



Research



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Temporal and environmental drivers of pre-migratory fuel loads in songbirds in West Africa

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Afro-Palaeartic migrants depart West Africa for breeding grounds in Europe during the transition from the dry to the wet season. Such timing can severely impact migration success because the onset of the rains varies between years, influencing food availability and migrants' body reserves, which are crucial for crossing the Sahara. We used a 23 year ringing dataset of seven migratory bird species from Nigeria to quantify changes in body mass and fat during the pre-migratory period as a function of recent and dry season rainfall and normalised difference vegetation index (NDVI). For a small subset of species, we also considered data from the wider non-breeding period. During the pre-migratory period, body reserves were positively correlated with pre-capture conditions in several species. Thus, body reserves increased after recent periods of high rainfall and NDVI, as well as with date. Effects of dry season conditions on pre-migratory body reserves were more variable, possibly linked to species-specific movement strategies in sub-Saharan Africa. During the non-breeding period, we found some support for reduced body reserves under good conditions, perhaps to enhance mobility. Limitations in fuelling due to poor recent conditions in West Africa could lead to birds departing later or in poorer condition, with potential carry-over costs to breeding.

1. Introduction

The traditional Northern Hemisphere perception is that Afro-Palaeartic migratory birds escape tough conditions (i.e. winter) in Europe to travel to Africa, where conditions are stable year-round. The limitations of this view are becoming evident with new data from bird ringing and spatio-temporal tracking of migratory species [1]. In fact, conditions in tropical Africa are highly seasonal, driven by the movement of the Intertropical Convergence Zone, which brings rain to West Africa during the boreal summer. It then moves southward, with rainy seasons in most of Africa's south and south-east during the boreal winter. In West Africa, the rainy season lasts from April/May to October [2]. Thus, Afro-Palaeartic migrants arrive on their post-breeding migration during the transition from the wet to the dry season and depart again towards their breeding grounds during the transition from the dry to the wet season in West Africa [3–5]. While some species continue to non-breeding sites further south in Africa, others remain in West Africa for the entire duration of the dry season [1,6]. The effects of this seasonal transition on migratory birds are not well understood, due to scarce long-term data from the non-breeding grounds, coupled with the diversity of behaviours among migrant species.

The arrival of the rains in West Africa leads to extensive vegetation green-up and a steep rise in arthropod biomass, though tree leaf-burst may anticipate the rainy season [7] and can lead to a small increase in arthropod biomass. As the vast majority of migrants use arthropods as their main food source [8,9], the start of the rains signifies a considerable increase in food resources, which arrive at a critical time: all Afro-Palaearctic passerine species, towards the end of the non-breeding season, must prepare for the long northward journey to their breeding grounds [10]. For this, they must accumulate fuel by depositing fat and building up muscles: during migration, fat is the predominant source of fuel in birds, but muscle can also be metabolized during the long flight bouts [11–13]. These fat and muscle reserves must be in place to allow birds to cross major ecological barriers, which from West Africa involves crossing the Sahara Desert [14]. Barrier crossing in migratory passerines can involve long bouts of uninterrupted flying, with limited or no opportunities for refuelling [14–16].

Individuals face the difficult choice of either not departing from the non-breeding grounds or stopover sites until they have accumulated sufficient body reserves, or pressing ahead to minimize time on their pre-breeding migration [12,17,18]. These elements point towards a period of heightened vulnerability in migratory landbirds, where they are dependent on finding sufficient food in the environment to fuel migration, or else risk costly delays to breeding or face additional risks during their journey [19]. Importantly, the precise timing of the onset of rains varies between years, and so does the severity of the dry season, when insect food is scarce [20]. Given the strong environmental seasonality in the non-breeding grounds and the inter-annual variation in the rains, effects of pre-migratory environmental conditions may depend on the severity of the preceding dry season [21–23]. However, thus far, the relative importance of short-term versus long-term non-breeding season conditions on birds remains unclear.

The exact timing of pre-migratory fuelling varies by species, with data from sub-Saharan Africa indicating a start from mid-January to February [12,24], and up to mid-March [10,17,25,26]. Birds build up fat and muscle once fuelling starts; however, there is a trade-off during this period because carrying body reserves impairs flight performance and increases predation risk [27,28]. Thus, as the non-breeding season progresses, the endogenous programme progressively switches to pre-migratory preparations [29,30], and thereby shifts priorities: earlier in the season, birds may maintain low levels of fat to prioritize predator avoidance, while later in the season, it becomes essential to fuel in preparation for migration [28]. However, if food supplies are uncertain, birds may choose to maintain body reserves even early in the non-breeding season to minimize the risk of starvation [27]. Indeed, an experimental study from the Caribbean showed that 2–4 weeks prior to pre-migratory fuelling, birds in sites with reduced food availability gained fat [31]. There is, therefore, a balance to be maintained between the priorities of avoiding predation, minimizing starvation risk and pre-migratory fuelling.

Several Neotropical studies conducted on Caribbean islands have established strong links between food availability during the non-breeding season, migrants' pre-migratory body condition and timing of migration. Birds spending the non-breeding season in poorer habitats (e.g. secondary scrub) tended to have lower body condition and survival than those in richer habitats (e.g. humid mangroves), with the body condition of birds in both habitats responding positively to rainfall during the dry season [32–34]. In turn, birds in poorer condition departed later for the breeding grounds and arrived there later and in poorer condition [31,32]. Processes occurring during the non-breeding period may then carry over to other stages of the annual cycle, with birds experiencing severe non-breeding conditions achieving poorer reproductive outputs and lower seasonal survival [35,36]. These studies demonstrate the importance of achieving good body condition during the non-breeding season, a process which in the Neotropics is strongly mediated by environmental conditions.

