

Tracking locally hatched pied flycatchers reveals masking of inherited trait variation during spring migration

Abstract

Climate change has been driving long-distance migratory birds to alter their schedules under the threat of being mismatched with their food peak at the breeding grounds. It is important to study the relative contribution of environmental, genetic and ontogenetic components in various spring timing traits in the wild in order to predict the true potential for migratory birds to adapt to the changing environment. We aimed to detect if heritable and ontogenetic components can explain variation in the timing of spring migration and breeding in pied flycatchers (*Ficedula hypoleuca*). Geolocator tracks of 44 locally hatched birds deployed during 2016-2019 in the Netherlands and the United Kingdom were used to investigate the role of early-life traits in the pre-fledging phase, as well as parental timings, in contributing to individual differences in the timing of spring migration and breeding in adulthood. We found a positive relationship between an individuals' birth date and spring departure date from Africa in adulthood, but not for breeding arrival or laying date. Variation in spring departure date could not be explained by any other early-life trait in the pre-fledging phase, yet was well explained by the arrival dates of its parents in its birth year. This suggests that under natural conditions, individual differences in spring departure timing have a strong heritable component (in the broad sense), but that environmental conditions experienced along the migratory route and at breeding sites are partially masking this expression in arrival and laying

schedules in these early breeding populations. Such environmental masking may reduce heritability in the timing of arrival and laying, thereby slowing down climatic adaptation towards earlier time schedules in pied flycatchers.

Keywords

Geocator, ontogeny, genetic, winter departure, arrival date, lay date

Introduction

Matching the timing of critical life-history events with suitable environmental conditions is essential in the animal kingdom. In the era of human-induced climate warming, many species are confronted with different rates of advance in phenology across trophic levels (Buse et al., 1999; Root et al., 2003; Thackeray et al., 2016). For instance, several migrant birds are pressed to advance arrival at breeding sites to ensure optimal timing to maintain breeding synchrony with prey peaks (Visser et al., 2006). Many migratory organisms are in decline, and migrants appear less responsive in adapting their time schedules to climate change than resident species, despite their evolved life-style to make use of seasonally changing resources at multiple locations (Both et al., 2009; Samplonius et al., 2016; Wilcove & Wikelski, 2008). Yet, the processes leading to or preventing annual-cycle adjustments are difficult to pinpoint, even in well-studied avian migrants.

The pied flycatcher is a key example of such a species that is intensely studied to better understand the ability of migrants to adapt to global warming at the breeding grounds. Rising

temperatures have resulted in advanced spring phenology of breeding areas. A prominent role for plasticity in laying decisions in response to these changes have been well demonstrated for many species, including flycatchers, in which the laying date-temperature correlation explains the majority of advancement of egg-laying date (e.g. Both et al., 2006; Both & Visser, 2001; Brommer et al., 2008). Some studies suggest that the response in breeding time may be insufficient, as the strength of directional selection for earlier breeding has increased (Both et al., 2006; Both & Visser, 2001; Burgess et al., 2018; Visser et al., 2015). In contrast, a recent study found shorter arrival-laying interval in pied flycatchers in the north of Great Britain without any detected consequence for productivity, suggesting that birds were able to adapt the arrival-laying interval (Nicolau et al., 2021). The causes proposed to underly the observed (insufficient) annual-cycle responses are variable, e.g. ranging from the inability for rapid microevolution of internal clocks to explain unchanged timing (Both & Visser 2001; but see Helm et al. 2019), to temperature constraints during spring migration that slow down adaptation via ontogenetic pathways (e.g. Both 2010). To falsify such hypotheses about the mechanisms driving the observed (lack of) responses to climate warming, it is vital to consider the sequence of traits involved, particularly including events that occur before breeding arrival and that have been little studied in this context.

Geolocator tracking now allows the study of multiple annual-cycle stages for individual birds, and investigation of where links across annual cycle stages occur *or* break down. Using geolocator tracking, Ouwehand & Both (2017) showed that the timing of pied flycatchers' migration in autumn was flexibly adjusted to breeding duties and contributed little to spring departure decisions. Moreover, these Dutch breeding pied flycatchers migrated fast, and revealed a tight correlation between African departure and breeding arrival timing

(Ouwehand & Both, 2017). The observed large variation in departure date from Africa in Dutch flycatchers implied a clear potential to further advance breeding by an earlier departure (Ouwehand & Both, 2017). In a recent geolocator meta-analysis, Schmaljohann (2019) showed the generality of a positive departure-arrival correlation within and across species and highlighted the general importance of earlier departure timing by which arrival dates at the breeding site could advance.

However, the mechanisms that underpin this variation in schedules is unknown and as such neither is the capacity for advancement in departure. Variation in timing decisions will likely result from a mixture of three key processes: genetic, ontogenetic and environmental processes. Moreover, the extent to which trait correlations, like departure-arrival-laying, are maintained (i.e. whether selection acts in a similar direction across traits), will influence whether this translates into adaptation towards earlier breeding schedules. Determining the relative importance of these three processes across traits, from spring departure to laying decisions, is needed to predict the adaptive potential of species with complex life-styles in their natural dynamic environments (Botero et al., 2015).

Substantial evidence exists for heritable/genetic factors to form the basis of an endogenous mechanism of timing in birds (Bazzi et al., 2016; Dor et al., 2011, 2012; Johnsen et al., 2007; Peterson et al., 2013; Saino et al., 2015; Udoh et al., 2015). Helm et al. (2019) showed a change in circannual clocks in pied flycatchers between 1982-2001, suggesting that phenotypic advances resulted from microevolution in timing traits. Further, most work on birds focuses on the heritability of arrival timing and laying, while data on departure is lacking. Heritabilities of arrival date appear low to moderate: in barn swallows *Hirundo rustica*, heritability of spring

arrival ranged from 0.11 to 0.32 in two populations (Teplitsky et al., 2011), and in Great reed warblers *Acrocephalus arundinaceus* this was estimated as 0.16 (Tarka et al., 2015). However, differentiating between genetic and ontogenetic factors is often difficult if using indirect methods, since it can be hard to disentangle genetic heritability from ontogenetic processes.

It has been argued that non-genetic inheritance mechanisms allow even for faster changes in traits across generations when environments change rapidly (Bonduriansky & Day, 2009).

