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Climate change relaxes the time constraints for late-born offspring in a long-distance migrant

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Animals in seasonal environments need to fit their annual-cycle stages, such as moult and migration, in a tight schedule. Climate change affects the phenology of organisms and causes advancements in timing of these annual-cycle stages but not necessarily at the same rates. For migratory birds, this can lead to more severe or more relaxed time constraints in the time from fledging to migration, depending on the relative shifts of the different stages. We tested how a shift in hatch date, which has advanced due to climate change, impacts the organization of the birds' whole annual cycle. We experimentally advanced and delayed the hatch date of pied flycatcher chicks in the field and then measured the timing of their annual-cycle stages in a controlled laboratory environment. Hatch date affected the timing of moult and pre-migratory fattening, but not migration. Early-born birds hence had a longer time to fatten up than late-born ones; the latter reduced their interval between onset of fattening and migration to be able to migrate at the same time as the early-born birds. This difference in time constraints for early- and late-born individuals may explain why early-born offspring have a higher probability to recruit as a breeding bird. Climate change-associated advancements of avian egg-lay dates, which in turn advances hatch dates, can thus reduce the negative fitness consequences of reproducing late, thereby reducing the selection for early egg-laying migratory birds.

1. Introduction

Animals need to synchronize their seasonal rhythms to the annual periodic changes in their environment. The different seasons of the year pose challenges and also create favourable conditions for demanding annual-cycle stages such as reproduction. Thus, decisions on when to initiate events like breeding or migration have major fitness impacts [1,2]. Apart from being synchronized to the environmental cycles, different rhythms also need to be appropriately timed in relation to one another. The energetic requirements of different stages often make their concomitant occurrence incompatible [3,4]. In organisms with complex annual cycles that need to allocate several of these energetically demanding activities in a single year, time constraints force the adoption of potentially costly time-saving strategies like overlapping stages, shortening their duration or shifting the stage in time, potentially moving it outside of its optimal window [4–7]. These decisions made in one stage may also have consequences that carry over to subsequent stages, eventually affecting the entire annual cycle [8]. For example, when the breeding time of blue tits (*Cyanistes caeruleus*) was experimentally delayed, it reduced winter survival and breeding performance in the subsequent year. This probably happened because late breeding imposes a time constraint on moult, decreasing the quality of the new feathers and thus, the bird's winter insulation, leading to higher energy expenditure in winter [9].

The temporal allocation of consecutive stages could be dictated solely by the timing of the previous stage [10] but could also involve one or more oscillators with annual periodicity [11,12]. Regardless of the endogenous time-keeping mechanism involved, the importance of a precise temporal organization within a year that allows events to happen at the appropriate time is obvious. The cyclic variations of photoperiod and temperature are important synchronizing cues for seasonal rhythms [4,13–15]. The photoperiodic cycle is practically invariable among years and, therefore, constitutes a very precise environmental cue. But temperatures can be used by organisms as a fine-tuning cue for certain decisions, such as onset of egg-laying in birds [14,16,17] and are particularly important when they correlate or predict the conditions that will ultimately affect fitness such as food availability for the young [14,18].

The temperature increase caused by climate change poses a threat to this fine temporal organization of annual-cycle stages. As climate change affects temperature cues, but not photoperiodic cues and the importance of cues is not uniform across stages, this means that different annual-cycle stages will also be differently affected by climate change [19]. It is currently known that changes in climate have caused changes in the onset of annual rhythms of many species [20,21]. A more complex question is how this is affecting the interaction among stages and the time constraints throughout the annual cycle. For example, if stages do not shift at the same rate, we can expect that the interval between events also change. In recent years, marmots (*Marmota flaviventris*) advanced both the termination of hibernation and weaning, for the offspring this meant more time for growth and fattening, increasing their survival and, at a larger scale, the population numbers [22]. Male and female red deer (*Cervus elaphus*), on the other hand, advanced their reproductive stages at different rates, suggesting that males are unable to track advancements in oestrus of females. Moreover, males rut (display/breeding season) ending dates advanced more than rut initiation dates, which resulted in a shorter breeding window and likely reduced breeding performance [23]. Finally in the pied flycatcher (*Ficedula hypoleuca*), a migratory bird, while breeding time advanced, arrival time to the breeding ground did not, causing an increased reduction in the time from arrival to breeding [19]. These examples suggests that climate change may cause a desynchronization among annual-cycle stages [5,19,23].

