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Experimental food supplementation at African wintering sites allows for earlier and faster fuelling and reveals large flexibility in spring migration departure in Pied Flycatchers

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By travelling vast distances, migratory birds take advantage of earth's seasonality. Afro-Palearctic migrants can profit from lush spring conditions in temperate regions for chick rearing, but must also gain sufficient energy reserves to cross the Sahara. Rainfall during the dry season in Africa may influence the food available to birds to accumulate reserves. Conflicts of interests in resource exploitation at locations thousands of kilometres apart may occur if migrants encounter poor food conditions during these migratory preparations. Studying how wild birds adjust their fuelling and migration decisions to dynamic environments allows us to understand how flexible migrants can be, which is particularly important in an era of rapid change. We performed supplemental feeding prior to migration in individual Pied Flycatcher *Ficedula hypoleuca* wintering territories in Ivory Coast and remotely monitored their body mass change until they started their spring migration flight over the Sahara. We tested how access to extra food causally affects fuelling, departure mass and departure date. Seasonal fluctuations in natural arthropod availability prior to migration were monitored in two years, to explore how natural resource dynamics alters fuel accumulation. Birds that fully accessed extra food in March–April put on weight earlier and faster than birds without extra food supply, and departed 12 days earlier. Birds accumulated fuel loads that were higher than required for the Sahara-crossing, regardless of their access to extra food. Fuelling rates fluctuated in synchrony with natural conditions, as non-supplemented birds achieved the highest body mass gains at the time that natural arthropod availability peaked in the study area. Fuelling rates were lower in 2020, i.e. the year when the first rains after the dry season started late, than in 2019. Our study showed that Pied Flycatchers modulated fuelling rates – but not departure fuel loads – to food dynamics in West Africa, causing flexibility in the timing of departure. This strategy probably enhances a safe Sahara crossing, but may limit the possibilities of migrants to anticipate advancing spring conditions at breeding sites.

Key words: pre-migratory fattening, seasonal interactions, food availability, climate warming, geolocator, non-breeding season, migration timing, annual cycle adaptation, ecological barrier, field experiment, Sub-Saharan Africa

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Migration behaviour is widespread across bird taxa and is considered an adaptation to exploit seasonality in resource abundance (Alerstam *et al.* 2003). It is still poorly known how annual-cycle decisions of migratory birds are shaped by seasonality within their tropical overwintering sites. Yet, most birds spend much of the year in the Tropics, where they prepare for their return journey to their temperate breeding grounds. Investigating how migrants respond to variability in tropical wintering resources is important to understand observed population declines in Afro-Palearctic birds and human-induced changes in both Africa and Europe (Both *et al.* 2006, 2010, Møller *et al.* 2008, Ockendon *et al.* 2012, Sanderson *et al.* 2006, Vickery *et al.* 2014). Insight into the ways in which migrants adjust their behaviours to tropical non-breeding resources can reveal critical constraints and pathways that determine how animals adjust to changes in Africa and at their breeding grounds.

A fundamental question is how migrants cope with seasonal dynamics in the tropics in order to optimize spring migration decisions and to be able to exploit food peaks during chick rearing. In Africa, seasonal dynamics is strongly linked to the annual arrival and retreat of the intertropical convergence zone that drives alternations between wet and dry seasons when moving from S(E) to N(W) and back again (Beresford *et al.* 2019). Decades ago, Moreau (1972) acknowledged how paradoxical it was that millions of Palearctic migrants choose to stay in Africa, where they experience seemingly deteriorating ecological conditions of the dry season during their stay. Although they arrive in lush and green conditions, they prepare their migration and leave before the start of the new rainy season.

Some species show migratory movements that seem to follow seasonal changes in vegetation greenness, which may possibly allow birds to circumvent resource limitation (Salewski *et al.* 2002a, Thorup *et al.* 2017). Yet, others remain in one area (Salewski 1999) or leave territories in late winter to fuel elsewhere (Risely *et al.* 2015). At locations where birds remain site-faithful over long periods and prepare their spring flights (Bayly *et al.* 2012, Ouwehand & Both 2016), birds must cope with the local conditions and dynamics. Birds that start migrating before the first rains may experience food shortage during the period when they fatten up for their energetically demanding flight across the Sahara, as was found for Montagu's Harriers *Circus pygargus* wintering in the Sahel (e.g. Schlaich *et al.* 2016). Species that start this barrier crossing later, especially when staying further south in more humid zones in West Africa, may take advantage of the onset of the upcoming rainy season, which triggers regreening of the environment and (presumably) increases food availability.

Correlational evidence suggests that wetter/greener conditions in late winter promote earlier timing in some Afro-Palearctic migrants resulting in earlier arrival or higher fitness (e.g. Balbontin *et al.* 2009, Both 2010, Finch *et al.* 2014, Goodenough *et al.* 2017, Robson & Barriocanal 2011). However, coarse environmental indices generally applied in correlative studies poorly and sometimes erroneously represent dynamics of food resources to which migrants are exposed (Beresford *et al.* 2019, Haest *et al.* 2020). Empirical and experimental studies are therefore needed to demonstrate the underlying pathways.

There are currently no studies on the causal links between food dynamics at tropical non-breeding sites and migration decisions in Afro-Palearctic migrants, but such studies are available for the Neotropical bird migration system. Poor rainfall conditions were found to delay the spring migration of individual birds in habitats where arthropod resources steeply declined, and this subsequently impacted fitness later in the annual cycle (Cooper *et al.* 2015, Marra *et al.* 1998, Studds & Marra 2007, 2011). Experimental reductions in late winter food led to poorer flight muscle condition, which was thought to be responsible for delayed departure (Cooper *et al.* 2015); however, since repeated measures of individuals during fuelling were not collected, the effect of food supply on pre-migration fattening could not be formally examined. It is unknown whether Afro-Palearctic migrants adjust their migration decisions in similar ways. The seasonal dynamics and ecological barriers unique to the Afro-Palearctic flyway may have resulted in different (hierarchy of) adaptations in the annual cycle.

Empirical data on how individual birds adjust pre-migration fuelling to conditions at their tropical wintering sites are rare (Bayly *et al.* 2020). Fuelling decisions during migration are much better documented (e.g. Schmaljohann & Eikenaar 2017), and indicate that food availability and body reserves affect migrants' decisions on when and where to replenish energy. The energetically demanding period of fuel accumulation makes up a large part of the whole spring migration process (Lindström *et al.* 2019). We expect that conditions during the pre-migration phase is a key factor in determining the outcome of barrier crossings and early arrival at breeding sites, especially for species that accumulate large fuel stores at their tropical overwintering sites (Alerstam 2011, Lindström *et al.* 2019).

We investigated the impact of food availability during the pre-migration period on fuelling and spring departure in European Pied Flycatchers *Ficedula hypoleuca*, an insectivorous songbird that overwinters in humid savanna in West Africa. This species has become a model system in organismal responses to climate change at the breeding grounds (e.g. Both & Visser 2001, Møller *et al.* 2010), but the phenological relations at their African wintering sites are poorly understood. Pied Flycatchers defend territories in winter (Salewski *et al.* 2000, 2002a), where they prepare for the long non-stop trans-Saharan flight at the end of the African dry season (Ouwehand 2016, Ouwehand & Both 2016). This allows us to experimentally test the causality between food dynamics and body mass increase, departure mass and departure date, by food supplementing free-living birds. Furthermore, we explore how natural fluctuations in arthropod resources alter fuelling of birds in two consecutive years, to provide insight into the extent and scale that food dynamics influence fuel accumulation and departure decisions under natural circumstances.

The arrival of Pied Flycatchers on breeding grounds is largely explained by departure date from wintering grounds (Ouwehand & Both 2017), and food availability in Africa may thereby potentially have a large impact on safe and timely migrations. Although Pied Flycatchers winter in the humid savanna zone in Sub-Saharan Africa, where they may profit from the onset of the first rainfall at the end of the dry season, we expect that birds will experience food shortage in dry years (in line with Both 2010) or when rains start late. Moreover, flycatchers have been shown to gain a selective advantage when laying early (Both & Visser 2001, Helm *et al.* 2019), and may therefore need to trade-off pre-migration fuelling and early arrival at their breeding sites. Departing with low reserves may entail large survival costs when crossing ecological barriers, while waiting for improved food conditions with the onset of the upcoming rainy season may delay migration and entail reproductive costs.

We hypothesize that improved food conditions during the pre-migration period influences the migration decisions of birds, by either allowing them to fuel and/or depart earlier, or, to do so with higher fuel stores (using departure mass as proxy). We expect that responses of non-supplemented birds to natural resource fluctuations mimic experimentally induced fluctuations, and impact birds especially in dry years or when rains are late and arthropod availability during fuelling is probably low. Fuelling and departure decisions may be further affected by age- and sex-specific differences in timing, experience or competitive ability, with potentially earlier timing in older birds and males, and/or a higher departure mass.

METHODS

Study system and general field methods

The European Pied Flycatcher (hereafter, Pied Flycatcher or flycatcher) is an insectivorous passerine that breeds in temperate and boreal forests in Eurasia, and occupies non-breeding residency sites (hereafter, wintering sites) in Sub-Saharan West Africa from September–March/April (Bell *et al.* 2022, Lundberg & Alatalo 1992, Ouwehand & Both 2017). Pied Flycatchers are generally considered to be site-faithful to wintering territories (Salewski *et al.* 2000, 2002a). In their African wintering sites, flycatchers undergo a pre-breeding moult, starting in February (Jenni & Winkler 1994, Salewski *et al.* 2004), and fatten-up prior to spring migration (Ouwehand & Both 2016, Salewski 1999). We studied Pied Flycatchers and ecological conditions in north-east Ivory Coast, in the centre of this species' range (Dowsett 2010), during the second half of their non-breeding season (i.e. from 7 December 2018 to 9 January 2019, from 28 February to 26 April 2019 and from 4 February to 15 April 2020). We followed the ethical standards for animal welfare as required in The Netherlands (e.g. Ouwehand & Both 2017) for data collection and sampling. No separate approval from animal experiments committee was required, but practices were covered by the permit provided by the Office Ivoirien des Parcs et Réserves.

The study site of approximately 1 km^2 is situated in close proximity to the Comoé River and the ecological research station in the southern part of Comoé National Park (8°45.875'N, 3°47.189'W; Figure S1), within the Guinean-Sudanian savanna zone. This part of the NP has high flycatcher densities and consists of a mixture of humid woodland, dry forests patches, tree and bush savanna and gallery forest. The climate is characterised by a distinct dry and rainy season, with an average annual amount of rainfall of c. 1000 mm. Most rainfall occurs between May and October, while drought conditions prevail from November until March (Figure S2).

Pied Flycatchers were caught using baited spring traps or 1–8 mist nets (individual length 3–6 m) with and without playback from 5:30–12:00 (sometimes 15:30–18:30). Individuals were fitted with an EURING inscription ring and one colour ring to improve recognition of birds based on an individuals' pre-breeding plumage characteristics (following Both *et al.* 2016).

Only one plastic or aluminium colour ring was placed respectively on top of the inscription ring (preventing direct foot contact with plastic) or on the opposite leg (preventing malformation of soft aluminium) to reduce the risk of leg problems (Pierce *et al.* 2007). Birds were measured (tarsus, wing length, p3), weighted (accuracy 0.1 g), aged (first winter or older) and sexed by plumage characteristics, and/or a blood sample taken for sexing (in case of unambiguous plumage; following Ouwehand 2016). To confirm that birds indeed departed directly on migration after fuelling in our study site, we mounted tracking devices with Rappole-Tipton leg-loop harness of elastane, using an Intigeo geolocator ($n = 17$ in 2019, $n = 7$ in 2020) with a 7-mm long light-stalk (P30Z11-7-Dip of Migrate technology, mass: 0.42 g, incl. harness) or solar-powered radio transmitter ($n = 1$ in 2020; LifeTag of Cellular Tracking Technologies; weight; 0.57 g incl. harness).

