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Research Article

Species-specific trends in migratory passage time in Nigeria based on long-term ringing data

Crinan Jarrett^{1,*}, Barbara Helm^{1,*}, Yahkat Barshep², Kwanye Zira Bitrus², Joy Akpanta Ishong², Michael Schaub¹ and Chima J. Nwaogu^{2,3}

¹Bird Migration Unit, Swiss Ornithological Institute, Seerose, Sempach, Switzerland

²A.P. Leventis Ornithological Research Institute, Jos, Nigeria

³FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

Correspondence: Barbara Helm (barbara.helm@vogelwarte.ch)

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As environmental conditions change, the ability of species to adjust their phenology is important for fitness. Advantageous adjustments are often specific to location, species, and annual cycle phase, and are particularly complex in migratory birds that must account for environmental change at vast spatio-temporal scales. Despite the heightened vulnerability of migrants, data on phenological shifts are largely unavailable for non-breeding areas. To reduce this gap, we used ringing data from 2001–2024 from Nigeria to model passage of 10 long-distance migrant species, accounting for a behavioural gradient between locally resident ‘stayer’ species and ‘movers’ which only occur on passage. By assessing temporal trends and environmental associations, we strove to discern effects of ‘pull factors’ from goal areas and locally acting ‘push factors’. Passage varied substantially, whereby typically stayers showed early-starting and long passage, whereas movers showed late-starting, fast passage, highlighting the importance of accounting for different movement behaviour. Peak passage across species changed only slightly over time, but a few species markedly delayed post-breeding migration and advanced pre-breeding migration, consistent with possible evolutionary adjustment to climate change. Our findings only partly confirm reported wide-spread delays of post-breeding migration and advances of pre-breeding migration. Environmental associations in Nigeria were species-specific. For some species, post-breeding passage was early in years with late vegetation senescence in Europe, while pre-breeding migration occurred early in years with early green-up in Nigeria, and particularly in cool years. These associations suggest that favourable local conditions enhance earlier departure in both migration seasons, possibly due to pull factors favouring timely post-breeding arrival in Africa and pre-breeding arrival in Europe. The sensitivity of pre-breeding migration to ambient temperature requires closer investigation of migratory birds’ ability to cope with warming non-breeding grounds, and warns that projected further warming could exacerbate difficulties to keep up with earlier springs on the breeding grounds.

Keywords: climate change, heat, NDVI, phenology, West Africa



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Introduction

Annual cycles of organisms have evolved to align seasonal activities with predictably fluctuating environmental conditions. As environments are rapidly changing, there is strong evidence that plants and animals are adjusting their phenology, i.e. the timing of seasonal processes (Walther et al. 2002). Although such adjustments occur at global scales, they typically differ between phases of the annual cycle, geographic locations and taxonomic groups (Walther et al. 2002, Thackeray et al. 2010, 2016, Cohen et al. 2018, Romano et al. 2023, Sullivan et al. 2024, Hickinbotham et al. 2025). Whether or not a species can track shifting environmental conditions is highly relevant to conservation as it can substantially affect fitness and demography (Visser and Gienapp 2019, Telenský et al. 2020, Youngflesh et al. 2023).

In highly mobile birds, assessing adjustments of full-annual cycle phenology is challenging. Avian breeding phenology has mostly advanced, and moult phenology is also shifting (Van Der Jeugd et al. 2009, Tomotani et al. 2018, Jenni and Winkler 2020a, Hanmer et al. 2022, Tattoni et al. 2025). However, migration adds a layer of complexity, as migrants must account for environmental change at multiple locations. Across the range migrants cover, environmental change, in particular in climate, progresses at different rates and differs in characteristics such as warming, precipitation, variability and extreme events (IPCC 2023). Thus, in migratory species, phenological adjustment appears to be complex and potentially insufficient for maintaining productivity (Both and Visser 2001, Johansson et al. 2015, Visser and Gienapp 2019, Telenský et al. 2020, Youngflesh et al. 2023, Robertson et al. 2024; but see Bellisario et al. 2023).

Adjustment of migration phenology is poorly understood across its vast spatio-temporal scale. Evidence for phenological change is heavily biased towards the breeding range and adjacent regions, with a focus on breeding, arrival, departure and passage (Jenni and Kéry 2003, Helm et al. 2019, Maggini et al. 2020, Telenský et al. 2020, Aharon-Rotman et al. 2021, 2022, Romano et al. 2023, Youngflesh et al. 2023, Dale et al. 2024, Robertson et al. 2024). There is urgent need to obtain phenology data from the Global South, where many migratory species spend the majority of their annual cycle (Moreau 1972, Lawrence et al. 2022, Romano et al. 2023). In the breeding range, reproductive timing in migrants has shifted less than in resident species, presumably because migration constrains early arrival at the breeding grounds (Both and Visser 2001, Romano et al. 2023, Youngflesh et al. 2023, Robertson et al. 2024). Pre-breeding arrival tended to advance in short-distance migrants, whereas shifts in long-distance migrants were moderate and sometimes non-detectable. Departure on post-breeding migration showed some delays with high interspecific variation (Jenni and Kéry 2003, Aharon-Rotman et al. 2021, Lawrence et al. 2022, Romano et al. 2023). Migratory behaviour and its spatio-temporal context are thus important factors for the adjustment of phenology near the breeding grounds, but corresponding data from the non-breeding grounds are almost completely lacking (but see

Bussière et al. 2015, Lawrence et al. 2022, Ouwehand et al. 2023, Ishong et al. 2025).

To better understand the challenges faced by migratory landbirds, in particular in the Eurasian–African migration system, we here present ringing data from West Africa from Jos, Nigeria. In combination with observational data, first arrival and last departure dates from ringing in Jos were recently used in a broad-scale comparison of two West African sites (Ishong et al. 2025), but the greater potential of the data remained unexplored. Taking advantage of the unique long-term ringing data from Nigeria, we first characterise the phenology of the locally most common European-breeding migrant landbirds. We then ask whether the phenology of pre-breeding and post-breeding migration is changing, and whether variation in time of migration passage (defined as the flux of birds through Jos during the two migration phases) is associated with selected environmental factors. The data were collected at the A. P. Leventis Ornithological Research Institute (APLORI) in Jos, central Nigeria, from 2001 to 2024. Parallel local studies on migratory and resident birds provide interpretational context on behaviour and on effects of climate on physiology (Blackburn and Cresswell 2016a, Nilsson et al. 2016, Nwaogu and Cresswell 2016, 2021, Jarrett et al. 2024).

We will first investigate species-specific migration phenology, identifying variation in the timing and duration of post-breeding and pre-breeding passage. The site sustains many migrant species throughout the non-breeding season, but there is large variation in movement behaviour. Long-distance migrants show a spectrum of migration strategies, ranging from the extreme of ‘stayers’ that remain at this single site for most of the non-breeding season. At the other extreme, ‘movers’ use Jos on passage to onward destinations, in some cases co-localising on a continental scale with vegetation green-up (Salewski et al. 2002, Blackburn and Cresswell 2016a, Thorup et al. 2017, Newton 2023, Teitelbaum et al. 2023). There are intermediate forms along this gradient, such as species that peak in numbers during passage times but are nonetheless found at Jos throughout the northern winter (Jarrett et al. 2025a). This local gradient in movement strategies is also closely linked to fuelling patterns, whereby stayers reached 50% of their gain in body mass and fat scores considerably earlier in the pre-breeding migration phase than mover species (Jarrett et al. 2025a). Thus, while the diverse movement strategies complicate analyses, they may influence the ability of species to respond to environmental factors on the non-breeding grounds (Teitelbaum et al. 2023), and we therefore consider them explicitly in our modelling approach.

We will then use the passage time series to assess trends over the study period and to test the role of potential environmental drivers. Throughout Africa, average and extreme temperatures have increased (Nicholson et al. 2018, IPCC 2023). Rainfall has decreased over much of the wider equatorial belt, and seasonal timings of rainfall have shifted (Omotosho et al. 2000, Sanogo et al. 2015, Nicholson et al. 2018, Biasutti 2019). Phenological responses are poorly known, but some studies of birds breeding in the Global South indicate high

inter-specific variation (Chambers et al. 2013, Bussière et al. 2015, Muller et al. 2025). We know of only three African studies that described phenological trends of European-breeding migrants, and they partly support some phenological adjustments (Romano et al. 2023). One compared South African atlas data across time and suggested advancing pre-breeding departure in some species (Bussière et al. 2015). The second study used year-round observations of 20 migratory songbird species in Kartong, The Gambia (1964 to 2019; Lawrence et al. 2022, Ishong et al. 2025). It reported advances in pre-breeding migration and delays in post-breeding migration, suggesting that these species now stay longer in Europe at the cost of time spent in Africa. The third study compared patterns in The Gambia with first-arrival and last-departure dates from observations and ringing in Jos, and found that the trends observed in The Gambia and Nigeria aligned only in part (Ishong et al. 2025). This motivates closer investigation as in Nigeria, we would have expected similar patterns as in Kartong because both sites are used by European-breeding birds as stop-over and residential non-breeding sites (Lawrence et al. 2022; Oliver Fox unpubl.). Specifically, these findings lead to questions about potential environmental drivers of phenological adjustments, which could then differ between sites.

Phenological adjustment in migrants, or lack thereof, has been attributed to 'pull factors' in remote target areas, to locally acting 'push factors', and to underlying mechanisms that constrain or enable the birds' responses to changing environments (Pageau et al. 2020, Helm and Liedvogel 2024, Bakner et al. 2025). Pull factors likely act mostly via evolutionary adjustments of a genetic, endogenous mechanism that triggers preparation for migration because long-distance migrants lack direct access to information on conditions in their target areas (Gwinner 1996, Both and Visser 2001, Helm et al. 2019, Åkesson and Helm 2020). The pull-factors that are commonly thought to affect phenological adjustments, in particular of pre-breeding migration, are reproductive benefits, given the common fitness advantages of timely breeding (Visser and Gienapp 2019, Youngflesh et al. 2023). High individual repeatability indeed supports hard-wired timing of pre-breeding migration (Franklin et al. 2022, Helm and Liedvogel 2024). However, hard-wiring of schedules by endogenous mechanisms may also constrain the migrants' response potential to currently rapidly changing environments (but see Helm et al. 2019), raising concerns about missing optimal reproductive opportunities (Both and Visser 2001, Youngflesh et al. 2023, Robertson et al. 2024). Despite the emphasis in the literature on reproductive phenology, pull factors are likely not restricted to the breeding grounds. Given the strong seasonality across Africa, it is likely that pull factors on the non-breeding grounds also shape migration phenology (Jenni and Winkler 2020a, Newton 2023).

Birds clearly also respond via plasticity to local 'push' factors, such as fluctuating resources or inclement weather (Tottrup et al. 2012, Haest et al. 2020, Pageau et al. 2020, Telenský et al. 2020, Davies et al. 2023, Ouwehand et al. 2023). Most data on such plasticity derive from short-term

studies of species, tracking data and experiments. They linked migration timing to environmental data or compared phenology across the annual cycle (Salewski and Jones 2006, Tottrup et al. 2012, Briedis et al. 2016, Newton 2023, Ouwehand et al. 2023). For example, on or near the breeding grounds, birds may delay arrival or advance departure to reduce risks of increased mortality from severe weather or from vegetation senescence (Brown and Bomberger Brown 2000, Pageau et al. 2020, Newton 2023, Taff and Shipley 2023). At non-breeding sites, some 'mover' species continue their journey when local conditions deteriorate (Newton 2023, Teitelbaum et al. 2023, Jarrett et al. 2025a). In the Afro-tropics, pre-breeding departure is sensitive to resources for the onward journey, as evident from documented effects of food availability and drought (Briedis et al. 2016, Lawrence et al. 2022, Davies et al. 2023, Ouwehand et al. 2023).

At Jos, environmental conditions are highly seasonal, largely due to the movement of the Intra-Tropical Convergence Zone, which drives the rhythmic, predictable alternation between dry and rainy seasons (Sanogo et al. 2015, Nicholson et al. 2018, Newton 2023). European-breeding migratory birds mostly arrive at Jos on post-breeding (autumn) migration at the end of the rainy season, when conditions are still favourable (Jarrett et al. 2025a), and depart on pre-breeding (spring) migration around the start of the following rainy season (Cresswell et al. 2009, Nwaogu and Cresswell 2016). Food availability differs markedly between seasons, affecting the phenology of locally breeding species (Nwaogu and Cresswell 2016, Nwaogu and Cresswell 2021, Jarrett et al. 2024). During the dry season, heat can constitute additional challenges to birds, as reported by Jan-Åke Nilsson (Nilsson et al. 2016). His research showed that during hot phases in Jos, body temperatures reached hyperthermic levels that carry considerable physiological risk, including in the long-distance migratory common whitethroat *Sylvia communis*.