Ontogenetic processes, such as environmental conditions during or after the hatching period, haven been shown to influence a bird's decision of timing at adulthood. In Black-tailed godwits *Limosa limosa*, researchers found that individuals were highly repeatable in arrival date, and that especially cohorts varied, suggesting that the advance in arrival dates unlikely worked through a genetic change (Gill et al., 2014). Other studies showed that photoperiodic shifts in early life in captive blackcaps *Sylvia atricapilla* affected the timing of moult and autumn departure (Coppack et al., 2001), and a similar experiment in wild Purple Martins *Progne subis* showed that autumn colony departure is affected by natal photoperiods (Bani Assadi & Fraser, 2021), but these studies did not cover the entire annual cycle and therefore it is uncertain whether effects may persist until the following spring. In pied flycatchers, it has been hypothesized that advancements in spring migration through North-Africa could also arise from non-genetic inheritance, in which earlier laying by female flycatchers facilitates earlier migration schedules in their offspring, via differences in the perceived photoperiodic environment during ontogeny (Both, 2010). This hypothesis was tested in Pied flycatchers using a multi-year study in which delayed hatching experiments in the field revealed that in one of three years birds arrived later when being born later in the season (Ouweland et al., 2017). However, because the experimental results were not in line with the natural birth-date

effects in the same years, it was argued that variation in arrival phenology was unlikely caused by the proposed ontogenetic pathway of hatch date *per se*, but more likely resulted from inherited timing traits (by other means) and environmental factors that can covary with parental egg-laying dates (Ouwehand et al., 2017).

The third key process that determines observed responses throughout the chain of timing traits, is phenotypic plasticity to environmental conditions. Pre-migratory environmental conditions have been associated with a bird's decision to depart from the wintering site, with most direct evidence coming from studies on American songbirds. For example, both rainfall and food-rich mangroves at the wintering site allow American redstarts *Setophaga ruticilla* to depart earlier compared to birds in secondary habitats (Studds & Marra, 2011). In contrast, Swainson's thrushes that were wintering in the high-quality native forest departed later than birds from poorer habitats, probably to make use of good fuelling conditions at these sites (González et al., 2020). So far, it is unclear to what extent Pied flycatchers can flexibly adjust departure dates in spring to wintering conditions, *or*, whether songbirds in general can make use of phenotypic plasticity to advance their departure dates.

More data exists on how birds adjust arrival dates and migration to environmental conditions. Phenotypic plasticity may allow migratory birds to speed up spring migration in order to arrive earlier to match the advancement at the breeding grounds (Coppack & Both, 2002). In some flycatcher populations, the observed advancements in arrival dates were likely caused by phenotypic plasticity in which migrants were capable of speeding up migration (Balbontin et al., 2009; Cadahía et al., 2017), particularly so when birds get close enough to their breeding sites to incorporate local environmental conditions into timing decisions (Ahola et al., 2004;

Lehikoinen et al., 2004). In contrast, the short and fast spring migration in pied flycatchers from a Dutch breeding population revealed little potential for earlier arrival via faster migration (Ouwehand & Both, 2017), although in a British population the earlier departing individuals had longer stop-overs and hence migrated more slowly (Bell et al., 2021). The potential to increase migratory speed appears non-universal across species or populations, and it mostly allows for a relatively small advancement in many species, because migration duration appears strongly dependent on stopover duration and refuelling conditions (Schmaljohann & Both, 2017).

The influence of environmental conditions may not only provide a solution to cope with change, but can act in the opposite direction, by masking innate trait variation where selection can act on (Visser, 2008). Such masking effects may in part explain the non-significant heritability of 0.16 previously found for egg-laying dates (between 1980-1999) of a Dutch pied flycatcher population (Both & Visser, 2001), which reveals that only a small genetic component is expressed in breeding timing. However, the heritability of egg-laying date in females of the same population calculated by using data collected between 2002 and 2012 is 0.33 (Visser et al., 2015), indicating the inevitable year variance. In line with this, individual flycatchers were found to show consistent differences in arrival schedules to their Dutch breeding site, but the strength of this repeatability differed among sets of consecutive years (Both et al., 2016). The long journey between wintering and breeding grounds likely leaves more potential for environmental factors to mask the expression of heritable trait variation, and was proposed to explain year-differences in the strength of naturally occurring relationships between an individuals' hatch date and breeding arrival date later in life (Ouwehand et al., 2017). An important reason why heritability and repeatability in arrival and

laying dates can thus be low or context-dependent, is due to the varying degree by which it is environmentally driven.

In the current study, we aim to investigate the extent to which spring timing in pied flycatchers is associated with inherited or ontogenetic factors by using geolocation tracking data from two early breeding populations: Drenthe, the Netherlands, and East Dartmoor, UK. First, we investigate the correlations between an individuals' hatch date and its Sahara departure (i.e. spring departure dates on which birds start flying across the Sahara), breeding arrival and laying schedule during adulthood. Next, we aim to test two hypotheses: 1) if early-life traits during the pre-fledging stage can explain this variation in spring timing (ontogeny hypothesis), or 2) if parental timing better explains the variation in (offspring) spring timing during adulthood. By focusing on various traits, i.e. Sahara departure dates, arrival and laying dates on the breeding grounds, we have the opportunity to explore to which extent and where in the annual-cycle the environmental impact may dilute or strengthen innate trait variation. Lastly, we discuss what our findings mean for the speed by which species with complex life-styles in their natural dynamic environments can advance breeding schedules to change.

Methods & Materials

Study system

The pied flycatcher is a migratory bird species that winters in West Africa in the Guinea-Savanna belt (BirdLife International, 2021) and breeds in Europe and Western Asia. They are hole-nesting birds that readily breed in artificial nest boxes, providing an excellent possibility

for researchers to observe their breeding attempts. In this study, we included data from two breeding sites in Europe: Drenthe in the Netherlands (52°49' N, 6°22' E), and East Dartmoor in the United Kingdom (50°36'N, 3°43'W). More than 1,000 nest boxes were placed in Drenthe from 2007, and the population consists of 200-350 pairs per year (Both et al., 2017). The East Dartmoor population has 306 nest boxes first established in the 1950s with approximately 95-100 pairs of pied flycatchers in recent years (Burgess, 2014).