Experimental set-up

Birds were first habituated to food bowls (diameter: 12 cm, depth: 3 cm) from 7 December 2018 to 9 January 2019 and from 28 February to 14 March 2019 (Photo 1D-E). Bowls were pinned at c. 0.1 m high into the ground at a location regularly visited by a bird and provided with 3 (c. 0.35 g) Mealworms *Tenebrio molitor* a day. After habituation, birds were assigned to an experimental treatment and provided with either 4 g of living Mealworms per day, or 3 Mealworms (c. 0.35 g) per day. The latter was the minimum to still attract birds to bowls for weighing and is hereafter referred to as birds without additional food. Since we aimed to alter food conditions during the fuelling phase, the experimental treatment started by 16 March until birds departed, since catching data from earlier years indicated that fuelling started mid to late March (Ouwehand unpubl. data). In spring 2020, all birds received only 3 Mealworms a day (c. 0.35 g), starting on 9 February. Food was always provided during the relatively cool morning period (5:30–11:30) to prevent Mealworms from dying through overheating.

During habituation and weighing sessions, we recorded food bowls by means of a video camera, which allowed us to confirm the identity of birds, and provide additional insight into unintentional food consumption by non-target birds (Figure 1C). Recordings revealed that at three of nine locations the focal bird accessed the food supply of 4 g only moderately, while Mealworms were frequently (c. 50% of recording days) eaten by other bird species instead. Since this likely influenced the effectiveness of the treatment in 30% of our food supplied birds, the three birds that moderately accessed extra food were separated from those that fully accessed the extra food supply and we evaluated the causal effect of food on fuelling and departure by a 3-level factor reflecting the ‘access to additional food’ that birds showed (i.e. no, moderate, full).

Remote body mass measurements

Body mass of individual birds was repeatedly measured using autonomous weight loggers, with an accuracy of 0.1 g (developed by Feldbrugge Prototyping), hereafter called ‘balances’. Measurements in 2019 were taken from 17 March until all birds departed. Measurements in 2020 ranged from 27 February to 15 April, when the COVID pandemic forced termination of fieldwork. Consequently, measurements from 2020 only covered the full fuelling trajectory of one individual that departed before 15 April. The balances consisted of an external weighing platform (diameter: 15 cm) with a food bowl, which was connected to a datalogger with SD memory card in a water-resistant casing (Figure 1). Balances had a measurement range of 0–80 g, with a sampling interval of 90 milliseconds (c. 11 measures per second) which allowed short visits to be measured. Measurements were started when we provided the birds their daily mealworm supply in the food bowl attached to one of the eight (randomly chosen) balances. The very first visit of a bird to the balance within a day reflected therefore the body mass prior to food supplementation on that day, providing a comparable measure of mass changes between days for birds in different treatment groups. After a weighing session stopped, any remaining food was returned to the pinned bowl.

For each weighing session, the birds’ identity and the precise start and end time of visits were annotated. The birds’ body mass was inferred by subtracting the calculated median baseline mass during a 10-s period prior to the visit from the median calculated mass during the visit (i.e. the period in which a bird was stationary on the balance). To guarantee robust measurements we excluded (1) visits where birds dived into the bowl or touched the balance for less than 1 s, (2) measurements that were inconsistent within visits, and (3) weighing sessions with unstable baseline measurements. The latter was common in three specific balances in 2019, and these data and devices were removed from the study (causing data gaps at the start of some fuelling trajectories, e.g. bird */O). If a bird carried a tag, its body mass was corrected accordingly. The remaining data were used to construct individuals’ fuelling trajectories.

Photo 1. To measure fluctuations in natural insect availability during the period that birds prepare their migration, we repeatedly monitored arthropods (A–C) at fixed locations using one malaise trap and three pitfalls to target flying and ground-dwelling insects. (A) Malaise trap at point 3-N on 5 April 2019. (B) One pitfall in the front with a cover to protect it against rain and Wender emptying the pitfalls on 10 March 2018 at point 1-S in a forest island (points refer to map locations in Figure S1). (C) After four days of trapping, arthropod yields were collected, sorted and identified. Insect abundance was based on the number of items, while the body length measurement of each trapped item allowed us to estimate insect biomass from length-mass regressions for each taxonomic group. To obtain repeated body mass measurements of birds with autonomous balances (Figure 1C), (D) individuals were first extensively observed (here by Armel and Bronwyn) to find perches and locations that they often used during foraging and resting, and (E) that could provide a suitable spot to place a food bowl for habituation. Prior to the start of the supplementary feeding experiment, as many birds as possible were habituated by providing three mealworms per day in a food bowl in their territory, while a video camera was used to monitor if birds were successfully attracted to the food bowl.

Departure date and departure mass

Within the subset of birds that returned with geolocators in the next year, we investigated if the date a bird was last seen on a balance or food bowl could be used to approximate spring migration date. Raw light data of geolocators was used to infer the onset of Sahara crossing in spring, i.e. using the evening prior to the onset of diurnal flight in these (normally) nocturnal migrants (following Ouwehand & Both 2016). The date that birds started their spring migration across the Sahara was tightly correlated (Figure S3) to the date a bird was last seen on a balance or food bowl, and we therefore used the latter to approximate spring departure date across all birds, hereafter referred to as departure date.

The first measurement on the last day a bird was weighted was used to estimate departure mass. We did not correct for potential body size-related differences in body mass, as body mass has previously been reported to be independent of body size (wing length) in Pied Flycatchers (Kelsey *et al.* 2019). We calculated departure fuel load (fat and protein) and fuel deposition rate (FDR) from respectively departure mass and mass changes relative to 9.3 g, which is the structural body mass of living Pied Flycatchers without visible subcutaneous fat stores and with breast muscle score 0 (following Salewski *et al.* 2010)

$$\text{departure fuel load}_i = (\text{departure body mass}_i\ (g) - \text{structural body mass}_i\ (g)) / \text{structural body mass}_i\ (g) \quad (1)$$

$$\text{fuel deposition rate}_i\ (1/d) = \text{mass change between two consecutive days}\ (g) / \text{structural body mass}_i\ (g) \quad (2)$$

Arthropod sampling

We sampled arthropods repeatedly (trapping duration of 4 days per round) to provide a proxy of natural fluctuations in food resources for flycatchers during the pre-migration period (Photo 1A-C). Sampling locations covered a gradient from forest interior to open savanna inhabited by Pied Flycatchers (Figure S1). In 2019, eight locations were continuously sampled during March–April. The four northern locations (Figure S1) were resampled in 2020, when sampling occurred once every eight days. At each location, one malaise trap and three pitfall traps were used to estimate abundance and biomass (expressed per 96 h of trapping) of respectively flying and ground-dwelling arthropods. The yield of three pitfalls were combined into a single pitfall arthropod sample. Malaise traps were 150 cm long and 120 cm high with one standard tube, and an additional tube and extra bottle added to the collection circuit to improve effectiveness. Pitfalls consisted of plastic cups (diameter: 7.8 cm, depth: 11.3 cm, 5 m apart) with a cover to prevent rain from entering (petri-dish on three wooden stick). Arthropod samples were collected using a 1-mm sieve. Specimen were stored in 70–96% ethanol in the fridge until further processing. After collection malaise traps and pitfalls were (re-)filled with respectively ethanol and cooling liquid.

Each sampled specimen with a body length of at least 3 mm (from abdomen to head, but excluding antennae, legs and wings) was identified, counted and its body length measured with an accuracy of 1 mm using graph paper. Insecta, Crustacea and Arachnida were mostly identified to order level (exceptions were ticks and mites identified as Arachnida spec., and Formicidae were separated from other Hymenoptera), and specimens in the subphylum Myriapoda to class, using Picker *et al.* (2002). Body length measurements were used to calculate fresh body mass by means of taxonomy-specific regressions provided by Sohlström *et al.* (2018), which allowed us to estimate body mass for more than 99% of our captured arthropods (but did not include mass for scorpions or specimen identified to a higher then required taxonomic level).

Although small arthropods (<3 mm) are very common in the environment (Bibby & Green 1980, Ouwehand 2016), these small items are considered to be underrepresented in the diet of Pied Flycatchers (Marchetti *et al.* 1998). Items larger than 30 mm likely require a longer searching and handling time. We hence only included items within a (presumed) edible and profitable size range in our analysis, to prevent masking of trends in potential prey abundance and biomass by respectively highly abundant small items or heavy larger items. Such prey are probably rarely taken except when slender or soft-bodied like Lepidoptera, Myriapoda and Odonata (for which we excluded specimens larger than 40 mm). Regarding bulky arthropods with hard body parts, we excluded specimens with a body length exceeding 30 mm in Orthoptera and 20 mm in Coleoptera, Hemiptera, Isopoda, Arachnida, Hymenoptera, Diptera and cockroaches.

Some samples were affected by ant raids, notably red driver ant *Dorylus* sp., which may have masked trends in total arthropod abundance and biomass. Samples (n = 5) in which more than 100 ants in malaise sampling or in one (pooled) pitfall sample occurred were therefore excluded.

Statistical methods

Two linear models (LMs) were fitted to estimate the causal effects of 'access to additional food' in 2019 (3-levels: 'no', 'moderate', 'full') directly on (1) the date at which birds departed from our study area (date fitted as April day: 1 = 1 April), and (2) body mass at departure (g). Both LMs included fixed effects for sex and age class. A similar LM tested if treatment groups (i.e. 'access to additional food') showed initial differences in body mass before fuelling and experimental treatments started, and included fixed effects for sex and age class. For this purpose, we used the most recent (balance or catching) mass measurement of birds before 6 March, which was the date when the earliest bird in our population showed considerable gains in body mass.

Although all birds were expected to gain mass and depart, the process of fuel accumulation in the wild may show strong non-linearity, and may vary within and between individuals. To investigate this non-linear process of fuel accumulation, we used hierarchical additive models (HGAMs) on natural log-transformed body mass changes over the season in relation to different factors that may contribute to variation in fuelling trajectories, while the shape of nonlinear functions are allowed to vary between different grouping levels without making assumptions about the shape of these patterns (Pedersen *et al.* 2018, Wood 2017). Each HGAM was fitted with the 'mgcv' package in R using REML estimation (Wood 2011). First, we studied the causal effect of food on fuelling using the experimental setup in 2019 with an HGAM that included a general smooth for Julian day (1 = 1 January, hereafter 'day'), factor-smooth interactions and intercepts for access to 'additional food' (levels: no, moderate or full), 'age' (first winter or older) and 'sex' (male or female), and individual-level random smooths to account for repeated measures and some additional degree of individuality in fuelling. Second, we investigated annual differences in fuelling between birds that received no additional food (beyond the 0.35 g), and thus most closely resembled natural conditions. The HGAM included a general smooth for 'day', factor-smooths interactions and intercepts for 'year', 'age' and 'sex', and individual-level random effects smooths. The maximum number of basis functions in both HGAMs were set to $k = 5$ to restrict the potential wiggliness of each smooth term. For model selection, we relied on an additional penalty to each term so that effects could be penalized to zero and which can effectively remove terms from the model (select = TRUE; Marra & Wood 2011). How well the HGAM captured patterns in the data is described by the total % deviance explained. Whether a smooth term significantly contributed to the model was inferred from the effective degrees of freedom (EDF); i.e. terms with EDF = c. 1 or <1 are equivalent to being linear terms, while a further increase in EDF indicates that more 'wiggliness' of terms is effective to improve the model. For each effective term, we discuss group-level factor differences using visual inspection of the whole fuelling trajectory and/or differences in smooth complexity (i.e. wiggliness).

To provide further insight into processes driving day-to-day modulations in fuelling rates, we fitted a third HGAM to the full dataset, optimized to best describe fine temporal scale fluctuations in body masses seen within individual trajectories. The HGAM included a general smooth for 'day', factor-smooths interactions and intercepts for 'additional food', 'year', 'age' and 'sex' (with $k = 5$), and 'individual-by-year' random effects smooths (with $k = 14$ to assure maximum flexibility within individual curves). High wiggliness in this model has higher potential to describe body mass changes even in individuals with irregular measures and strong inter-annual variation, and allow for stronger deviations of shared trends from other factor smooths. From the model predictions, we estimated daily mass changes (g/day) for each individual per year over the date range for which we had raw data measurements for that specific bird. We excluded one bird (individual */Y2) in subsequent analyses for which raw data measures were more than 25 days apart and for which HGAM predictions showed large uncertainty (dashed line in Figure S4B). A linear mixed model (LMM) was fitted to investigate if access to additional food (3-levels: 'no', 'moderate', 'full') created consistent differences in fuelling rates (i.e. HGAM-derived daily mass changes in g/day) of birds in 2019, and included fixed effects for 'sex' and 'age', and random intercepts for 'individual'. Another LMM tested for year differences in daily mass changes in birds without additional food during the period when data were collected in both years (i.e. day 76–105), and included fixed effects for 'sex' and 'age', and 'individual-within-year' as random intercept.

