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RESEARCH ARTICLE

Shifts in hatch dates do not provide pied flycatchers with a rapid ontogenetic route to adjust offspring time schedules to climate change

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Abstract

1. Environments change rapidly, and it is unclear whether organisms with complex life-styles, such as avian migrants, are able to adjust sufficiently. For understanding human impacts on ecosystem functioning, it is crucial to understand how well, and by which mechanisms species are able to adapt.
2. To improve the understanding of migrants' ability to adjust their annual timing to climate change, we investigated ontogenetic hatch date effects on adult spring migration timing and female egg-laying dates. We experimentally delayed hatch dates of pied flycatchers *Ficedula hypoleuca* by 1 week in three breeding seasons by delaying incubation onset. We investigated if natural and experimental (shifts in) hatch date affected timing of recruiting individuals up to at least 3 years after the manipulation.
3. Spring arrival dates were positively correlated with natural variation in hatch dates in three of the 5 years considered, but no such effects were found in egg laying. Experiments showed that delayed hatching resulted in delayed arrival and laying only in 1-year-old and not in older birds. These effects were mostly observed during one of the study years.
4. The discrepancy between experimental and natural hatch date effects indicates that a causal hatch date effect is not generally responsible for the correlation between a birds' birth date and timing during adulthood. Instead, we propose that natural hatch date effects on spring arrival arise from genetic variation in migration schedules, while delays in hatching induced carry-over effects on arrival and laying dates in offspring (e.g. the experimental effect in 2010). Strong support for year-specific expression of hatch date and delay effects on time schedules imply that trait-variation can be easily obscured. The latter may explain the lack of hatch date effects on female egg laying.
5. Our results imply that plasticity in breeding phenology does not provide pied flycatchers with a non-genetic inheritance route to rapidly advance annual cycles. Instead, plasticity may rather masks (genetic) trait-variation for selection to act on, and thereby slow down micro-evolutionary adaptation to changing environments.

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KEYWORDS

breeding phenology, constraints, early-life environment, heritability, migration schedule, ontogenetic effect, photoacceleration, photoperiod

1 | INTRODUCTION

Organisms are wonderfully adapted to the environments they live in. In this era of global change, species should adapt to the enormous human impact on the planet, or they will likely face declines, ultimately leading to severe loss of biodiversity. Climate change has affected many organisms in different ecosystems (e.g. Root et al., 2003), with the main responses being shifts of species' ranges (Thomas et al., 2001) and advances in phenology, which often change at different rates across trophic levels (Thackeray et al., 2016). It seems paradoxical that migrants have more difficulty in adapting to environmental changes than resident species, despite their evolved life-style to traverse vast distances and make use of seasonally changing resources (Both et al., 2010; Wilcove & Wikelski, 2008). Yet, it may depend on the specific response modes of all the involved traits throughout their annual routines whether environmental changes can be successfully tracked (Botero, Weissing, Wright, & Rubenstein, 2015). If we want to understand human impacts on the functioning of ecosystems, it is crucial to study how well species, including those with complex life-styles, are able to adapt whole suites of traits to their environments.

The long-distance migratory pied flycatcher *Ficedula hypoleuca* has been intensively studied for understanding migrants' ability to adapt to climate change. Increased spring temperatures have led birds to advance their egg-laying dates, and/or arrival dates in some populations (Ahola et al., 2004; Both & te Marvelde, 2007; Both & Visser, 2001; Both et al., 2004; Lehikoinen, Sparks, & Zalakevicius, 2004; Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016). As in most long-distance migrants, pied flycatchers start their spring migration at their wintering grounds, where they lack direct information on the progress of spring at their breeding sites (e.g. Berthold, 1996). The observed responses have often been explained as phenotypic plasticity, with birds incorporating local environmental conditions into timing decisions once they get closer to or are at their breeding sites (e.g. Ahola et al., 2004; Lehikoinen et al., 2004; Phillimore et al., 2016). The lack of change in spring arrival dates, as observed in some populations (Both, Bijlsma, & Visser, 2005; Hüppop & Winkel, 2006), was interpreted as inflexibility associated with the mechanism controlling migration departure.