Evidence from the Afro-Palaearctic points not only towards similar processes but also to differences. For instance, consistent with patterns in the Neotropics, after poorer dry seasons in West Africa, the arrival of migrants in Europe is delayed [22,23,37]. In these studies, authors consider that this delay may be mediated through body condition, so that in poorer seasons, birds take longer to accumulate sufficient body reserves and thus must delay migration departure or take longer for their journey [3,37]. In African non-breeding ranges, there may be important differences in how species respond to environmental conditions, driven by their behaviour along a gradient of movement strategies. During the non-breeding season, some species ('movers') may either move short distances, for example within West Africa [38], or even track the seasonal emergence of resources on continental scales, by moving through multiple sites across rainfall gradients [5,6,39,40]. For mover species, there may not be a clear distinction between what is considered a non-breeding site and a stopover site [1]. On the other extreme are species ('stayers'), whose movements during the non-breeding season are very limited, so that they arrive in one site and remain there throughout the season [6,41,42]. These stayer species may be strategically adapted to endure unfavourable conditions at their non-breeding site [43], while more mobile species may depart from areas with limited food to reach richer areas. This gradient of movement strategies may also exist in the Neotropics, though studies thus far have mostly focused on territorial 'stayer' species [44].

A recent experimental study investigated a 'stayer' species, the pied flycatcher (*Ficedula hypoleuca*), on its non-breeding grounds in Côte d'Ivoire. When given supplementary food during the pre-migratory period, birds put on mass earlier and faster, and departed 12 days earlier [26]. Additionally, over 2 years, in non-supplemented birds, fuelling rates were correlated with the biomass of arthropods in the environment [26]. In contrast, other species appear to strive to keep the timing of departure from non-breeding grounds fixed, so that variation in arrival time is driven by conditions encountered en route [45]. An example is a mover species, the Eurasian cuckoo (*Cuculus canorus*). For this Afro-Palaearctic migrant species that winters in southern Africa, departure from stopover sites in West Africa was largely consistent [46]. For cuckoos to be able to depart with consistent timing between years, they must be able to accumulate sufficient body reserves despite inter-annual variation in resources [46]. Whinchats (*Saxicola rubetra*) in central Nigeria appear to have a mixed strategy, where some individuals fuel slowly and depart early, likely allowing for additional fuelling at more northern sites, while other individuals fuel more steeply and depart later, perhaps aiming for non-stop desert crossing [47].

Based on the accumulated knowledge from the Afrotropics and Neotropics, some questions remain open. First, there is theoretical evidence and some empirical evidence for the different pressures affecting birds during the non-breeding and pre-migratory periods, balancing predator avoidance, minimizing starvation risk and fuelling [26–28,31]. However, these expectations are not always met, particularly in birds that initiate fuelling very early [12] or in birds increasing fat reserves during the non-breeding season when additional food is available [48]. Second, it is not clear whether the most important factor in determining bird body reserves is dry season conditions or more recent conditions during the fuelling period, with evidence for the former in Saino *et al.* [49] and Balbontín *et al.* [21], and for the latter in Studds & Marra [50] and Robson & Barriocanal [37]. And third, given the different movement strategies in Afro-Palaeartic migrants, it is not clear whether the patterns of body reserves in relation to food availability observed in stayer species in the Neotropics will apply.

To address these questions, we require data from the non-breeding and pre-migratory periods from a range of migrant species across the mover-stayer gradient. These data should span a sufficiently long duration to capture inter-annual variation in these processes. Here, we harness a rare opportunity of a 23 year dataset of Afro-Palaeartic migratory bird captures from Jos, Nigeria, to quantify relationships between body mass and fat in birds, and rainfall and NDVI (Normalized Difference Vegetation Index). We investigated, for birds captured during the non-breeding and pre-migratory periods (January to mid-March and mid-March to May, respectively), the influence of local conditions and date on body reserves at two temporal scales. We linked fat scores and body mass at capture to the effect of the overall conditions experienced in the dry season (1 November to 28 February), and the effect of recent conditions experienced over 2 weeks prior to capture. In addition to cross-sectional data from all birds, we used a subset of recaptured birds to investigate individual patterns of fuel deposition. Using both fat score and body mass allowed us to quantify the systematic build-up of long-term reserves in preparation for departure (i.e. fat [11]) as well as more instantaneous fluctuations in fuel loads (i.e. body mass). Importantly, changes in the body mass of birds may reflect different processes, including changes in muscle mass, water and fat. For simplicity, we use the term ‘reserves’ to describe fat and mass jointly.

Our aim was to determine whether body reserves of migratory birds varied as a function of local rainfall and NDVI, to test the hypothesis that poor pre-capture conditions affect the ability of birds to build up pre-migratory reserves. Additionally, driven by the endogenous migration programme, and possibly facilitated by pre-rain green-up, we expect increasing body reserves with advancing date. We predict that priorities may be different between the non-breeding and pre-migratory periods, so that in the non-breeding period, bird body reserves may decrease in response to improved conditions, while in the pre-migratory period, birds may prioritize body reserve build-up and thus increase mass and fat under favourable conditions. We predict that in years with more severe dry seasons, body reserves of migratory birds prior to migration would be lower, especially in stayer species that remain in central Nigeria. We expected mover species, that just pass through Nigeria in spring, to be primarily influenced by pre-capture conditions rather than dry season conditions.

2. Methods

(a) Field data collection

We used a dataset of mist-net captures of migratory birds around the A.P. Leventis Ornithological Research Institute (APLORI, Jos, Nigeria, 09°52'N, 08°58'E; 1336 m a.s.l.) from 2002 to 2024 [51]. Birds were captured, ringed and released regularly throughout the year, but here we focused on the non-breeding and pre-migratory periods (1 January until the end of May). All captures were made in a similar habitat, consisting of heterogeneous woodland savannah patches with inselbergs and riparian forests. We measured body mass (g), using a digital precision scale, and wing length (mm), using a wing ruler, for each captured individual [52]. We also collected fat scores, based on the amount of fat visible in the tracheal pit and the body. Fat scores range from 0 (no visible fat) to 8 (fat entirely covering breast muscles [52]). For each bird, we also recorded the date and time of extraction from the net. We excluded from the analysis three outliers, which are likely recording errors: one Icterine warbler with mass = 51.6 g, one wryneck with mass = 79.7 g and one whinchat with fat score = 0.5. After this, our dataset consisted of 2840 captures, including 95 individuals recaptured at least once during the pre-migratory season (table 1), featuring the following species: garden warbler (*Sylvia borin*), common whitethroat (*Curruca communis*, henceforth ‘whitethroat’), whinchat (*Saxicola rubetra*), willow warbler (*Phylloscopus trochilus*), pied flycatcher (*Ficedula hypoleuca*), spotted flycatcher (*Muscicapa striata*) and Icterine warbler (*Hippolais icterina*).