Furthermore, we investigated if natural fluctuations in arthropod availability in the study site could explain fluctuations in fuelling rates in birds without additional food. For this we only considered daily body mass changes after 5 March, which represented the moment that the earliest bird in our population showed considerable gains in body mass. To match the 4-day arthropod sampling duration with HGAM-derived body mass change estimates, we first calculated a mean mass change per bird over each 4-day sampling period. Since mass change estimates did not always perfectly overlap with 4-day periods, i.e. periods can be shorter at the end and start of a fuelling trajectory, we only calculated mass means when the overlap with an arthropod sampling period was at least two days. To subsequently establish if arthropods sampled across the whole study sites could explain the fuelling rate at the flycatcher population level, we fitted four separate LMs to establish per arthropod proxy how well the mean yield across all sampling locations explained the (population) mean mass change across birds without extra food supply.

RESULTS

In 2019 we measured body mass of 17 individuals repeatedly until the birds had departed (8 females, 9 males, 12 first winter, 5 older birds). All 17 birds took part in a field experiment in which birds differed in their access to extra food supplements; i.e. 6 birds ‘full’, 3 ‘moderate’ and 8 ’no’ access to extra food supply. In 2020 eight birds, which received no additional food, were repeatedly measured for part of the fuelling period (3 females, 5 males, 2 first winter, 6 older birds). Four of the latter individuals had also been measured in 2019 (Table S1). COVID-19 restrictions in 2020 forced measurements to end on 15 April, before most birds departed on migration.

Birds that fully accessed extra food supply started fuelling earlier and increased body mass faster over time (Figure 1B, Table S3) compared to birds that received no additional food. Pied Flycatchers without access to additional food supply departed on average on 13 April, which was 12 days later than birds with full access to the extra food supply ($F_{2,12} = 17.75$, $P < 0.001$; Figure 1A, Table S2). If we consider the average departure date as the end of fuelling, and the start of the experiment (16 March) as the beginning, the fuelling duration of birds that only accessed natural resources was 29 days, compared to 17 days in birds with full access to the extra food supply. At locations where access to supplemented food was moderate and where (unintentional) consumption by (larger) heterospecific birds occurred, Pied Flycatchers showed

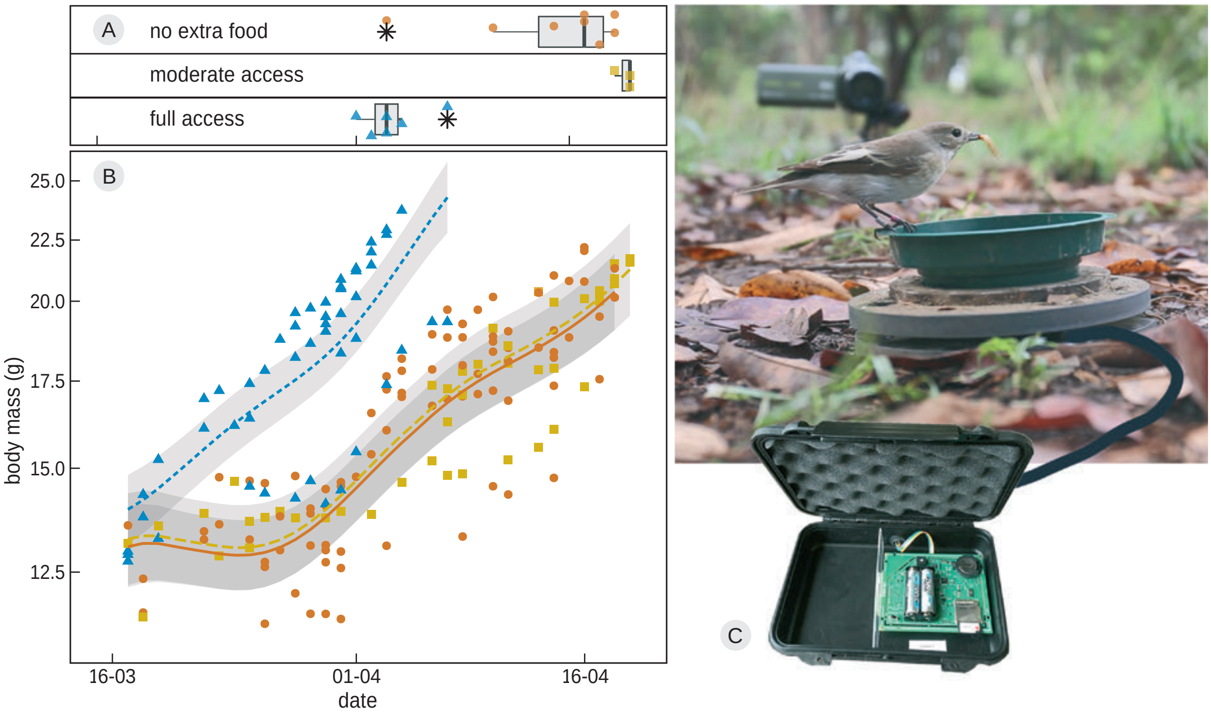

Figure 1. (A) Spring departure decisions and (B) fuelling trajectories in 2019 in Pied Flycatchers wintering in Ivory Coast in relation to access to experimental food supplementation with Mealworms. After birds were habituated to visit a food bowl, repeated body mass measures in the field were obtained by luring birds to a food bowl connected to an autonomous balance (C). Boxplots and (jittered) raw data in A show approximated spring departure dates of birds (incl. one bird of 13 g; i.e. */red dot) based on the date a bird was last seen at a balance (see Figure S3). Each point in B refers to the body mass in grams of a bird on a specific date. Lines and confidence intervals show the predicted fuelling trajectories per group (from models in Table S3).

fuelling trajectories that largely overlapped with birds that received no additional food. A positive effect of full access to food supplementation was also apparent within individuals (Figure 2), and allowed birds to achieve higher body mass at earlier dates than they did in the next year when no additional food was provided.

The extra food supply did not significantly affect the mass of birds when they departed for spring migration ($F_{2,12}$ = 0.8, P = 0.46; Table S4), and ranged from 17.5 to 23.6 g (i.e. excluding one outlier of a 13-g bird; Figure S5A). Nor did body mass of birds in different treatment groups differ significantly prior to fuelling ($F_{2,9}$ = 0.13, P = 0.88; Table S5, Figure S5A). Assuming the same structural body mass across Pied Flycatchers, the recorded mass range of 17.5–23.6 g corresponded to a fuel load of 88–154% of structural body mass. Birds equipped and returning with geolocators reached body masses of 20.2–22.6 g at the day (or day before) they start crossing the Sahara, corresponding to fuel loads of 117–143% of structural body mass. These results confirm that Pied Flycatchers commonly accumulate fuel stores at their wintering territories from where they start to cross the Sahara directly (see also Figure S3 and Ouwehand & Both 2016, 2017). However, we consider it likely that the early 'departing' individual without extra food in Figure 1A, which had a final mass of only 13 g, moved to another fuelling site or died, rather than having started migration, as this reflects energy stores that doesn't allow crossing the Sahara without refuelling.

Fuelling trajectories of non-supplemented birds varied clearly between years (Table S6), suggesting that birds flexibly adjusted fuelling prior to spring migration to perceived natural conditions in these years. In 2019 birds generally started to gain mass later but did so more rapidly than in 2020 (Figure 2, Figure S6). By comparing the (incomplete) predicted fuelling trajectories of flycatchers in 2020 with those in the previous year (Figure S6), we find that average body mass during the last observation date (which for most birds was not the departure date) in 2020 was already achieved a week earlier in 2019. The within-individual patterns recorded in four birds (Figure 2) illustrate that flexibility can result from various factors. For three of

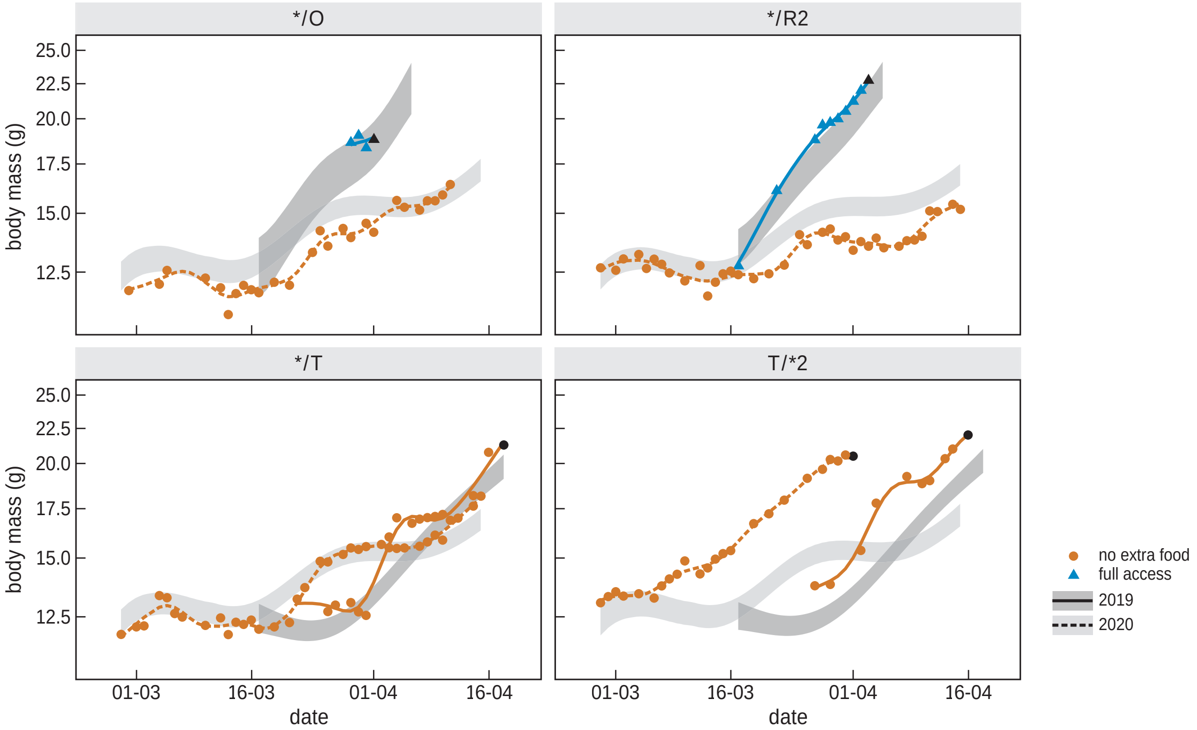

Figure 2. Body mass measurements over time in four birds that were repeatedly measured in 2019 and 2020. Birds differed in their access to experimental food supplementation in 2019. Points reflect body mass in grams and the associated lines show the predicted fuelling trajectories of individual birds (see Figure S4 for trajectories of other individuals). Black symbols indicate if birds were measured until departure (n = 1 in 2020, all in 2019). Grey ribbons depict confidence intervals of the predicted (population) trajectories in the age class, sex, year and experimental group to which an individual belonged (i.e. using model outputs of Table S3 for 'full access' and Table S6 for 'no extra food').

these birds (individuals */T, */O, */R2) the observed within-individual variation in fuelling seem to roughly be the same as the predicted fuelling trends arising from year and food treatment differences (Figure 1, Figure S6). In contrast, female T/*2 in 2020 clearly deviated from general trends (Figure 2); she steeply increased mass early in the season and was the first of all flycatchers to depart, in contrast to the other birds without access to food supplementation that fuelled slower and departed later, especially in 2020 (Figure S6).

We found no consistent sex and age differences in departure dates (Table S2), fuelling trajectories (Table S3, S6–S7, Figure S7), and mass prior to fuelling and mass at departure (Table S4–S5, Figure S5B–C).