Pied flycatchers and other migratory birds are good examples of animals with a particularly time-constrained annual cycle: in a single year they have to fit in a large number of different stages (i.e. breeding, moult, migration) and perform large scale movements between breeding and wintering grounds. This means that even relatively small shifts at any point of the cycle may have an effect on the whole annual cycle [5,19]. New born chicks of migratory species are severely time-constrained as these have a very short interval to grow and prepare for their first migration [24,25]. In particular, late-born birds need to speed up their development to prevent a too late departure to the wintering grounds before conditions at the breeding grounds deteriorate too much [25–27]. One potential cue chicks use to assess whether they are born early or late is photoperiod, as most song birds have a breeding season that terminates before or around the longest day of the year [13]. Exposure to different photoperiods during the first days of life often results in an adjustment of the onset and/or duration of the annual-cycle stages, from development of first plumage to onset of migration [28–30], a phenomenon referred to as the 'calendar effect'. Despite this adaptation there are still costs for being born late as these birds often have a lower recruitment probability [1,2,31].

As climate change advances the onset of egg-laying in birds [20,32], this also means that the chicks nowadays hatch earlier in the season and thus their time constraints are partly lifted. Assuming that the optimal autumn migration time has not been advanced by climate change (which might not necessarily be the case, as climate change could affect several factors related to migration decisions [33,34]), they either have more time between hatching and migrating or are able to migrate earlier [30]. Understanding how climate change will lead to a re-organization of the annual cycle will help us to understand if and how animals cope with anthropic changes.

Although field studies have demonstrated that different annual life cycle stages shift at different rates due to climate change, thus increasing or reducing the available time for other stages [19,22,23,35], they mostly rely in correlations observed at the population level. To causally conclude whether or not the change in one annual-cycle stage affects the timing of subsequent stages it is necessary to manipulate timing alone, controlling for possible confounding factors such as 'individual quality' [2]. Therefore, we experimentally manipulated the hatch dates of pied flycatcher chicks as this is a trait affected by current climate change and which will impact the timing of a number of annual-cycle stages in their first year. This way we can determine where in the annual cycle late-born chicks pay the cost of being late (i.e. a later time of migration or a shortened time for development up to migration) and what happens when hatching dates are advanced.

2. Material and methods

(a) Study area and study species

Pied flycatchers (*Ficedula hypoleuca* ([Pallas], 1764); Muscicapidae) are small long-distance migratory birds that breed in Europe and winter in West Africa (respectively, the Netherlands and Ivory Coast for the population of the present work). As these long-distance migrants need to fit in several annual stages (breed, moult and preparation for back migration), allocating breeding into the (short) spring–summer of the temperate regions, pied flycatchers are excellent models for the study of annual temporal organization. Owing to their acceptance of artificial nest-boxes and low nest desertion rates it is also possible to conduct field experiments and precisely monitor their breeding success.

The fieldwork was conducted in the forests of the Hoge Veluwe National Park (The Netherlands; 52°02′07″ N, 5°51′32″ E). Forested areas in the park are dominated by pedunculate oaks (*Quercus robur*), northern red oaks (*Quercus rubra*), Scots pines (*Pinus sylvestris*), European larches (*Larix decidua*) and birches (*Betula* sp.). We provide around 400 nest-boxes year-round in an area of 171 ha which are occupied in spring by cavity-nesters such as pied flycatchers, great tits (*Parus major*), blue tits (*C. caeruleus*), nuthatches (*Sitta europaea*) and coal tits (*Periparus ater*).

(b) Experimental design

All nest-boxes in the study area were checked twice per week until we detected the presence of pied flycatcher nest material. As soon as nest building started, we inspected nests daily to determine the date that the first egg was laid. When we found three or more nests with first eggs laid at the same date, we randomly assigned them to a treatment (or randomly excluded them from the experiment, in cases where there were sufficient experimental groups or there were not enough nests to create additional groups).