We wished to test potential differences between the non-breeding and pre-migratory period, putatively based on different potential drivers. However, there is no clear cut-off between these two periods, especially considering the differences between species’ movement patterns. For most species, even those that may remain in Nigeria throughout the non-breeding season, there was a perceptible phase of increased captures marking migration (though not apparent for species with few captures, e.g. wryneck, nightingale and tree pipit). This phase presumably represents individuals from more southern non-breeding populations travelling north (appendix I: electronic supplementary material, figure S1). We thus separated the time period of the high capture phase from the time period before it (electronic supplementary material, appendix II), resulting in two periods: 1 January to 17 March as non-breeding and 18 March to 31 May as pre-migratory, with the pre-migratory period capturing pre-migratory fuelling and individuals on stopover. These timings broadly match data on pre-migratory fuelling phenology from other studies in West Africa [10,17,25,26].

We considered species to be on a scale of ‘stayers’ (birds that remain in Nigeria throughout the non-breeding season) to ‘movers’ (birds that pass through). We sorted the species on the scale of stayers to movers according to the relative frequency of captures from the non-breeding period (1 January to 17 March; figure 1; table 1; electronic supplementary material, appendix

Table 1. Species overview. For each species, we show the total number of captures made between 1 January and 31 May, number of captures made during the non-breeding period (1 January to 17 March), average yearly proportion of captures from the non-breeding period (see electronic supplementary material, appendix I, for details), number of captures made during the pre-migratory period (18 March to 31 May) and number of recaptures during the pre-migratory period. Species are sorted following the mover-to-stayer order.

species	total captures	non-breeding captures	average proportion non-breeding captures	pre-migratory captures	pre-migratory recaptures
spotted flycatcher	307	0	0	307	1
Icterine warbler	285	2	0.02	283	11
garden warbler	582	17	0.13	565	17
whinchat ^a	336	116	0.37	220	8
willow warbler	163	51	0.39	112	3
whitethroat ^a	936	500	0.55	436	51
pie flycatcher ^a	231	133	0.55	98	4

^aFor these species, we also analysed data from the non-breeding period.

I). Of the full list of the 10 species above, whitethroat, pied flycatcher, willow warbler and whinchat are the most likely stayers, while spotted flycatcher, Icterine warbler and garden warbler are the clearest movers (electronic supplementary material, appendix I; [51]).

(b) NDVI and rainfall data

We downloaded rainfall data from the Climate Hazards Center Infrared Precipitation with Stations (CHIRPS) v.2.0 (<https://data.chc.ucsb.edu/products/CHIRPS-2.0/>), which provides daily precipitation since 1981 at a $0.05^\circ \times 0.05^\circ$ scale resolution (approximately 5 km $\times$ 5 km) [53]. We downloaded data corresponding to the APLORI coordinates (9.877 N, 8.980 E) from the period 2001 to 2024 using the R package 'chirps' v.0.1.4 [54]. For NDVI, data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra Vegetation (1 km resolution) [55]. We extracted data corresponding to a 5 km diameter buffer around APLORI, to match the rainfall data spatial resolution, and then averaged across grid cells to achieve one NDVI value per time point. As NDVI data were available at 16 day intervals, we interpolated linearly between these values to estimate a daily NDVI value. Rainfall data showed a clear distinction between the dry season in Jos (approximately November to March) and the rainy season (from April to May; figure 1; electronic supplementary material, appendix III), with NDVI showing similar somewhat lagged patterns (figure 1). Given these clear patterns, we defined 'dry season' as the period between 1 November and 28 February (figure 1).

Rainfall and NDVI values were strongly correlated with day of year (electronic supplementary material, appendix III) and thus, instead of including these variables directly into our analysis, we calculated standardized daily anomaly values. We calculated the mean and standard deviation (s.d.) of the daily value of rainfall and NDVI across our study years, and then for each daily value, we calculated standardized anomaly as:

$$\text{standardized anomaly} = (\text{daily value} - \text{mean}) / \text{s.d.}$$

These anomaly values can thus be interpreted as the variation with respect to mean trends: if a day is particularly wet or green compared with the same day over the 23 year period, then it would receive a high positive anomaly value. The standardization (dividing by s.d.) scales the anomaly according to the variability on that day.

We wished to investigate the effects of long-term (i.e. dry season) and short-term (i.e. pre-capture) environmental conditions on migratory bird body mass. Using NDVI and rainfall standardized anomaly data, for long-term conditions, we considered the mean NDVI anomaly for each dry season (1 November to 28 February; henceforth, 'dry season NDVI'). For the short term, we calculated mean rainfall and NDVI anomaly over the 14 day period prior to capture (henceforth, 'pre-capture rainfall/NDVI'). To account for the potential dependence between short- and long-term conditions, we included an interaction term in the analyses.

(c) Data analyses

For the population-level analysis, we built a general linear mixed model (GLMM) for each species and period, with body mass (Gaussian) or fat score (Poisson) as the response variable. Based on the number of captures of each species during non-breeding and pre-migratory periods, we excluded some species and periods from statistical analyses. As explanatory variables in the GLMMs, we included pre-capture rainfall and NDVI, dry season NDVI, the interaction between pre-capture NDVI and dry season NDVI, and day of year. Additionally, as fixed effects, we included wing length (mm) and time of day to account for potential variation in body mass or fat as a function of body size or time. Finally, we included the year as a random effect to account for potential yearly variation driven by factors not considered in our models. However, the fat score models (Poisson distributed) did not converge with the random factor, so we made year a fixed effect for fat score analyses. We scaled and centred all continuous explanatory variables and used the package 'lme4' v.1.1.37 to build the GLMMs [56]. We inspected plots