Field observations

Arrival monitoring was performed according to Both et al. (2016), through daily (Drenthe) or once every other day (Dartmoor, Drenthe) surveys of the nest box areas. As male pied flycatchers vary in appearance (dorsal colour, wing patch and forehead patch sizes/shapes), in combination with various combinations of (colour) rings, individuals were uniquely identifiable by experienced observers within the spatially-separated sub-populations (up to 60 pairs per plot). Previous work has shown that the Dutch arrival estimate was generally within two days of the arrival date as estimated from a sub-set of individuals with geolocators (Both et al., 2016). Arrival dates of pied flycatchers were recorded as the first day that individual was observed at a nest box from daily surveys, or as the mid-point day between the observation day and the previous visit if visits occurred every other day (Bell et al., 2017; Both et al., 2016). In Drenthe, female pied flycatcher arrival date was recorded as the first day when paired with a male. In Dartmoor, initiation of nest building was recorded and used as proxy of female arrival (Visser et al., 2015). Nest-building initiation was detected by checking the nest building stage using a five-point scale in Drenthe (Both et al., 2016) and the similar British Trust of Ornithology's Nest Record Scheme method in East Dartmoor (Crick et al., 2003).

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213 All nest boxes in the study areas were checked regularly (at least once per week) throughout
214 the breeding season April-June, with a higher frequency prior to crucial life history events,
215 such as first egg laying date and hatching. From the 13th day of incubation, the nest boxes in
216 Drenthe and East Dartmoor were checked every day to have an accurate hatch date of each
217 brood (date the first chick was born). In Drenthe, chicks were ringed and weighed (to nearest
218 0.1 g) at age day 7, and again weighed at day 12, when also tarsus length and wing length
219 were measured. In East Dartmoor, only the body weight of chicks were taken at 12 days old
220 (Bell et al., 2017). In a few cases, the second weight measurement was taken at age day 11 or
221 13, since chicks reach their asymptotic mass around day 11.

222

223 **Geolocator deployment and data analysis**

224 Adult flycatchers were deployed with geolocators between 2016-2019 using a leg-loop
225 harness. In Drenthe 151 loggers were deployed of which 25% returned (n=6/23 females;
226 n=32/128 males), and in East Dartmoor 170 loggers of which 28-30% returned (n=13/57
227 females; n=38/113 males). The selection of birds for geolocator deployment was aimed to
228 cover a wide range of breeding dates, and mostly targeted males because of a higher local
229 return rate (Both et al., 2017). Among all 86 recaptured birds with readable data, we used
230 four different models of geolocator (5*Intigeo-W30 (0.32g), 10* Intigeo-W50 (0.45g), 65*
231 Intigeo-P30 (0.36g), 6* Intigeo-P50 (0.50g), Migrate Technology Ltd., Cambridge, UK). P30 and
232 P50 models are the same as the W30 and W50 models, but additionally have a 7mm long light
233 tube to minimise feather shading (thereby providing more accurate sunrise and sunset
234 estimates inferred from measured light intensity). We retrieved loggers upon return to the
235 breeding sites, during arrival, incubation or breeding. From this full set of successfully

returning geolocator birds, we used only the 46 tracks of locally hatched birds known from uniquely numbered rings fitted as chicks in our study areas for which we have data available that relates to early-life traits collected in their hatch year.

In the current study, we primarily use the geolocator data to extract the date that individuals started their Sahara crossing in spring, hereafter referred to as Sahara departure. This event can be clearly identified by the full light pattern anomalies (FLP) from plotted light-levels recorded by the geolocators (Adamík et al., 2016; Ouwehand & Both, 2016), that occur when pied flycatchers – that are otherwise nocturnal migrants – perform prolonged 40-60 h non-stop flights that include diurnal flights when crossing the Sahara Desert. Sahara departure was assumed to have started at dusk the evening prior to the first FLP recorded, unless clear shading at the start of the first identifiable FLP bout indicated that a bird started flying during the day. In the Dutch breeding population, most individuals departed directly from their wintering grounds (Ouwehand & Both, 2017). Although this appears the general pattern, the Sahara departure can differ from the departure from main non-breeding areas in some cases (Bell et al. 2021: difference > 2 days in 5 out of 86 tracks, with a range of 5 to 26 days of difference). We chose Sahara departure instead of departure from main non-breeding area as this allowed us to extract timing of spring departure with greater accuracy and in a similar way for all tag models used, since FLPs were consistently distinguishable from all geolocator models (including W30, for which full geolocator analysis could not be performed). Moreover, we assume that for individuals where departure from the main non-breeding area deviates from the Sahara departure, e.g. due to an extra fuelling/resting stop, the Sahara departure is most closely related to an individuals' departure decision to start spring migration.

We used a threshold of 0.8 for log-transformed lux values to define sunrise and sunset times in the R-package TwGeos (Lisovski et al., 2016, 2020). Twilight events were used to define movement and stationary periods by applying the `invChanges` and `extractMovements` function from the R-package GeoLight v2.0.1 (Lisovski & Hahn, 2012). We used tag specific settings for the thresholds in both the `extractMovements` function and `mergeGroups` function considering the variation in the levels of ambient and feather shading and individual movements. Then we modelled individual migration tracks and locations of stationary periods using grouped-threshold models in R-package SGAT (Wotherspoon et al., 2016), which applies a Bayesian framework combining the observed sunrise and sunset data with a priori knowledge of bird behaviour to provide location estimates with the associated uncertainty (see Lisovski et al., 2020). Models were underpinned using a tag-specific zenith_0 inferred from a gamma light error distribution by using an optimization procedure during the period November-February when birds are at their main non-breeding site and shading events are less pronounced than during the post-breeding period. This procedure is similar to a Hill-Ekstrom calibration in that it seeks to minimize variance in latitude positions, but in this case assuming a gamma light error distribution during a stationary period (for details, see Bell et al in prep.). Next, the group threshold model was parameterised using a twilight model with this tag-specific zenith_0 , and a shape and scale parameters set to 2.5 and 0.1 respectively, to depict a broad error distribution. The latter was used to temper the confidence that the resultant peak zenith is representative for all stationary non-breeding periods (for details, see Bell et al in prep.).