Long-distance migrants must thus balance their responses to pull and push factors, depending on costs and benefits of adhering to schedules or moving on. We will investigate species-specific trends over time alongside two candidate environmental drivers, the temporal dynamics of local vegetation (i.e. NDVI) and, in Nigeria, ambient temperature (Cohen et al. 2018, Romano et al. 2023, Sullivan et al. 2024). For post-breeding migration, we investigate effects of the timing of vegetation senescence in Europe, and for pre-breeding migration, we investigate effects of timing of vegetation greening and ambient temperature in Nigeria (Lawrence et al. 2022, Briedis et al. 2024). Specifically, we expect that for pre-breeding migration, either birds are prioritising the 'pull' of trying to breed earlier (i.e. reflecting temporal trends on the breeding grounds), or the 'push' of local conditions (i.e. responding directly to NDVI and ambient temperature), or that they are hard-wired and therefore show no change. For post-breeding migration, the birds could prioritise early arrival in West Africa as a pull factor (temporal trend), or stay longer in Europe as milder conditions

diminish push factors (responding directly to NDVI), or they are hard-wired and show no change.

Material and methods

Capture data

We used a dataset of mist-net captures of migratory birds around APLORI (Jos, Nigeria, 09°52'N, 08°58'E) (Nilsson et al. 2016, Ishong et al. 2022). Birds were captured, ringed and released throughout the year, though effort (number of nets, days and hours open) was variable. In later years, the site has become a constant-effort site, but throughout the study period there have been many additional captures, depending on local research projects and capacity (Ishong et al. 2022). Since we used all available capture data, the effort represented in our study varied over the years, but there was no consistent trend over time in the number of captures nor of capture days. Each of the years achieved total captures of > 1000 birds, representing substantial mist-netting effort.

We used capture data from 2001 to 2024, and selected the 10 most commonly-caught Afro-Palearctic bird species: garden warbler *Sylvia borin* (n = 2417), common whitethroat (n = 1354), whinchat *Saxicola rubetra* (n = 903), willow warbler *Phylloscopus trochilus* (n = 436), pied flycatcher *Ficedula hypoleuca* (n = 612), tree pipit *Anthus trivialis* (n = 381), spotted flycatcher *Muscapa striata* (n = 310), icterine warbler *Hippolais icterina* (n = 296), nightingale *Luscinia megarhynchos* (n = 128) and wryneck *Jynx torquilla* (n = 76). These species follow different migratory routes and strategies, with some remaining in Jos throughout the non-breeding season, whilst others spend part of the European winter further south and pass through Jos on their southward and northward

journeys (Jones 1995, Ottosson et al. 2005, Cresswell et al. 2009, Risely et al. 2015, Blackburn and Cresswell 2016b, Newton 2023). Throughout this article, we will use the following terms to describe the different processes that are parts of the birds' life-cycle: 'post-breeding migration' are the movements made during the boreal autumn, involving flight to Africa; 'non-breeding phase' is the presumed stationary phase at APLORI between migrations, and 'pre-breeding migration' is the northward movement to the breeding grounds conducted in boreal spring. Additional movements of birds during the non-breeding season are not the focus of our study (Teitelbaum et al. 2023).

We considered species to be on a gradient from 'stayers' (birds that remain resident in Jos between the migration phases) to 'movers' (pass-through). To quantify the position of each species on this site-specific gradient, we considered the mean yearly proportion of captures made during the non-breeding phase, defined following (Jarrett et al. 2025a, Table 1). We assume that species that tend to stay in Jos from post-breeding migration through to pre-breeding migration will have a higher proportion of captures during the non-breeding phase than species that pass through. When considering the proportion of captures during the non-breeding phase, species can be ordered as follows (from lowest – 'movers', to highest – 'stayers'): spotted flycatcher, icterine warbler, garden warbler, whinchat, willow warbler, pied flycatcher and common whitethroat (Table 1; Jarrett et al. 2025a). Spotted flycatcher and icterine warbler have almost no captures (0 and 1, respectively) during the post-breeding and non-breeding phases because they only pass through Jos during the pre-breeding migration. Note that for three of the species, results should be interpreted with caution. Nightingale and wryneck had overall low sample sizes, but we kept them in the analyses because data from these species in the non-breeding grounds

Table 1. Sample size and first and last capture for each species in Jos, Nigeria. To classify species on the mover–stayer spectrum, we considered the mean proportion of captures across years made during the non-breeding phase (considered as 1 January to 17 March, based on Jarrett et al. 2025a). Species are sorted from the top as movers (lowest capture proportion) to stayers (highest capture proportion) at the bottom, and yearly means of proportions and numbers of captures during the non-breeding season are shown. Spotted flycatcher and icterine warbler only pass through Jos during pre-breeding migration (dark grey shading). Tree pipit, nightingale and wryneck (pale grey shading) have low numbers of captures in the first half of the year, and thus the classification into stayers versus movers was made visually as the proportions may be biased.

Species	Total captures	Mean yearly captures	Earliest post-breeding capture	Latest pre-breeding capture	Mean across years of proportion (and of number) of captures in non-breeding phase
Spotted flycatcher	310	13		17 May	0.00% (0.00)
Icterine warbler	296	12		18 May	1.04% (0.04)
Garden warbler*	2417	101	24 August	24 May	1.49% (0.71)
Tree pipit**	381	16	27 September	28 April	-% (1.08)
Whinchat	903	38	28 September	05 May	37.36% (4.88)
Willow warbler	436	18	15 September	02 May	44.03% (2.21)
Pied flycatcher	612	26	31 August	08 May	59.47% (5.58)
Common whitethroat	1354	56	24 September	10 May	60.11% (21.29)
Nightingale**	128	5	09 September	15 April	-% (0.83)
Wryneck**	76	4	29 September	30 April	-% (1.04)

*One garden warbler was captured on 2 July 2016. We did not include this capture in the analysis as presumably it represents an exceptional case where the bird did not perform pre-breeding migration and remained in Jos throughout the summer months (Kwanye Zira Bitrus, pers. comm.).

**Calculations of mean proportions for these species were unreliable due to small sample sizes during the pre-breeding season (< 45 captures per species over 24 years).

are rare. Tree pipit had considerable capture numbers, but heavily skewed towards the autumn, so that captures in the non-breeding and pre-breeding periods were limited ($n=45$ over 24 years). Thus, classification into stayers versus movers for these three species was unreliable due to very low number of captures from the pre-breeding season, leading to unreliable estimation of proportions (Table 1). For these three species, we sorted them as stayers or movers based on the apparent shape of capture distributions: if there were evident peaks during post- and pre-breeding passage and almost no captures in between, we considered the species a mover (the case of tree pipit), whereas if the number of captures appeared more or less stable throughout the non-breeding period, we considered the species a stayer (the case for nightingale and wryneck).

For subsequent modelling (below), we needed to put species along the gradient into categories in order to fit the most appropriate model, as the models for different behaviours had slightly different structures. Allocation to categories followed the large leap in the proportion of non-breeding captures from < 2 to $> 37\%$ (Table 1). The three species with unreliable proportions were classified according to continuity of the captures distribution (indicating stayers), or to bimodality of captures or limitation to a single migration season (indicating movers).

Effort data

Detailed mist-netting effort data (number of nets or hours open) were not available for our capture dataset. However, there was a parallel dataset to that of the migratory bird captures that contains all captures from all species (i.e. including resident birds; Ishong et al. 2022). Given that it is very rare for no birds to be caught when nets are opened (Chima Josiah Nwaogu, pers. comm.), we used the days in which any bird was captured as an approximation of effort. To do this, we created a binary effort variable describing whether nets were or were not open on a given day. Thus, for each day of the year, capture data for each migrant species could then either be a given number of captures, 0 (if nets were open – i.e. at least one bird was caught, but no individuals of the focal species were captured) or NA (if, to our knowledge, no nets were opened).

Environmental covariate data

To test whether timing of migration was influenced by conditions in the breeding and non-breeding grounds, we downloaded NDVI data for the period 2001–2024 for Western Europe and Nigeria (date range for both datasets: 01 January 2001 to 18 December 2024). We used the MOD13A2 ver. 6.1 product (Didan 2021), downloaded via Google Earth Engine. We defined the European breeding grounds as 7°W – 21°E and 40° – 65°N , following (Lawrence et al. 2022). Whilst we mostly do not know from which breeding populations the birds caught in Jos come, this defined area likely encompasses for most study species the highest breeding richness and the majority of range extents of the populations captured in West Africa (Blackburn et al. 2019, Briedis et al. 2020, Lawrence et al. 2022, Tapia-Harris et al. 2022, Briedis et al. 2025).

The NDVI data from Nigeria cover 4° – 12°E and 3° – 12°N , which spans most of the country and thus broadly represents conditions in the area where birds were captured and in neighbouring areas to which they could easily travel (Cresswell et al. 2009). For these two areas, we downloaded 16-day NDVI values at 500 m resolution, and then, for each date, we calculated an average across all grid cells of the area (Supporting information). In Jos, each year there is a single dry season ($\sim$ November to March) and a rainy season ($\sim$ April to October). The rainy season is usually interrupted around August by a short, dry break from rains, as the region borders on areas with bimodal rainy seasons (Omotosho 1988). Before the proper onset of the rainy season deciduous trees start greening up, and there may be minor precipitation, both leading to early increases in NDVI (Adole et al. 2018).

NDVI values are strongly influenced by land-use, and thus, comparing values of the same area between years may not be representative of different patterns of greening but rather of changes in land-use. This is especially relevant for datasets such as ours that cover an extensive area and a long-time span, as it is highly probable that land-use has changed considerably over this period. Therefore, rather than quantifying environmental conditions using NDVI data directly, we calculated timing of vegetation green-up (in the pre-migratory phase in Nigeria) and senescence (in autumn in Europe Lawrence et al. 2022, Briedis et al. 2024).

NDVI in Nigeria is at its lowest at the end of the dry season ($\sim$ January–February), and then increases steeply throughout the pre-migratory phase until a first peak around June (Supporting information). Thus, to capture vegetation green-up, for each year we extracted all NDVI measurements (consisting of means across spatial extents, see above) between the day of the year with lowest NDVI value (mean = 18 February, range = 17 January to 22 March) and the day with the highest NDVI value prior to day 200 (mean = 9 June, range = 9 May to 12 July). By doing so, we captured the peak prior to the pre-breeding migration phase, rather than the second peak that occurs later in the year around October. For Western Europe, NDVI is at its lowest at the start of the year, increases until a peak around late June, and then declines throughout the autumn, representing vegetation senescence (Supporting information). Thus, for each year, we selected NDVI values between the day of maximum NDVI (mean = 24 June, range = 24 May to 27 July) and the day of minimum NDVI in the second half of the year (mean = 12 December, range = 17 November to 19 December), to capture autumn senescence.

To these data, we fitted logistic curves with smoothing (to allow for noisy time-series; Supporting information), using the *loess* function in R (www.r-project.org). We then generated predicted data from the loess model, and from this we extracted parameter t_{50} , which represents the time point in the curve at which NDVI reaches 50% (Briedis et al. 2020). For Nigerian data, t_{50} thus represents the 50% point of green-up during the pre-migratory phase, whilst for European data t_{50} represents the point at which vegetation senescence in autumn reaches 50%.

In addition to local productivity, we wanted to test the effect of high ambient temperatures in Nigeria on birds while preparing for pre-breeding migration, following (Nilsson et al. 2016). We thus downloaded temperature data spanning 2001–2024 for Nigeria (same extents as NDVI data) from the Climatic Research Unit (CRU; Harris et al. 2014, as in Lawrence et al. 2022). The CRU data are monthly mean temperatures, which in Nigeria are at their lowest in December to January, and at their highest in March to May (Supporting information). We selected data for February and March, covering the main phase prior to migration, and calculated an average between the two months.

We tested for correlation between the t_{50} values, temperature and year, and found overall low correlation (all Spearman's correlation coefficients ≤ 0.25 ; Supporting information). The closest correlations were between t_{50} in Europe (autumn senescence) and year (Spearman's correlation coefficient = 0.25, $p = 0.17$), indicating that vegetation is senescing later, between t_{50} in Nigeria (green-up) and year (Spearman's correlation coefficient = -0.23, $p = 0.59$), indicating that vegetation is greening earlier, and between t_{50} in Nigeria (green-up) and ambient temperature (Spearman's correlation coefficient = 0.23, $p = 0.16$), indicating that vegetation greening was delayed in hot years (Supporting information).

General modelling framework

We constructed three different model variants depending on the movement strategy of the species: one model for stayers, one for movers, and one for species recorded only during pre-breeding-migration. The basic way of modelling migration passage was the same across model variants (Fig. 1), but we added an element to describe the non-breeding phase in the stayer model, and we considered only pre-breeding phase captures in the pre-breeding-phase only model. Given the nature of our data with inconsistent effort, we could not directly

extract date of first arrival and departure from the raw capture data, as is often done in other studies (Romano et al. 2023, Dale et al. 2024). Instead, we used the data to estimate passage timing, and from this we derived estimated dates for start and end of passage.