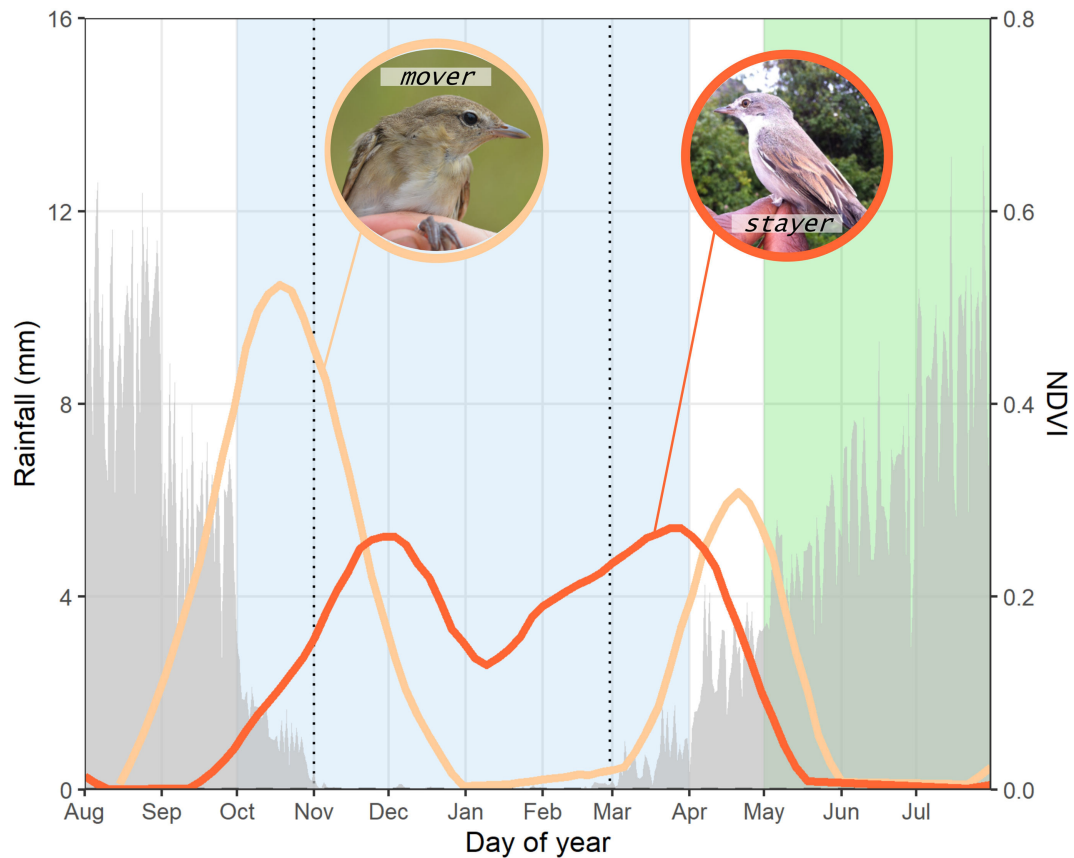


Figure 1. Rainfall and NDVI seasonality in Jos, Nigeria, in relation to the passage of Afro-Palaearctic migrants. The grey shaded area shows mean daily rainfall (mm), and the dashed grey line shows mean daily NDVI. The orange lines show passage of migrants through Jos: the paler orange represents mover species that pass through Nigeria on their way to more southerly non-breeding sites (represented by garden warbler). The darker orange represents stayers that may remain in Nigeria throughout the non-breeding season (represented by whitethroat). In the background of the panel, the blue rectangle represents the non-breeding season, the green rectangle the breeding season, the white areas are migration periods and the dotted black lines indicate the Nigerian dry season as defined in this study.

of residuals to check the assumptions of normal distribution. For each species, we present the coefficient estimates (mean and 95% confidence intervals (95% CIs)) for all fixed effects. Additionally, we carried out analyses of overall seasonal trends in body mass, fat, wing length and sex, as detailed in electronic supplementary material, appendix V.

For the individual-level analysis, we considered birds that were caught more than once (on separate days) in a given pre-migratory season. We considered only the pre-migratory period because recapture sample sizes for the non-breeding period were very small, and because our main goal with this part of the analysis was to further understand influences on fuelling prior to migration. There were 95 individuals that were recaptured at least once during the pre-migratory period. However, only garden warbler and whitethroat were represented by sufficient individuals ($n \geq 15$; total sample size = 68 individuals; table 1). The overall mean time between recaptures for these two species was 5.1 days (s.d. = 4.8), and species specifically for garden warbler mean = 4.2 days (min = 1, max = 13), and for whitethroat mean = 5.4 days (min = 1, max = 25). For recaptured individuals, we calculated the change in body mass and fat scores between subsequent recaptures and divided this by the number of days between captures to get a daily rate of mass and fat change. We used daily change in mass and fat as response variables in a GLM that included as explanatory variables pre-capture NDVI and rainfall, dry season NDVI, day of year, and the interaction between pre-capture and dry season NDVI.

3. Results

Mean body mass of birds captured in Jos, Nigeria, throughout the entire study period was 21.5 g (s.d. = 3.6) for garden warbler, 15.8 g (s.d. = 2.5) for Icterine warbler, 20.8 g (s.d. = 2.5) for nightingale, 13.0 g (s.d. = 2.9) for pied flycatcher, 17.8 g (s.d. = 2.9) for spotted flycatcher, 22.5 g (s.d. = 2.7) for tree pipit, 18.2 g (s.d. = 3.5) for whinchat, 15.0 g (s.d. = 2.1) for whitethroat, 9.4 g (s.d. = 2.4) for willow warbler and 37.1 g (s.d. = 5.5) for wryneck. For all species, mean mass during the pre-migratory period was considerably higher than structural body mass (range 42%–72%; electronic supplementary material, appendix IV). Timing of fuelling varied by species, with strong alignment along the mover-stayer gradient, so that movers tended to fuel substantially later than stayers (electronic supplementary material, appendix V).

(a) Effects of environmental conditions on non-breeding body reserves

Considering the three stayer species with sufficient data from the non-breeding period, the body mass of whitethroat showed a positive association with date, whereas no relationship was detectable in pied flycatcher and whinchat (figure 2). We did not detect any significant effects of environmental conditions on body mass, aside from a positive association with pre-capture rainfall in whitethroat (figure 2). Considering fat scores of non-breeding birds, there was no evidence of changes in fat with day of year, but we did detect environmental effects. Whitethroat fat scores decreased with dry season NDVI and increased with pre-capture rainfall. For whinchat, there was also a negative association with dry season NDVI, and for pied flycatcher, fat scores were positively associated with pre-capture NDVI.

