthermore, we cannot exclude the possibility that geolocator deployment affected timing events that disrupt such correlations, especially during migration when the potential for geolocators to affect performance is presumably at its peak.

The importance of wintering conditions for pied flycatchers has been described by correlative studies showing that after wet seasons spring migration and breeding is earlier

in several populations (Both et al. 2006, Both 2010). Early arrival at the breeding destinations is important as early birds have more choice in obtaining the best available territory and mate (Kokko 1999). This prior occupancy is assumed to promote strong selection in spring on migration strategies (e.g. fuelling decisions) that allow fast migration (Alerstam 2011, Nilsson et al. 2013). The consequences of wintering site selection by pied flycatchers might be most prominent for pre-migratory fuelling, since this takes place at the end of the dry season at the wintering sites (Moreau 1972, Salewski et al. 2002c). Extensive work on American redstarts *Setophaga ruticilla* in the New World has shown that occupancy of high quality habitats in winter advanced timing of spring departure, as mediated by food availability, that carried over to enhance fitness later in the annual cycle (Studds and Marra 2005, 2007). At the west-African wintering grounds of pied flycatchers, food conditions vary in time and space due to differences in habitat, the amount of rainfall and the onset of spring rains (Smith 1966, Zwarts et al. 2009). This raises the question if the observed wintering distribution of pied flycatchers may be related to the timing of spring migration because wintering sites differ in spring fuelling conditions?

If fuelling conditions vary in time and space, the sites that birds from various populations will need to fuel will depend also on their own spring migration schedule. Despite our small sample size, we found that late versus early breeding populations also differed in spring departure dates (mean day: FI = 12 April, NO = 15 April, NL = 3 April, UK = 28 March). These differences were similar to trends estimated in these populations for spring passage through north-Africa, as inferred from long-term ringing recoveries (Both 2010). Bell (1996) showed for yellow wagtails (Bell 1996) how migratory connectivity (leap-frog) patterns could be explained by populations differences in breeding phenology and spring departure, and hence the ability of populations to rely on the rainfall dynamics for fuelling in spring. Besides selecting wintering sites for their improved feeding conditions in response to early rains, pied flycatchers may alternatively select sites or habitats that provide stable fuelling conditions even without early rainfall, as shown in American redstarts (Studds and Marra 2007), or that allow fast migration by other means (e.g. minimize migration distance). A rough approximation of migration distance towards the breeding grounds (assuming winter latitudes of 9°N), suggests that populations with the earliest breeding phenology wintered at longitudes that allow them the shortest possible great circle flight between wintering and breeding destinations (deviation of actual mean location to the closest possible wintering site; NL = Δ 148 km, UK = Δ 26 km). In contrast, the Fennoscandian populations wintered further west than the nearest possible wintering site (FI = Δ 622 km, NO = Δ 365 km). By wintering west of the Dutch and British birds, they may avoid competition with early birds, as well as with birds that winter in the eastern part of the wintering range.

We currently lack data that directly describe habitat quality as well as fuelling conditions of these wintering sites. For the birds that we tracked by geolocation we could not detect a relationship between longitude and δ values in wintering sites that was indicative of differences in habitat quality. However our small sample sizes might hamper infer-

ences of these patterns as variation within habitats in $\delta^{13}C$ and $\delta^{15}N$-values is likely large (as found in site-faithful flycatchers in Ghana: JO unpubl.) while the longitude gradient in these δ-values is subtle (Hobson et al. 2012). Moreover, variation in rainfall dynamics is expected to also occur along a latitudinal gradient (as spring rains move from SE to NW), and thus wintering latitude may be ecologically important. We found no indication for strong migratory connectivity with respect to wintering latitudes in the ring recovery data, but we currently lack proper geolocation data on wintering latitude to confirm this. To unravel if migratory connectivity in pied flycatchers is possibly driven by the dynamics in fuelling conditions, we first need more detailed ecological work at the wintering grounds incorporating temporal dynamics in food availability across space and see how this affects their migrations.

Currently the wintering range of pied flycatchers is subject to large-scale habitat transformation from Guinea savanna into cropland (Ockendon et al. 2012), with losses up to 20% of the dry forests in the Guinea-Congolia/Sudania and Sudanian regions between 1975–2000 (Brink and Eva 2009). These changes affect the extent and location of available habitat remaining for individuals to choose from. If populations evolved to winter at specific sites (e.g. differences in migration direction or predefined goal areas; Thorup and Rabøl 2001, Fransson et al. 2005, Thorup et al. 2011, Liechti et al. 2012, Willemoes et al. 2014) they might be more vulnerable to changes and local habitat loss (Taylor and Norris 2010) than when wintering distributions have the potential to shift (Cresswell 2014). Population differences in migration directions and wintering locations in pied flycatchers (Chernetsov et al. 2008, this study) tend to suggest that wintering site selection is non-random. A complex pattern of migratory connectivity as observed in this study might be explained by juveniles having predefined goal areas embedded in their genes (Thorup and Rabøl 2001, Fransson et al. 2005, Thorup et al. 2011, Willemoes et al. 2014, contra Cresswell 2014). However, since we tracked adults, rather than juveniles prior to selection, it remains to be tested if the observed migratory connectivity patterns arose at the juvenile stage. Because the full implication of strong migratory connectivity in pied flycatchers and their ability to respond to environmental changes may depend on the flexibility of wintering site selection, future studies are needed to unravel both ultimate (e.g. benefits to winter at specific sites) and proximate factors (e.g. migratory programme) that shape wintering distributions.

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Supplementary material (Appendix JAV-00721 at <www.avianbiology.org/appendix/jav-00721>). Appendix 1–2.