Data selection

Starting from 86 geolocator records (see Fig. S1), we first excluded repetitive records from individuals that were tracked in multiple years by only selecting the first record. 8 second-track records were removed from the original 86 records and resulted in 78 birds. We further excluded extremely late records from the dataset using the following cut-off: Arrived after 20 May (day 81 of March Julian date), or nests with first eggs laid after 25 May (day 86 of March Julian date). Based on previous years' data, those records are highly probable to be a replacement clutch, or, missed arrival, or initial arrival outside the local study area (see Both et al., 2016 for rare cases in which individuals moved between study plots). This resulted in 75 birds of which 48 were local recruits. Combining the hatch date with Sahara departure, we yielded a set of 43 locally hatched individuals for which we have Sahara departure date during adulthood (age at the year of return ranging from 3 to 8 years): 29 birds in Drenthe, NL (6 females and 23 males), and 14 birds in Dartmoor, UK (4 females and 10 males). Of this dataset, for 32 birds the egg laying dates were also known.

For birds with data of both hatch date and Sahara departure, we primarily used field-observed arrival (N= 37) and laying (N= 32) date at the breeding site (if known). Geolocator inferred estimates of arrival are closely related to field observed arrival dates (Both et al. 2016), but geolocator arrival estimates will have a lower spatial accuracy and precision due to the nature of geolocator data analysis. Field-observed arrival dates at the breeding ground were available for 37 of 43 pied flycatchers. For 6 birds we used geolocator-inferred arrival estimates as substitutes for those birds that lacked field observation of arrival.

Data sets differed depending in the traits analysed. For one individual arrival date was lacking, so we had 47 out of 48 local recruits with arrival dates (41 field observed arrivals, 6 geolocator

inferred arrival estimates). For laying date we had a restricted data set of 36 out of 48 local recruits, since several males failed to obtain a female.

Within all local hatched birds with departure dates, paternal arrival was known for 33 paternal arrival dates (27 males from Drenthe and 6 males from East Dartmoor). 27 maternal arrival dates for Drenthe were also available. The maternal arrival dates for East Dartmoor (N = 11) were absent but all missing records were substituted by nest building initiation dates, since this is a good proxy of female arrival dates (Visser et al., 2015); yielding in total 38 maternal arrival records (27 from Drenthe, 11 from East Dartmoor).

Statistical analysis

We first studied if there was a hatch date effect on the three spring timing traits: Sahara departure, arrival and laying. In case we detected a positive correlation between hatch date and any timing trait, we further investigated two different pathways by which such an effect might be caused: 1) How various early-life traits correlated with migratory/breeding timing (ontogeny hypothesis); and 2) How parental traits correlated with the offspring traits (trans-generational hypothesis).

The statistical analyses were performed in R 4.0.3 (R Core Team, 2020) using general linear models as no indication of substantial deviation from normality was shown under normality test, unless mentioned otherwise. In the models explaining variation in Sahara departure and breeding arrival, we always include sex as a fixed effect to account for migratory timing difference between male and female pied flycatchers (Alatalo & Lundberg, 1984; Ouweland et al., 2017). The model with laying date as a response variable did not include sex, because

the different sexes do not differ in laying date. We first describe the support for a hatch date effect by adding this as a term to our null models. Next we test the support for the different pathways by describing if significant hatch date effects can be similarly well described by another trait associated with these two different hypothesis. To test support for the first pathway (ontogeny hypothesis), each of four early-life traits replaced the hatch date in the starting model: i.e. fledgling body weight (at day 12), fledgling tarsus length, natal clutch size, and natal number of fledglings. For birds that lacked tarsus measurements at the nestling phase (N = 22), we took the individuals' adult tarsus length as a proxy of early-life tarsus length since the tarsus length of pied flycatchers has reached its asymptote before age day 12 (Alatalo et al., 1992). For the second pathway, i.e. the trans-generational hypothesis, the potential of a cross-generational effect on timing during adulthood, we run models for three parental timing traits in the hatch year of the tagged birds: i.e. maternal arrival dates, paternal arrival dates, and mid-parental arrival dates. The mid-parental arrival dates were calculated by the average arrival dates of the paired male and female in the hatch year of the tagged birds. Pearson correlation was used to describe the correlation between maternal arrival dates and paternal arrival dates.

All date variables were expressed as Julian date from 1 March. Breeding area (Drenthe or East Dartmoor) was included as a fixed effect in all general linear models, to account for potential differences in timing traits among birds that arise from these birds originating and migrating from/to different areas (Ouweland et al., 2016). Year was not included, because sample sizes per year were small.

Results

Sahara departure positively correlated with hatch date ($F_{1,40} = 4.415$, $P = 0.042$, $\beta = 0.423$ day by day; Fig. 1A). There was a significant sex effect in this model where male pied flycatchers departed on average 8.87 days earlier than females ($F_{1,40} = 11.71$, $P = 0.001$), but no difference between breeding areas on departure date was detected ($F_{1,40} = 0.887$, $P = 0.352$). The variation in Sahara departure dates was substantial, ranging from 11 March to 14 April in males and from 27 March to 25 April in females (Fig. 1), but was consistent across the two locations (Drenthe/East Dartmoor males: 12/11 March to 14/5 April, $N=25/11$; Drenthe/East Dartmoor females: 27/31 March to 17/25 April, $N=6/N=4$).

We found no significant hatch date effect on breeding arrival date ($F_{1,43} = 0.005$, $P = 0.942$, $\beta = -0.013$ d/d; Fig. 1B). Neither did we detect an effect of hatch date on laying date ($F_{1,33} = 0.222$, $P = 0.641$, $\beta = -0.076$ d/d; area: $F_{1,33} = 1.107$, $P = 0.301$; Fig. 1C). Sex differences in arrival timing was again significant, with male pied flycatchers arriving on average 6.81 days earlier at the breeding grounds than females ($F_{1,43} = 8.462$, $P = 0.006$). No difference was found between breeding areas in their arrival date ($F_{1,43} = 1.732$, $P = 0.195$) and egg laying date ($F_{1,33} = 1.107$, $P = 0.301$).