We observed synchronous daily changes in body mass across birds without access to additional food (red lines in Figure 3A). Fuelling rates showed striking peaks in 2019 and daily rates were on average higher (0.28 ± 0.03 g/d, i.e. FDR of c. 3%) than during the same 29-day period in 2020 (0.13 ± 0.04 g/d, i.e. FDR c. 1%; year effect: $\chi^2_1 = 8.74$, $P < 0.005$). Synchronous mass gains (Figure 3A) in birds without extra food were particularly visible in 2019, and coincided with temporal peaks in 4-day arthropod sampling yields (Figure 3B). Under natural circumstances birds achieved higher fuelling rates when abundance and biomass of arthropods in our study area was higher (ground arthropods: biomass: $F_{1,11} = 17.1$, $P < 0.005$, $r^2 = 0.57$, abundance: $F_{1,11} = 3.9$, $P = 0.073$, $r^2 = 0.20$; flying arthropods: biomass: $F_{1,11} = 5.1$, $P < 0.05$, $r^2 = 0.26$, abundance: $F_{1,11} = 8.2$, $P < 0.05$, $r^2 = 0.37$; Figure 4).

The maximum mass gain observed in our study site was 1.28 ± 0.04 g/d (i.e. FDR c. 14%) in a bird in 2019 that had moderate access to additional food, at a time that most birds had already departed on migration. Fuelling rates larger than 0.8 g/d (i.e. FDR > 9%) were only recorded in 2019, and mostly after the majority of birds with full access to extra food had already departed (Figure 3A). Food supplementation in 2019 allowed birds to overcome low availability in natural arthropod resources, especially at the start of fuelling

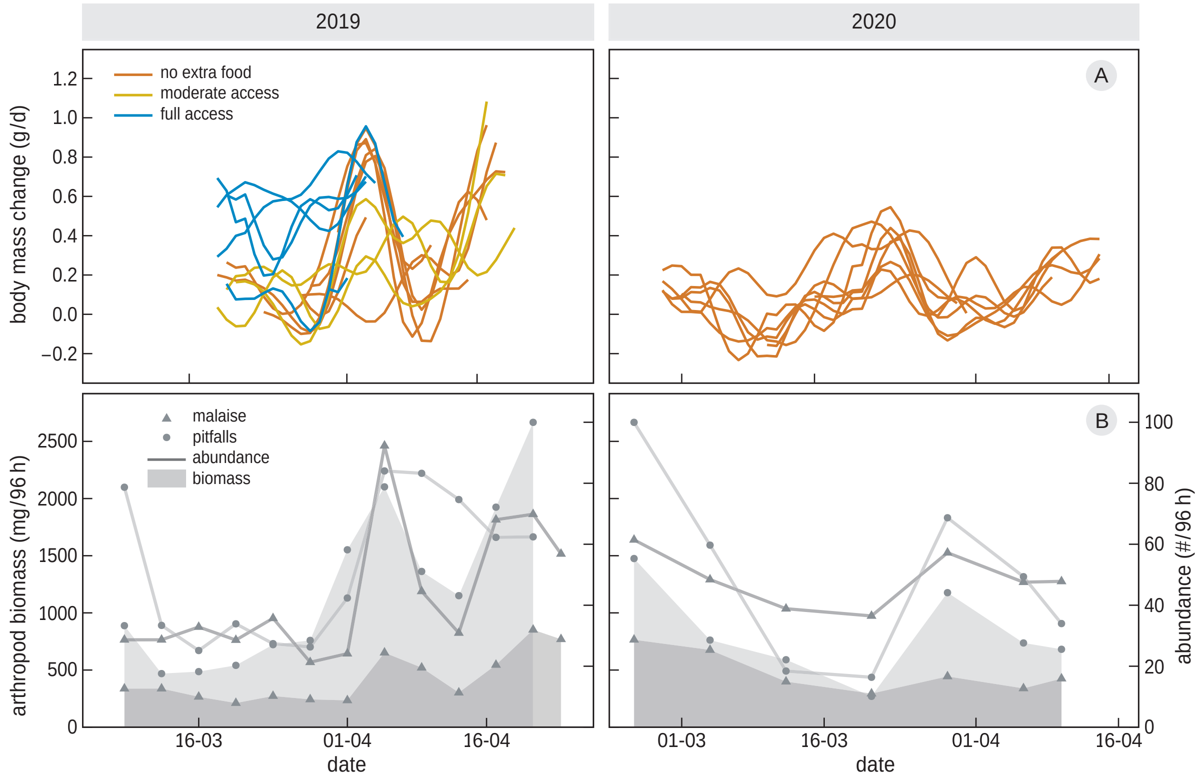

Figure 3. Seasonal fluctuations in daily body mass change of Pied Flycatchers in 2019 and 2020. Daily body mass change was calculated using the model predictions at individual level within seasons (Table S7, Figure S4). B shows fluctuations in natural arthropod resources during the same seasons. Arthropod yields reflect mean biomass in mg (shaded area) and mean abundance (lines) per 4-day sampling period, measured with malaise and pitfall traps to target respect. flying and ground-dwelling arthropods in eight (2019) or four (2020) sampling locations in the study site (see Figure S1, S8).

(blue lines in Figure 3A). This led to overall higher fuelling rates in birds with full access to additional food (0.46 ± 0.05 g/d, i.e. FDR around 5% of structural body mass) compared to birds with no or moderate access to additional food (respectively, 0.30 ± 0.03 g/d and 0.25 ± 0.04 g/d; FDR of c. 3%; $\chi^2_2 = 9.58$, $P < 0.01$).

DISCUSSION

How ecological conditions determine departure of long-distance migratory birds from African overwintering areas is poorly understood. We showed that Pied Flycatchers at their African wintering site, when preparing for a non-stop trans-Saharan flight, were strongly affected by food availability. Fuelling rates of flycatchers correlated positively with within-season fluctuations of arthropod abundance and biomass. Food supplementation revealed that effects of food availability on fuelling and timing of departure are causal. Individuals with full access to food supplements increased their body mass earlier in the season and departed 12 days earlier than non-supplemented birds. The fuelling trajectories of individuals recorded in two consecutive years revealed large individual flexibility in fuelling under different (food) conditions.

These findings confirm our hypothesis that food availability in Africa prior to migration modifies timing of spring departure in Afro-Palearctic migrants, as was previously described in Neotropical migrants (Cooper *et al.* 2015, Studds & Marra 2007, 2011). The ability of individuals to modify innate time schedules to ecological conditions may result from programmed flexibility (Åkesson & Helm 2020) that allows the fine-tuning of endogenous time keeping mechanisms. Although rigid endogenous rhythms and local photoperiodic conditions at non-breeding sites (Gwinner 1989, 1996) will determine when birds can start migratory preparations, the observed departure schedules may thus show considerable flexibility. When the potential time window over which fuelling can occur is large, not only the duration and rates of fuelling may be variable, as recorded for some Palearctic migrants (Bayly *et al.* 2012), but also the observed onset of fuelling can vary (this study). This may explain why males and females

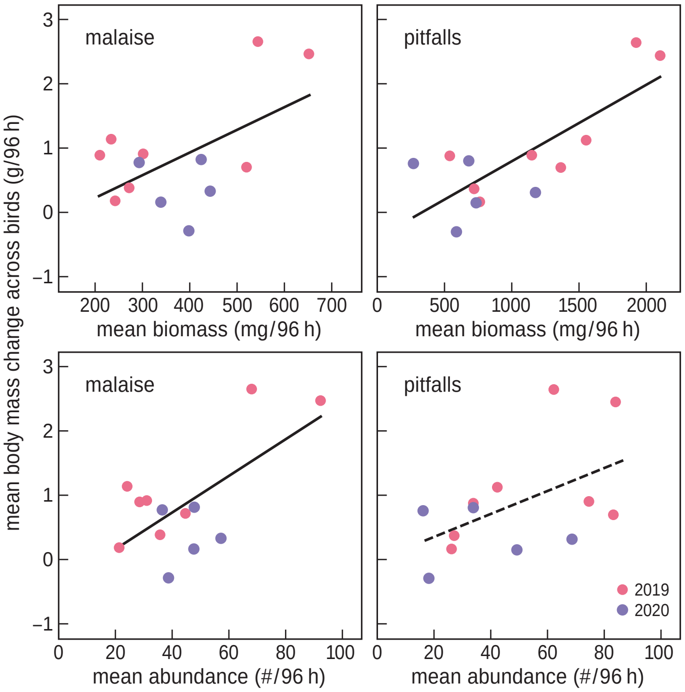

Figure 4. Fuelling rates of Pied Flycatchers at population level in relation to four proxies of natural food availability during migration preparations. The mean fuelling rate of each bird during a 4-day arthropod sampling period was first estimated, and included only birds without food supplementation and mass changes after 5 March (i.e. the earliest observed instance of fuelling), before expressing fuelling rates at population level. Each symbol shows the mean fuelling rate across birds during a 4-day arthropod sampling period. Lines indicate trends (dashed: $P = 0.05–0.10$) or significant (solid: $P < 0.05$) relationships from LMs.

showed – in contrast to our expectations – similar fuelling and departure decisions, despite previous findings that male Pied Flycatchers migrate approximately one or two weeks ahead of females in spring (Bell *et al.* 2022, Both *et al.* 2016, Ouwehand & Both 2017).

We found that effects of arthropod availability on fuelling rates generally acted throughout the (shared) local environment, as indicated by synchronous fuelling responses of site-faithful Pied Flycatchers across different territories. This resulted in stronger modulations in the fuelling rates in birds without access to extra food in comparison to the more constant and overall higher fuelling rates in birds that fully accessed food supplements. Differences in fuelling rates between experimental groups were most pronounced early in the season (Figure 3A). Later in the season when arthropod resources peaked in our study area (Figure 3B), birds without extra food accumulated fuel at faster rates (Figure 3A) than typically seen in birds with full access to 4 grams of Mealworms per day (respectively FDR around 9% vs. c. 5% of structural body mass). It seems likely that our food supplementation did not create *ab libitum* food conditions, although it did help birds to start earlier with fuelling. The shortest achievable fuelling duration is estimated at c. 10 days when circumstances were really good (i.e. assuming FDR of 9% and departure mass of 17.5 g). On the other hand, fuelling duration can be considerably longer when conditions are poor.

Fuelling was especially slow in the study year 2020, when rainfall started late. The period Jan–April 2020 was dryer than in 2019, with later onset of the rainy season, despite relatively large amounts of rainfall at the start of the dry season in October/November (Figure S2). The fact that fuelling of most birds was slower in 2020 than in 2019, suggests that particularly the onset and amount of rain in the second half of the non-breeding season in Africa (i.e. Jan–April) may be critical in determining fuelling conditions. Synchronous and steep peaks in arthropod yields and fuelling rates were very apparent in 2019 (Figure 3 and 4). Non-continuous (and less extensive) arthropod sampling in 2020 allowed only a partial description of arthropod fluctuations in 2020, and prevent a formal year comparison over the whole period. Visual inspection suggests less pronounced peaks in 2020, and larger overall arthropod availability in 2019 compared to 2020 during fuelling in the first half of April (Figure 3). Slower fuelling probably also resulted in later departure dates in 2020, as radio tracking in the study area revealed that Pied Flycatchers left the study area mostly in May (Bil *et al.* 2023), which is relatively late compared to previous years when birds departed between early and late April (Ouwehand unpubl. data 2017–2019).

Long-term arthropod and fuelling data are not available to indicate how often migrants modulate fuelling and departure timing to local food conditions at their wintering site, but rainfall data helps to place our findings in a wider perspective. The onset and amount of rainfall in 2019 at the end of the dry season was relatively normal compared to the 5-year averages in the study area (Figure S2), while conditions in 2020 were much dryer than average. Satellite-derived daily rainfall estimates (RFE2 of the U.S. Climate Prediction Centre) from NE Ivory Coast provide a reasonable predictor for the weekly Jan–April rainfall sums at Comoé station (data available for 2015–2020: $\beta = 0.65 \pm 0.11$, $r^2 = 0.24$). This suggests that local rainfall at Comoé station in Jan–April 2019 was also normal when compared to long-term average RFE2 rainfall Jan–April sum (2001–2020) in NE Ivory Coast. However a situation of local drought conditions occurred during Jan–April 2020 at our study site, since plentiful rain only fell at Comoé station during May, while RFE2 values for NE Ivory Coast in 2020 (compared to 2001–2020) indicate relatively wet conditions (elsewhere) during Jan–April. Given that rainfall conditions in 2019 were normal, we expect that birds in this region regularly modulate their departure timing, while even larger effects might be expected in years with late onset of rains such as in 2020.