To create differences in the hatch date of the chicks we combined a manipulation of the start of egg-incubation date, and thereby hatch date, and a split brood design (electronic supplementary material, figure S1). We took advantage of the fact that these birds lay a single egg per day and only start incubating their eggs when the last egg is laid. Each experimental group consisted of three nests, one 'advanced', one 'control' and one 'delayed'. When the three females in a group laid their second egg, we collected all these six eggs and replaced them with plastic dummy eggs to prevent desertion. This clutch of six eggs (the typical clutch size for a pied flycatcher), composed of a mixture of eggs from all three nests, was then placed under an already incubating great or blue tit. This made the start of the incubation 4 days earlier than normal. On the following days, we continued collecting the remaining eggs until the sixth egg was laid, always replacing them with dummy eggs. When the sixth egg was laid, we considered the females' clutch complete and, in case it laid a seventh egg, the egg was collected and not replaced. All these newly collected eggs (lay order three to six) were stored in a field shed at ambient temperature and turned twice per day.

Once the female assigned as 'control' laid her sixth egg, we swapped all plastic dummy eggs with a clutch created from eggs with lay order four and five. Because we gave the female six eggs on the same day that she laid her sixth egg, we did not modify the time when she started incubating or the hatching date of the eggs (electronic supplementary material, figure S1). Eventual seventh eggs were removed as explained above.

As soon as the female assigned as 'advanced' started incubating her dummy eggs continuously (approx. 1 or 2 days after laying the last egg), we replaced the dummy eggs by the six pre-incubated eggs. As mentioned above, because the females of pied flycatchers only start incubating their clutch once it was completed (six eggs), this meant that we advance the hatching of these eggs by 4 days (electronic supplementary material, figure S1).

The females assigned as 'delayed' only received a clutch of six eggs (with lay order three and six), replacing the dummy eggs, 5 days after the female laid the sixth egg (on the hypothetical 'egg day 11'). This meant that start of incubation of these eggs was 4 days later than normal (electronic supplementary material, figure S1).

This procedure was repeated throughout the season as we tried to span the whole range of egg-laying dates as long as we found three females laying eggs on the same day. We created 20 triplets in total, a sample size defined for studying the effect of our manipulations on adult birds, which will be reported elsewhere [36]. To distribute these 20 triplets over the range of egg-laying dates, we avoided using more than three groups (nine nests) per day.

(c) Laboratory conditions

From three of the 20 experimental triplets (nine nests), with originally early, intermediate and late laying dates, all chicks were collected on day 12 post-hatching (with exception of one nest that had to be collected when chicks were 10 days old as the female was abandoned by her partner and chicks were starving). Chicks were taken to the Netherlands Institute of Ecology where they were hand-raised following a standardized protocol [37] until independence (approx. 30 days old) after which they were transferred to individual cages (90 × 50 × 40 cm), equipped with a normal wooden perch and a perch connected to a microswitch to continuously measure perch-hopping activity. From the moment they were taken in, chicks were checked regularly for onset of moult and fattening.

The photoperiod during both hand raising and when in individual cages followed the natural Dutch pattern until the duration of the light phase reached 12 h of light and 12 h of darkness in autumn (equinox), when we kept the photoperiod constant at 12 L : 12 D. The photoperiod is an important factor in the regulation and expression of migration and migratory restlessness in captivity [13]. We needed to choose the condition that would allow a proper comparison across the treatments (and not add an additional photoperiodic treatment). We opted to not simulate changes in day length experienced during migration time because it is totally dependent on the timing and route taken by an individual bird. By keeping the photoperiod constant at 12 L : 12 D, we avoid simulating the timing and route of an 'average' bird, thus all birds experienced the same condition.

We used the boundaries of the civil twilight without simulation of dawn and dusk as the effective photoperiod, which means our equinox refers to the 'civil twilight equinox'. Light intensity measured inside the cages at perch height was on average 200 lx during daytime and 0.02 lx at night and in all parts of the experiment the birds were kept in room temperatures (20–25°C).

Throughout the experiment, chicks were offered food and water ad libitum and diet consisted of a recipe based on cottage cheese, eggs, bread and vitamin supplements, commercial mix for insectivore birds, a variety of frozen insects and live mealworms.

Out of the original 54 chicks, five died in the field due to natural causes before being collected and one chick died during hand raising in laboratory from unknown reasons, therefore, our starting sample size was 48 chicks. It was not always possible to reliably estimate the onset of all annual stages for all chicks as a few animals died during the course of the experiment. This small variation in the sample sizes is reflected in the variation of degrees of freedom across annual stages (electronic supplementary material, table S1).