The notion of a rigid photoperiodic control of migration comes from laboratory studies that described (inherited) circannual clocks and photoperiodic responses (Gwinner, 1989, 1996). However, the relative importance of ontogenetic effects and plasticity for fine-tuning the onset of spring migration in the wild to external conditions are not well understood. Although earlier studies showed no changes in arrival (Both & Visser, 2001; Hüppop & Winkel, 2006), recently pied flycatchers breeding in western and central Europe have been observed to migrate progressively earlier during spring through North

Africa (Both, 2010). Several mechanisms can potentially explain advances in migration onset.

Population advances in arrival or laying dates in other migrants have been suggested to be of genetic origin (Jonzen et al., 2006), the result of phenotypic plasticity (Charmantier & Gienapp, 2014; Phillimore et al., 2016; Tarka, Hansson, & Hasselquist, 2015), or driven by ontogenetic processes (Gill et al., 2014). Non-genetic inheritance has been argued to allow faster transmission of adaptive traits across generations when environments change rapidly, as the lag-time associated with evolutionary (genetic) adaptation is eliminated (Bonduriansky & Day, 2009).

Both (2010) proposed that advancements in spring migration through North Africa resulted from non-genetic inheritance in which earlier laying by female flycatchers facilitated earlier migration schedules in their offspring due to changes in the perceived environment during ontogeny. The variation in spring recovery dates in North Africa was partly explained by variation in hatch date, in interaction with breeding latitude in Europe (Both, 2010). At Southern breeding populations all chicks are born before the summer solstice, and later born chicks were found migrating later through Northern Africa. In contrast, more Northern born individuals were mostly born after the summer solstice, and at these sites a negative correlation between hatch date and migration date through Northern Africa was observed. Both (2010) hypothesized that a photoperiodic response during ontogeny could underlie this date effect in pied flycatchers. Photoperiod is a well-known and reliable anticipatory cue for the timing of future important life-history events (Bradshaw & Holzapfel, 2010). Photoperiod allows adult migrants to synchronize their "internal clock" (Berthold, 1996) and trigger migration preparations (Gwinner, 1989), while photoperiodic cues at hatching can affect the onset of moult and autumn migration in young birds (Coppack, Pulido, & Berthold, 2001). Positive effects of light on the development (the so-called photoacceleration) of embryos or juveniles have been commonly found (e.g. Berthold, 1996; Clark & Reed, 2012; Cooper, Voss, Ardia, Austin, & Robinson, 2011). In the wild, seasonally changing photoperiods can covary with many other factors that may also cause hatch date effects, and influence offspring traits via carry-over effects, phenotypic plasticity, genetic and non-genetic inheritance (Bonduriansky & Day, 2009; Gienapp, van Noordwijk, & Visser, 2013; Senner, Conklin, & Piersma, 2015).

The aim of our study is to experimentally test the hypothesis that hatch date causally affects the timing of spring arrival and egg laying in pied flycatchers during their adulthood. If photoperiod is the main cause underlying "hatch date-timing" correlations, we expect that chicks born later in the season—thus perceiving longer day lengths in our study population—will migrate later during adulthood and females lay their eggs later. However, migratory life cycles as we observe them

will not only depend on the control mechanisms and cue use, but also on the individual ability to behave accordingly (Winkler et al., 2014). Constraints during migration may potentially uncouple the onset of migration from the arrival dates (Both, 2010). To test the existence of early-environmental effects in a migrant's naturally complex environment, we therefore repeated our delayed hatching experiments in 3 years (2009–2011) and monitored arrival and egg-laying dates of control and experimental recruits in subsequent years (2010–2014). We do not know to which extent response modes and constraints vary across individuals, and therefore take differences among sexes and age classes into account. This field study will help judging how important a causal hatch date effect on timing events during adulthood may be for long-distance migrants, and whether this can facilitate rapid adjustments to climate change.