The fact that local rainfall in 2020 deviated strongly from regional rainfall in NE Ivory Coast during the fuelling period, demonstrates the limitations of using coarse rainfall estimates. This is an even greater issue when using the Sahel rainfall index, a commonly used proxy of rainfall conditions affecting Afro-palearctic migrants. The Sahel rainfall index poorly predicted the annual rainfall sum measured in a weather station located c. 150 km SE of our study site (Bondoukou data available for 1920–2017: unpubl. analysis Zwarts). For example, Jan–April rainfall conditions in NE Ivory Coast were fairly good in the period of the Great Drought in the Sahel, during 1969–1991. Local rainfall conditions also deviated strongly from the Sahel rainfall index in our study years, since 2019 and 2020 are both considered relatively wet years according to the Sahel rainfall index (Figure S50 in Zwarts *et al.* 2023).

An important next step is to quantify more precisely which prey species allow flycatchers to sufficiently increase their body mass, and describe their relation to climatic drivers. Although we found that ground-dwelling and flying arthropod availability predicted fuelling rates, this does not mean that these specific groups are especially important. Pied Flycatchers forage on a wider range of substrates then we sampled (e.g. bark, tree canopies; Salewski *et al.* 2003, Zwarts & Bijlsma 2015). We observed flycatchers exploiting caterpillar outbreaks in freshly (de)foliated tree canopies of *Daniellia olivieri* during our study (Ouwehand unpubl. data). Tree canopy-dwelling arthropods were poorly quantified in our study, but were previously found to become more abundant in the study area when monthly rainfall during the non-breeding season increased (Salewski 1999). Such prey may thus have changed in synchrony with arthropod proxies. On the contrary, arthropod availability also fluctuates at finer spatial scale (Figure S8), and habitats and arthropod groups may differ considerably in their responses to climatic drivers (see also Bil *et al.* 2023). A better knowledge of diet preferences in relation to available resources within and between seasons will improve quantification of food availability for fuelling birds, by concentrating on the most relevant trapping techniques and insect groups.

Birds reached high body masses by the time they left the study site (Figure S5A), and did not need supplemented food *per se* to achieve this. Despite the ability of birds to fine-tune fuelling decisions to food, birds in our study did not use food supplements to reach a higher departure fuel load. When food was plentiful prior to departure, birds achieved higher fuelling rates and reached this threshold more quickly which allowed birds to depart earlier on migration. Birds may wait for suitable weather conditions to start migration (e.g. Deppe *et al.* 2015, Shamoun-Baranes *et al.* 2017), but our birds departed as soon as they had gained large fuel loads (Figure S4). Also, the flycatchers did not slow down fuel accumulation prior to departure (Figure 3A). The proximate mechanisms that determine how feeding conditions regulate decision-making at wintering sites might be similar to those operating during migration (e.g. Alerstam 2011, Biebach 1985, Hedenström 2008, Klinner *et al.* 2020, Schmaljohann & Eikenaar 2017). Klinner *et al.* (2020) proposed a critical 'fuel-threshold' below which the survival probability is higher when staying at the fuelling site and above which departing is the best option to reach the migratory destination in time. Pied Flycatchers probably need a specific fuel-threshold to depart on migration. Our results on flycatchers indicate that a fuel-threshold may correspond to a body mass of at least 17.5 g and a fuel load of 88%. When birds fly non-stop (Ouwehand & Both 2016) at speeds of 50 km/h (Schmaljohann *et al.* 2008), a fuel load of 88% would facilitate a flight of c. 3160 km (assuming 1%/h body mass decrease, following Delingat *et al.* 2008), which is under normal flight conditions more than sufficient to cover the distance of 2250 km over the Sahara.

Given the pressure on birds of arriving earlier to match chick rearing with warming spring conditions (Helm *et al.* 2019), it seems counterintuitive that Pied Flycatchers alter their departure timing in order to achieve a seemingly excessive fuel-load. A potential consequence could be that food shortage prior to departure delays the timing of arrival and breeding, since we previously found that breeding arrival in Dutch Pied Flycatchers was strongly determined by the date birds leave their wintering sites (Ouwehand & Both 2017). Our current study shows that differences in food conditions created large differences in departure, and did so already in a year when local rainfall conditions were normal. This may even imply that fuelling constraints that delay departure and carry over to impact on breeding arrival and laying, can slow down observed adaptation towards earlier migration schedules (Helm *et al.* 2019). Human induced change potentially increases the 'natural' conflict in resource exploitation of migrants that want to travel earlier to track advancing food resources at warming breeding sites. However, we lack sufficient data in our current study to make direct inferences that can support this interpretation about the consequences of later departure for subsequent annual cycle events. Whether poor rainfall conditions cause food constraints and places migrants in jeopardy will depend on a whole series of decisions that individuals make. Each individual makes decisions on wintering site selection, when to (re)fuel, how fast to migrate, and what to do when arriving at the breeding grounds.

Complex ecological interactions at the wintering sites may allow birds to compensate for negative rainfall effects. This may be particularly important because rainfall in the Guinea zone is highly unpredictable across years, as shown by large deviations around the average rainfall sum in Jan–April in NE Ivory Coast (unpubl. analysis Zwarts; Bondoukou data 1920–2017). Our observation of one female flycatcher in 2020 that fuelled and departed exceptionally early, despite slow fuelling seen in other flycatchers that year, nicely illustrate the potential of birds to overcome 'shared' environmental impacts. This may happen if individuals can access natural resources that occur heterogeneously. Our study site is a mosaic of habitats with considerable vegetation heterogeneity in space and time that sedentary Pied Flycatchers selectively use over the course of non-breeding season (Bil *et al.* 2023). Occupying high quality wintering habitats improved the ability of Neotropical songbirds to cope with dry-season conditions, and was especially important for timely departure in years with poor rainfall conditions (Studds & Marra 2011). Previously described earlier breeding and higher fitness in Pied Flycatchers that occupied wintering sites with more mesic isotope profiles (Goodenough *et al.* 2017) may reflect similar small-scale habitat mediating effects. Differences in territory quality or flexibility in how birds make use of spatial-temporal heterogeneity in their home range (Bil *et al.* 2023) may help birds to mitigate effects from the shared environment. This may directly arise from changes in the birds' diet or experienced food availability, or, act indirectly through effects of predation risk, competition or heat stress on foraging behaviour. High quality wintering habitats for flycatchers might be particularly located on the edge of forest and savanna, resulting in high densities of site-faithful flycatchers, from where birds can profit from the different dynamics associated with two different habitats (Figure S8 and Bil *et al.* 2023). Ongoing deforestation in Africa will likely reduce the availability of forests and thereby limit the possibilities of flycatchers to make use of seasonal dynamics, or, mitigate drought effects.

Factors such as habitat quality, predation pressure, competition and health may also exaggerate environmental impacts, or, influence birds in unexpected ways. The latter was apparent in the three Pied Flycatchers in our study that only moderately accessed food supplementation. Video recordings illuminated an unintended effect of food supplementation, where supplies were regularly eaten by larger African bird species. Rather than the anticipate positive effect of food supplementation in the flycatchers' territory, this may have enhanced competition for food or influenced how birds trade-off fuelling decisions.

The flexibility in fuelling behaviour may also be larger than apparent from our results of fuelling in site-faithful individuals. Although Pied Flycatchers are generally considered site-faithful, other wintering strategies reported in flycatchers involve 'floating' (i.e. not having a territory), and habitat-related territory switches (Salewski 1999, Ouwehand unpubl. data). Pied Flycatchers could potentially leave their wintering territories in search of better fuelling locations, albeit this strategy seems relatively rare (Salewski *et al.* 2002b, Smith 1966). Experiments in the Neotropics revealed that free-living territorial songbirds can respond to food shortage by becoming floaters (Cooper *et al.* 2015). Future research is needed to investigate if similar solutions occur in flycatchers and are suitable alternatives to cope with local food limitation in their unpredictable environments, or, that floating and occupying new fuelling sites is the less preferred strategy that involves high costs associated with switching (Cresswell 2014).

Mechanisms underlying the observed fuelling decisions likely evolved in such a way that birds depart at the time that maximizes fitness, presumably by reducing costs of migration and/or to match timing of reproduction with seasonality of food at the breeding site. It is well known that accumulating a fuel surplus enables birds to withstand unpredictable adverse conditions during barrier-crossing, which is especially sensible when risks during migration are high, or when conditions during barrier-crossings are difficult to predict (see Schmaljohann *et al.* 2013). Flexible fuelling decisions – in contrast to rigid time schedules – allow birds to immediately make use of seasonal peaks in food when available to achieve this fuel surplus. Flexible fuelling may even have evolved to allow birds to cope with unpredictable rainfall dynamics during the pre-migration phase in Africa. A potential consequence may be that birds can only leave timely on migration if the food conditions in winter allow them to do so. If suitable conditions for fuelling happen relatively early in the season, birds may not want to risk deteriorating conditions or wait with full fuel loads that are costly to carry. Yet, birds could use any left-over reserves after Sahara-crossing to flexibly adjust their migration pace on their way to the breeding sites (but see Ouwehand & Both 2017). Early departure of these individuals may thus not directly result in arriving too early at the breeding grounds if birds extend staging in southern Europe after crossing the Sahara, where conditions may be more predictable. Late departing birds may invest into continuing their flight directly towards their breeding sites to compensate for a delayed departure. The extent to which birds and populations can take advantage of this plasticity to compensate for delays likely varies and may depend on the phenology in a breeding population, the quality of wintering areas and conditions that birds encounter en route.

If poor fuelling conditions force flycatchers to delay departure and arrive late at the breeding grounds, birds could adjust their breeding decisions. Breeding opportunism has been found in Pied Flycatchers and could include active breeding dispersal strategies to match local resources, skipping breeding when conditions are not suitable (Both *et al.* 2017) or modulating breeding investment according to current conditions. Although breeding opportunism may seem counterintuitive for short-lived songbirds, this could be a viable option for birds like flycatchers that seem to favour fuelling strategies that promote safe migration (rather than early departure) and if the high food surplus at temperate breeding grounds provides good survival prospects.

Describing how migrants choose their environments and investigating the fitness consequences of these choices are thus key elements to better predict the abilities and limits of migrants to cope with ongoing environmental change. Integrated tracking studies of the annual cycle of individual birds are an essential step forward to achieve this. Even so, ground studies in Africa would be a fruitful avenue for future studies on the cost and benefits of different annual cycle strategies that are difficult to measure when studying birds only in breeding populations. Field studies at non-breeding residency areas are still under-represented, and especially so in Afro-Palearctic migrants. Ground studies in Africa provide the ground-truthing needed for interpreting the growing body of data from birds carrying tracking and geolocator devices. Our study highlights the need for such studies, as we found that fuelling and migration decisions in Pied Flycatchers are strongly shaped by local ecological conditions in Africa, which are difficult to describe by coarse rainfall estimates and geolocator devices. Tracking birds is one thing, learning what is going on *in situ* is quite something else.

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Data Accessibility

Data described in this article are available at https://doi.org/10.34894/EIUWB3

SAMENVATTING

Door over grote afstanden te trekken kunnen vogels de seizoensveranderingen op aarde benutten. Vogels die in Afrika overwinteren maar in Europa broeden, kunnen zo profiteren van een groter maar tijdelijk beschikbaar voedselaanbod in gematigde streken om hun jongen groot te brengen. Om dit te kunnen doen moeten vogels daar op tijd arriveren, maar ook voldoende energiereserves aanleggen voordat ze de Sahara oversteken. Als de voedselomstandigheden in Afrika in het droge seizoen slecht zijn, kan dit leiden tot conflicten tussen deze belangen. Door te onderzoeken hoe vogels deze beslissingen maken in een dynamische en veranderende leefomgeving, kunnen we inzicht krijgen in hoe flexibel trekvogels hun gedrag aanpassen. Hiertoe vingen we Bonte Vliegenvangers *Ficedula hypoleuca* in hun winterterritoria in Ivoorkust en gaven hun een geolocator. Een deel van deze vogels werd experimenteel bijgevoerd, en alle werden tot aan het vertrek herhaaldelijk gewogen op autonome gewichtsloggers. Op die manier hoopten we inzicht te krijgen in het effect van (extra) voedsel voorafgaande aan de voorjaarstrek op het opvetproces, de vertrekdatum en het gewicht waarmee de vogels de voorjaarstrek over de Sahara beginnen. In beide jaren van het onderzoek (2019 en 2020) kwantificeerden we het natuurlijke aanbod van geleedpotigen gedurende de opvetfase, om te onderzoeken hoe de natuurlijke voedseldynamiek het opvetproces van vogels beïnvloedt. De vogels die in maart–april extra voedsel kregen en benutten, begonnen eerder met opvetten en deden dit sneller dan vogels zonder toegang tot extra voedsel, wat resulteerde in 12 dagen eerder vertrek naar het broedgebied. Vogels legden grotere vetreserves aan dan strikt noodzakelijk voor de Sahara-oversteek en dat deden ze onafhankelijk van het experimentele voedselaanbod. Opvetsnelheden van vogels veranderden mee met de natuurlijke omstandigheden binnen en tussen jaren. Vogels zonder extra voedsel bereikten de hoogste gewichtstoename op momenten dat het natuurlijke aanbod van geleedpotigen piekte. De gemiddeld geringere gewichtstoenames in 2020 in vergelijking met 2019 suggereren dat vogels trager opvetten in jaren met late regens. Het laat een grote flexibiliteit zien in de timing van de voorjaarstrek onder invloed van de voedseldynamiek op overwinteringslocaties in West-Afrika die de opvetsnelheid van trekvogels, maar niet hun streefgewicht bepaalt. Deze strategie bevordert waarschijnlijk een veilige oversteek over de Sahara, maar kan de mogelijkheden beperken om (vervroegde) voedselpieken in het broedgebied te blijven benutten.