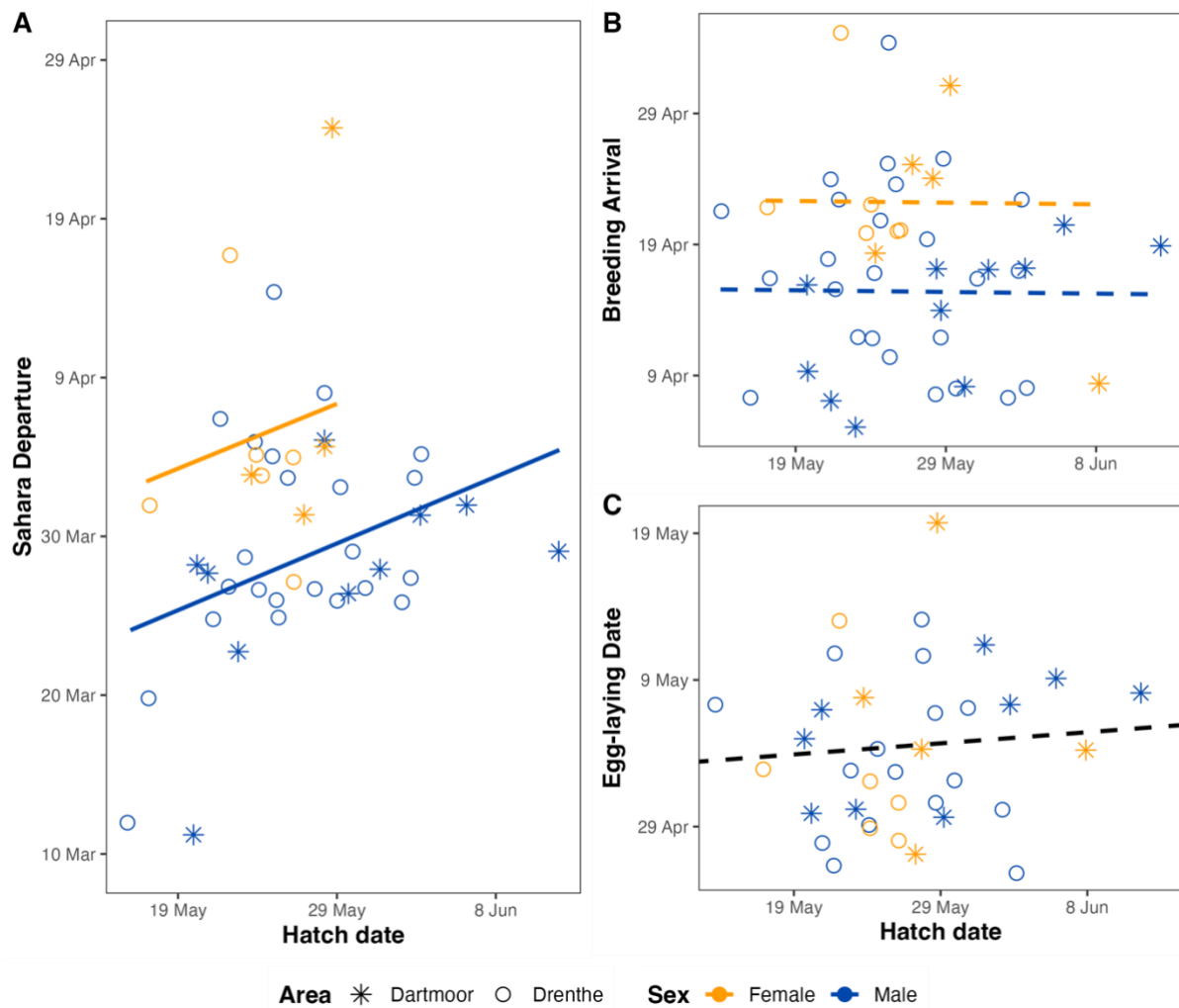


Fig. 1 The relationship between a pied flycatchers' hatch date and three timing events during its' adulthood: A) Spring departure date for Sahara crossing, B) Spring arrival date at the breeding grounds, C) First-egg laying date in the breeding season (here lines were not shown separately by sex since sex was not included as a variable in this model). Solid lines represent significant correlations while dashed lines are non-significant correlations. The points were jittered to avoid overplotting.

Early life traits (other than hatch date) did not explain variation in Sahara departure (Fig. 2). Hence, we found little support that the birth date effect on Sahara departure date arises through an ontogenetic effect that acts via nestling traits.