(b) Effects of environmental conditions on pre-migratory body reserves

The seven study species showed variable responses to date and environmental factors. Body mass of all species except spotted flycatcher and willow warbler increased significantly with day of year (figure 2). Pre-capture rainfall and NDVI were generally better predictors of pre-migratory body mass compared with dry season NDVI (figure 2; electronic supplementary material, appendix VI). Body mass increased significantly and similarly with pre-capture rainfall in four species (Icterine warbler, pied flycatcher, spotted flycatcher and whinchat), whereas effects were non-significant for pre-capture NDVI (figures 2–3). At the lowest pre-capture rainfall, the body mass of these species was at its lowest. With increasing pre-capture rainfall, body mass increased by up to approximately 20%. There were no significant effects of dry season NDVI on migratory bird body mass.

For fat scores, day of year was positively associated in all species except for the spotted flycatcher (figure 2). Pre-capture rainfall was positively associated with fat scores in Icterine warbler, spotted flycatcher and whinchat (electronic supplementary material, appendix VI). At low pre-capture rainfall or NDVI, fat scores were between 0 and 3 for these species, while at high pre-capture rainfall, fat scores increased up to 3–6 (figure 4). Pre-capture NDVI had a similarly positive association in whitethroat (figures 2 and 4; electronic supplementary material, appendix VI) but was negatively associated with fat scores in spotted flycatcher. For two species (Icterine warbler and spotted flycatcher), dry season NDVI was positively associated with pre-capture fat scores. NDVI during our two predictor periods, pre-capture and dry season, had interactive effects on fat scores of whitethroats and willow warblers, with the interaction showing opposite directions for each species (figures 2 and 4).

Wing length was significantly positively correlated with body mass in most species, but only in three species with fat scores (figure 2), and we found no evidence of variation in wing length over the season in any species (electronic supplementary material, appendix V). Concerning sex, from the species with available data, we only detected sex differences in body mass in whitethroats (electronic supplementary material, appendix V).

(c) Effects of environmental conditions on individual fuelling rates of birds recaptured in the pre-migratory season

At the individual level, there was a general, although variable, increase in mass and fat across subsequent recaptures in a season across all species. For mass, 52 out of 95 recaptured birds increased in mass, 1 maintained the same mass (slope = 0), and 42 decreased. For fat, 42 birds increased in fat, 30 maintained and 23 decreased. Our detailed analysis of garden warbler and whitethroat revealed no environmental effects on fuelling in garden warblers. In whitethroats, mass change was positively associated with pre-capture rainfall, with mass loss at times of low pre-recapture rainfall (minimum fuel deposition rate = -3.9 [57]), and mass gain when pre-recapture rainfall was high (up to fuel deposition rate = 4.1). In contrast, pre-recapture NDVI had the opposite effect on fat change, so that when pre-recapture NDVI was high, fat change was negative and *vice versa*. In addition, there was a negative association between dry season NDVI and mass change (electronic supplementary material, appendix VI).

4. Discussion

The body reserves of Afro-Palaearctic migrants in Nigeria were influenced by environmental conditions, with varying effects between non-breeding and pre-migratory periods and species. The day of the year and recent rainfall and NDVI appeared to be of stronger influence during the pre-migratory period, with strong evidence of accumulation of reserves as the season advances and of improving conditions correlating with higher body reserves. During the non-breeding period, there was a more common negative association between body reserves and dry season conditions, likely reflecting different priorities of this life-cycle period. In addition, we found some evidence that species' responses to environmental conditions may depend on their non-breeding ground movements.

Our results for the three species studied during the non-breeding period provide mixed evidence regarding the responses of birds to conditions early in the season (January to mid-March). First, there was some evidence of fuelling, though not widespread, with only mass in whitethroats increasing with date over the non-breeding period. In a parallel study from the same site in Jos, whitethroats were shown to be one of the species with the earliest pre-breeding migration [51]. Thus, we interpret that fuelling in Jos may begin as early as January or February for some species, matching Bayly *et al.* [12], while for others, it may begin later. Second, during the non-breeding period, whinchat and whitethroat, but not pied flycatcher,