RÉSUMÉ

En migrant sur de longues distances, les oiseaux mettent à profit l'alternance des saisons sur Terre. Ceux qui hivernent en Afrique et se reproduisent en Europe exploitent l'abondance de nourriture dans les régions tempérées au printemps et en été pour y élever leurs petits. Pour cela, ils doivent y arriver à temps, mais aussi constituer des réserves d'énergie suffisantes avant de traverser le Sahara. Si les conditions alimentaires en Afrique sont mauvaises pendant la saison hivernale qui correspond à la saison sèche au Sahel, ces deux exigences peuvent devenir contradictoires. En étudiant les choix qu'ils effectuent en fonction des changements trophiques survenant dans leurs habitats hivernaux, il est possible de comprendre comment les oiseaux migrateurs adaptent leur comportement. À cette fin, nous avons capturé des Gobemouches noirs *Ficedula hypoleuca* dans leurs territoires hivernaux en Côte d'Ivoire et les avons équipés d'un géolocalisateur. Certains de ces oiseaux ont reçu un complément d'alimentation et tous ont été pesés à plusieurs reprises avec des balances autonomes jusqu'à leur départ en migration. Cette expérience visait à étudier l'effet de la complémentation alimentaire sur le processus d'engraissement, la date de départ et le poids des oiseaux jusqu'au début de la migration prénuptiale à travers le Sahara. Au cours des deux années de l'étude (2019 et 2020), nous avons quantifié l'approvisionnement naturel en

arthropodes pendant la phase d'engraissement prémigratoire afin d'étudier comment la disponibilité alimentaire naturelle affecte ce processus. Les oiseaux qui ont reçu et consommé de la nourriture complémentaire en mars et avril ont commencé à grossir plus tôt et plus rapidement que les oiseaux qui n'y ont pas eu accès. Ils ont débuté leur migration vers les zones de reproduction en moyenne 12 jours plus tôt. Tous les oiseaux ont constitué des réserves de graisses plus importantes que celles strictement nécessaires à la traversée du Sahara et ce, indépendamment du nourrissage complémentaire. Leurs vitesses d'engraissement ont évolué en fonction des conditions trophiques naturelles que ce soit au cours d'une même année et d'une année à l'autre. La prise de poids des oiseaux non complémentés a culminé au moment où l'offre naturelle d'arthropodes a atteint son maximum. Elle a été moindre en 2020 qu'en 2019, ce qui suggère que les oiseaux engraissent plus lentement les années où les pluies sont tardives. L'étude démontre que la disponibilité alimentaire dans les sites d'hivernage en Afrique de l'Ouest détermine le taux d'engraissement des oiseaux migrateurs, mais pas leur poids de départ en migration : elle influence donc fortement le calendrier de la migration printanière. Cette stratégie semble privilégier la sûreté de la traversée du Sahara, au détriment de la capacité à exploiter efficacement les pics d'abondance alimentaire qui surviennent de plus en plus précocement sur les sites de reproduction.

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SUPPLEMENTARY MATERIAL

Table S1. Overview of individual birds (IDs) of which we measured pre-migratory fuelling (by means of body mass increase) at their wintering location in Comoé NP in Ivory Coast, and whether we were able to estimate their departure date by means of the last day a bird was seen on a bowl. Tag type and tag departure indicate how birds were tracked and if a departure date could be obtained from the tag. NA indicates that no data was available for the date a bird was last seen on a bowl, tag departure, or return of birds. Missing data resulted from closure of the field station that prevented collecting these data, tag failure, or birds not returning to the study area (i.e. return = 0).

Year	IDs	Age class	Sex	Food access	Last seen on bowl (1 = 1 April)	Return	Tag departure (1 = 1 April)	Tag type
2019	*/O	older	F	full	1	1	NA[1]	Geolocator
2019	*/R1	1st winter	F	no	17	0	NA	Geolocator
2019	*/R2	1st winter	M	full	3	1	3	Geolocator
2019	*/Rot	1st winter	F	moderate	19	0	NA	Geolocator
2019	*/T	1st winter	M	no	18	1	18	Geolocator
2019	*/Y1	1st winter	M	moderate	19	1	19	Geolocator
2019	*/Y2	1st winter	F	no	18	1	19	Geolocator
2019	*/Yr	1st winter	M	full	4	0	NA	Geolocator
2019	–/gw*	1st winter	M	full	2	0	NA	Geolocator
2019	–/pz*	older	M	no	16	1	NA[1]	Geolocator
2019	–/s*	1st winter	F	no	10	0	NA	Geolocator
2019	–/zy*	older	M	full	3	0	NA	Geolocator
2019	G/*1	1st winter	F	no	3	0	NA	Geolocator
2019	O/*	1st winter	F	moderate	18	0	NA	Geolocator
2019	Ob/*	older	M	no	14	0	NA	Geolocator
2019	T/*2	1st winter	F	no	16	1	16	Geolocator
2019	v*/–	older	M	full	7	0	NA	Geolocator
2020	*/O	older	F	no	NA	NA	NA	Geolocator
2020	*/R2	older	M	no	NA	NA	NA	Geolocator
2020	*/T	older	M	no	NA	NA	NA	Geolocator
2020	[SB]/O	1st winter	M	no	NA	NA	NA	Geolocator
2020	m*/–	older	F	no	NA	NA	33	Radio transmitter
2020	T/*	older	M	no	NA	NA	NA	Geolocator
2020	T/*2	older	F	no	0	NA	NA	Geolocator
2020	V/[SB]	1st winter	M	no	NA	NA	NA	Geolocator

[1] Bird returned with malfunctioning geolocator

Table S2. Model summary of a LM investigating the causal effect of food availability on approximated spring departure date from Africa in free-living Pied Flycatchers that took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with 'full' access to food supply, 'moderate' access, or 'no' access to additional food). Departure date was described as April day (1 = 1 April) and the model included sex and age class (first winter or older) and included all birds in 2019 regardless of their departure mass. The intercept reflect first winter females with 'no' access to additional food.

Parameter		**β**	**SE**	***t***	P_r
(Intercept)		12.98	1.650	7.859	**< 0.001**
Food	(full)	–11.89	2.363	–5.035	**< 0.001**
	(moderate)	4.864	2.720	1.788	**0.099**
Age (older)		0.379	2.334	0.162	0.87
Sex (male)		2.483	2.201	1.128	0.28

Table S3. Model summary of hierarchical additive mixed models (HGAM) investigating the causal role of food availability on $\log_e$-transformed body mass change during the premigration period in free-living Pied Flycatchers that took part in a supplementary feeding experimental in north Ivory Coast in 2019. In total 181 weight measures were taken from in total 17 birds, with measurements continuing until birds left the study site. Access to experimentally provided additional food was either 'full', 'moderate', or, 'no'. The effective degrees of freedom (EDF) increases as the 'wiggliness' of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females with 'no' access to additional food. Total deviance explained by the model is 97.2%.

Parametric terms		**β**	**SE**	***t***	P_r
(Intercept)		2.717	0.034	79.7	**< 0.001**
Age (older)		–0.021	0.051	–0.41	0.683
Sex (male)		0.037	0.047	0.80	0.425
Food	(full)	0.292	0.065	4.49	**< 0.001**
	(moderate)	0.014	0.049	0.27	0.786

Smooth terms	**EDF**	**Ref *df***	***F***
ƒ(Day)	**2.53**	4	22.6
ƒ(Day : Age *older*)	**1.90**	4	0.88
ƒ(Day : Sex *male*)	**2.18**	4	1.12
ƒ(Day : Food *full*)	**2.56**	4	3.64
ƒ(Day : Food *moderate*)	0.0002	4	0.00
ƒ(Day, Individual)	**40.92**	79	12.6

Table S4. Model summary of a LM investigating the causal effect of food availability on approximated departure mass of free-living Pied Flycatchers at the moment that they left on spring migration departure. Birds took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with 'full' access to food supply, 'moderate' access, or 'no' access to additional food). The model included mass (g), sex and age class (first winter or older) and included all birds in 2019 regardless of their departure mass. The intercept reflect first winter females with 'no' access to additional food.

Parameter		**β**	**SE**	***t***	P_r
(Intercept)		18.78	0.99	18.82	**< 0.001**
Food	(full)	1.36	1.43	0.95	0.36
	(moderate)	1.80	1.65	1.09	0.30
Age (older)		–1.06	1.41	–0.75	0.47
Sex (male)		2.19	1.33	1.64	0.13

Table S5. Model summary of a LM investigating the initial differences in body mass prior to fuelling in free-living Pied Flycatchers that took part in a supplementary feeding experiment in north Ivory Coast in 2019 (i.e. with 'full' access to food supply, 'moderate' access, or 'no' access to additional food). The model included mass (g), sex and age class (first winter or older). The intercept reflects first winter females with 'no' additional food.

Parameter		**β**	**SE**	***t***	P_r
(Intercept)		12.13	0.53	22.63	**< 0.001**
Food	(full)	–0.29	0.69	–0.42	0.68
	(moderate)	–0.11	0.75	0.15	0.88
Age (older)		0.39	0.67	0.58	0.57
Sex (male)		0.32	0.62	0.52	0.61

Table S6. Model summary of hierarchical additive mixed models (HGAM) investigating the effects of the natural environment by means of a year-effect on $\log_e$-transformed body mass change during the premigration period in free-living Pied Flycatchers in north Ivory Coast in 2019 ($n = 8$) and 2020 ($n = 8$) that receive no additional food supply (i.e. only a minimal amount of food, c. 0.35 g to still attract them to a balance). NB. In 2019 measurements continued until all birds left the study site for migration, but in 2020 measurements stopped at 15 April before most left the study site. In total 298 weight measures were taken. The effective degrees of freedom (EDF) increases as the 'wiggliness' of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females in 2019. Total deviance explained by the model is 95.6%.

Parametric terms	**β**	**SE**	***t***	P_r
(Intercept)	2.611	0.031	85.41	**< 0.001**
Year (2020)	–0.002	0.037	–0.045	0.964
Age (older)	0.065	0.033	1.98	**0.049**
Sex (male)	–0.005	0.033	–0.146	0.884

Smooth terms	**EDF**	**Ref *df***	***F***
ƒ(Day)	**3.825**	**4**	**51.6**
ƒ(Day : Year *2020*)	**3.772**	**4**	**30.3**
ƒ(Day : Age *older*)	0.742	4	0.23
ƒ(Day : Sex *male*)	1.170	4	0.40
ƒ(Day, Individual)	**37.74**	67	21.1

Table S7. Model summary of hierarchical additive mixed model (HGAM) describing fuelling in free-living Pied Flycatchers from $\log_e$-transformed body mass changes during the premigration period in north Ivory Coast, optimized to best fit 'individual-within-year' trajectories (n = 25), while accounting for effects of year, access to additional food supply, age class and sex. Access to additional food supply was either 'full', 'moderate', or 'no'. In 2019 measurements continued until all birds left the study site, but in 2020 measurements stopped at 15 April before most birds left on migration. In total 393 weight measures were taken. The effective degrees of freedom (EDF) increases as the 'wiggliness' of the terms increase. An EDF of c. 1 or <1 is consistent with a linear effect. The reference category are first winter females with 'no' access to additional food in 2019. Individual curves were fitted as individual-within-year level random effect smooth with high with wiggliness (k = 14) to allow deviations from factor smooths (see Methods). Total deviance explained by the model is 99.1%.