We divided all capture data into seasons, which consist of half-year blocks; data for each year were divided into one season spanning 1 July to 31 December (broadly speaking capturing post-breeding migration and the first half of the non-breeding phase, 183 days), and a second season spanning 1 January to 30 June (capturing the second half of the non-breeding phase and pre-breeding migration, 182 days; Fig. 1). In total, our capture data spanned 47 seasons (i.e. 23.5 years: northern autumn 2001 to autumn 2024). We modelled count data ($C_{d,y,i}$) on capture day of season, d (1:183 for the post-breeding phase, 1:182 for the pre-breeding phase), season y ($y = 1, 3, 5, 7 \dots$ for the post-breeding phase, $y = 2, 4, 6, 8 \dots$ for the pre-breeding phase) and species i as a Poisson-distributed variable. Number of captures $C_{d,y,i}$ was dependent on the total captures for each season and species $n_{y,i}$ and parameter $a_{d,y,i}$, which is a function of the underlying migration and non-breeding phase processes and corresponds to the relative frequency of captures:

$$C_{d,y,i} \sim \text{Poisson}(n_{y,i} a_{d,y,i}) \quad (1)$$

This model does not incorporate imperfect detection, but rather just considers relative abundance – i.e. $n_{y,i}$ is an index of population size. We considered that, depending on time of year and species, capture data from birds on each day could represent either just post-breeding passage, a mixture of post-breeding passage and non-breeding phase, just non-breeding phase, a mixture of the non-breeding phase and pre-breeding passage, or just pre-breeding passage.

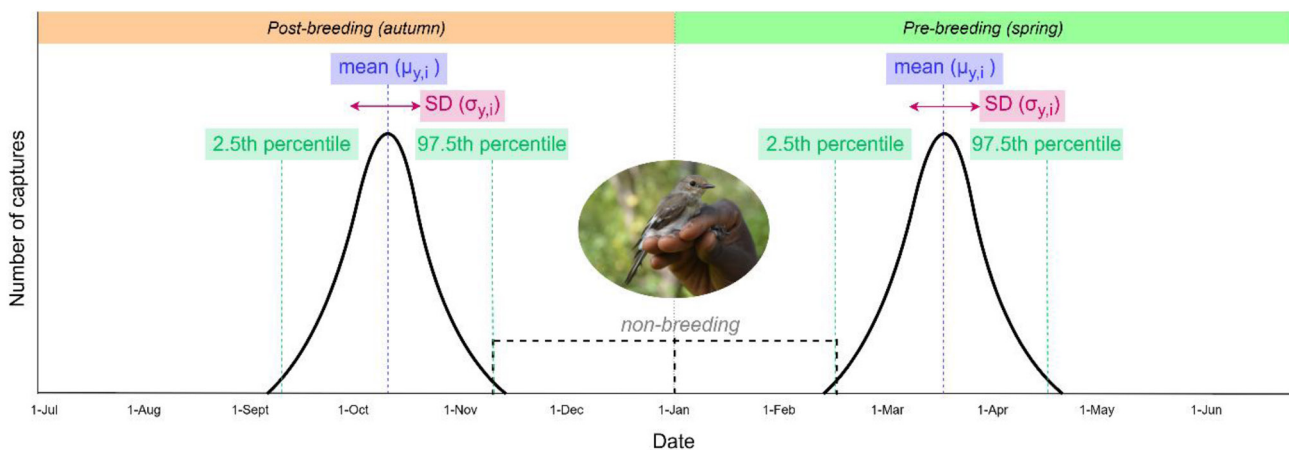


Figure 1. Schematic representation of model used to quantify phenology of migration through Jos, Nigeria. The model considers capture data from each season (post-breeding or pre-breeding of each year) to represent two potential processes, migration passage and residency during the non-breeding phase. Migration passage is modelled using a Gaussian density function defined by parameters $\mu_{y,i}$ (mean) and $\sigma_{y,i}$ (standard deviation). From these two parameters, we then derived the 2.5th and 97.5th percentiles of post-breeding and pre-breeding migration passage, which broadly capture start and end of passage. The non-breeding phase is modelled as a uniform distribution spanning 97.5th percentile to end of year for post-breeding captures, and start of year to 2.5th percentile for pre-breeding captures.

Mover model

For mover species (garden warbler and tree pipit), we considered that data represent just post-breeding and pre-breeding passage, with no non-breeding phase process. The relative frequency $a_{d,y,i}$ was modelled via a Gaussian density as a function of capture date (d), date of peak relative abundance $\mu_{y,i}$ and a scale parameter $\sigma_{y,i}$ (equivalent to standard deviation, SD) which describes the width of the curve (Fig. 1, Table 2):

$$a_{d,y,i} = \frac{1}{\sigma_{y,i}\sqrt{2\pi}} \exp\left(-\frac{(d - \mu_{y,i})^2}{2\sigma_{y,i}^2}\right) \quad (2)$$

This model for pre-breeding and post-breeding passage processes was based on the phenomenological within-season model presented by (Dennis et al. 2016), and demonstrated in Chapter 1 of Applied Hierarchical Modelling in Ecology (Kéry and Royle 2021). Given the nature of our capture data, we modelled migration passage as a Gaussian distribution with an estimated mean and SD. The assumed symmetry in the Gaussian distribution is supported by the distributions of arrival and departure dates that were recently reported for combined observational and ringing data from APLORI (Ishong et al. 2025), as well as by the distribution of arrival times from a European mist-netting scheme in the Baltic Sea (Tøttrup et al. 2006). In our data, exploratory plotting of the captures confirmed reasonable fit with a Gaussian distribution (see the Supporting information for the most common species, the garden warbler). The Gaussian distribution had additional advantages by allowing some flexibility (e.g. varying SD), without an unreasonable number of parameters to estimate, but other distributions with heavier tails such as the t-distribution could also be used.

The count model describes a unimodal symmetric temporal pattern in abundance of a species, estimating the Gaussian parameters $\mu_{y,i}$ and $\sigma_{y,i}$ to describe the date of maximum captures, and the spread around it (Fig. 1). From the parameters mean and SD, we could derive 2.5th and 97.5th quantiles. Thus, we use four parameters (mean $\mu_{y,i}$, SD $\sigma_{y,i}$, 2.5th and 97.5th quantiles) to characterise timing of migration, where the 2.5th and 97.5th quantiles broadly represent start and end of post-breeding and pre-breeding passage. We estimated the duration of passage by subtracting the date of the 2.5th from that of the 97.5th quantile. Using quantiles to represent start and end dates mitigates some of the bias and distortion commonly associated with absolute first and last observation dates, or with looking only at mean passage times (Tøttrup et al. 2006, Sparks et al. 2008, Dale et al. 2024). However, our estimates do not reflect empirical quantiles, as in the works cited above, because here they are derived from the modelled distribution.

Pre-breeding-only model

For pre-breeding-only species (icterine warbler and spotted flycatcher), we used a model identical to the mover model but considering only pre-breeding captures, i.e. $y=2, 4, 6, 8, \dots$

Stayer model

For stayers, $a_{d,y,i}$ is given by a mixture of either the pre-breeding or post-breeding migration process, and the non-breeding phase process (Fig. 1). This is modelled as a mixture of two distributions with probabilities, $p_{1,y,d,i}$ for the migration process, and $p_{2,y,d,i}$ for the non-breeding phase. Thus, we defined $a_{d,y,i}$ as follows:

$$a_{d,y,i} = p_{1,y,d,i} \frac{1}{\sigma_{1,y,i}\sqrt{2\pi}} \exp\left(-\frac{(d - \mu_{1,y,i})^2}{2\sigma_{1,y,i}^2}\right) + p_{2,y,d,i} \frac{1}{\delta_{2,y,i} - \delta_{1,y,i}} \quad (3)$$

The migration processes are modelled as in the mover model, via a Gaussian density as a function of capture date (d), date of peak relative abundance $\mu_{y,i}$ and parameter $\sigma_{y,i}$ which describes the width of the curve (SD). The non-breeding phase process is modelled as a uniform density with parameters $\delta_{1,y,i}$ and $\delta_{2,y,i}$ corresponding to the range of the distribution (Fig. 1, Table 2). During the post-breeding phase, $\delta_{1,y,i}$ was assumed to be identical to the 97.5th percentile of post-breeding passage and $\delta_{2,y,i}$ was set to 183 corresponding to the last day of the year counted from 1 July. During the pre-breeding phase, $\delta_{1,y,i}$ was set to 1 and $\delta_{2,y,i}$ was assumed to be identical to the 2.5th percentile of pre-breeding migration. The probability parameter for the residential non-breeding phase process $p_{2,y,d,i}$ was modelled using a logistic function with parameters $k_{1:2,i}$ (where 1=post-breeding and 2=pre-breeding), representing the logistic growth rate (steepness of the curve) and $m_{1:2,i}$ the midpoint of the curve (Table 2). This logistic function represents the increasing likelihood of a non-breeding phase with increasing day of year (d ; during the post-breeding phase), and the equivalent decrease during the pre-breeding phase (Table 2).

$$p_{2,y,d,i} = \frac{1}{1 + \exp(-k_{1:2,i}(d - m_{1:2,i}))} \quad (4)$$

The daily probability of the migration process was therefore 1 minus the probability of the non-breeding phase, as these are mutually exclusive processes.

$$p_{1,y,d,i} = 1 - p_{2,y,d,i} \quad (5)$$

Covariates affecting passage timing

To test our hypotheses, we modelled peak passage timing $\mu_{y,i}$ as a function of a species-specific intercept ($b_{1:2,i}$), representing the mean date of post-breeding and pre-breeding passage across years, plus covariates ($v_1 \dots v_5$; Table 2). Specifically, for post-breeding migration (stayer and mover models), we included a continuous variable for year to capture the potential linear temporal trend over the study period in post-breeding passage timing, and a covariate describing the effect of timing of vegetation senescence in Western Europe (quantified using t_{50} parameter). For pre-breeding migration (stayer, mover and pre-breeding-only models), we included the continuous

Table 2. Description of parameters used in models, including prior distributions and definitions. Subscripts are used as follows: y =season (either post-breeding or pre-breeding phase each year, counted progressively over the study period), i =species, d =day of year.

Parameter	Description	Prior distribution or linear model	Included in model
$\mu_{y,i}$	Mean of Gaussian distribution describing migration process, i.e. timing of peak captures	$\mu_{y=\text{autumn},i} = b_{1,i} + v_{1,i}\text{Year}_y + v_{2,i}t50\text{Eur}_y + \varepsilon_{1,y,i}$ $\mu_{y=\text{spring},i} = b_{2,i} + v_{3,i}\text{Year}_y + v_{4,i}t50\text{Nig}_y + v_{5,i}\text{TempNig}_y + \varepsilon_{2,y,i}$	All
$b_{1:2,i}$	Intercept of linear predictor describing timing of peak captures $\mu_{y,i}$ in the post-breeding ($b_{1,i}$) and pre-breeding phase ($b_{2,i}$), i.e. mean timing of peak captures across years	Normal(80, 20)	All
$\nu_{1,i}$	Coefficient describing the effect of year (continuous variable 2001–2024, scaled and centered) on timing of peak passage $\mu_{y,i}$ during the post-breeding phase	Normal(0, 3.2)	All
$\nu_{2,i}$	Coefficient describing the effect of vegetation senescence (t_{50}) in Western Europe (continuous variable, scaled and centered) on timing of peak captures $\mu_{y,i}$ during the post-breeding phase	Normal(0, 3.2)	All
$\nu_{3,i}$	Coefficient describing the effect of year (continuous variable 2002–2024, scaled and centered) on timing of peak captures $\mu_{y,i}$ during the pre-breeding phase	Normal(0, 3.2)	All
$\nu_{4,i}$	Coefficient describing the effect of vegetation green-up (t_{50}) in Nigeria (continuous variable, scaled and centered) on timing of peak captures $\mu_{y,i}$ during the pre-breeding phase	Normal(0, 3.2)	All
$\nu_{5,i}$	Coefficient describing the effect of mean temperature in Feb–Mar in Nigeria (continuous variable, scaled and centered) on timing of peak captures $\mu_{y,i}$ during the pre-breeding phase	Normal(0, 3.2)	All
$\varepsilon_{1:2,y,i}$	Random error term describing potential inter-year variation in timing of peak captures during the post-breeding and pre-breeding phase	Normal(0, 3.2)	All
$\sigma_{y,i}$	Standard deviation of Gaussian distribution describing migration process, i.e. spread of captures around peak	$\sigma_{y,i} = \exp(\omega_{1:2,i} + \tau_{1:2,y,i})$	All
$\omega_{1:2,i}$	Intercept of linear predictor describing spread in timing of captures $\sigma_{y,i}$ during the post-breeding ($\omega_{1,i}$) and pre-breeding phase ($\omega_{2,i}$)	Normal(3.4, 0.15)	All
$\tau_{1:2,y,i}$	Random error term describing potential inter-year variation in spread of captures during the post-breeding and pre-breeding phase	Normal(0, 0.15)	All
$\delta_{1:2,y,i}$	Upper and lower bounds of Uniform distribution describing the residential non-breeding phase process.	During post-breeding $\delta_{1,y,i} = 97.5\text{th percentile of post-breeding passage}$ and $\delta_{2,y,i} = 183$. During pre-breeding $\delta_{1,y,i} = 1$ and $\delta_{2,y,i} = 2.5\text{th percentile of pre-breeding passage}$.	All
$p_{1,y,d,i}$ $p_{2,y,d,i}$	Probability of captures belonging to migration process. Probability of captures belonging to the residential non-breeding phase process.	$p_{1,y,d,i} = 1 - p_{2,y,d,i}$ $p_{2,y,d,i} = \frac{1}{1 + \exp(-k_{1:2,i}(d - m_{1:2,i}))}$	Stayers Stayers
$k_{1:2,i}$	Logistic growth rate (steepness of curve) of the probability of the residential non-breeding phase as a function of day of year (d)	During post-breeding $k_{1,i} \sim \beta(0.7, 2.6)$ and during pre-breeding $k_{2,i} = -1 \times \beta(0.7, 2.6)$	Stayers
$m_{1:2,i}$	Mid-point of curve describing change in probability of a residential non-breeding phase with day of year.	During post-breeding, $m_{1,i} = \text{Normal}(150, 10)$, and during pre-breeding $m_{2,i} = \text{Normal}(60, 10)$, which is equivalent to 1 December for post-breeding and 1 March for pre-breeding.	Stayers

temporal covariate describing a potential linear yearly trend, a covariate describing the effect of pre-migration green-up timing in Nigeria, and a covariate for mean temperature in February to March in Nigeria. For both post-breeding and pre-breeding passage models, we added a temporal residual

term (random effect) $\varepsilon_{1:2,y,i}$ to capture potential variation between years not described by the covariates. This random effect was informed by a diffuse prior with commonly used parametrization of mean=0 and variance=10 (SD=3.16; Eq. 6).