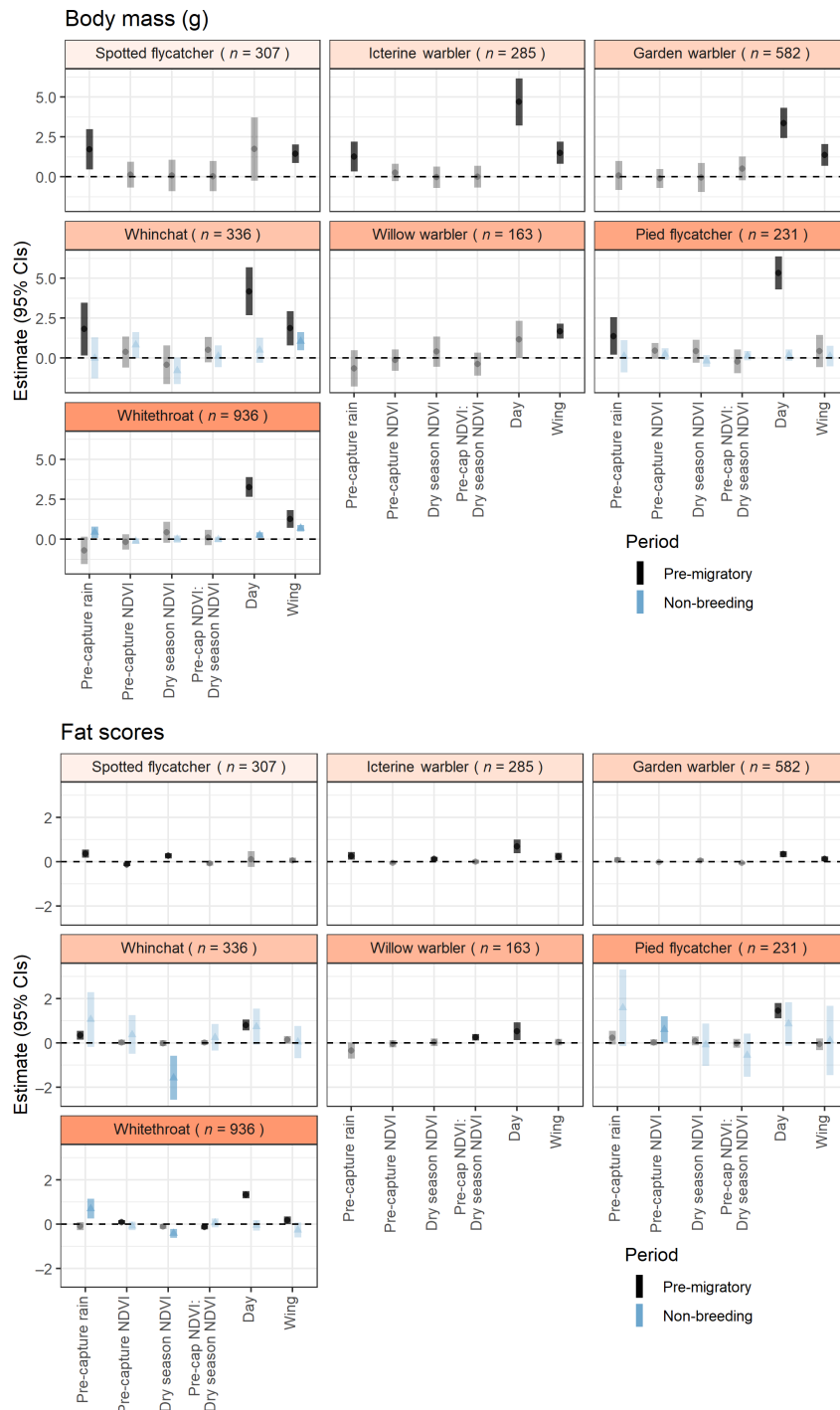


Figure 2. Overview of environmental effects on migrant body mass and fat (blue = non-breeding, black = pre-migratory). Estimates and 95% CIs from GLMMs investigating the effects of pre-capture rainfall and NDVI, dry season NDVI, the interaction between pre-capture and dry season NDVI (with interaction indicated with a colon), day of year and wing. A darker colour shade indicates statistical significance of terms ($p < 0.05$; see also electronic supplementary material, appendix VI). The panel titles are colour-coded according to the position of each species on the stayer-mover scale, with deeper red indicating stayer species, and lighter colours indicating movers.

followed the patterns expected for strategic body mass regulation by reducing body reserves when dry season conditions are good, perhaps prioritizing leanness and thus more efficient predator avoidance when food is guaranteed [28,58]. However, both whitethroat and pied flycatcher responded positively to good recent conditions, showing that short-term increases in food abundance may still trigger reserve build-up [48]. Thus, during the non-breeding season, there is a species-specific distinction between the effects of long-term and short-term food abundance, with the former leading to reserve loss and the latter to reserve gain. These findings partly match patterns from the Neotropics, which suggest that high, consistent food availability leads to lower fat reserves [31], while short peaks in food (perhaps interpreted by birds as unpredictability in food resources) lead to mass gain [48].

We found a stronger signal of pre-capture conditions on body reserves during the pre-migratory period, with increases in mass or fat with recent rainfall or NDVI in several species, matching findings of Ouwehand *et al.* [26] on pied flycatcher. It appears that even for species that spend most of the non-breeding season at more southerly latitudes [6], such as the clear ‘mover’ species in our study (Icterine warbler, spotted flycatcher), conditions in West Africa are influential [20]. This is likely

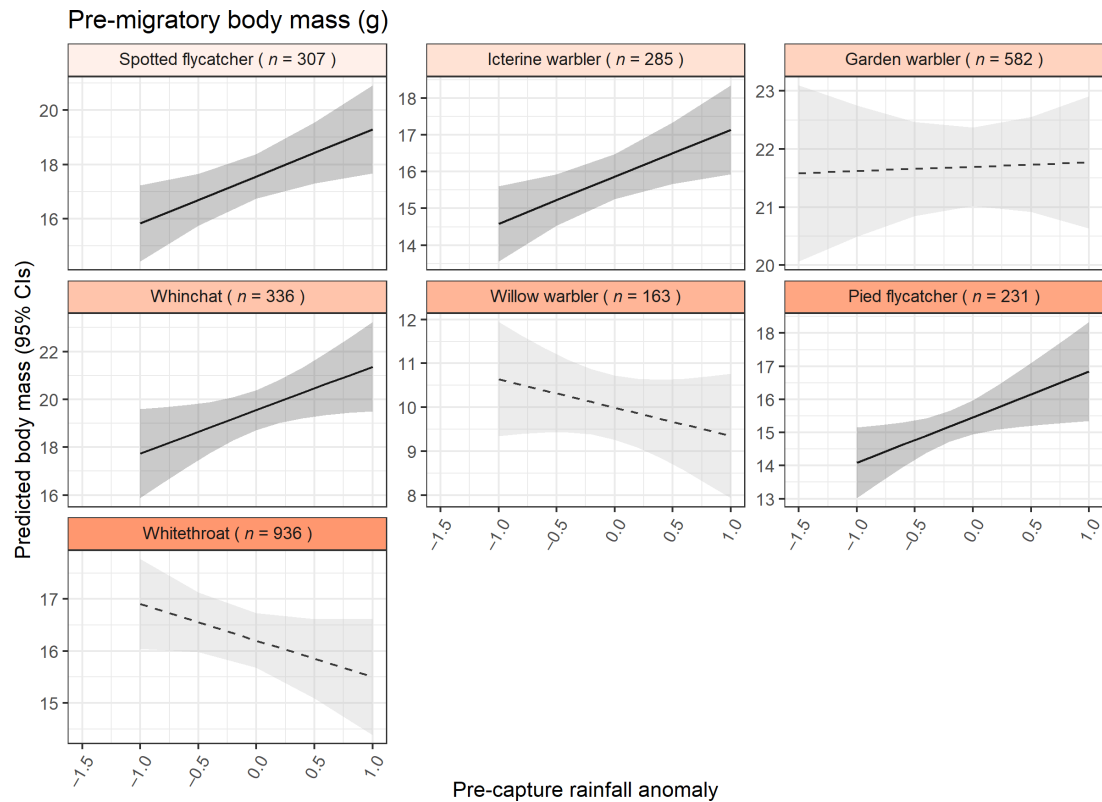


Figure 3. Change in pre-migratory body mass (g) with pre-capture rainfall, predicted from GLMMs. Represented are the mean and 95% CIs of model predictions. Solid lines and darker shading indicate significant effects. The panel titles are colour-coded following the mover-to-stayer gradient. We did not include predicted values for NDVI as there were no significant effects.

because no matter where birds overwintered, their endogenous migration programme during the pre-migratory period will have activated physiological mechanisms of hyperphagia and fuel deposition [59]. Indeed, our data showed clear evidence of fuelling behaviour, with day of year predicting mass and fat during the pre-migratory period in most species. That birds are able to increase reserves is likely enabled by high pre-migratory fuelling efficiency [11,57], in combination with some resources becoming available by partial pre-rain green-up [7]. Here, the fuelling behaviour of Afro-Palaearctic migrants can be clearly distinguished from intra-African migrants, that show substantially smaller gains in mass during this period despite the assumed increase in food availability [10]. The strong environmental effects described here underline the importance of conditions in the Jos area, which appear to influence the ability of birds to meet their endogenously driven fuelling programme.