(d) Data collection

(i) Basic field data

We collected data on the date of first egg of the original parents and hatching of the young. On the day the chicks were taken to the laboratory, we measured their tarsus and third primary length to the nearest 0.1 mm and weighed to the nearest 0.01 g. This last field weight is the fledgling weight (when most of the structural growth is completed) and used in the models as a measure of the chick's condition before the start of the experiment where we standardized feeding. All chicks were also blood sampled for paternity assignment and sexing [36], families could be completely reconstructed even after the cross fostering.

(ii) Post-juvenile moult

After fledging juvenile pied flycatchers undergo an incomplete moult in which they only renew the body feathers and a few wing feathers (small coverts and part of the medium coverts). The greater coverts, primaries, secondaries, tertials (components of the wing feathers) and the rectrices (tail feathers) are retained [27]. We scored post-juvenile moult every 4 days, from the moment birds reached 19 days of age, by blowing the body feathers across the whole body and detecting new growing feather patches. For each day that moult was scored, we inspected 17 pre-defined body areas and six wing tracts looking for growing feathers. The number of areas with growing feathers comprised the moult score for that day [26]. As expected, the chicks moulted all body tracts but not all wing tracts nor the tail.

To get a standardized moult onset, we defined that moult started on the day the chicks had eight moulting body areas (i.e. moult score 8). This number of moulting body areas gradually increases until the maximum of 19 and then declines, forming a bell-shaped curve. The choice of eight moulting areas as a measure of moult timing was based on the shape of this curve, as score 8 is

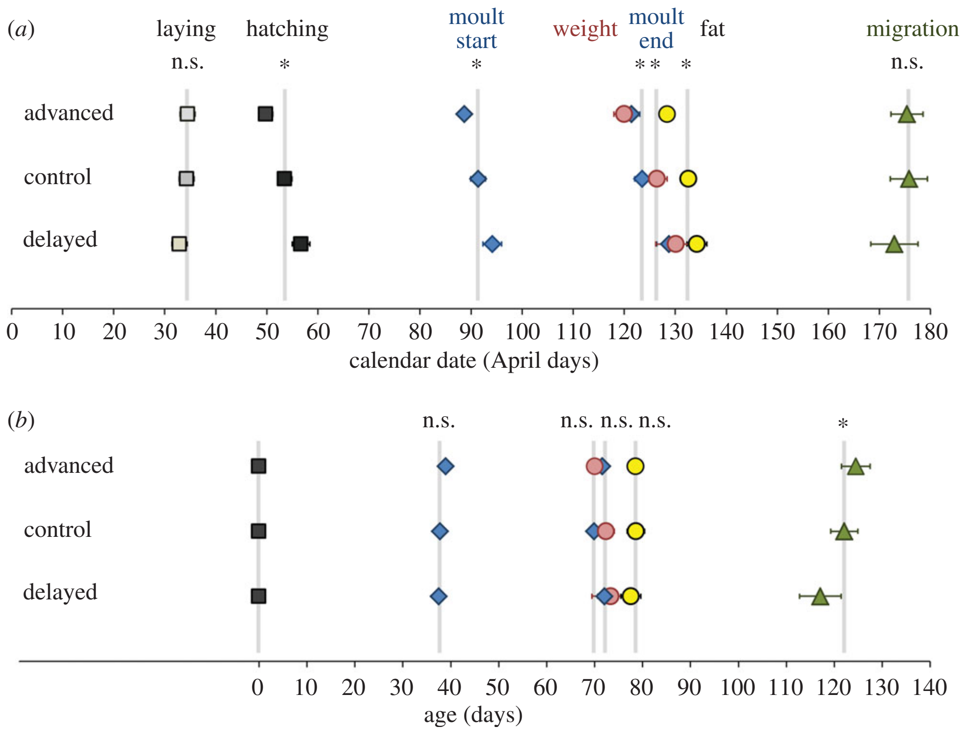

Figure 1. Timing of life-history stages during the first six months of the pied flycatcher chicks' life in relation to treatment: onset of moult, onset of weight gain, timing of mid-migration (migratory restlessness), termination of moult and onset of fat deposition. The vertical lines (centred at the control treatment value) are meant solely to facilitate visual comparison of timing between treatments. Graphs are plotted in relation to (*a*) the calendar date in April days (day 0 = 31st of March) or (*b*) the age of the chicks in days (day 0 = hatch date). (Online version in colour.)

its steepest slope; therefore, we expected the highest temporal accuracy (lowest amount of measurement noise) at this point. Likewise, termination of moult was defined when the moult score reached 8 again after peaking. Moult duration was defined as the number of days between the start and ending moult dates.