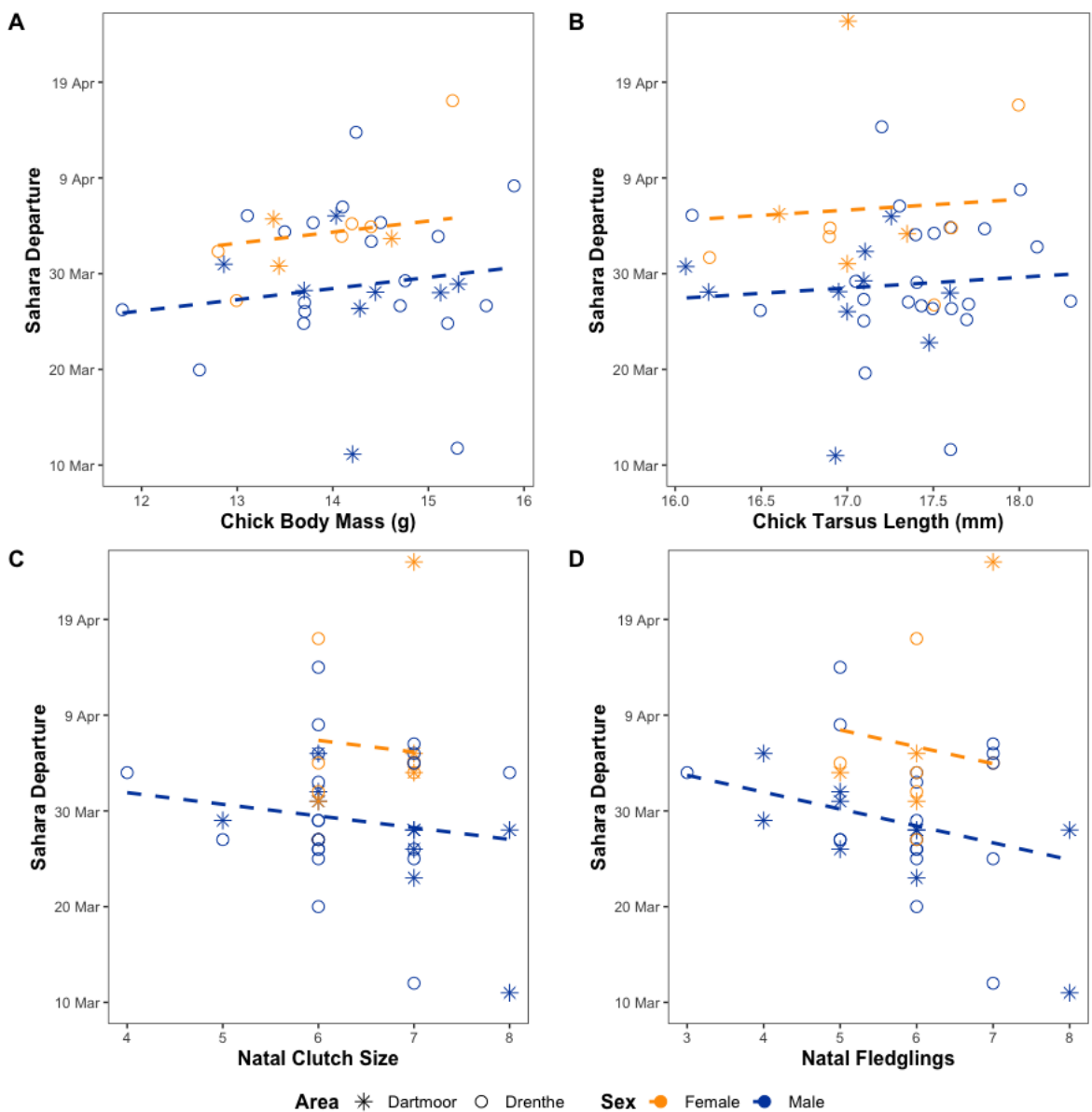


Fig. 2 The effect of various early-life traits (A: fledgling body mass ($F_{1,32} = 0.787$, $P = 0.382$); B: fledgling tarsus length or adulthood ($F_{1,39} = 0.218$, $P = 0.643$); C: natal clutch size ($F_{1,40} = 0.681$,

P = 0.414); D: natal brood size at fledging ($F_{1,34} = 2.143$, $P = 0.152$)) on the spring departure date of Sahara crossing in pied flycatchers. The points were jittered in figure A and B to avoid overplotting. All models included a significant effect of sex, and a non-significant effect of area.

Parental arrival dates significantly explained variation in the offspring Sahara departure date during adulthood, but not in their arrival dates at the breeding grounds (Fig. 3). This was true for the separate parents (paternal arrival date: $F_{1,30} = 4.687$, $P = 0.038$, $\beta = 0.431$; maternal arrival date: $F_{1,36} = 5.485$, $P = 0.025$, $\beta = 0.318$), and for mid-parental arrival date ($F_{1,30} = 7.060$, $P = 0.013$, $\beta = 0.491$). Paternal and maternal arrival dates of the tagged individuals were positively correlated (Pearson's $r = 0.704$, $df = 37$, $p < 0.0001$). Furthermore, the correlation between maternal arrival and hatch date was positive ($\beta = 0.443$; Pearson's $r = 0.573$, $df = 44$, $p < 0.0001$), as well as for paternal arrival ($\beta = 0.559$; Pearson's $r = 0.558$, $df = 37$, $p < 0.0001$).