Even during the pre-migratory period, in a few cases, we detected negative associations between pre-capture conditions and body reserves, indicating a loss of fat when food is abundant. Notably, spotted flycatcher fat scores decreased with increasing pre-capture NDVI, and recapture data from whitethroats showed a decrease in fat accumulation under high pre-capture NDVI. This behaviour, expected for the non-breeding season but less so for the pre-migratory period, may still reflect conflicting priorities in birds prior to departure. Additionally, given that in both these cases there were parallel but opposite trends with rainfall (increase in fat score with rainfall in spotted flycatcher and increase in fuelling rate with rainfall in whitethroat), this behaviour may suggest differential responses to rainfall when compared with NDVI. Thus, rainfall may reflect immediate food availability (such as ant and termite eruptions after the first rains) while NDVI may reflect food abundance over a longer period prior to capture. When food availability spikes, birds may be triggered to fuel, while over longer periods of high food abundance, the opposite may occur. For whitethroats, which are stayers in Jos, there could be a link to subsequent movements. Recent tracking studies show that whitethroats may stop over in sites further north than Jos prior to crossing the Sahara [39,60]. Thus, birds may be less likely to increase body reserves under good conditions in Jos if they have further opportunities for fuelling prior to barrier crossing. Additionally, with recapture data, we cannot discard the possibility that noise is introduced into the data due to stress-related losses of mass or fat after handling events.

In contrast to the fairly consistent positive association between pre-capture conditions and body reserves during the pre-migratory period, we found more limited evidence of dry season effects. For body mass, there were no associations with dry season conditions, and for fat scores, there were dry season effects in four species. Against expectations, for the two most extreme mover species (Icterine warbler and spotted flycatcher), pre-migratory fat scores were positively linked to dry season NDVI in Jos, although these species do not remain in Jos throughout the dry season. The main interpretation here could be that higher dry season NDVI leads to overall higher food abundance at the time of pre-migratory fuelling or that there is some correlation between dry season conditions in West Africa and in their further range. For whitethroat and willow warbler, interactive effects evidenced that dry season conditions influenced birds' responses to recent conditions. Thus, drier seasons led to steeper gains in fat under improving recent conditions in whitethroat, while in willow warbler, greener seasons led to steeper fat gain under improving recent conditions, a difference we can not currently explain. For the remaining species, dry season conditions did not appear to be linked to pre-migratory body condition. This could potentially be explained by reduced