(iii) Pre-migratory fattening

Weight was measured together with all moult scores, i.e. every 4 days until the birds completed moulting, and then once every week until the end of the experiment. Onset of pre-migratory weight gain was defined as the date when birds reached 10% of their weight gain (10% of maximum weight minus baseline weight). The maximum weight was reached in November, while the baseline weight was the mean weight when animals were 30–60 days old: an age in which field condition differences would probably have disappeared but birds were still under development and not in the pre-migratory fattening state.

Amount of stored fat was also scored with every weighing and was based on the regular scoring system used in bird ringing protocols, in this specific case we followed [38]. Similar to the onset of moult, we defined onset of fat deposition as when the birds reached the 'fat score 2' (fat present in the furcular depression and also starting to accumulate in the abdominal region), which was more easily recognizable and less prone to observation errors than the 'fat score 1' (small amounts of fat in furcular depression).

(iv) Migration and total weight gained until migration

Perch-hopping activity–rest rhythm was continuously monitored using the cage's perches connected to microswitches until the last bird stopped nocturnal activity in December. We used this nocturnal migratory restlessness as a proxy for nocturnal migration [39]. The day-to-day variation in amount of migratory restlessness was much more variable than the variation in moult or weight gain. Therefore, rather than using a threshold we defined timing of migration as the day when the median of the total cumulative nocturnal activity was reached. Although not correspondent to the 'real' onset of migration in the field, this 'mid-migration' time was a much more accurate measurement. The difference between the bird's fledgling weight and their weight at this pre-defined migration date was used as a measure of the total weight the animals accumulated during moult and prior to migration.

(e) Data analysis

Analyses were performed in R v. 3.2.1 [40]. We tested for treatment effects on the onset of the different annual-cycle stages of the first year of the chicks. For that, we used generalized linear mixed effect models ('lme4' and 'pbkrtest' R packages) with treatment, egg-laying date, sex of the chick, and fledgling weight as fixed effects and the foster nest (ontogenetic effect) and parental nest (genetic effect) as random effects. Because there was an expected order that the treatments would affect each stage, after defining the minimal model, we used ordered heterogeneity tests (OH test) to test whether differences across treatments followed that expected direction. The minimal model for the OH tests was defined with backwards model selection, dropping non-significant terms in each step. In a few cases, treatment effects were significant in the presence of the egg-laying date term even though egg-laying date effects were not significant. In those cases, the egg-laying date term was kept in the model. Full statistics can be found in electronic supplementary material, table S1.

The nest that was taken before day 12 due to desertion by the male and thus lacked fledgling weight was only included in the analyses if and once fledgling weight was dropped in the model selection phase.

Results can be interpreted from two different perspectives: (i) the timing of seasonal stages in relation to the actual day (i.e. calendar day in April days, figure 1*a*) or (ii) the timing of seasonal stages in relation to the age of the chick (figure 1*b*). Both interpretations are based on the same set of data but the implications differs in each case: while the first will show if the date of occurrence of events differ when hatch date is manipulated, the second will reveal if the age at which the event happens is altered when hatch date is manipulated (altered development), possibly also affecting the individual quality of the chick.

3. Results

(a) Egg-hatching and pre-treatment egg-laying

Treatment was not significantly related to the egg-laying date of the female ($F_{2,44} = 0.3$, $p = 0.74$) but had a highly significant effect on hatch date ($F_{2,41} = 13.4$, $p < 0.01$). Therefore, we are confident that our experimental manipulation was successful.

(b) Post-juvenile moult

We detected a significant treatment effect on the onset of post-juvenile moult, with advanced birds starting to moult at an earlier calendar date than controls and controls starting earlier than delayed (rsPc = 0.99, $p < 0.01$; figure 1*a*). If age is used as reference, there is no significant treatment effect (electronic supplementary material, table S1; figure 1*b*). So advanced and delayed birds started moulting at the same age and experimentally shifting their hatch date also shifts their moult date.

There was also a significant effect of egg-laying date of the original parents when using calendar date as reference ($F_{1,6.22} = 75.42$, $p < 0.01$): chicks from late egg-laying dates moulted later (almost 1 day later for every egg-laying date day).