2 | MATERIALS AND METHODS

2.1 | Study species and area

Pied flycatchers breed in temperate forests across Europe and into West Asia. These long-distance migratory passerines winter in sub-Saharan Western Africa, with our study population being concentrated around $7.4^{\circ}\text{W} \pm 1.0^{\circ} \text{SD}$ (Ouwehand & Both, 2017). They are single-brooded with bi-parental brood care and females lay between four and eight eggs (Lundberg & Alatalo, 1992), usually one egg per day. Our study area was located in Drenthe, The Netherlands (NL, $52^{\circ}49'\text{N}$, $6^{\circ}22'\text{E}$) where 1,100 nest boxes (inner dimensions: $90 \times 120 \times 230 \text{ mm}$, entrance hole 32 mm) were subdivided over 12 study plots that are dominated by oak (primarily *Quercus robur*), oak-mixed or coniferous (mainly *Pinus* ssp.) habitat. The annual number of pied flycatcher breeding pairs rose from 187 at the establishment in 2007 to around 350 in 2011, when it stabilized (Both, Bijlsma, & Ouwehand, 2016; Both et al., 2017). Nest boxes were visited on intervals of 5 days or fewer from the beginning of April.

Spring arrival was visually monitored at least every other day from early April until mid-May. For male flycatchers, arrival was based on territorial behaviour. Female arrival dates were estimated from observations on either female appearance, male behavioural changes that indicated pair formation, or, from the onset of nest-building. Male and female identities as inferred from these observations were checked and confirmed when captured later in the season. Arrival dates of birds also tracked by geolocation indicated a high accuracy of our field methods to determine individual arrival dates (see Both et al., 2016). Newly built nests were checked at least every other day for egg laying. Actual egg hatch dates were defined by daily nest checks around predicted hatch dates. At day 7 of nestling age, parents were caught, ringed, sexed and nestlings were ringed and weighed. The sex of adults was determined from plumage characteristics and the presence of a brood patch. Nestlings were measured again (fledgling weight) at day 12, i.e. shortly before they fledge at an age of around 15 days. Since 2007, all chicks are ringed and >90% of breeding adults are captured (Both et al., 2017).

2.2 | Experimental procedure

We delayed hatch dates to study the causal effect of hatch date on timing during adulthood. Experiments were conducted during the breeding seasons of 2009, 2010 and 2011. Nests with similar laying dates were randomly assigned to a control or delay treatment. Both treatments started when nests contained one or two eggs, and we daily replaced freshly laid eggs with dummy eggs, and stored the eggs in a cup with cotton wool at a cool place. Local storage, in a hole in the ground beneath the nest box, kept the eggs cool and minimized handling. We assumed the clutch to be completed if clutch size reached six eggs, and no new egg was found the subsequent day. For smaller clutches, we waited another day before we assumed a complete clutch, to circumvent the possibility of laying gaps and return of the eggs before clutch completion. For control nests, all original eggs were returned to the nest at that point, which resulted in delayed hatching of 1 day relative to unmanipulated nests. For delayed nests, original eggs remained in the ground for 7 more days in 2009 or 6 more days in 2010 and 2011 and were then returned to the nest. Females with delayed broods thus incubated dummy eggs for a week, before incubating their own eggs. In total 401 nests were manipulated as control or delay (Burger, 2014). For eggs laid early in the season, the shift in hatch date reflects a bit larger chance in day length than for eggs laid later in the season (respect. a 20- or 14-min shift per 7 days' delay in hatching, see Figure S1).

Cold storage of eggs could affect hatching success of eggs and subsequent development of the young (Wiggins, Pärt, & Gustafsson, 1998). A comparison between unmanipulated nests, non-supplemented control and delay nests, revealed only marginal negative effects on nestling parameters, and somewhat higher hatching failures in 2009 (especially in delayed nests) due to moisture in the cups used for storage and late nests being abandoned by females (Burger, 2014). Therefore, protocols in 2010–2011 were changed towards a shorter delay time (6 days) and the cotton wool in the cups was kept as dry as possible. No abnormalities were observed during chick growth in any of the successfully hatched eggs that hint at developmental problems in the embryo. We expect that the slight differences in egg storage were therefore negligible.

We monitored arrival and laying date in at least three subsequent years after each experimental season (i.e. 2010–2014), since many chicks do not recruit locally in their first year, but only in later years (Both et al., 2017). We obtained in total 102 arrival observations for control (female: $n = 44$; male: $n = 58$) and 69 for delayed chicks (female: $n = 34$; male: $n = 35$), which includes observations of birds seen in several years.