Parametric terms	**β**	**SE**	***t***	***P*$_r$**
(Intercept)	2.639	0.036	72.91	**< 0.001**
Year (2020)	–0.000	0.048	–0.019	0.984
Age (older)	0.0458	0.036	1.264	0.207
Sex (male)	–0.0019	0.033	–0.057	0.954
Food (full)	0.234	0.060	3.878	**< 0.001**
(moderate)	0.030	0.054	0.549	0.584

Smooth terms	**EDF**	**Ref *df***	***F***
f(Day)	**3.067**	4	33.3
f(Day : Year *2020*)	**3.424**	4	6.86
f(Day : Age *older*)	0.0003	4	0.00
f(Day : Sex *male*)	0.0000	4	0.00
Food (full)	**2.289**	4	3.77
(moderate)	0.0007	4	0.00
f(Day, Individual-within-year)	**140.63**	271	25.2

Photo S1. Female Pied Flycatcher in Comoé National Park; 8 April 2018 (photo Sander Bot).

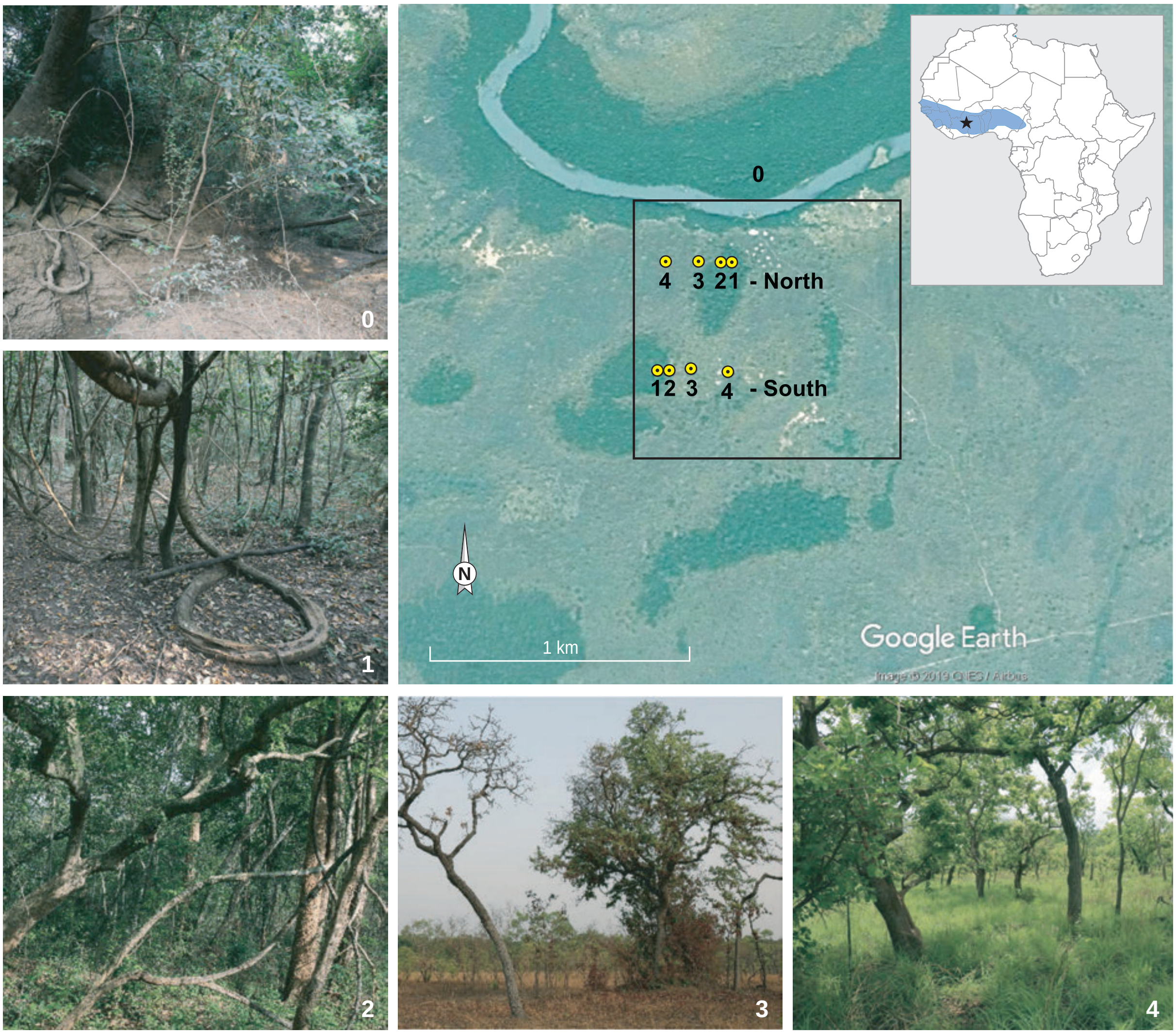

Figure S1. The study region in Comoé NP in northeastern Ivory Coast is located (indicated by a star) in the centre of the wintering range of Pied Flycatchers (range in blue; redrawn from Ouwehand 2016). The study site of c. 1 km^2, shown as the box in the google earth map, is dominated by savanna (picture and sampling locations 3–4). Other habitats commonly used by Pied Flycatchers during non-breeding are dry forest patches (pictures and sampling locations 1–2; forest interior and edge). Repeated arthropod sampling during the fuelling period was performed across these four habitats in four sampling locations in 2020 (1–4 North; yellow dots) and eight locations in 2019 (1–4 North and South). Gallery forests adjacent to the Comoé River (0) were not systematically sampled in this study, and were less used by flycatchers during the pre-migratory period.

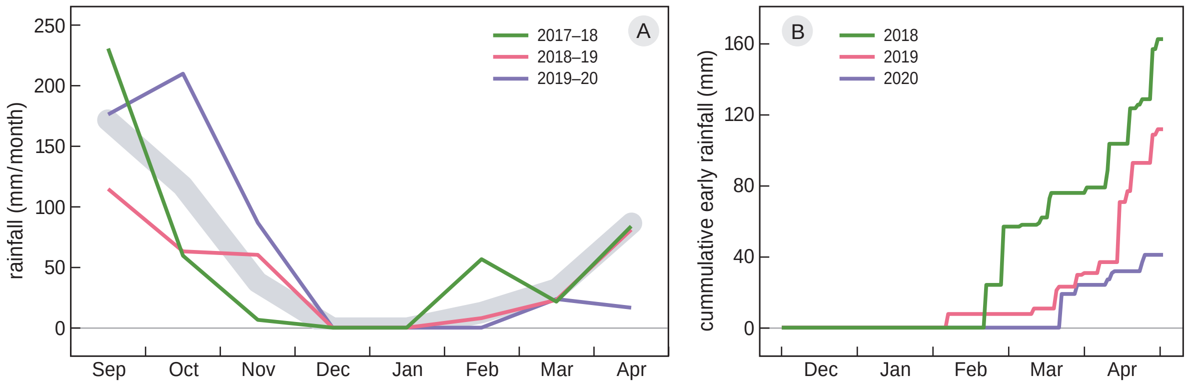

Figure S2. Local rainfall estimates in Comoé NP of (A) monthly rainfall sum (mm) for the wintering season in three different years, and the 5-year average from 2015–16 until 2019–20 (show as grey ribbon), and (B) cumulative daily rainfall (mm) during the second half of the dry season (i.e. 1 December – 30 April). Rainfall was measured at the study site (Comoé Research Station, Ivory Coast).

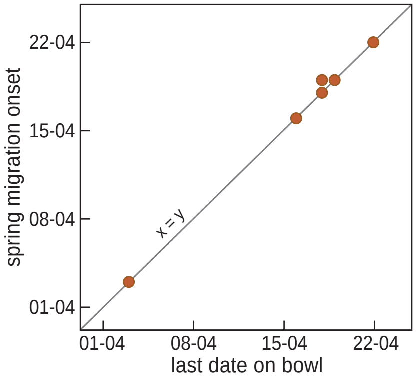

Figure S3. The spring migration onset of Pied flycatchers in relation to the date of departure as estimated from the last day a bird was seen accumulating fuel stores on the bowl in its wintering territory (with $x = y$ line). The onset of spring migration departure could only be confirmed for birds that successfully returned with geolocator loggers (5 birds from 2019 (Table S1) and 1 bird from a pilot in 2018) and for which raw geolocator data were available to estimate the moment that birds started their non-stop flights across the Sahara. All these birds had body masses between 20.2 and 22.6 g on the last measurement day, corresponding to fuel loads of 117–143% of structural body mass.

Photo S2. Pied Flycatchers in this study were all ringed and deployed with tags to track their migration. A colour ring allowed us to recognize individuals on the video footage. Knowing the identity of a bird was important to monitor if habituation and supplementary feeding was successful and to confirm that remote body mass measurements and observed departure belonged to the focal bird (see Figure 1C). In the subset of birds that returned the next year with their geolocator, we could show that the actual start of Sahara crossing was tightly linked to the last day a bird was seen and measured on the balance (Figure S3). The picture was taken on 8 April 2018, which was two days before this first winter female started with her flight over the Sahara Desert (photo Sander Bot).

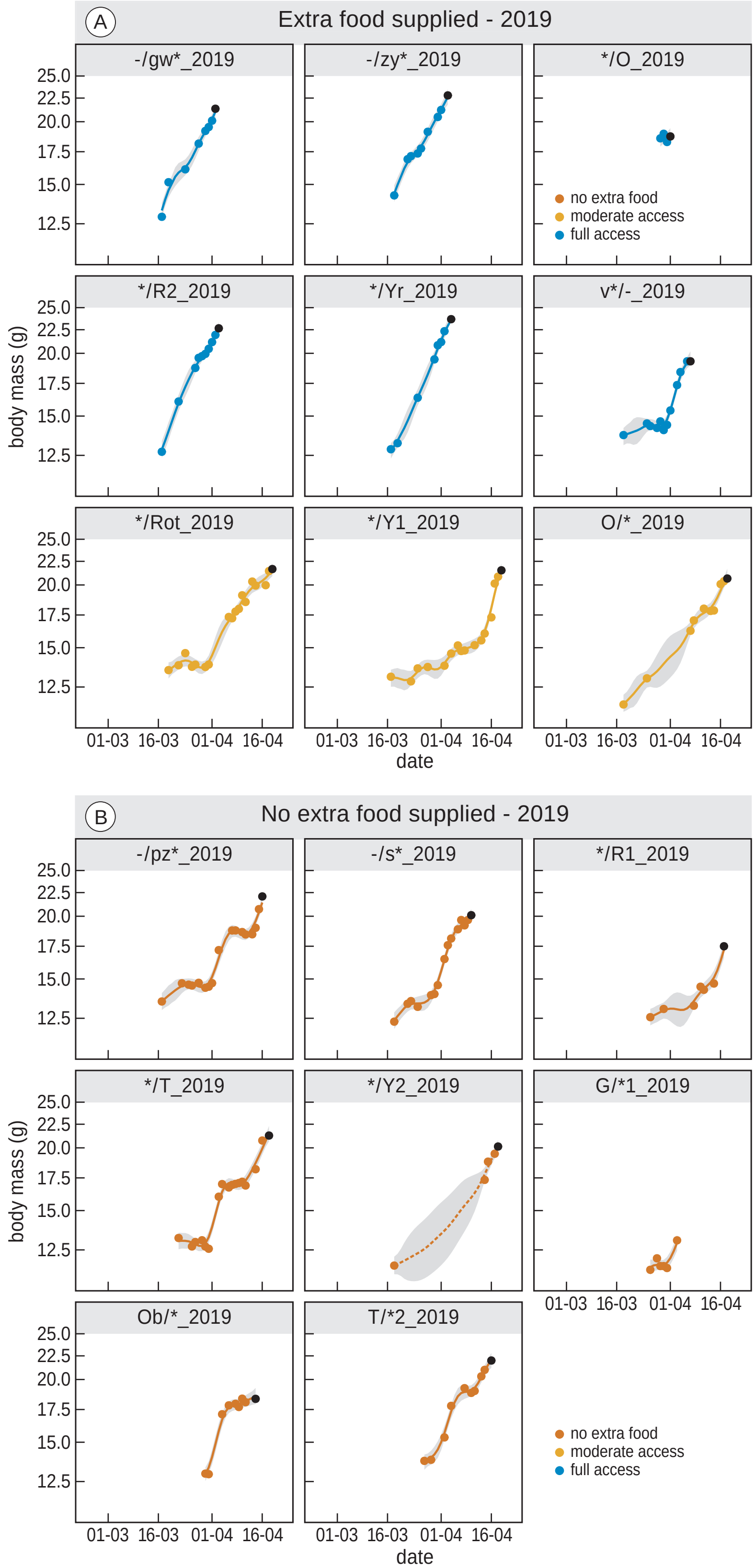
A
Extra food supplied - 2019
-/gw*_2019
-/zy*_2019
*/O_2019
*/R2_2019
*/Yr_2019
v*/-_2019
*/Rot_2019
*/Y1_2019
O/*_2019
no extra food
moderate access
full access
body mass (g)
25.0
22.5
20.0
17.5
15.0
12.5
01-03
16-03
01-04
16-04
date
B
No extra food supplied - 2019
-/pz*_2019
-/s*_2019
*/R1_2019
*/T_2019
*/Y2_2019
G/*1_2019
Ob/*_2019
T/*2_2019

Figure S4.