A similar pattern was found for the termination of moult where there was a significant treatment effect when using calendar date as reference (figure 1*a*) but only when the egg-laying date term was kept in the model (rsPc = 0.99, $p < 0.01$; electronic supplementary material, table S1): chicks from delayed nests finished moulting at a later calendar date, but at the same age as advanced chicks. There was also a significant sex effect ($F_{1,7.17} = 38.49$, $p = 0.01$), with females finishing their moult before the males. This significant sex effect also appeared in the moult duration: males took longer to moult than females ($F_{1,41.58} = 5.16$, $p = 0.03$). Again, there was no treatment effect on the age of termination of moult, so chicks finished moulting at the same age (electronic supplementary material, table S1; figure 1*b*).

(c) Pre-migratory fattening

Fattening and weight gain followed a similar pattern: the treatment effect was significant for these two pre-migratory fattening components when calendar date was used as a reference (fat: rsPc = 0.93, $p < 0.01$; weight: rsPc = 0.94, $p < 0.01$; figure 1*a*). Individuals that had their hatching advanced started to store fat and increase mass significantly earlier relative to calendar date than birds that were born later. Again, there was no age difference across treatments (electronic supplementary material, table S1; figure 1*b*).

(d) Migration and total weight gained until migration

There was no effect of treatment on timing of migration (migratory restlessness) when we used calendar date as reference (electronic supplementary material, table S1; figure 1*a*). When age was used as a reference, we detected a significant effect of treatment on timing of migration (rsPc = 0.71, $p < 0.05$; figure 1*b*). Therefore, birds that had their hatching date delayed started at a younger age, but not at a different calendar date, than birds that had their hatching date advanced (figure 1).

There was also a significant treatment effect on the total weight gain before migration when egg-laying date was kept in the model (rsPc = 0.76, $p = 0.04$; electronic supplementary material, table S1). Individuals from the advanced group gained on average slightly more weight than controls before migration, while delayed birds gained much less weight than both control and advanced birds (advanced = 4.48 ± 0.88; control = 4.22 ± 0.86; delayed = 2.71 ± 1.03; electronic supplementary material, figure S2).

(e) Genetic and ontogenetic effects

There was no interaction between treatment and foster nest on all stages analysed. An interaction between treatment and parental nest was only found for onset of weight gain (in relation to chick age, $p = 0.02$). This suggests that, with the exception of onset of chick weight gain, different (original or foster) families do not respond differently to treatments (electronic supplementary material, table S2). There were also no effects of the early-life rearing environment (foster nest) in any of the annual-cycle stages (electronic supplementary material, table S2). There was a significant effect of the parental nest on the timing of pre-migratory fattening (weight: $p < 0.01$ and fat gain: $p = 0.03$), on the maximum weight reached ($p < 0.01$) and on the timing of migration ($p = 0.01$; electronic supplementary material, table S2). This indicates that some of the variation in timing of pre-migratory fattening and migration is explained by a genetic component or by a maternal effect on the eggs. In the case of moult, there was no significant effect of family (neither foster nor parental) and this could be related to the significant effect of egg-laying date. Family and laying date effects are correlated because chicks come from families that have the same laying date. This results show that early egg-laying families will also produce chicks that moult earlier (calendar date), this pattern was not observed for other stages.

4. Discussion

Our study shows that individuals with experimentally delayed (or advanced) hatch dates did not compensate by moulting at a younger (or older) age, speeding up (or slowing down) plumage development or by initiating pre-migratory fattening at a younger (or older) age. However, the timing of migration of the delayed individuals occurred at a younger age and for advanced birds at an older age (figure 1*b*). For delayed birds, this comes at the cost of a shorter interval between moult, pre-migratory fattening and migration which results in a lower weight at mid-migration (in comparison with early-born siblings; electronic supplementary material, figure S2). This means that late-hatched birds are more likely to suffer from energy limitation that could compromise their migration performance. This is a potential explanation for the reduced fitness of late-born birds.

Timing of consecutive stages could be dictated solely by the timing of the previous stage [10]. In the case of the stages described in this work, this would point to a ‘developmental timer’ instead of an endogenous oscillator that would give information on time of year [41]. Our experiment was not designed to differentiate between control via an endogenous oscillator or via sequence of developmental stages.