$$\mu_{y=\text{autumn},i} = b_{1,i} + v_{1,i}\text{Year}_y + v_{2,i}t50\text{Eur}_y + \varepsilon_{1,y,i}$$

$$\varepsilon \sim \text{Normal}(0, 3.16) \quad (6)$$

$$\mu_{y=\text{spring},i} = b_{2,i} + v_{3,i}\text{Year}_y + v_{4,i}t50\text{Nig}_y$$

$$+ v_{5,i}\text{TempNig}_y + \varepsilon_{2,y,i} \quad (7)$$

We modelled the log of $\sigma_{y,i}$ (to ensure positive values) as a function of a species-specific intercept $\omega_{1,2,i}$ and a random error term for year $\tau_{1,2,y,i}$ (Table 2):

$$\sigma_{y,i} = \exp(\omega_{1,2,i} + \tau_{1,2,y,i}) \quad (8)$$

To visualise the effects of covariates, we sampled the parameters by taking 2000 random draws from their posteriors. We considered covariates to have a significant effect on phenology when 95% credible intervals (CRI) of posteriors did not overlap 0. We used the random draws to generate predicted values; when generating predicted values for a focal predictor, we fixed other predictors at their mean value.

We used the Bayesian framework for model fitting, requiring the definition of a prior distribution of each quantity we estimate (Table 2). We ran the process model with 3 chains for 100 000 MCMC iterations each (plus 6000 burn-in) with a thinning rate of 5, resulting in 60 000 samples from the posterior distributions. Convergence of the chains was ensured with these specifications (R-hat < 1.1). We fit all models using the JAGS 4.3.0 software (Plummer 2023) executed using the runjags (Denwood 2016) in the R statistical computing environment (www.r-project.org). We report posterior means and the 95% CRI.

Results

Timing of peak, start and end of passage in Jos

Afro-Palearctic migrants were captured in Jos from 24 August (first recorded capture of post-breeding phase, garden warbler in 2005) to 24 May (last recorded capture of pre-breeding phase, garden warbler in 2022). Considering all species jointly, average timing of peak passage during the post-breeding phase was 23 October (95% range of captures: 20 September to 26 November). During pre-breeding migration, average peak timing of captures was 6 April (95% range of captures: 1 March to 12 May).

Variation between species in peak timing of passage was considerably larger during pre-breeding than post-breeding migration (Fig. 2, Table 3). In the post-breeding season, peak passage timing varied from 19 October in pied flycatcher, the earliest-peaking species, to 31 October in whinchat, the latest species (Fig. 2, Table 3). Peak pre-breeding passage timing varied from 15 March in tree pipit to 28 April in spotted flycatcher. The spread in timing of captures also varied between species and seasons. During the pre-breeding

phase, spotted flycatcher, icterine warbler and whinchat had the lowest spread (Fig. 2, Table 3). Wryneck, nightingale, and pied flycatcher had the largest spread of captures during the pre-breeding phase, although there were limited data for nightingale and wryneck (Fig. 2, Table 3).

Considering the mean across years, the start of post-breeding passage (2.5th quantile) occurred on 10 September in common whitethroat, the earliest starting species, to 6 October in whinchat, the latest starting species (Table 3; not considering wryneck and nightingale due to limited data). End of post-breeding passage (97.5th quantile) ranged from 9 November in pied flycatcher to 5 December in common whitethroat. During the pre-breeding phase, start of passage ranged from 27 January in tree pipit to 16 April for spotted flycatcher (Table 3). End of pre-breeding passage ranged from 29 April in whitethroat to 25 May in garden warbler.

Overall, species that started passage earlier had a longer passage duration than late-starting species (Fig. 3), evidenced by a negative relationship between start of passage and duration. This was true for both seasons, with birds aligning on a spectrum of 'early-slow' to 'late-fast' passage (Fig. 3). Whilst this negative association between dates and duration held up in both seasons, it was steeper during the pre-breeding phase. During the pre-breeding phase in particular, this relationship arose because the start of passage differed far more among species (range 2.5 months) than its relatively synchronous end (range < 1 month; Fig. 3).

For the post-breeding phase, the earlier starters with longer passages included common whitethroat (start=10 September, duration=86 days) and garden warbler (start=20 September, duration=60 days), as well as nightingale and wryneck. The species with later starts and shorter passages included pied flycatcher (start=28 September, duration=42 days), whinchat (start=6 October, duration=51 days) and willow warbler (start=2 October, duration=48 days). During the pre-breeding phase, pied flycatcher (start=1 February, duration=113 days) and whitethroat (start=7 February, duration=82 days), as well as nightingale, tree pipit and wryneck, and thus mostly stayer species, belonged to the early-slow passage group (Fig. 3, Table 3). In contrast, icterine warbler (start=11 April, duration=33 days), spotted flycatcher (start=16 April, duration=25 days) and whinchat (start=28 March, duration=40 days), and thus mainly movers, belonged to the group with late-fast passage (c.f. Fig. 3, colour-shading).

Temporal and environmental effects on migration phenology

When considering all species together by taking the mean peak passage times for each year, post-breeding passage has become slightly later, and pre-breeding passage slightly earlier (Supporting information). Mean post-breeding passage across species was 21 October in 2001 (DOY=294, 95% CRIs=283–303) and 25 October in 2024 (DOY=298, 95% CRIs=285–315). Mean pre-breeding passage was 7 April in 2002 (DOY=97, 95% CRIs=71–119) and 4 April in 2024 (DOY=94, 95% CRIs=64–120).

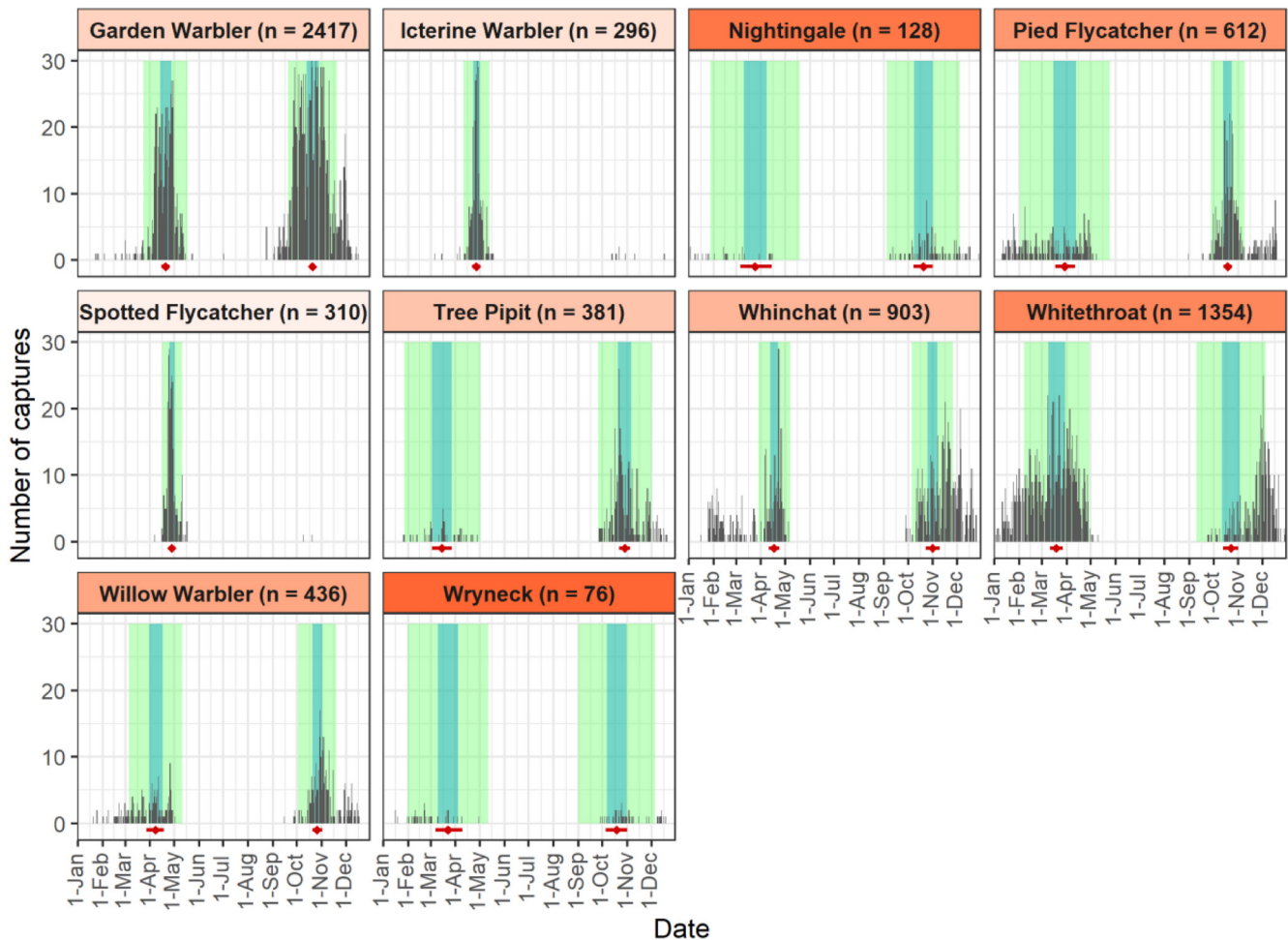


Figure 2. Timing of passage of each species throughout the year in Jos, Nigeria. Bars represent captures from all years (2001–2024). Red dots and bars below graphs represent the posterior mean and 95% CRIs of peak timing of passage ($\mu_{y,i}$), averaged across years. The light blue band (embedded within the green band) shows parameter $\sigma_{y,i}$, representing the spread of captures around peak passage timing. The light green bands show the 95% range in passage timing based on the estimated distribution. The shading around the panel titles are colour-coded according to the position of each species on the stayer–mover gradient, with lighter red indicating movers, and deeper red indicating stayers.

Three species showed significant trends in passage timing over the study period (Fig. 4, Table 4, Supporting information). We found that date of peak post-breeding passage was significantly delayed since 2001 for tree pipit and whinchat (Fig. 4, Table 4). Effect size was largest for tree pipit, with date of post-breeding passage shifting from 20 October (DOY=293, 95% CRIs 288–298) in 2001 to 6 November (DOY=310, 95% CRIs=306–316) in 2024, a shift of 17 days in 24 years ($0.70 \text{ days year}^{-1}$). For whinchat, post-breeding passage shifted from 25 October (DOY=298, 95% CRIs=292, 305) to 6 November (DOY=310, 95% CRIs=303, 316), a delay of 12 days in 24 years ($0.50 \text{ days year}^{-1}$). For pre-breeding passage, we found a significant advancement over time in whitethroat, from 27 March (DOY=86, 95% CRIs=83, 91) to 10 March (DOY=69, 95% CRIs=61, 76), representing 17 days advancement ($0.70 \text{ days year}^{-1}$). For pied flycatcher, we found possible evidence of pre-breeding advancement: 95% CIs included zero,

but the posterior probability that the effect was negative (i.e. advancement) was 95.8%, indicating a strong negative association of pre-breeding passage with year (Fig. 4).

We found some evidence for associations between the timings of local productivity and migration (Table 4 Supporting information). For three species, common whitethroat, whinchat and willow warbler, passage was earlier in years when vegetation senescence occurred later, as represented by the negative relationship between timing of vegetation senescence in Western Europe and timing of post-breeding passage (Table 4). During the pre-breeding phase, we found that timing of pre-breeding passage in common whitethroat (and likely spotted flycatcher, with 96.6% posterior probability) was later when green-up in Nigeria occurred later (Table 4).

Temperature in Nigeria during the pre-migratory phase was closely associated to passage timing in two species, with several additional strong associations where 95% CIs overlapped 0 (Fig. 5, Table 4). For whinchat, hotter seasons were

Table 3. Summary of parameters describing migration phenology in Jos, Nigeria. Parameters represent the mean across years (2001–2024), and include timing of peak passage (i.e. mean of Gaussian distribution describing migration), standard deviation, and start and end of passage estimated by the 2.5th and 97.5th quantiles. Timing parameters are represented as day of year (where 1 = 1 January).