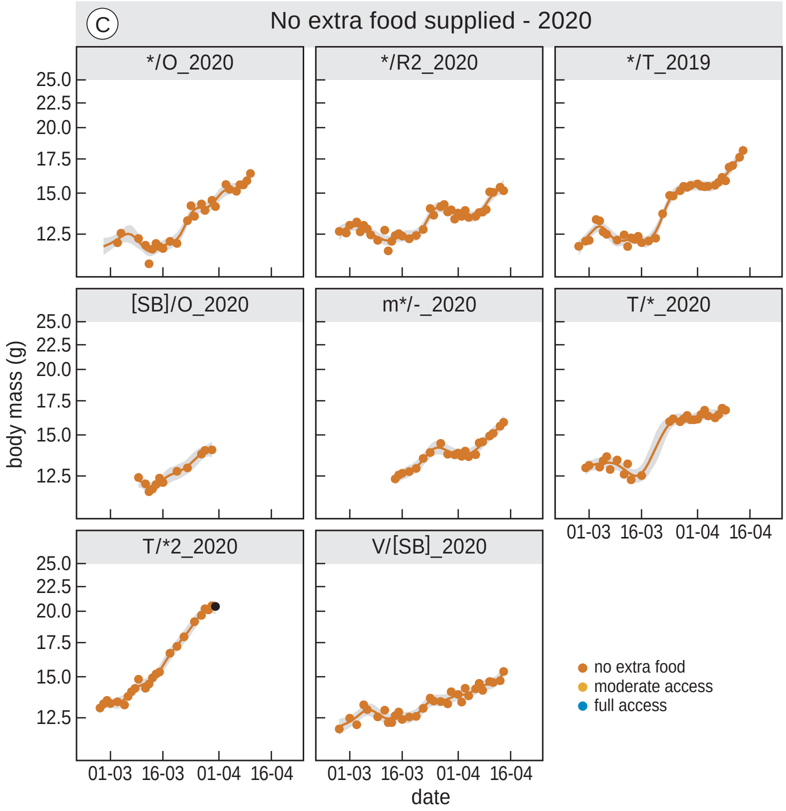

Figure S4. Change in body mass over time for each individual within a year during the premigration phase. In (A–B), birds were exposed to experimental food supplementation in 2019 in which birds showed full access to extra food (blue), moderate access (orange), or received no extra food (red). In 2020 (C), none of the birds received extra food. NB. In 2020 most fuelling trajectories were incomplete and only one bird, compared to all birds in 2019, could be measured until birds left on spring migration (black symbols). Shown are raw body mass measurements and the associated predicted line and confidence intervals from a HGAM model optimized to fit log$_e$-transformed mass change trajectories of individual birds within years (see Table S7 and Methods). The dashed line depicts one bird where model interpolation between subsequent measures was more than 25 days.

Photo S3. Armel providing food and setting up the balance to measure the body weight of a flycatcher being faithful to this site.

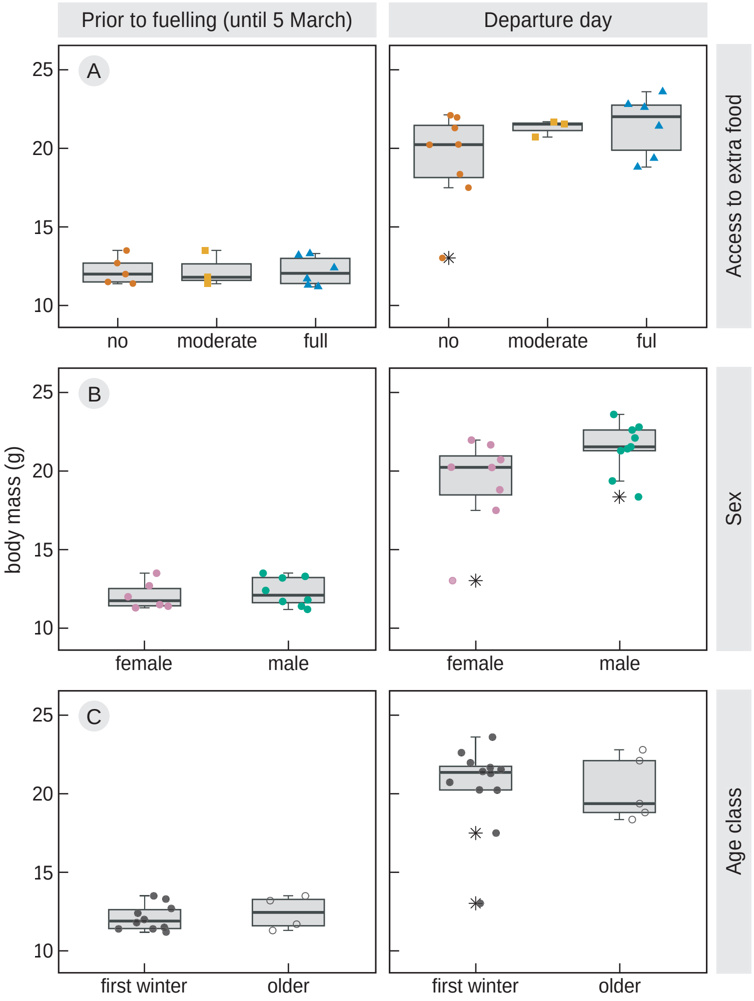

Figure S5. Body mass of Pied Flycatchers in 2019 in relation to (A) access to extra food, (B) sex and (C) age class. Body mass was measured prior to fuelling (left) and at departure using the last day a bird was measured (right). Masses in B–C are shown regardless of a birds' access to extra food. Each panel shows the boxplots and jittered raw data in each group.

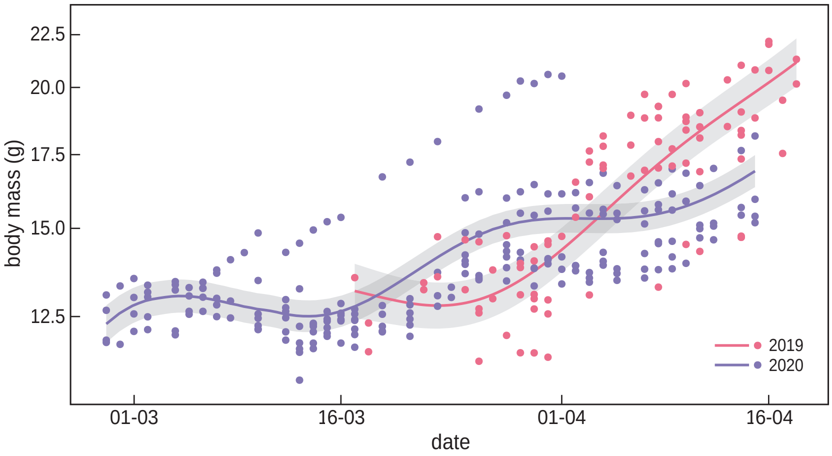

Figure S6. Natural variation in body mass increases over time of birds that receive no extra food, shown for two fuelling seasons in Ivory Coast. Shown are body mass measurements and the associated predicted lines and confidence intervals per year (from the model in Table S6).

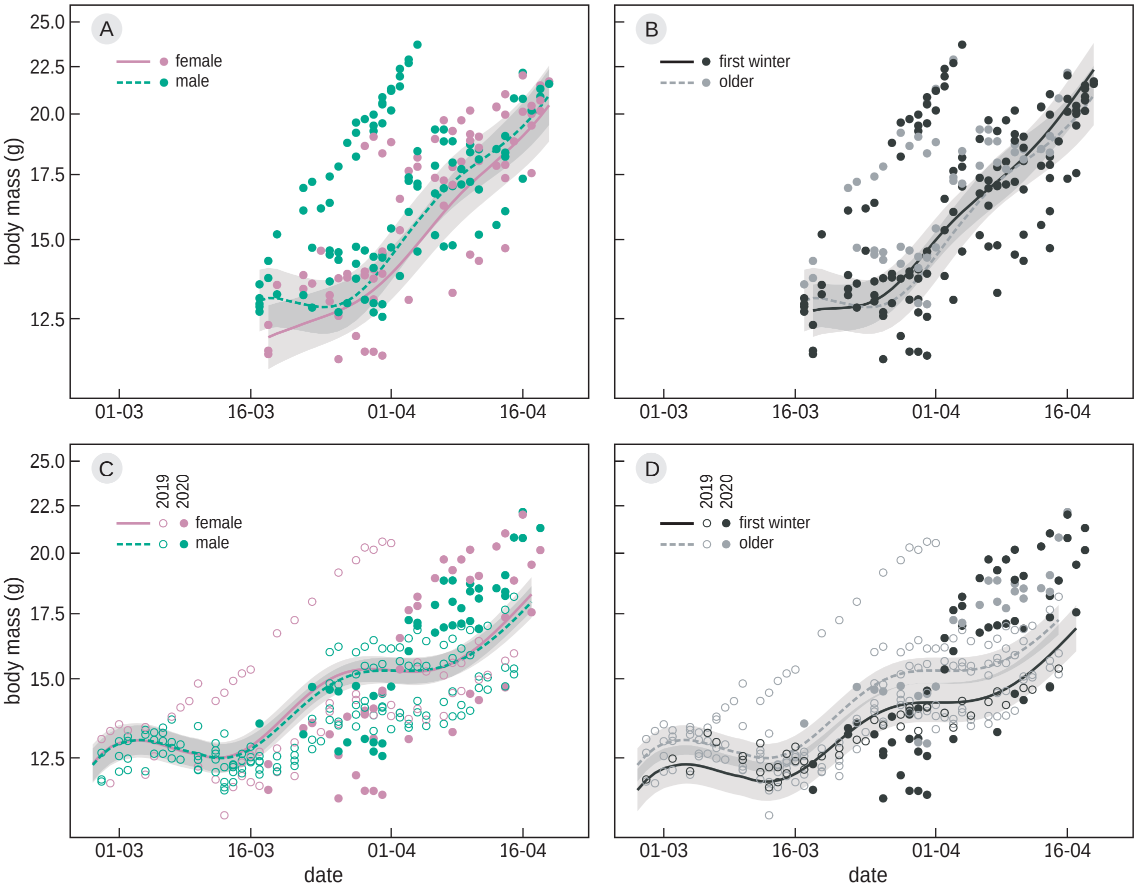

Figure S7. Body mass increase over time in Ivory Coast shown for Pied Flycatchers in different sex (A, C) and age classes (B, D). Birds in A–B were part of a supplementary feeding experiment in 2019 with varying access to extra food, while C–D show only birds with 'no extra food' in 2019 or 2020. Shown are body mass measurements and the associated predicted lines and confidence intervals per sex and age class (using models provided in Table S3 for A–B and Table S6 for C–D).

Figure S8. Spatio-temporal variation in arthropod biomass and abundance during the dry season in two years, shown per sampling location. Flying and ground-dwelling arthropods were repeatedly sampled by one malaise trap and three pitfall traps per sampling location (trapping duration of 96 h) for in total 4–8 sampling points. Sampling points were spread across the study site and covered a range of habitats used by Pied Flycatchers (Figure S1).