This study was part of a larger experiment in which half of all control and delay nests also received supplemental food, from chick age of 3 days until the young fledged (Burger, 2014). These nests were provided daily 30 g of mealworms, i.e. the amount that is thought to account for about one-third of the daily energy needs of the brood (Verhulst, 1994). Parents used this food to feed their young, but they could also use it for themselves. We pooled nests with and without food supply, since (1) we expect the photoperiodic effect

to be independent of food availability, (2) previous analysis revealed only marginal (and variable) effects of food supplementation on fitness components of young and offspring recruitment rates (Burger, 2014), (3) no effects of food supply on chick mass at an age of 12 days ("food": $F = 0.76$, $p = .39$, mean difference = 0.013 g; "food \times treatment": $F = 0.11$, $p = .74$) or recruitment (see "Statistics" section) were found within this study.

2.3 | Statistics

We describe the effect of hatch date on timing of adult arrival and egg laying (expressed as day: 1 = 1 April) for a large dataset with natural variation in hatch dates (hereafter, descriptive dataset), and for an experimental dataset of control and delay chicks born in 2009–2011 (data available at the Dryad Digital Repository <https://doi.org/10.5061/dryad.d0cp4>). In the descriptive dataset, hatch date represents natural date variation, while in the experimental dataset, hatch date variation is a combination of natural hatch date variation and the experimental delay in hatch date (also referred to as "experimental hatch date"). Spring arrival and laying dates were analysed for 2010–2014.

The descriptive dataset consists of almost 500 young born locally between 2007 and 2013 (with $n = 265$ arrival estimates in females and $n = 412$ in males) in non-experimental nests and the control nests of the experiment with a maximum of five observations per bird. The analyses on the natural hatch date variation will reveal whether there is a general positive correlation between hatch date and timing later in life, and whether this effect differs among arrival years. This among year variation will indicate when we have a good ability to test for causal hatch date effects with our delayed hatching treatment in the experimental dataset. We only expect to find experimental hatch date effects in control and delayed chicks when environmental conditions allow for the expression of such individual variation (i.e. thus, when also found in our descriptive dataset).

Because egg-laying dates in males are largely determined by their females and were not repeatable within males (Both et al., 2016), effects on laying dates were only investigated in females. In our study, egg laying dates were correlated with arrival dates in females in all years, in both the descriptive and experimental dataset (i.e. respect. for 2010 $\beta_{2010} = 0.84$, 0.85, $\beta_{2011} = 0.72$, 0.45, $\beta_{2012} = 0.61$, 0.74, $\beta_{2013} = 0.33$, 0.40, $\beta_{2014} = 0.72$, 0.83; $p = .06$ for 2013_{exp}; all other $p < .05$). For males, this relation was strong in 2011 and 2014 in the descriptive and experimental dataset ($\beta_{2011} = 0.63$, 0.56, $\beta_{2014} = 0.74$, 0.70; $p < .05$), but weaker ($\beta_{2010\text{-descr.}} = 0.27$, $\beta_{2012} = 0.37$, 0.24, $\beta_{2013\text{-descr.}} = 0.43$; $p < .05$) or absent in other years ($\beta_{2010\text{-exp.}} = 0.14$, $\beta_{2013\text{-exp.}} = 0.11$; NS).

For arrival and laying dates (analysed separately), we ran linear mixed models (LMMs) in both the descriptive and experimental dataset to test for the effect of hatch date (expressed as day: 1 = 1 April), a factor "year of arrival" (in short "year"), the interaction "hatch date \times year", and included "individual" as a random intercept. Significance of fixed effects was inferred with likelihood ratio tests against models without these terms (using maximum likelihood). Because timing of spring

migration in pied flycatchers varies according to a birds' age and sex (our population: Both et al., 2016), LMMs always included "sex" and "true age" (continuous: i.e. 1 = 1-year-old bird in its second calendar year, etc.) as predictors.

In addition, we tested more directly for treatment effects in the experimental dataset by studying whether a change in hatch date affected timing of arrival and laying, using an LMM with "treatment" (two levels: delayed vs. control), the interaction "treatment \times year," "true age" and "sex" as independent variables and "individual" as random effect.