Species	Post-breeding				Pre-breeding			
	Timing of peak passage ($\mu_{y,p}$)	SD of passage ($\sigma_{y,p}$)	Start of passage (2.5th quantile)	End of passage (97.5th quantile)	Timing of peak passage ($\mu_{y,p}$)	SD of passage ($\sigma_{y,p}$)	Start of passage (2.5th quantile)	End of passage (97.5th quantile)
Garden warbler	293.3	15.4	263.1	323.6	110.4	13.9	83.1	137.6
Icterine warbler					117.0	8.4	100.6	133.4
Nightingale	292.9	23.2	247.5	338.4	83.4	28.4	27.8	139.1
Pied flycatcher	291.6	10.8	270.5	312.7	88.6	28.7	32.2	144.9
Spotted flycatcher					118.4	6.5	105.7	131.1
Tree pipit	301.6	17.0	268.3	335.0	74.1	24.2	26.6	121.5
Whinchat	304.5	13.0	279.0	329.9	107.3	10.2	87.4	127.2
Common whitethroat	295.8	21.9	252.9	338.6	78.3	20.9	37.3	119.3
Willow warbler	299.2	12.2	275.3	323.1	98.1	17.0	64.9	131.3
Wryneck	291.8	24.5	243.8	339.7	81.7	25.8	31.2	132.2

associated with later pre-breeding passage (Fig. 5). The same association was present in garden warbler, icterine warbler and willow warbler despite 95% CIs overlapping 0, with posterior probabilities of positive associations of 95.4, 95.8 and 90.6%, respectively. In contrast, for common whitethroat, hotter seasons were associated with earlier pre-breeding passage (Fig. 5). Notably, the four species moving northward later in higher temperatures belong to the late-fast group, whilst the species leaving earlier in higher temperatures belongs to the early-slow group (Fig. 2, 3, Table 3).

Discussion

Palaearctic migrants in Jos showed species-specific patterns in passage phenology. We also detected species-specific changes

in phenology through time. The timing of vegetation senescence in autumn in Europe, and of green-up in Nigeria, correlated with substantial phenological adjustments in several species. We also identified associations of pre-breeding migration phenology with ambient temperatures in Nigeria in five of the ten study species. These findings from unique long-term ringing data in West Africa point to diverse, and partly surprising, links between migration phenology, and to underappreciated effects of environmental seasonality in Africa.

A movers–stayers gradient

In Jos, we observed a wide range of movement behaviours along a spectrum ranging from extreme movers that only passed through in one or both migration seasons, to extreme stayers that were captured throughout the non-breeding season. Such a mix of strategies may be common at many

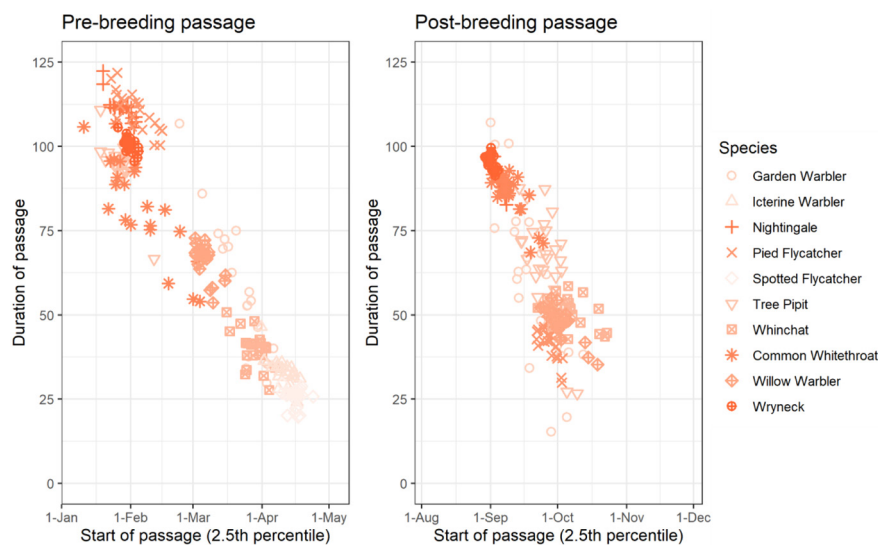


Figure 3. Duration of pre-breeding and post-breeding migration passage in relation to start of passage (2.5th quantile of the estimated distribution). Symbols represent yearly values and are coloured and shaped by species.

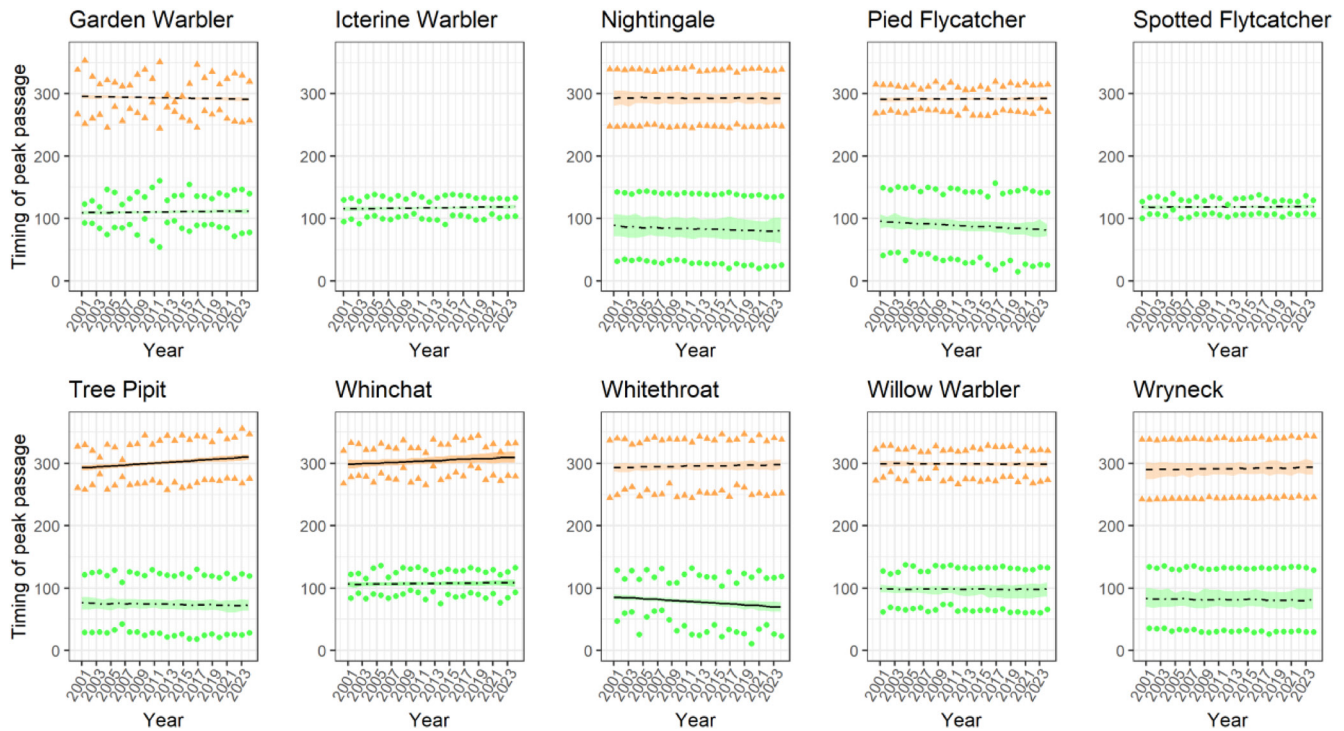


Figure 4. Mean timing of peak passage (μ) during post-breeding (orange; dashed line) and pre-breeding (green; dot-dash line) migration of each species in 2001–2024 (lines and ribbons), and estimated start and end of passage (means of posterior distributions for the 2.5th and 97.5th quantiles of passage; triangles for post-breeding and points for pre-breeding). Black lines and coloured shaded areas represent mean and 95% CRIs of the model predictions for timing of peak passage. We considered trends to be significant when the 95% CRIs of the posterior distribution of the parameter $\nu_{1,i}$ and $\nu_{3,i}$ (capturing yearly trends during the post-breeding and pre-breeding phase, respectively) did not overlap 0, and in these cases the lines are solid and shaded areas are darker. Predicted values were generated by keeping other covariates (t_{50} , temperature, year random effect) fixed at their mean values.

other locations, and may occur to varying extent across the annual cycle in both the non-breeding and breeding ranges (Salewski et al. 2002, Thorup et al. 2017, Newton 2023, Teitelbaum et al. 2023). Recently, also in Jos, the gradient in movement strategies was shown to be closely aligned with the timing of fuel deposition in preparation for pre-breeding migration (Jarrett et al. 2025a). Pronounced stayers such as common whitethroat reached 50% of mass and fat

accumulation roughly one month earlier than extreme movers such as spotted flycatcher (Jarrett et al. 2025a). These observations indicate far-reaching implications of differences in non-breeding movement behaviour. We propose that future considerations of the impact of ecology during the non-breeding season (often termed ‘wintering’) on phenology or on population trends of migrants should take these differences into account (Teitelbaum et al. 2023). In our

Table 4. Coefficients affecting timing of peak captures of post-breeding and pre-breeding migration (mean [95% CRIs]). Year captures the long-term temporal trend in timing of peak captures, vegetation covariates capture responses of birds to environmental productivity, and temperature represents responses of birds to mean temperature during the main pre-migratory phase (February to March).

Species	Post-breeding		Pre-breeding		
	Year ($\nu_{1,i}$)	Vegetation senescence in Western Europe ($\nu_{2,i}$)	Year ($\nu_{3,i}$)	Vegetation green-up in Nigeria ($\nu_{4,i}$)	Temperature in Nigeria ($\nu_{5,i}$)
Garden warbler	−1.31 (−3.05, 0.52)	−0.16 (−1.84, 1.54)	0.92 (−0.81, 2.74)	−1.41 (−3.87, 0.98)	1.84 (−0.28, 3.82)
Icterine warbler			0.96 (−0.97, 2.95)	1.08 (−1.09, 3.26)	1.65 (−0.30, 3.54)
Nightingale	−0.26 (−5.12, 4.69)	−0.20 (−4.35, 4.92)	−2.90 (−8.21, 2.83)	0.25 (−5.47, 6.28)	1.05 (−4.27, 6.05)
Pied flycatcher	0.42 (−1.60, 2.58)	−0.80 (−2.86, 1.37)	−4.00 (−8.32, 0.59)	2.85 (−1.36, 6.86)	−2.30 (−6.74, 2.01)
Spotted flycatcher			0.31 (−1.45, 2.11)	1.85 (−0.16, 3.91)	0.04 (−1.64, 1.79)
Tree pipit	5.37 (2.71, 8.06)	1.13 (−1.83, 4.20)	−1.42 (−5.99, 3.19)	2.51 (−2.78, 8.22)	−1.09 (−6.21, 4.30)
Whinchat	3.64 (0.21, 7.30)	−6.94 (−9.73, −4.28)	0.81 (−1.42, 3.17)	1.73 (−1.82, 5.32)	2.72 (0.31, 4.95)
Common whitethroat	1.65 (−2.20, 5.31)	−3.85 (−7.85, 0.06)	−5.06 (−8.76, −1.91)	5.09 (1.83, 8.20)	−6.61 (−9.72, −3.44)
Willow warbler	−0.42 (−2.99, 2.07)	−3.49 (−5.87, −0.95)	−0.22 (−5.56, 3.94)	0.52 (−3.76, 4.77)	2.25 (−1.20, 5.66)
Wryneck	1.12 (−4.08, 6.39)	0.46 (−4.73, 5.76)	−0.94 (−6.06, 4.04)	0.00 (−5.20, 5.45)	−1.44 (−6.71, 3.60)

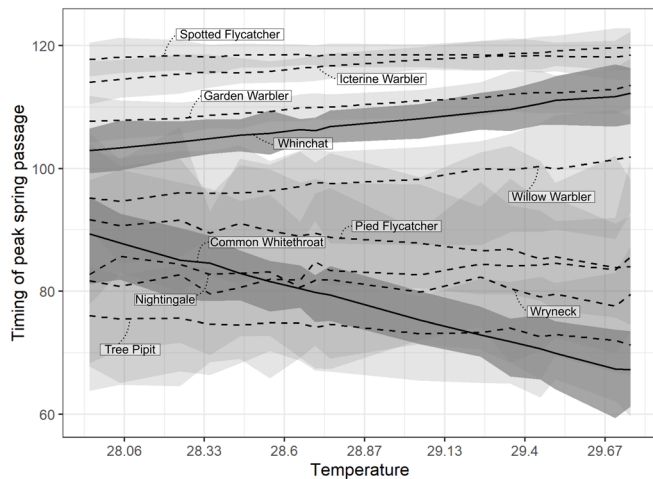


Figure 5. Effect of temperature during the pre-migratory phase in Nigeria (mean February to March) on timing of peak pre-breeding passage from Jos (mean and CRLs of posterior distribution). Significant relationships (CRLs not overlapping 0) are indicated with solid lines and darker shading.

study, the placement of species on the mover–stayer gradient was highly specific to the study location. Thus, a species may be a mover in Jos, but then be a stayer if considered at a subsequent non-breeding site, where it may remain throughout the non-breeding season. A striking diversity of onward movements after a first major migration leg has been observed along several global flyways, calling for closer investigation (Thorup et al. 2017, Newton 2023, Teitelbaum et al. 2023). Future studies could develop a more robust characterisation of migrants along this strategy spectrum, ideally using high-resolution tracking methods (Nussbaumer et al. 2023).