Nevertheless, our results point to post-juvenile moult and fattening being 'purely developmental' stages, as the occurrence of these two stages was fairly fixed in relation to the hatching date. This means that animals had to reach a certain age before the initiation of moult and (to a lesser extent) fattening. On the other hand, timing of migration occurred at the same moment, independent of the animals' hatching dates. Thus, it is not related to developmental stage and could be controlled by an endogenous oscillator set by the photoperiod or by photoperiod directly.

Self-sustained annual rhythms of moult, fattening and migration have already been demonstrated in several bird species, including pied flycatchers [42], suggesting the involvement of a true circannual clock. Those rhythms were not only demonstrated to free-run, but also to be strongly synchronized by photoperiodic variation [13]. While this would initially contradict our findings (that moult and fattening are dependent on age rather than calendar date), the control of seasonal rhythms of moult and fattening in adult birds could potentially differ from the post-juvenile moult and first-year fattening: while the first is cyclic, the latter would reflect the time to grow and develop in a species- or population-specific manner [25,26].

Our results are, to a certain extent, analogous to what was argued by Pittendrigh & Skopic [41] for pupal emergence rhythms in fruit flies (*Drosophila pseudobscura*). They showed that adult emergence from the pupa was controlled by an oscillator which 'gated' the event, meaning that all animals emerged at the same time, independently from the manipulated pupation time. However, intermediate steps were dependent solely on the development state (in hours), occurring at fixed times after pupation [41]. More recently, a similar pattern was observed for winter moths (*Operophtera brumata*), which have a single generation per year. In these insects, the time between egg-hatching and pupation had a fixed duration, while adult eclosion was dependent on whether animals perceived to be early or late in the year [43]. This suggests that certain key stages of development (e.g. eclosion and first migration) are constrained to a restricted time window in the day (fruit fly) or year (pied flycatcher, winter moth) and that it is preferable for late individuals to sacrifice developmental/preparation time rather than delaying the onset of the critical event (figure 1).

Interestingly, we also observed a significant genetic effect on timing of migration in the absence of effects of egg-laying or hatching date. This would mean that there is (additive) genetic variation for the timing of autumn migration in pied flycatchers but no genetic covariation with the egg-laying date, which is known to be heritable in flycatchers [44,45]. Therefore, for some families there is a shorter interval between date of egg-laying and departure. This suggests that the timing of reproduction is under a different (genetic) control than timing of migration, which means that these two traits could evolve independently. This means that the two systems could also respond differently, either increasing or decreasing time available between them, especially if summer and spring conditions change unequally with climate change.

Although we found an effect of time constraints on body mass, the growth rate of flight feathers did not differ between treatments. A similar pattern was observed in adult starlings with experimentally delayed moult. In that experiment, growth rate of flight feathers was not affected by a delayed moult, but birds replaced more feathers at the same time [6]. The growth rate of flight feathers seems to be rather fixed in most bird species, without much room for variation [46]. This could be related to the structure of the growing region of the feather follicle, rather than the energetic requirements of moult, which constrains how many cells can divide and differentiate to form the full vane [46].

This relationship between hatching date and timing of first-year stages has been previously investigated in other bird species, but results were not always consistent across studies (and they also differ from our results). The effect of late-season photoperiod is believed to influence the timing of first-year stages by accelerating juvenile moult, fattening and migration, which allows late-hatched birds to be ready for migration—the so-called 'calendar effects' [11,12]. Although some studies found a consistent effect of late-season photoperiodic conditions in the speed of development [25,28], our results did not point to a faster moult or occurrence of moult or fattening at an earlier age. For example, while we did not find evidence for change in age of moult in advanced or delayed birds (figure 1), in blackcaps (*Sylvia atricapilla*) simulated (photoperiodic) conditions of very early hatching made birds initiate moult at a younger age and finish at an older age in comparison with controls, meaning that manipulated hatch dates caused a prolongation of moult duration for the earlier hatched birds [29]. However, in vireos (*Vireo flavoviridis*) naturally hatched at different times, early hatched birds moulted, fattened and initiated migration at an older age than late birds and no change in moult duration was observed. A similar effect on age of migration was also observed in the same blackcaps of the previously mentioned study [29], in stonechats (*Saxicola torquata*) [47] and various short distance migrants [48] naturally hatched at different moments of the season. In all these cases, late-hatched birds initiated migration at a younger age. This is similar to what we found in our experimentally shifted pied flycatcher hatching dates (figure 1). However, in a Russian population of great tits (*P. major*), late-hatched migration at younger age was only observed in seconds broods, as chicks from first broods migrated at the same age [49].