We started with a balanced design in which delay and control nests were paired according to their laying date, that would under non-experimental conditions thus have had a similar expected hatch date (hereafter called: "original hatch date"; see Figure S1). We cannot control who survives to the next year, and the experimental design thus becomes more "loose" over time, which can be a problem if birds from specific groups are affected differently. Previous research using the same experiment, however, suggest that selective disappearance is probably not large or biased towards specific groups: experimental and naturally early-born offspring did not recruit more often than late-born offspring (Burger, 2014). Within our own dataset, recruitment rates were not affected by experimental hatch date ($\chi^2 = 1.92$, $df = 1$, $p = .17$), delay treatment ($\chi^2 = 1.43$, $df = 1$, $p = .23$) or food supplementation ($\chi^2 = 0.13$, $df = 1$, $p = .72$), as inferred from quasi-binomial generalized linear models. In total 8% of the control chicks and 6.6% of delayed chicks recruited into the population. Similarity in the means and overall distributions of "original hatch date" among control and delayed birds for which we had timing data indicate that our experimental design was reasonably well maintained within those birds that survived and returned to our population (arrival date: Mann–Whitney U : $W = 3505.5$, $p = .97$, Kolmogorov–Smirnov: $D = 0.13$, $p = .52$); female laying date: Mann–Whitney U : $W = 712.5$, $p = .76$, Kolmogorov–Smirnov: $D = 0.22$, $p = .31$). For birds recruiting into our population, delayed chicks had thus similar original hatch dates as controls, while their experimental hatch date was on average 5.8 days later. To account for more subtle changes in the experimental set up, we included "original hatch date" (i.e. experimental hatch date *minus* the experimental shift in hatch days) as covariate to the LMMs.

In a post hoc analysis, we explored if "food supply" (yes or no) indeed did not influence timing traits in our study (as we assumed: see Experimental procedure section), by expanding final LMMs (Table 1) with "food supply" or replacing "treatment" by "food supply."

Lastly, we investigated how sex-specific and permanent hatch date effects were in both datasets. For spring arrival timing, we expanded the final LMMs (Table 1) with an interaction "sex \times hatch date" (both datasets) or "sex \times treatment" (experimental dataset). In case the final model in our previous analyses also included an interaction of "year \times hatch date" or "year \times treatment" we also tested its three-way interaction with sex. To investigate whether hatch date effects only occur in young birds or are present also in older birds, we ran separate LMMs to test for interactions of age and "hatch date" or

TABLE 1 Most adequate linear mixed models that describe the role of hatch date and delayed-hatching treatment on timing of spring arrival (a) and female egg laying date (b) in pied flycatchers. Likelihood ratio statistics (χ^2) and p -values for fixed effects or interactions were obtained by comparing them to reduced models (using ML). Cases where hatch date or treatment effects dropped from the final models are denoted by —. In case of significant interactions, associated main terms were kept in the model (significance not shown). Estimates of fixed effect terms in the final models are calculated using REML (year “2010”, “female” sex and “control” birds were chosen as reference categories). Year reflects always to the year of laying or arrival. ID refers to the individual, and was fitted as a random intercept. In the descriptive dataset, hatch date refers to natural date variation, while in the experimental dataset hatch date is a combination of natural hatch date variation and experimental delays in hatch days. “Original hatch date” refers to the hatch date *minus* the experimental change in hatch days