A linked gradient: early-slow to late-fast passage

In the present study, we discovered that the mover–stayer spectrum largely aligned with a second spectrum, ranging from early-slow to late-fast passage. In both migration seasons, the earlier a species' passage through Jos started, the longer it lasted. We observed extremes of an early-slow group, whereby early-migrating species had long passage windows, and these species were mainly stayers. On the other extreme was a late-fast group, whereby species tended to migrate late through Jos, but thereafter showed rapid onward passage (Risely et al. 2015, Blackburn et al. 2019). This late-fast group consisted mostly of movers. Along the gradients, species with an early passage might thus have a higher potential than late-passing species to respond to conditions that affect their journey, the progress of which they could then adjust. Our observation that differences in response to ambient temperature also partly aligned with the gradients (below), gives some support to these ideas. Alignment of species on these gradients could indicate different endogenous programmes with respect to time windows for the readiness to migrate, with time windows set aside for moult, or with respect to structured onward migration (Gwinner 1996, Åkesson and Helm 2020, Sjöberg et al. 2025). Alternative interpretations

are also conceivable, for example early-slow species could derive from a wider geographical range than late-fast species (Moreau 1972). We recommend to further explore how patterns in phenology, such as the gradient of early-slow to late-fast passage, relate to differences in avian life histories and to the vulnerability of species to environmental change.

Trends over time

Accounting for mover–stayer differences in our model, we found slight overall trends in phenology for post-breeding and pre-breeding peak migration passage at Jos. For post-breeding (autumn) migration, two of 10 species, tree pipit and whinchat, delayed passage at Jos over the 23 study years, while none clearly advanced it. Most species showed no detectable adjustment of post-breeding phenology. For garden warbler specifically, our findings are supported by data collected from 1960–1965 at Vom, Nigeria, 27 km from Jos, which indicated stable phenology (Smith 1963, Smith 2007). Mean passage was in the third week of October, close to our peak estimate of 21 October, and earliest birds and latest birds were captured ca 5 weeks to either side, close to our 2.5% percentiles of ca 30 days. For pre-breeding migration, we found a slight general advancement in the dates of migratory passage. On a species-specific level, we detected an advance in pre-breeding migration in whitethroat and likely in pied flycatcher. Garden warblers showed no trend, but our estimated peak passage on 10 April was markedly earlier than at Vom from 1960–1965 (peak passage 4th week of April), although the passage time range was again similar (Smith 1963, Smith 2007). In many species, however, no trends were detectable. Interpretations of species-specific responses are limited by lacking detailed life-history information, for example on the number of broods (Jenni and Kéry 2003, Dale et al. 2024), and by lacking geographical information on breeding range. Birds ringed at Jos could derive from an extensive Eurasian breeding area, within which breeding biology could differ substantially (Lawrence et al. 2022, Newton 2023, Ishong et al. 2025).

At Jos, we thus observed only little phenological trend, possibly indicating that migrants are too hard-wired for rapid change (Both and Visser 2001, Åkesson and Helm 2020, Robertson et al. 2024). How these species will keep up with progressively shifting phenology is largely unclear. However, elsewhere, slight to moderate adjustments of migratory phenology have been widely reported (Both and Visser 2001, Lawrence et al. 2022, Romano et al. 2023, Youngflesh et al. 2023, Robertson et al. 2024). Some studies reported variable pre-breeding advancements for several long-distance migrants (Romano et al. 2023, Robertson et al. 2024), and observed particularly heterogeneous trends in resident and migrant species within Africa (Chambers et al. 2013, Bussière et al. 2015, Muller et al. 2025). Thus, beyond the passage of our study species through Jos, changes may have occurred further along migration routes, for example via greater migration speed enabled by resource availability (Davies et al. 2023, Lameris et al. 2025). Furthermore, changes in the climate can have multiple effects on migratory species. For example, a

possibly shortened migration distance could affect the timing and composition of migrants on the non-breeding grounds, but such patterns are mostly observed in short-distance migrants (Visser et al. 2009).

Our findings contrast with a strong overall pre-breeding migration advance detected in The Gambia (Lawrence et al. 2022), as also noted in a recent direct comparison between the two sites (Ishong et al. 2025). The different findings of the studies might be partly explained by differences in study methods, in local conditions (Kartong is coastal and wetter), in patterns of climate change, or in location (Ishong et al. 2025). Kartong and Jos differ in latitude (Kartong is 4° further north) and longitude (Kartong is 25° further west), which could affect the migrants' breeding origins or the stage of migration during passage at the respective sites. Nonetheless, our findings confirm also for Jos some delays in post-breeding migration and advances in pre-breeding migration, albeit being weaker than those observed in The Gambia (Lawrence et al. 2022, Ishong et al. 2025). Overall, the findings highlight specificity of trends depending on species and sites.

Push and pull factors

In both migration seasons, our findings gave some support for the prediction that birds might adjust passage time in response to progressively changing climatic conditions (Jenni and Kéry 2003, Lawrence et al. 2022, Romano et al. 2023, Dale et al. 2024), although patterns were highly species-specific. For post-breeding migration, the slight delays in some species matched expectations associated with warming in Europe, which might reduce the action of push factors (Jenni and Kéry 2003, Dale et al. 2024). The results were also consistent with possible evolutionary adjustment of post-breeding schedules in response to a lengthening growing season (Helm et al. 2019). Additionally, our analyses of environmental effects in some species suggested the action of pull factors. When autumn sets in later in the European breeding areas (i.e. delayed vegetation senescence), whinchat and willow warbler counter-intuitively advanced their post-breeding passage at Jos. This pattern might suggest that under favourable conditions, these species might prioritise early arrival in West Africa before the dry season sets in (Moreau 1972, Jenni and Winkler 2020a, Newton 2023). Alternatively, early passage in years with delayed autumn senescence in Europe might be due to faster migration thanks to conditions favourable for fuelling (Lindström et al. 2019).

For pre-breeding migration, our findings gave some support for the prediction that birds might shift pre-breeding passage time in response to the pull factor of early breeding. The advances were consistent with indication of some evolutionary adjustment of pre-breeding schedules, namely in the pied flycatcher (Helm et al. 2019). Responses to environmental factors mostly supported the action of pull factors, as under apparently favourable conditions, some species advanced pre-breeding migration. Common whitethroat and spotted flycatcher migrated early when green-up in Nigeria occurred early, and four species migrated earlier in cooler

years. These relationships might indicate the lifting of constraints to fuel deposition that slow the pre-breeding journey (Ouwehand et al. 2023, Jarrett et al. 2025a). Our alternative hypothesis of the action of local push factors, specifically advanced pre-breeding migration in years of delayed greening and hot ambient temperatures in Nigeria, saw limited support.

Responses to ambient temperature

Ambient temperature in Nigeria proved to be a strong predictor of pre-breeding migration phenology in more than half of the study species. Whinchats, alongside garden warbler, icterine warbler and willow warbler, delayed pre-breeding migration in hot years, whereas common whitethroats migrated early in hot years. The delayed pre-breeding passage in the four species was linked to environmental conditions in Nigeria that are considered challenging for European-breeding migrants (Ottoosson et al. 2005, Tøttrup et al. 2012, Risely et al. 2015). Generally, in Nigeria, hotter seasons are likely seasons with later rainfall (Omotosho et al. 2000). However, the measures we used (mean temperature in February and March; green-up t_{50} : 50% point of green-up) were only weakly correlated ($r=0.23$) and did not directly capture timing of rains. It nonetheless seems surprising that common whitethroats responded to hot years with advanced pre-breeding migration, whereas late rains delayed their migration. Likely, the whitethroats' discrepant phenological responses indicate differential responses to ambient temperature versus rain timing. In hot years with timely rains, whitethroats apparently leave early. Conversely, when rains are delayed but temperatures are not excessively hot, common whitethroats leave late, supporting notions that they are particularly robust towards drought (Wilson and Cresswell 2006). Other study species delayed their passage linked to either heat or late green-up, but not to both, further suggesting that these two environmental characteristics had at least partly separate effects.

Sensitivity to heat might play a major role for birds' ability to keep up with ever earlier spring conditions on the breeding grounds. At our ringing site in Jos, earlier physiological and ecological research has reported that hot ambient temperature poses challenges to birds (Nilsson et al. 2016): under hot conditions, birds' body temperature rose to hyperthermic levels that were physiologically risky. Notably, findings included a common whitethroat whose body temperature exceeded 45°C (Nilsson et al. 2016). A recent experimental comparison suggested that European trans-Saharan migrants may be better able to cope with heat than short-distance migrants (Hasenbichler et al. 2025), and it is possible that the hyperthermia observed in Jos is a short-term coping strategy (Nilsson et al. 2016). However, this strategy is unsustainable and costly in terms of water and energy needs. Research at Jos also showed that birds preferred to feed near water sources, even if patches were sub-optimal (Molokwu et al. 2008, 2010). Thus, the observed delayed passage in hot years in some species could be due to insufficient resources for their onward journey, as shown by food

supplementation experiments on pied flycatchers in Ivory Coast (Ouwehand et al. 2023). However, alternatively to staying at Jos, birds can also move towards more productive sites to enhance fuel deposition. Such movements have been suggested for whinchats (Risely et al. 2015, Blackburn et al. 2019) and may also be supported by data on re-distributions of migrants within Nigeria during the dry season, including the common whitethroat (Cresswell et al. 2009).

While we have no definitive explanation for species differences in response to hot years, the observed associations between temperature response and passage characteristics provide some cues. The four species that delayed passage in hot years all belonged to the 'late-fast' group, whereas the species that advanced pre-breeding passage in hot years belonged to the 'early-slow' group. Thus, the heterogeneous responses to pre-migratory conditions may be influenced by the species' migration programmes (Gwinner 1996, Åkesson and Helm 2020), heat tolerance (Nilsson et al. 2016), or fuel thresholds required to initiate migration (Lindström 2003, Marra et al. 2005, Nwaogu and Cresswell 2016, Aharon-Rotman et al. 2021, 2022).

Annual-cycle interpretation of species' phenology

Fitting important life history events into the annual cycle may be a key determinant of the observed differences in migration strategies. In an annual-cycle context, one possible explanatory factor for species differences in migration phenology is the timing and location of moult (Jenni and Winkler 2020a, 2020b, Jarrett et al. 2021). Most European-breeding long-distance migrants moult during the non-breeding season (Jenni and Winkler 2020a, 2020b). While moulting flight feathers (remiges), birds are poorly equipped for onward migration, implying that the goal area for this phase of the annual cycle must be safely chosen (Jarrett et al. 2021). Because moult may also require specific nutrients, difficult conditions could delay its completion for a safe onward journey (Jenni and Winkler 2020b, Jarrett et al. 2025b). European migrant landbirds that remain in West Africa north of the equator for the dry season (i.e. stayers) mostly moult completely on the breeding grounds, so that only partial feather replacement is needed, or they suspend moult (Jenni and Winkler 2020a). Conversely, species that only stage in West Africa (i.e. movers), delay moult until reaching more southerly non-breeding grounds (Jenni and Winkler 2020a). In our study the three most extreme movers, spotted flycatcher, icterine warbler and garden warbler, belonged to the group that generally perform complete moults on the non-breeding grounds. Conversely, six species including the most extreme stayers showed the northern pattern of complete moult on the breeding grounds (Remisiewicz et al. 2019, Jenni and Winkler 2020a, 2020b). These species either do not moult in Africa (nightingale) or renew only secondaries (common whitethroat, pied flycatcher) or body plumage (whinchat, tree pipit, wryneck) (Remisiewicz et al. 2019, Jenni and Winkler 2020a, 2020b). Willow warblers, which are exceptional by undergoing two complete annual moults, were intermediate on the mover-stayer gradient. Hence, moult patterns appear to align well

with the mover-stayer migration strategy spectrum (Jenni and Winkler 2020a). Likewise, the association of movers with late-fast passage, and of stayers with early-slow passage, might also be explained by the position of moult in the annual cycle, and by the birds' endogenous migration programmes that regulate it (Gwinner 1996, Åkesson and Helm 2020, Jarrett et al. 2021, Helm and Liedvogel 2024).

Strengths and weaknesses of our modelling approach

Our dataset posed a number of challenges which we addressed in our modelling approach. Firstly, sampling effort differed over the years and was not recorded, including gaps in trapping within seasons that we partly filled by assigning migrant absence based on resident captures and partly through modelling. Inspired by (Dennis et al. 2016), we developed an innovative statistical model to describe the passage of migratory birds based on capture data. By estimating the spread of the distribution of passage volumes, our model provides additional insights into migratory behaviour. For example, the model allows us to test for trends in mean passage time, but also in passage duration. We modelled migration passage as a Gaussian distribution. Although exploratory plotting (Supporting information), as well as literature data (Tøttrup et al. 2006, Ishong et al. 2025), supported a Gaussian distribution of passage times, our data suggested that the Gaussian shape is less clear for stayers than for movers (c.f. Fig. 2). We addressed the additional challenge of modelling captures for species that were not on passage but rather remained residential in the study area by incorporating a new element to the model which explicitly describes the residential non-breeding process. Thereby, we modelled captures as a combination of a Gaussian distribution (for passage) and a uniform distribution (for non-breeding). Due to the complexity of the model, we used the Bayesian approach, which requires the definition of priors for all estimated quantities. Our priors were vague, so they should only have a minimal effect on the posteriors. We found that the model requires reasonable sample sizes, as for species with few captures the resulting estimates are quite imprecise. Estimation could be improved if variables characterising capture efficiency (e.g. netting effort or wind speed) were recorded. These could then be included as additional variables to explain variation in the number of birds captured. Importantly, the model could also be applied to data from counted birds that were not captured (but only observed).