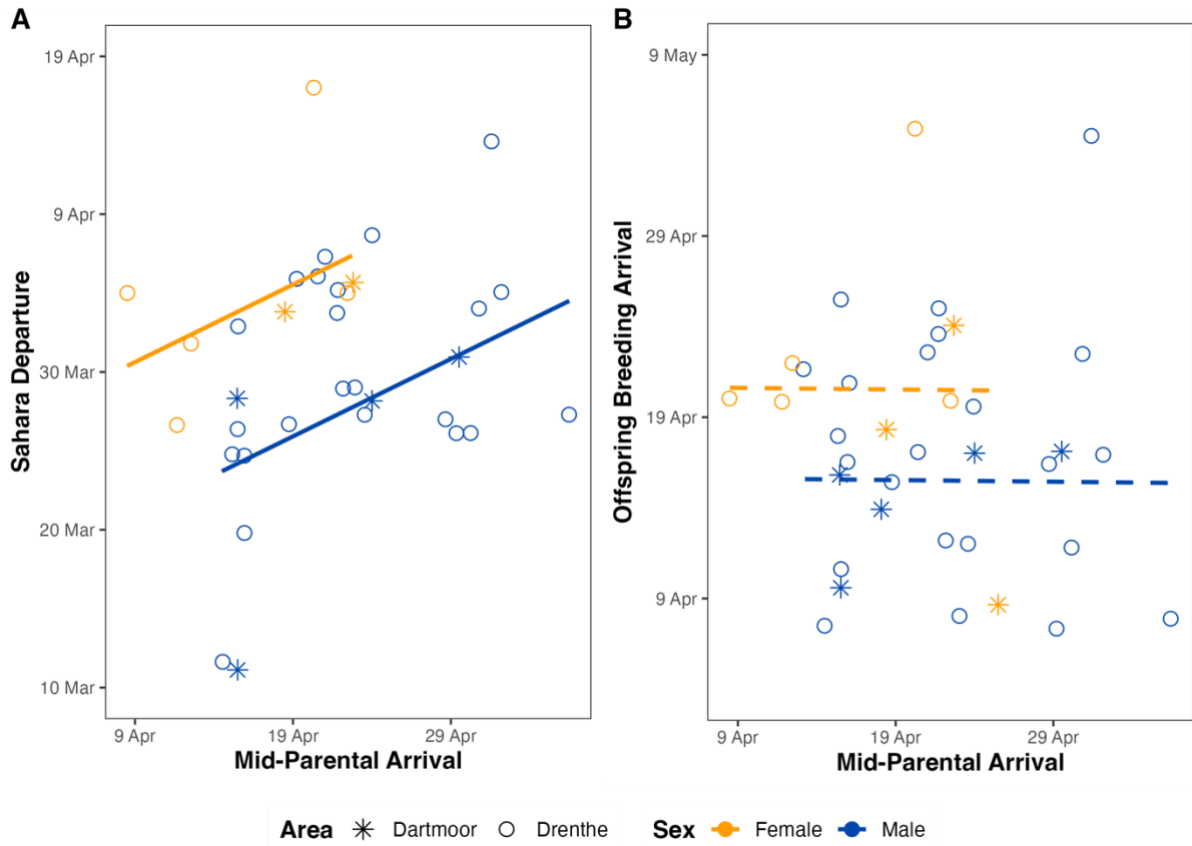


Fig. 3 The effect of mid-parental arrival timing at the breeding ground on African spring departure date (A) and arrival date (B) of the tracking year of their offspring produced from that year. The points were jittered to avoid overplotting.

Despite the lack of a significant relation between hatch date and arrival date later in life, we did find a significant positive correlation between Sahara departure and spring arrival (Fig. 4; $F_{1,39} = 26.698$, $P < 0.001$, $\beta = 0.564$ d/d; sex: $F_{1,39} = 3.493$, $P = 0.069$, males 3.80 d earlier than females; area: $F_{1,39} = 0.677$, $P = 0.415$).

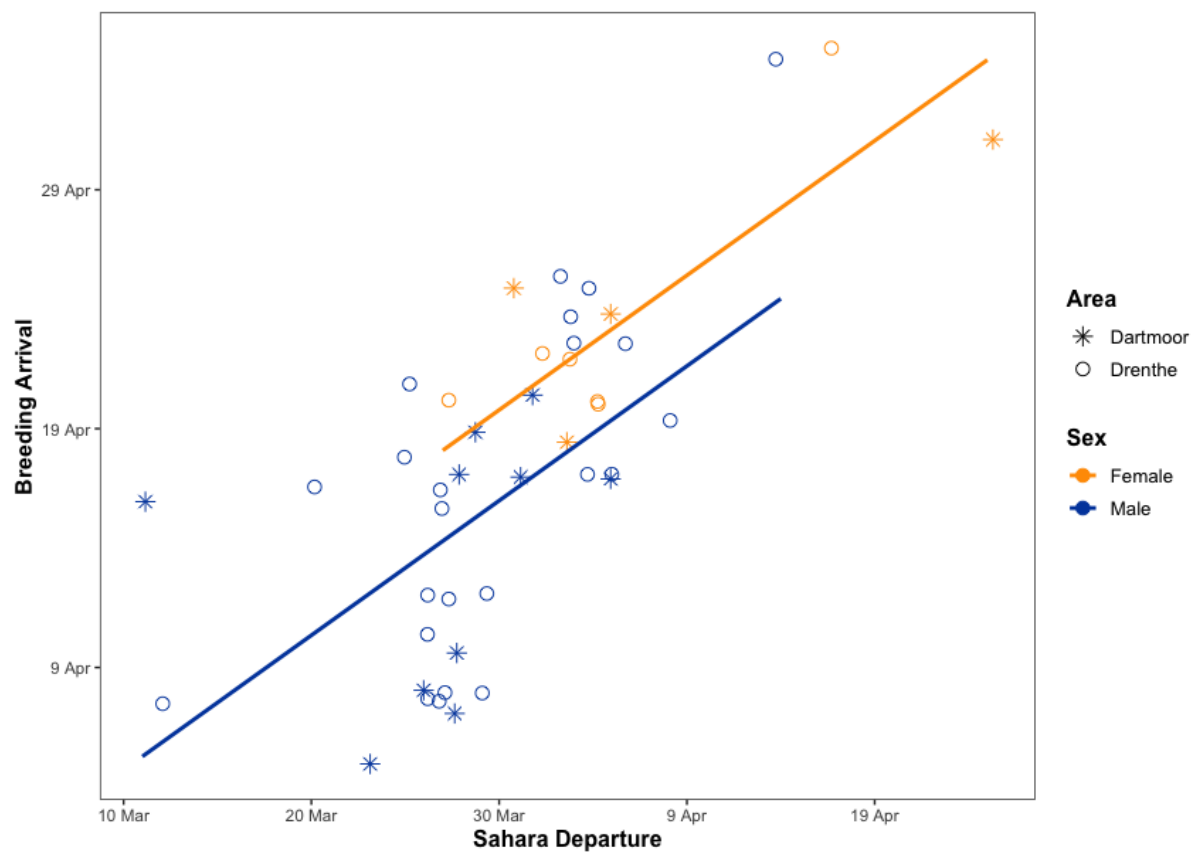


Fig. 4: The relationship between spring arrival date at the breeding grounds and Sahara departure for pied flycatchers from two breeding populations. The points were jittered to avoid overplotting.

Discussion

In this study, we found a positive effect of hatch date on spring Sahara departure timing of pied flycatchers in adulthood, but we found no evidence that other early-life traits during the pre-fledging stage explained this variation in Sahara departure timing. On the contrary, the positive association between spring Sahara departure and the arrival dates of their parents to the breeding areas suggests a role of transgenerational factors as a plausible cause of

variation in timing schedules. Below we discuss potential pathways to explain the phenotypic variation in and relation among these timing traits, and discuss their potential implications for adjustments of annual timing to climate change.

Our study aimed at distinguishing between ontogenetic and transgenerational effects. Some previous studies suggested annual timing in migrants could be explained by ontogeny (Both, 2010; Gill et al., 2014; Pulido & Coppack, 2004; Coppack et al., 2001; Bani Assadi & Fraser, 2021). Correlations between early-life conditions and spring migration or arrival dates (Both, 2010; Gill et al., 2014) were hypothesized to represent ontogenetic effects on time schedules later in life via the early-life environment. Yet, an experimental study in the wild revealed an age-specific effect, where experimental delays only delayed arrival in the first year of life, suggesting this effect to be a carry-over rather than a permanent ontogenetic effect via which non-genetic inheritance can act (Ouwehand et al., 2017). Our possible ontogenetic effect on timing in adult life was restricted to an effect of hatch date on spring Sahara departure, whereas no effects of fledgling body mass, tarsus length, clutch size or number of fledglings were observed. Our results as such do neither hint at carry-over effects (via e.g. body mass, number of fledglings) nor at more permanent ontogenetic effects (e.g. via tarsus length). Our results indicate a positive correlation between hatch date and Sahara departure in spring, but not on subsequent timing traits such as breeding arrival or laying date. It thereby confirms Ouwehand et al. (2017), in that the correlation between a birds' hatch date and timing during adulthood can only be observed as an effect on arrival date at the breeding grounds if environmental conditions between departure and arrival do not mask these links.