(a) Spring arrival date						(b) Female egg laying date				
Parameter	β	SE	χ^2	df	p	β	SE	χ^2	df	p
<i>Descriptive dataset</i>										
ID	10.52	3.24				15.93	3.92			
Intercept	16.18	7.51				37.11	0.99			
Sex “male”	−7.86	0.59	152.05	1	<.00001					
True age	−0.83	0.25	11.29	1	.0008	−0.94	0.34	7.69	1	.0055
Hatch date	0.24	0.14				—	—	1.77	1	.18
Year								23.17	4	<.0005
“2011”	−6.46	9.85				−2.49	1.09			
“2012”	18.16	9.31				0.72	1.14			
“2013”	4.81	9.11				2.30	1.13			
“2014”	−6.66	9.17				0.81	1.18			
Hatch date × year			10.94	4	.027	—	—	4.2	4	.38
Hatch date, “2011”	0.04	0.19								
Hatch date, “2012”	−0.32	0.18								
Hatch date, “2013”	−0.13	0.18								
Hatch date, “2014”	0.12	0.17								
<i>Experimental dataset</i>										
ID	6.52	2.55				7.30	2.70			
Intercept	14.71	6.08				37.31	1.90			
Sex “male”	−5.91	1.08	27.91	1	<.00001					
True age	−1.78	0.86	4.23	1	.039	−0.18	1.04	0.03	1	.86
Year			30.31	4	<.00001			11.11	4	.025
“2011”	−2.51	1.89				−4.81	2.21			
“2012”	4.95	1.92				−1.56	2.13			
“2013”	−0.33	2.48				0.65	2.85			
“2014”	3.44	3.11				−3.23	3.55			
Hatch date	0.23	0.10	5.02	1	.025	—	—	1.60	1	.21
Hatch date × year	—	—	5.77	4	.22	—	—	5.62	4	.23
ID	5.10	2.26				4.61	2.15			
Intercept	8.96	6.78				33.34	7.52			
Original hatch date	0.30	0.13	5.78	1	.016	−0.02	0.15	0.02	1	.89
Sex “male”	−5.87	1.05	29.57	1	<.00001					
True age	−2.41	0.89	7.61	1	.0058	−0.22	1.14	0.04	1	.83
Year										
“2011”	0.66	2.37				−1.48	2.76			
“2012”	9.73	2.38				3.51	2.64			
“2013”	4.81	2.93				5.62	3.39			
“2014”	10.56	3.59				3.37	4.28			

(Continues)

TABLE 1 (Continued)

(a) Spring arrival date						(b) Female egg laying date				
Parameter	β	SE	χ^2	df	p	β	SE	χ^2	df	p
Treatment "delay"	7.77	2.80				12.41	3.14			
Treatment \times year			13.26	4	.010			16.18	4	.0028
"Delay", "2011"	-5.91	3.48				-9.11	4.00			
"Delay", "2012"	-9.38	3.38				-12.35	3.68			
"Delay", "2013"	-9.08	3.57				-12.24	3.98			
"Delay", "2014"	-12.58	3.80				-15.82	4.28			

"treatment". Age upon arrival was included as a two-level factor "age class": i.e. birds arriving in the year after the experimental treatment (hereafter, "first-year") or at older ages, as we expect such differences to be largest between these life stages. For the descriptive dataset, we expanded the final LMM with "age-class \times hatch date" and in case the LMM included also "year \times hatch date," also the three-way interaction "age-class \times hatch date \times year". For the experimental dataset, age-interactions were investigated in more simple models, excluding all interaction terms with "year," because these terms are partly confounded in our experimental dataset. For example, all birds in our experimental dataset that arrived in 2010 are first-year birds, while in 2013 and 2014 all are older, since experimental delays only were done in 2009–2011.

All analyses were performed in the R statistical environment (v. 3.2.2; R Development Core Team), with "lmer" function from the R-package "lme4" to run LMMs (Bates & Maechler, 2009). Model estimates of timing values are illustrated, using the means \pm 95% confidence intervals using the "effects" package (Fox, 2003).

3 | RESULTS

Spring arrival dates during adulthood (2010–2014) correlated positively with variation in hatch date in our descriptive dataset (individuals born between 2007 and 2013), but this effect differed between years in which birds arrived (Figure 1a; "hatch date \times year": $\chi^2 = 10.94$, $df = 4$, $p = .027$). Spring arrival dates were positively correlated with birth dates in 2010, 2011 and 2014, arriving respect. 0.24, 0.28 and 0.36 days later per day of later hatching, while flat or very shallow regression lines occurred in 2012 and 2013 (respect. -0.08, 0.18 day/day). In contrast, we found no significant effects of hatch date on the timing of egg laying in females (Figure 1c; $\chi^2 = 1.77$, $df = 1$, $p = .18$), neither in interaction with year ($\chi^2 = 4.2$, $df = 4$, $p = .38$).