Our decision to model passage time, and to extract estimated 95% percentiles to broadly represent start and end of passage, impacted the level of detail in our phenological analyses. Because the Gaussian distribution assumes symmetry, we were not able to assess potential trends in quantiles, as in some other phenological studies that extracted quantiles directly from raw capture data to estimate start and end of migration (Tøttrup et al. 2006, Lawrence et al. 2022, Romano et al. 2023, Dale et al. 2024). A focus on mean timing, as in our study, can greatly underestimate phenology trends of the fastest-responding parts of a population (Tøttrup et al. 2006,

Romano et al. 2023, Dale et al. 2024; but see Lawrence et al. 2022). The precise breeding origin of the birds that migrate through Jos is mostly unknown. To link migration phenology to European NDVI, we thus used a single definition of the geographic extent of the European breeding grounds as (7°W–21°E, 40–65°N; Lawrence et al. 2022). Relative to an estimated migratory divide for 23 species between western and eastern flyways at 15°E (Briedis et al. 2020), our cut-off generally errs towards extending too far east, but it is broadly inclusive and allows for direct comparison with work from The Gambia (Lawrence et al. 2022). We however acknowledge that in some species the defined breeding range might not fully cover the origin of birds, in particular for common whitethroat and whinchat (Moreau 1972, Blackburn et al. 2019, Tapia-Harris et al. 2022). Geolocators and ringing recoveries showed that common whitethroats captured in Jos bred across a vast area of Europe, reaching eastward to ca 35°E (Tapia-Harris et al. 2022), and the species is known to vary in annual-cycle phenology across its range (Remisiewicz et al. 2019, Briedis et al. 2025). For whinchat, geocator data suggested that the breeding range extended even further to the east (range ca 20–55°E; Blackburn et al. 2019). Our broad definition of potential breeding grounds may have reduced the chance of detecting links to NDVI senescence, as the large spatial extent likely introduces noise to the senescence timing data. However, as we did not use NDVI data directly, but instead derived the mid-point of vegetation green-up and senescence, we consider the expected effects of precise breeding range to be minor (Lawrence et al. 2022, Briedis et al. 2024).

Conclusions

Our analyses of long-term ringing data from Nigeria provided novel insights into patterns of migration behaviours across the study species. These patterns followed two largely aligned gradients, one between stayers and movers, and another between early-slow and late-fast migration passage. The position along the mover–stayer gradient was broadly associated with the species' trends in migration phenology, whereby stayers tended to show an early-slow passage, and movers a late-fast passage. The mover–stayer gradient was also associated with the timing of moult, and with the species' responses to environmental factors. We interpret the gradients as resulting from differences in the endogenous timing programme, possibly linked to the position of moult in the annual cycle.

Across species, we found some support for phenological shifts. During post-breeding migration, trends over time and responses to the environment indicated the action of both push factors on the breeding grounds and pull factors on the non-breeding grounds, depending on species. During pre-breeding migration, pull factors on the breeding grounds appeared to dominate, with also some indication for push factors in Nigeria. Among the investigated environmental factors, ambient temperature had the greatest impact on pre-breeding migration phenology, a finding that calls for further study as the planet warms.

Importantly, in our study, many observed patterns were unexpected, indicating that there is much to learn from studying migratory birds on the non-breeding grounds and from accounting for environmental seasonality in Africa. Therefore, long-term data from African research have tremendous potential for a comprehensive and nuanced understanding of the phenology of African–Eurasian migration systems. Such long-term data need not be perfect, as new analytical tools such as our modelling approach are becoming available; however, rigorous recording of effort data alongside bird survey data should always be the priority if feasible.

Our study suggests complex patterns and species-specific responses to a changing climate which are currently hard to disentangle. We thus strongly encourage further, long-term (ringing) studies in Africa. Major contributions of such studies could include clearer insights into the diversity of movement strategies and on ecological and physiological responses to environmental factors that underlie phenology. Studies could look at changes and challenges during the vulnerable phase of moult in Africa, when birds potentially require specific resources (Jenni and Winkler 2020b, Jarrett et al. 2021, 2025b). Studies should also investigate thermal tolerance of migratory birds to rising temperatures, to identify risks and limits to the birds' flexibility (Nilsson et al. 2016). The patterns of climate change in West Africa are not entirely clear, and while warming is inescapable, changes to precipitation patterns and phenology are still difficult to predict (Omotosho et al. 2000, Sanogo et al. 2015, Nicholson et al. 2018). A deeper understanding of the migrants' life in Africa is essential for supporting the species that connect our continents.

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Author contributions

Crinan Jarrett: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Barbara Helm:** Conceptualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Yahkat Barshep:** Data curation (equal); Investigation (equal). **Kwanye Bitrus Zira:** Investigation (equal). **Joy Ishong Akpanta:** Data curation (equal); Investigation (equal); Writing – review and editing (supporting). **Michael Schaub:** Conceptualization (equal); Methodology (equal); Software (equal); Writing – review and editing (equal). **Chima J. Nwaogu:** Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data and scripts are available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.29098775> (Jarrett et al. 2025c).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adole, T., Dash, J. and Atkinson, P. M. 2018. Large-scale prerain vegetation green-up across Africa. – *Global Change Biol.* 24: 4054–4068.
- Aharon-Rotman, Y., Perlman, G., Kiat, Y., Raz, T., Balaban, A. and Iwamura, T. 2021. Limited flexibility in departure timing of migratory passerines at the East-Mediterranean flyway. – *Sci. Rep.* 11: 5184.
- Aharon-Rotman, Y., McEvoy, J. F., Kiat, Y., Raz, T. and Perlman, G. Y. 2022. Time to move on: the role of greenness in Africa and temperatures at a Mediterranean stopover site in migration decision of long-distance migratory passerines. – *Front. Ecol. Evol.* 10: 834074.
- Åkesson, S. and Helm, B. 2020. Endogenous programs and flexibility in bird migration. – *Front. Ecol. Evol.* 8: 00078.
- Bakner, N. W., Mastro, N. M., Highway, C. J., Keever, A. C., Holmes, L. P., Steelman, N. J., Hagy, H. M., Feddersen, J. C., Pierce, A. R. and Cohen, B. S. 2025. Balancing opposing cues: seasonal shifts in push–pull drivers of migration in a temperate waterfowl species. – *Mov. Ecol.* 13: 91.
- Bellisario, B., Cardinale, M., Maggini, I., Fusani, L. and Carere, C. 2023. Co-migration fidelity at a stopover site increases over time in African–European migratory landbirds. – *R. Soc. Open Sci.* 10: 221043.
- Biasutti, M. 2019. Rainfall trends in the African Sahel: characteristics, processes, and causes. – *Wiley Interdiscip. Rev. Clim. Change* 10: e591.
- Blackburn, E. and Cresswell, W. 2016a. High site fidelity in northern wheatears *Oenanthe oenanthe* wintering in Africa revealed through colour marking. – *Bird Study* 63: 284–288.
- Blackburn, E. and Cresswell, W. 2016b. High within-winter and annual survival rates in a declining Afro-Palaearctic migratory bird suggest that wintering conditions do not limit populations. – *Ibis* 158: 92–105.
- Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C. and Cresswell, W. 2019. Spring migration strategies of whinchat *Saxicola rubetra* when successfully crossing potential barriers of the Sahara and the Mediterranean Sea. – *Ibis* 161: 131–146.
- Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – *Nature* 411: 296–298.
- Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. and Adamík, P. 2016. Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. – *J. Avian Biol.* 47: 743–748.
- Briedis, M., Bauer, S., Adamík, P., Alves, J. A., Costa, J. S., Emmenegger, T., Gustafsson, L., Koleček, J., Krist, M., Liechti, F., Lisovski, S., Meier, C. M., Procházka, P. and Hahn, S. 2020. Broad-scale patterns of the Afro-Palaearctic landbird migration. – *Global Ecol. Biogeogr.* 29: 722–735.
- Briedis, M., Hahn, S. and Bauer, S. 2024. Duration and variability of spring green-up mediate population consequences of climate change. – *Ecol. Lett.* 27: e14380.
- Briedis, M., Wong, J. B., Adamík, P., Lislevand, T., Funts, K., Hromádka, M., Hromádka, K., Porkert, J. and Hahn, S. 2025. Seasonal variation in migration routes of common whitethroat *Curruca communis*. – *J. Ornithol.* 166: 29–38.
- Brown, C. R. and Bomberger Brown, M. 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). – *Behav. Ecol. Sociobiol.* 47: 339–345.
- Bussière, E. M. S., Underhill, L. G. and Altwegg, R. 2015. Patterns of bird migration phenology in South Africa suggest Northern Hemisphere climate as the most consistent driver of change. – *Global Change Biol.* 21: 2179–2190.
- Chambers, L. E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L. J., Crawford, R. J. M., Durant, J. M., Hughes, L., Keatley, M. R., Low, M., Morellato, P. C., Poloczanska, E. S., Ruoppolo, V., Vanstreels, R. E. T., Woehler, E. J. and Wolfaardt, A. C. 2013. Phenological changes in the Southern Hemisphere. – *PLoS One* 8: e75514.
- Cohen, J. M., Lajeunesse, M. J. and Rohr, J. R. 2018. A global synthesis of animal phenological responses to climate change. – *Nat. Clim. Change* 8: 224–228.
- Cresswell, W., Boyd, M. and Stevens, M. 2009. Movements of palaearctic and Afrotropical bird species during the dry season (November–February) within Nigeria. – *Proceedings of the 12th PanAfrican Ornithological Congress*.
- Dale, V. R., Bolton, M., Dornelas, M., Magurran, A. E., Dennis, R., Broad, R., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D. and Reid, J. M. 2024. Among-species variation in six decades of changing migration timings explained