The positive correlation between parental arrival dates and spring departure dates of their offspring could be caused by genetic inheritance of timing across generations. The finding that mid-parental arrival timing explained departure dates better than hatch date, supports the hypothesis that variation in migratory timing may have a heritable component, consistent with the conservative internal clock of spring departure in pied flycatchers and other species (Gwinner, 1986). Indeed variation in timing of migratory behaviour has been suggested to have a genetic basis based on quantitative genetics of spring arrival date (Tarka et al., 2015; Teplitsky et al., 2011), captive studies (Helm et al., 2019), and correlations between genetic variation in potentially functional genes and timing. For instance, the CLOCK poly-Q allele length variation was found to be correlated with migration timing and distance in some bird species (Bazzi et al., 2016; Krist et al., 2021; Peterson et al., 2013; Saino et al., 2015). However, so far the studies on variation in arrival date in *Ficedula* flycatchers show very low and non-significant heritability based on pedigree-resemblance (Krist et al., 2021; Potti, 1998), whereas repeatability is moderate (Both et al., 2016; Krist et al., 2021). In this respect it is quite remarkable that our study still reveals a positive correlation between parental arrival dates and their offspring's spring Sahara departure in adulthood.

Disentangling ontogenetic, genetic and environmental effects on annual cycle variation is difficult, especially because different annual cycle traits (such as spring departure date from Africa or laying date) likely vary in how strongly they are affected by environmental factors. The start of preparation for departure might be strongly innate and variance between individuals mostly resulting from genetic differences, but this innate timing likely is modified by the quality of the wintering habitat (Studds & Marra, 2011), which may weaken the correlation between start of preparation and actual spring departure. Subsequently,

environmental conditions *en route* will modify how strongly variance in departure date translates into variance in breeding ground arrival date (e.g. Tottrup et al., 2012). Interestingly, the significant, but much weaker correlation found between Sahara departure and arrival in the current study, suggests that such effects are likely more pronounced than previously found (Ouwehand & Both, 2017). Subsequently, conditions at the breeding grounds will add more environmental noise when it comes to laying and hatching dates (Low et al., 2019; Nicolau et al., 2021). In this study we show how the role of environmental variation increases – both in Sahara departure-arrival relation, but also in parental arrival-hatch date relation – and whereby the trait-correlation between parental and offspring arrival is weakened. Although it seems plausible that the combination of a genetic effect and the masking of such an effect by environmental conditions can explain our findings (Fig. 5), there are potentially other explanations. If arrival dates indeed are to a large extent determined by environmental conditions, a positive correlation between parental arrival dates and offspring spring departure dates may also arise by other means, when acting in the same direction. Carry-over effects could potentially strengthen trait-correlations in this way, as was suggested to explain previously found experimental effects of hatch date on arrival timing (Ouwehand et al., 2017). In our case, a strong correlation between hatch dates and parental arrival dates, and assortative mating among pair members (in term of their arrival dates) potentially strengthened trait-correlations between parental arrival and Sahara departure of their offspring.

511 timing has a strong genetic component, it is uncertain whether this has evolutionary
512 implications if little of this variation is expressed when arriving at the breeding grounds,
513 where most of the selection will take place. In *Ficedula* flycatchers, spring departure and
514 arrival timing often show intermediate repeatabilities (0.2-0.5, Both et al., 2016; Krist et al.,
515 2021), likely because of these large environmental effects during migration. The increased
516 selection for earlier breeding in response to climate change (see Both & Visser, 2001) can act
517 directly on spring departure schedules in years when innate timing schedules are also
518 expressed into arrival (as likely happened in Ouweland & Both, 2017; reviewed by
519 Schmaljohann, 2019). When more plasticity occurs in response to encountered
520 environmental conditions *en route* that disrupts this relation, selection would then rather be
521 on the environmental part of the variation and not on the genetic part (Tarka et al., 2015).
522 Hence, we should not just consider heritability as a population-specific trait, but rather should
523 focus on annual variation in heritability and how this annual heritability is associated with
524 variation in selection (Husby et al., 2011). If we assume that variation in arrival dates is mostly
525 due to a non-genetic effect of hatch date on Sahara departure date in later life, the expression
526 again likely depends on environmental conditions. Again, the lack of correlation with
527 subsequent arrival dates would preclude a directional change in arrival dates through such
528 ontogenetic inheritance. The extent to which variation in Sahara departure dates is translated
529 into arrival is hence most important in determining the speed of directional changes. Mean
530 arrival dates of early breeding populations of pied flycatchers have advanced during the last
531 decades (Schmaljohann & Both, 2017), despite the role of high year-to-year variation in
532 expressing birth date-arrival correlations and expression of individual differences in arrival
533 schedules (Both et al., 2016). The observed advance in arrival date implies that repeatability
534 of Sahara departure is probably high, and thereby allows the (generally) weaker correlation

of birth-arrival to be maintained and expressed in some years (Ouwehand et al., 2017). This thus leaves room for micro-evolution under climate change, as shown in the advance of annual cycle timing in captivity from the same wild flycatcher population with a 20-year interval (Helm et al., 2019). The observed assortative mating among parents with similar arrival phenotypes may also positively contribute to this advance, especially since this could strengthen the selective response by counteracting the (weakened) expression of inherited variation.

Our study highlights the importance of studying a whole chain of annual-cycle events in order to pinpoint where trait-associations break-down or are maintained. Despite the limits to tackle exact causes of transgenerational resemblance in timing traits with descriptive data, field studies – like ours – provide key insights about how expression of timing trait variation can influence the speed of climatic adaptation towards earlier breeding schedules under natural conditions.

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