In the experimental dataset, hatch date affected timing of arrival ($\chi^2 = 5.02$, $df = 1$, $p = .025$; Table 1) of birds during adulthood, with a 0.23 day later arrival in spring with each day chicks were born later. Given the year-specific expression of the hatch date effect on adult arrival in the descriptive dataset, it is surprising that we found no proof for significant year-specific variation in slopes in the experimental dataset ($\chi^2 = 5.77$, $df = 4$, $p = .22$). Consistent with the

descriptive dataset, hatch date did not affect female laying dates ($\chi^2 = 1.6$, $df = 1$, $p = .21$) nor in interaction with year ($\chi^2 = 5.62$, $df = 4$, $p = .23$).

Based on the descriptive data, we expected to detect an experimental delay effect mostly in timing of arrival in 2010–2011 and 2014. In 2010, an experimental delay in hatching resulted in a 7.8 day later arrival in spring compared to control birds (Figure 2a), but weak or no delays in later years ("treatment \times year": $\chi^2 = 13.26$, $df = 4$, $p = .010$; Table 1). Interestingly, a year-specific treatment effect occurred also in egg-laying dates of females (Figure 2b; $\chi^2 = 16.18$, $df = 4$, $p = .0028$), despite the presumed low power to detect experimental effects in egg laying. Females that perceived delayed hatching, laid their eggs 12.4 days later in 2010 than control chicks, while weak (3.3 days in 2011) or no delays occurred in later years (see Table 1). Thus, an experimental delay resulted in later spring arrival and egg-laying dates in 2010 (and less so in 2011) compared to control birds (Figure 2). In contrast, delayed birds arrived and laid their eggs in 2014 on average earlier (respect. 4.8 and 3.4 days) than controls, rather than later, although variation in each group was large (Figure 2, Table 1). Despite their non-significance (Table 1), the year-specific slopes of experimental hatch date effects on timing during adulthood (Figure 1b,d) illustrate that the experimental effects are not necessarily in line with the effects found in the descriptive dataset (Figure 1a,c). The later arrival and laying in 2010 of delayed chicks compared to controls (Figure 2) also led to seemingly steeper slopes of the experimental hatch date effect in 2010 (Figure 1b,d; respect. $\beta = 0.58$, $\beta = 0.65$), compared to those found for the natural hatch date variation in that year (Figure 1a,c; $\beta = 0.24$ for arrival and $\beta = 0.06$ for laying in 2010).

3.1 | Role of sex in hatch date effects

Spring arrival and egg laying showed seemingly different relations with hatch dates. This difference might result from different response modes of these timing traits, or arise from sex-specific responses. We tested the latter by considering sex specific effects on arrival date. In the descriptive dataset, the strength of the year-specific correlations between arrival timing and natural hatch date differed among sexes ("hatch date \times sex \times year", $\chi^2 = 28.03$, $df = 8$, $p = .0005$). In males the effects were most pronounced in 2010 and 2014 (respect. $\beta = 0.41$,