The reported differences in the organization of life cycles in early- and late-hatched offspring may come from different methods than our experimental manipulation of hatch date, such as correlative measurements of early- and late-hatched individuals (vireos [28]; great tits [49]; stonechats [47]; short distance migrants [48]); comparisons between first and second broods (great tits [49]); photoperiodic manipulations simulating early moments in the season (blackcaps [29,50]) or comparison across different populations (different subspecies of stonechats [25,26]). Moreover, migration distance could also play a role as short distance migrants and residents are supposedly less constrained [19,49]. For example, naturally early- and late-hatched birds may differ in terms of quality of their parents as it is known that late egg-laying birds have smaller clutches [51], worse territory quality [52] and may be younger than early breeders [1]—all of which may affect the amount of parental investment and thus development and success of the offspring. Birds invest less in raising a second brood due to, for example, moult–breeding overlap in the adults which happens later in the season [9], which will again lead to developmental differences between chicks from first and second broods [2]. In both cases, the effects of timing will be confounded by quality. Photoperiodic manipulations avoid such issues, but they test whether a modified perception of timing of year, rather than a different birth date *per se* that would also change other cues than photoperiod, will affect timing of subsequent stages. Finally, comparison across populations or subspecies may simply reflect the differences in local optima. Our manipulations allowed the comparison between nests that were initiated at the same time, thus presumably with the same initial 'quality', but that were moved in time. Therefore, our experiment was successful in causally testing the effects of hatching dates on timing of subsequent stages. We also attempted to keep our manipulations within the expected range of hatching dates, in order to not create extremely early or late hatching, later than very last broods or earlier than very early broods, thus avoiding aberrant responses to environmental conditions under which the birds did not evolve.

Over the past 30 years the pied flycatchers of the Hoge Veluwe population have advanced their egg-laying date [19], as have many other birds species [53,54]. Despite this advancement, there has been an increasing difference in fitness between early and late egg-laying birds—from 1980 to 2000 early birds had higher breeding success than late birds leading to directional selection for early egg-laying. However, over the past 15 years, the directional selection on timing of reproduction for the Hoge Veluwe pied flycatcher population has weakened again. The pattern was not explained by an increasing match between the birds' seasonal timing and the time of their maximal food abundance, thus the so-called phenological mismatch is not a major selective pressure for flycatcher timing of breeding [45]. A possible explanation for this is the differential recruitment of chicks depending on the temperatures on the year of recruitment: early chicks would only have a higher probability to recruit if they return in a warm year [45]. Our results provide an additional explanation for the reduction of the selection for early egg-laying: the advancement of egg-laying dates, and thus birth date of the chicks, will reduce the time constraint for late-born birds. This means that the advancement of egg-laying dates gives the chicks more time to complete the development and preparation before the migration date. This could be one of the components that explain why selection for early egg-laying dates has weakened over the past years.

This weakening of the selective pressure on egg-laying, however, does not necessarily imply that climate change imposes no costs for the birds. The gain in time in the interval from breeding to migration means that time is lost in another portion of the annual cycle because the period of the whole cycle is set by the duration of the year. While the earlier egg-laying of the females increases the time available for their young from hatching to migration, the adult birds seem to be constrained in their time from migration (from the African wintering grounds) to breeding: while egg-laying dates are advancing, arrival dates at the breeding grounds did not change [19]. This means that for adult birds climate change may shorten their preparation time between arrival and breeding, which will impose a fitness cost on the breeding birds.

Ethics. All procedures were carried out under licences of the Animal Experimental Committee of the KNAW (protocols NIOO-13.04, NIOO-13.06 and amendment and NIOO 14.04).

Data accessibility. Complete analyses and additional figures supporting this article have been uploaded as part of the electronic supplementary material. Complete datasets are stored at the Netherlands Institute of Ecology (NIOO-KNAW) repository and are available upon request.

Authors' contributions. B.M.T. and M.E.V. designed the study; B.M.T. collected the data; B.M.T., P.G., D.G.M.B. and M.E.V. analysed the data and wrote the manuscript. All authors gave final approval for publication.

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