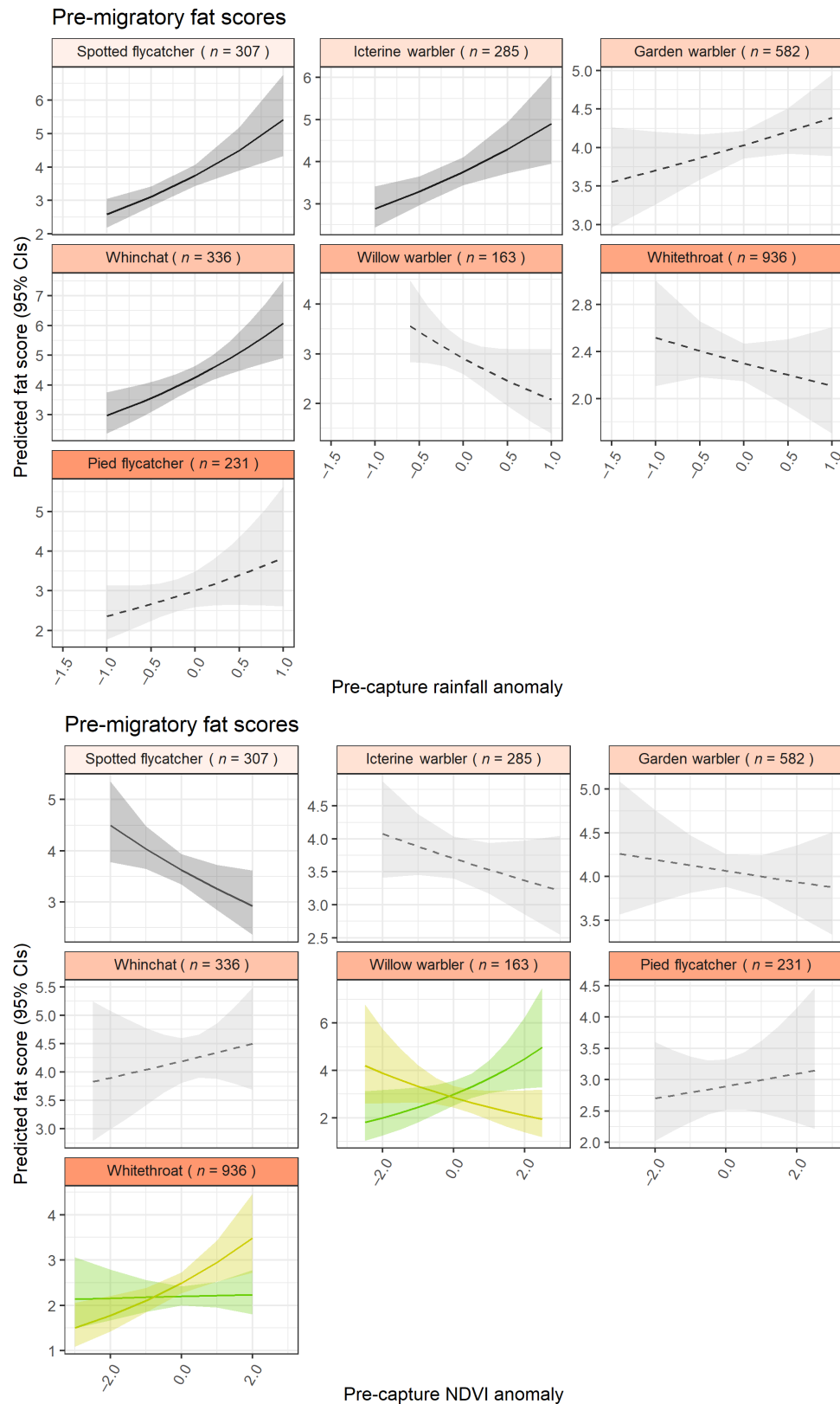


Figure 4. Change in pre-migratory fat scores with pre-capture rainfall and NDVI, predicted from GLMMs. Represented are the mean and 95% CIs of model predictions. Solid lines and darker shading indicate significant effects. For whitethroat and willow warbler fat scores, there was a significant interaction term between pre-capture NDVI and dry season NDVI: for these species, we present the slope of fat score with pre-capture NDVI during years with drier seasons (yellow) and wetter seasons (green). The panel titles are colour-coded following the mover-to-stayer gradient.

survival during severe dry seasons, leading to only robust individuals remaining in spring, though this hypothesis is not supported by studies of winter survival of migratory birds in our study area [61]. Alternatively, this trend could be explained by the movements of species, as some species may depart from Jos if the dry season conditions become too severe [6]. In our study, the diverse movement strategies of birds likely introduced noise to our results: even in a given period (non-breeding versus pre-migratory), there may be individuals at different stages of migratory preparation, leading to divergent responses to environmental conditions. Future analyses should focus on generating in-depth data for specific individuals (e.g. via tracking), to further understand this variation.

Our results of mixed evidence for dry season effects on pre-migratory fuelling match previous studies. In the Neotropical system, there appears to be a strong influence of pre-migratory conditions on fuelling birds [36,50], while effects of conditions early in the season are more mixed and possibly mediated by habitat [34,50,62]. In the Afro-Palaearctic system, some species appear to arrive later in Europe after dry seasons with lower NDVI in West Africa [22,49], while for certain species, dry season NDVI or rainfall appears to have limited influence on pre-breeding migration phenology [19,63]. In a parallel study from Jos, there were some links between dry season conditions and timing of migration, so that for certain species, years with later arrival of the rains resulted in later pre-breeding migration [51].

Our parallel measures of body mass and fat reserves supported scenarios of strategically and physiologically differentiated resource use. The data suggest different functions of mass versus fat, with some indication that mass change may reflect short-term fluctuations in food, while fat reflects longer-term strategic reserve build-up. In our results, body mass did not vary with dry season conditions in any species, while fat did. In addition, NDVI, which may represent the more long-term availability of resources, had a stronger influence on fat reserves than body mass in our data. Our findings emphasize the importance of ringing efforts, which include consistent morphometric data collection, as they can provide detailed insight into ecological processes. Additionally, it may be important in the future to consider further reserves (e.g. muscle mass), additional to body mass, to represent diverse physiological processes. Unfortunately, in our study, we could not make direct links between body reserves and departure timing due to the unstandardized nature of the capture data (but see [51]), though seasonal body mass patterns provided some indication of the timing of fuelling across species (electronic supplementary material, appendix V). Further data collection on the ground in Africa is thus essential to build towards a more comprehensive understanding of how environmental change (seasonal, but linked to climate and land-use change) is affecting birds.

Overall, the mean pre-migratory body mass of birds in our study, as expected, was higher than the mass of these species upon arrival in the southern Mediterranean [64], and similar to the body mass of birds in the Sahel, prior to desert crossing [12]. Previous data on body mass of garden warblers in Nigeria prior to migration broadly matched our pre-migratory data [4]. Our measures of body mass from Nigeria were considerably higher than the structural body mass of these species, with the most extreme differences being for garden warbler and whinchat, with mean body mass in Nigeria approximately 70% higher than structural body mass (electronic supplementary material, appendix IV [65]). These differences imply that, on average, birds fuelling prior to migration in Nigeria are accumulating sufficient reserves to fly >1000 km based on mean fuel loads, and up to 3000 km for garden warbler and whinchat (electronic supplementary material, appendix IV). Such high fuel loads for these species may allow desert crossing without the need to stop and refuel, matching expectations of pre-barrier crossing fuel deposition [4,66]. Other species with lower fuel loads may be better adapted to refuel along the way—an ability that may depend on species' foraging tactics and habitat requirements [16,47,66]. Even within a species, there can be substantial variability in strategies, with some individuals stopping during desert crossing and others less so, depending on fuel loads [16,47].

Considering our findings, which show that birds' body reserves respond to recent fluctuations in rainfall and NDVI, ensuring a continued and consistent source of food in West Africa during the pre-migratory period is essential for species that over-winter and stop over there. Measures that involve restoring and conserving Sahel habitats can help maintain resources for migratory birds and ultimately could mitigate potential impacts of drought in the pre-migratory period [20]. While predictions of climate change-driven shifts in total rainfall in West Africa are thus far varied depending on climate models, the general agreement seems to be that these areas are experiencing increasing extreme and erratic rainfall, as well as a delay and low amount of rainfall during the onset of the rainy season [67,68]. These changes in conditions during the pre-migratory period may pose a significant threat to birds attempting to accumulate body reserves in West Africa, as evidenced by the strong declines in migratory birds after the Sahel droughts in the 1970s and 1980s [20] and recent anthropogenic habitat degradation [69]. Constraints on fuelling in migratory birds can pose a substantial dilemma: birds must depart from Nigeria with sufficient reserves to survive desert crossing, but they cannot delay departure considerably without risking costly delays to breeding [18,19].

Ethics. Fieldwork in Nigeria was conducted with all appropriate national and local permissions. Bird capture and ringing in Nigeria does not require specific permits. The head ringer (Y.B.) is licensed by SAFRING (ringer number 1518).

Data accessibility. For data and code see Jarrett *et al.* [70].

Supplementary material is available online [71].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.J.: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; B.H.: conceptualization, investigation, methodology, supervision, writing—review and editing; Y.R.: formal analysis, methodology, writing—review and editing; Y.B.: data curation, project administration, writing—review and editing; K.B.: data curation, methodology, project administration, writing—review and editing; J.A.I.: data curation, methodology, project administration, writing—review and editing; C.N.: conceptualization, data curation, investigation, methodology, project administration, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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