- through ecology, life-history and local migratory abundance. – *Global Change Biol.* 30: e17400.
- Davies, J. G., Kirkland, M., Miller, M. G. R., Pearce-Higgins, J. W., Atkinson, P. W. and Hewson, C. M. 2023. Spring arrival of the common cuckoo at breeding grounds is strongly determined by environmental conditions in tropical Africa. – *Proc. R. Soc. B* 290: 20230580.
- Dennis, E. B., Morgan, B. J. T., Freeman, S. N., Roy, D. B. and Brereton, T. 2016. Dynamic models for longitudinal butterfly data. – *J. Agric. Biol. Environ. Stat.* 21: 1–21.
- Denwood, M. J. 2016. runjags: an R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. – *J. Stat. Softw.* 71: 1–25.
- Didan, K. 2021. MODIS/terra vegetation indices 16-day L3 global 1km SIN grid V061. – In: NLPDAA Center (ed.). <https://doi.org/10.5067/MODIS/MOD13A2.061>.
- Franklin, K. A., Nicoll, M. A. C., Butler, S. J., Norris, K., Ratcliffe, N., Nakagawa, S. and Gill, J. A. 2022. Individual repeatability of avian migration phenology: a systematic review and meta-analysis. – *J. Anim. Ecol.* 91: 1416–1430.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. – *Ibis* 138: 47–63.
- Haest, B., Hüpopp, O. and Bairlein, F. 2020. Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. – *Proc. Natl Acad. Sci. USA* 117: 17056–17062.
- Hanmer, H. J., Boersch-Supan, P. H. and Robinson, R. A. 2022. Differential changes in life cycle-event phenology provide a window into regional population declines. – *Biol. Lett.* 18: 20220186.
- Harris, I., Jones, P. D., Osborn, T. J. and Lister, D. H. 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. – *Int. J. Climatol.* 34: 623–642.
- Hasenbichler, J., Bittermann, F., Hafner, G., Zechmeister, T. and Maggini, I. 2025. Response to high ambient temperatures in short-distance and trans-Saharan migratory species. – *J. Avian Biol.* 2025: e03375.
- Helm, B. and Liedvogel, M. 2024. Avian migration clocks in a changing world. – *J. Comp. Physiol. A* 210: 691–716.
- Helm, B., Van Doren, B. M., Hoffmann, D. and Hoffmann, U. 2019. Evolutionary response to climate change in migratory pied flycatchers. – *Curr. Biol.* 29: 3714–3719.e4.
- Hickinbotham, E. J., Ridley, F. A., Rushton, S. P. and Pattison, Z. 2025. 30 years of climate related phenological research: themes and trends. – *Int. J. Biometeorol.* 69: 1459–1473.
- IPCC 2023. Climate Change 2023: synthesis report. – In: Lee, H. and Romero, J., (eds), Contribution of Working Groups I, II and III to the sixth assessment report of the Intergovernmental Panel on Climate Change, pp 35–115.
- Ishong, J., Afrifa, J., Iwajomah, S., Deikumah, J., Ivande, S. and Cresswell, W. 2022. Population trends of resident and migrant West African bird species monitored over an 18-year period in central Nigeria. – *Ostrich* 93: 1–16.
- Ishong, J. A., Howard, C., Barlow, C. R. and Willis, S. G. 2025. Phenological trends of Palearctic passerine bird species wintering in the Gambia and Nigeria. – *Afr. J. Ecol.* 63: e70108.
- Jarrett, C., Powell, L. L., Claire, T. T. R., Tchoumbou, M. and Helm, B. 2021. Moults of overwintering wood warblers *Phylloscopus sibilatrix* in an annual-cycle perspective. – *J. Ornithol.* 162: 645–653.
- Jarrett, C., Simon, O. G., Tchana, C. N., Pev, T. A., Meigang Kamkeng, M. F., Wandji, A. C., Manu, S. A., Tchoumbou, M. A., Helm, B., Powell, L. L. and Nwaogu, C. J. 2024. Differences in phenology across three trophic levels between two Afrotropical sites separated by four degrees latitude. – *Ecol. Evol.* 14: e70274.
- Jarrett, C., Helm, B., Rime, Y., Barshep, Y., Bitrus, K. Z., Ishong, J. A. and Nwaogu, C. J. 2025a. Temporal and environmental drivers of pre-migratory fuel loads in songbirds in West Africa. – *Proc. R. Soc. B* 292: 20251988.
- Jarrett, C., Nwaogu, C. J., Tchana, C. N., Kamkeng, M. F. M., Quiñones, A. L. S., Olguin-Villa, M. C., Helm, B., Powell, L. L. and Welch, A. J. 2025b. Moults is associated with higher diversity of food items in the diet of common bulbuls (*Pycnonotus barbatus*) in Cameroon. – *Ibis* 167(3): 803–811.
- Jarrett, C., Helm, B., Barshep, Y., Bitrus Zira, K., Akpanta, J. I., Schaub, M. and Nwaogu, C. J. 2025c. Data from: Species-specific trends in migratory passage time in Nigeria based on long-term ringing data. – Figshare Digital Repository, <https://doi.org/10.6084/m9.figshare.29098775>.
- Jenni, L. and Kéry, M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. – *Proc. R. Soc. B* 270: 1467–1471.
- Jenni, L. and Winkler, R. 2020a. Moults and ageing of European passerines. – Academic Press.
- Jenni, L. and Winkler, R. 2020b. The biology of moults in birds. – Christopher Helm Publishers.
- Johansson, J., Kristensen, N. P., Nilsson, J.-Å. and Jonzén, N. 2015. The eco-evolutionary consequences of interspecific phenological asynchrony – a theoretical perspective. – *Oikos* 124: 102–112.
- Jones, P. J. 1995. Migration strategies of Palearctic passerines in Africa. – *Isr. J. Zool.* 41: 393–406.
- Kéry, M. and Royle, J. A. 2021. Chapter 1 - Relative abundance models for population dynamics. – In: Kéry, M. and Royle, J. A. (eds), Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. – Academic Press, pp. 3–64.
- Lameris, T. K. et al. 2025. Migratory birds advance spring arrival and egg-laying in the arctic, mostly by travelling faster. – *Global Change Biol.* 31: e70158.
- Lawrence, K. B., Barlow, C. R., Bensusan, K., Perez, C. and Willis, S. G. 2022. Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. – *Global Change Biol.* 28: 375–389.
- Lindström, Å. 2003. Fuel deposition rates in migrating birds: causes, constraints and consequences. – In: Berthold, P., Gwinner, E. and Sonnenschein, E. (eds), Avian migration. – Springer, pp. 307–320.
- Lindström, Å., Alerstam, T. and Hedenström, A. 2019. Faster fuelling is the key to faster migration. – *Nat. Clim. Change* 9: 288–289.
- Maggini, I., Cardinale, M., Sundberg, J. H., Spina, F. and Fusani, L. 2020. Recent phenological shifts of migratory birds at a Mediterranean spring stopover site: species wintering in the Sahel advance passage more than tropical winterers. – *PLoS One* 15: e0239489.
- Marra, P. P., Francis, C. M., Mulvihill, R. S. and Moore, F. R. 2005. The influence of climate on the timing and rate of spring bird migration. – *Oecologia* 142: 307–315.
- Molokwu, M. N., Olsson, O., Nilsson, J.-Å. and Ottosson, U. 2008. Seasonal variation in patch use in a tropical African environment. – *Oikos* 117: 892–898.
- Molokwu, M. N., Nilsson, J.-Å., Ottosson, U. and Olsson, O. 2010. Effects of season, water and predation risk on patch use by birds on the African savannah. – *Oecologia* 164: 637–645.

- Moreau, R. E. 1972. The Palaearctic–African bird migration systems. – Academic Press.
- Muller, R., Nwaogu, C., Helm, B., Irene Tieleman, B. and Amar, A. 2025. Exploring the use of the South African nest record scheme to detect changes in phenology: a case study using four well represented species. – *J. Avian Biol.* 2025: e03376.
- Newton, I. 2023. The migration ecology of birds. – Academic Press.
- Nicholson, S. E., Funk, C. and Fink, A. H. 2018. Rainfall over the African continent from the 19th through the 21st century. – *Global Planet. Change* 165: 114–127.
- Nilsson, J.-Å., Molokwu, M. N. and Olsson, O. 2016. Body temperature regulation in hot environments. – *PLoS One* 11: e0161481.
- Nussbaumer, R., Gravey, M., Briedis, M. and Liechti, F. 2023. Global positioning with animal-borne pressure sensors. – *Methods Ecol. Evol.* 14: 1104–1117.
- Nwaogu, C. J. and Cresswell, W. 2016. Body reserves in intra-African migrants. – *J. Ornithol.* 157: 125–135.
- Nwaogu, C. J. and Cresswell, W. 2021. Local timing of rainfall predicts the timing of moult within a single locality and the progress of moult among localities that vary in the onset of the wet season in a year-round breeding tropical songbird. – *J. Ornithol.* 162: 265–276.
- Omotosho, J. B. 1988. Spatial variation of rainfall in Nigeria during the 'little dry season'. – *Atmos. Res.* 22: 137–147.
- Omotosho, J. B., Balogun, A. A. and Ogunjobi, K. 2000. Predicting monthly and seasonal rainfall, onset and cessation of the rainy season in West Africa using only surface data. – *Int. J. Climatol.* 20: 865–880.
- Ottosson, U., Waldenström, J., Hjort, C. and McGregor, R. 2005. Garden warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes. – *Ibis* 147: 750–757.
- Ouwehand, J., Asso, A. A., Johnston, B., Bot, S., Bil, W., Groenewoud, F. and Both, C. 2023. Experimental food supplementation at African wintering sites allows for earlier and faster fueling and reveals large flexibility in spring migration departure in pied flycatchers. – *Ardea* 111: 343–370.
- Pageau, C., Tonra, C. M., Shaikh, M., Flood, N. J. and Reudink, M. W. 2020. Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines. – *Biol. Lett.* 16: 20200155.
- Plummer, M. 2023. rjags: Bayesian graphical models using MCMC. – R package ver. 4-15, <https://CRAN.R-project.org/package=rjags>.
- Remisiewicz, M., Bernitz, Z., Bernitz, H., Burman, M. S., Rajmakers, J. M. H., Rajmakers, J. H. F. A., Underhill, L. G., Rostkowska, A., Barshep, Y., Soloviev, S. A. and Siwek, I. 2019. Contrasting strategies for wing-moult and pre-migratory fueling in western and eastern populations of common whitethroat *Sylvia communis*. – *Ibis* 161: 824–838.
- Risely, A., Blackburn, E. and Cresswell, W. 2015. Patterns in departure phenology and mass gain on African non-breeding territories prior to the Sahara crossing in a long-distance migrant. – *Ibis* 157: 808–822.
- Robertson, E. P., La Sorte, F. A., Mays, J. D., Taillie, P. J., Robinson, O. J., Ansley, R. J., O'Connell, T. J., Davis, C. A. and Loss, S. R. 2024. Decoupling of bird migration from the changing phenology of spring green-up. – *Proc. Natl Acad. Sci. USA* 121: e2308433121.
- Romano, A., Garamszegi, L. Z., Rubolini, D. and Ambrosini, R. 2023. Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: a global meta-analysis. – *Ecol. Monogr.* 93: e1552.
- Salewski, V. and Jones, P. 2006. Palearctic passerines in Afrotropical environments: a review. – *J. Ornithol.* 147: 192–201.
- Salewski, V., Bairlein, F. and Leisler, B. 2002. Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies? – *Ibis* 144: 85–93.
- Sanogo, S., Fink, A. H., Omotosho, J. A., Ba, A., Redl, R. and Ermert, V. 2015. Spatio-temporal characteristics of the recent rainfall recovery in West Africa. – *Int. J. Climatol.* 35: 4589–4605.
- Sjöberg, S., Macías-Torres, P., Andersson, A., Bäckman, J., Thorup, K., Tøttrup, A. P. and Alerstam, T. 2025. The structure of the annual migratory flight activity in a songbird. – *Proc. R. Soc. B* 292: 20250958.
- Smith, V. W. 1963. Arrival dates of the garden warbler *Sylvia borin* in Central Nigeria. – *Ibis* 105: 561–563.
- Smith, V. W. 2007. Garden warbler *Sylvia borin* migration in sub-Saharan West Africa: a comment on Ottosson et al. (2005). – *Ibis* 149: 412–413.
- Sparks, T. H., Huber, K. and Tryjanowski, P. 2008. Something for the weekend? Examining the bias in avian phenological recording. – *Int. J. Biometeorol.* 52: 505–510.
- Sullivan, M. K., Fayolle, A., Bush, E., Ofosu-Bamfo, B., Vlem-inckx, J., Metz, M. R. and Queenborough, S. A. 2024. Cascading effects of climate change: new advances in drivers and shifts of tropical reproductive phenology. – *Plant Ecol.* 225: 175–187.
- Taff, C. C. and Shipley, J. R. 2023. Inconsistent shifts in warming and temperature variability are linked to reduced avian fitness. – *Nat. Commun.* 14: 7400.
- Tapia-Harris, C., Izang, A. and Cresswell, W. 2022. Migratory routes, breeding locations and multiple non-breeding sites of common whitethroats *Curruca communis* revealed by geolocators. – *PLoS One* 17: e0274017.
- Tattoni, D. J., Labarbera, K. and Hendershot, J. N. 2025. Moulting phenology advances under hot or dry conditions for two passerines across 16 years in a Mediterranean climate. – *Ibis* 167: 979–990.
- Teitelbaum, C. S., Bachner, N. C. and Hall, R. J. 2023. Post-migratory nonbreeding movements of birds: a review and case study. – *Ecol. Evol.* 13: e9893.
- Telenský, T., Klvaňa, P., Jelínek, M., Cepák, J. and Reif, J. 2020. The influence of climate variability on demographic rates of avian Afro-Palearctic migrants. – *Sci. Rep.* 10: 17592.
- Thackeray, S. J. et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. – *Global Change Biol.* 16: 3304–3313.
- Thackeray, S. J. et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. – *Nature* 535: 241–245.
- Thorup, K., Tøttrup, A. P., Willemoes, M., Klaassen, R. H. G., Strandberg, R., Vega, M. L., Dasari, H. P., Araújo, M. B., Wikelski, M. and Rahbek, C. 2017. Resource tracking within and across continents in long-distance bird migrants. – *Sci. Adv.* 3: e1601360.
- Tomotani, B. M., van der Jeugd, H., Gienapp, P., de la Hera, I., Pilzecker, J., Teichmann, C. and Visser, M. E. 2018. Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. – *Global Change Biol.* 24: 823–835.
- Tøttrup, A. P., Klaassen, R. H., Kristensen, M. W., Strandberg, R., Vardanis, Y., Lindström, Å., Rahbek, C., Alerstam, T. and Thorup, K. 2012. Drought in Africa caused delayed arrival of European songbirds. – *Science* 338: 1307.
- Tøttrup, A. P., Thorup, K. and Rahbek, C. 2006. Patterns of change in timing of migration in north European songbird populations. – *J. Avian Biol.* 37: 84–92.

- Van Der Jeugd, H. P., Eichhorn, G., Litvin, K. E., Stahl, J., Larsson, K., Van Der Graaf, A. J. and Drent, R. H. 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. – *Global Change Biol.* 15: 1057–1071.
- Visser, M. E. and Gienapp, P. 2019. Evolutionary and demographic consequences of phenological mismatches. – *Nat. Ecol. Evol.* 3: 879–885.
- Visser, M. E., Perdeck, A. C., Van Balen, J. H. and Both, C. 2009. Climate change leads to decreasing bird migration distances. – *Global Change Biol.* 15: 1859–1865.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. and Bairlein, F. 2002. Ecological responses to recent climate change. – *Nature* 416: 389–395.
- Wilson, J. M. and Cresswell, W. 2006. How robust are Palearctic migrants to habitat loss and degradation in the Sahel? – *Ibis* 148: 789–800.
- Youngflesh, C., Montgomery, G. A., Saracco, J. F., Miller, D. A. W., Guralnick, R. P., Hurlbert, A. H., Siegel, R. B., LaFrance, R. and Tingley, M. W. 2023. Demographic consequences of phenological asynchrony for North American songbirds. – *Proc. Natl Acad. Sci. USA* 120: e2221961120.