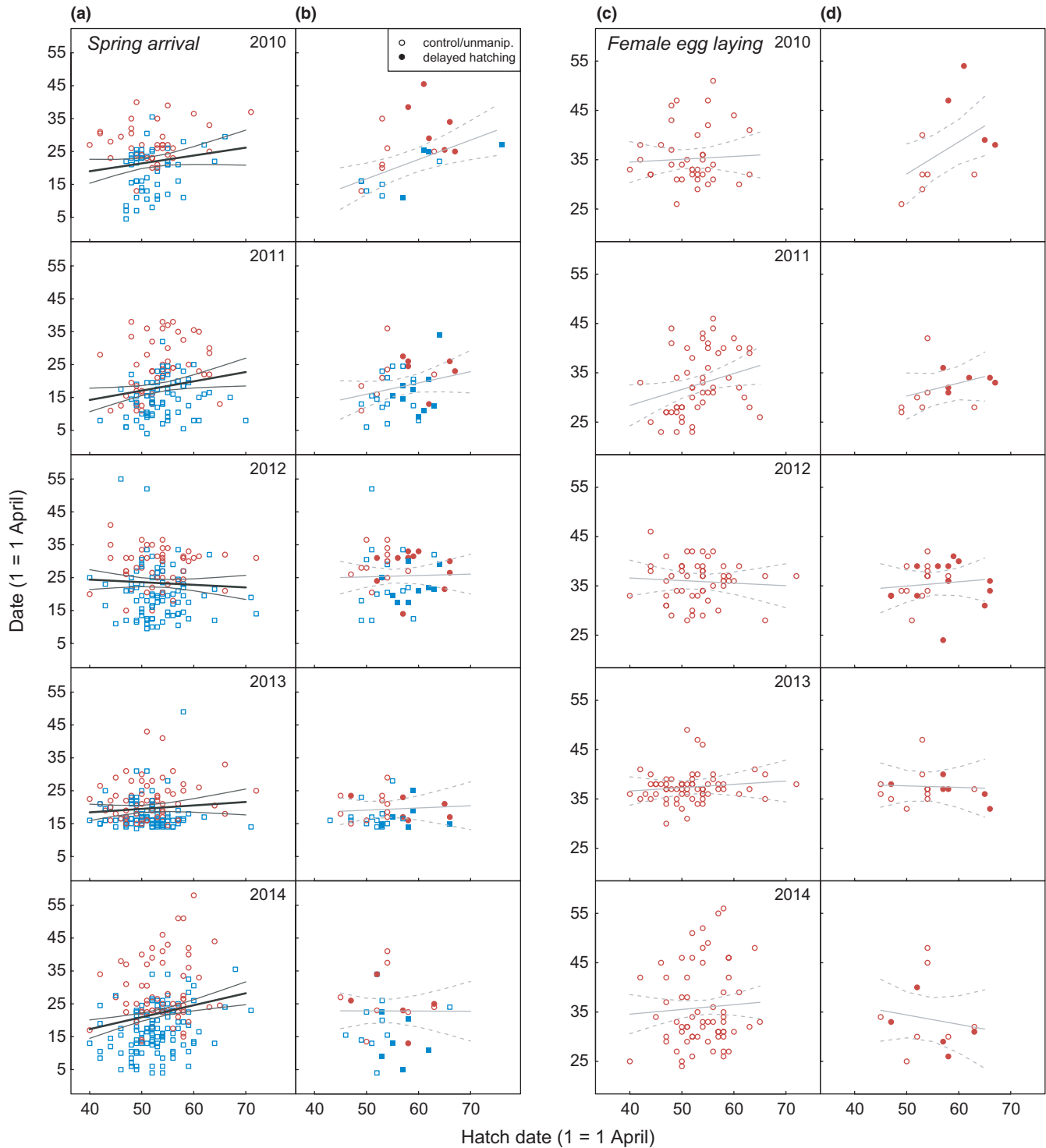


FIGURE 1 Timing of spring arrival and laying of adult pied flycatchers in relation to their hatch date (males in blue squares; female in red dots). The relation between natural variation in hatch date of chicks born in 2007–2013 and timing later in life (2010–2014) varied significantly across years in (a) spring arrival date. No such natural hatch date effects were found on egg laying dates (c). The experimental hatch date (b, d) of control and delayed chicks that received a hatching treatment in 2009–2011 positively influenced spring arrival, but not egg laying, without proof for significant variation in slopes between years (b, d). Regression lines indicate the estimated mean hatch date effect on timing and 95%-confidence intervals in interaction with year (significant interactions are shown in bold) as inferred from LMMs with individual as random intercept, and also included “true age,” and for spring arrival, “sex”

$\beta = 0.39$ day/day), whereas in females this was true in 2011 ($\beta = 0.42$ day/day). Experimentally manipulated males and females did not show different responses in arrival date when their hatch dates were

delayed, as inferred from non-significant interaction terms (i.e. “treatment \times sex”, “treatment \times sex \times year”, “hatch date \times sex” or “hatch date \times sex \times year”: all $p > .45$; see Table S1).

3.2 | Role of age in hatch date effects

We found a clear positive effect of experimental hatch date on arrival date in the first year of life, but not at older ages (Figure 3a; “age class \times hatch date”: $\chi^2 = 4.32$, $df = 1$, $p = .038$; model incl. year, sex). For each day a chick was born later, it arrived 0.50 (± 0.16 SE) days later in the first year of life. First-year females that received delayed hatching as chicks laid their eggs 5.3 (± 2.2 SE) days later than control birds (Figure 3b), but no difference was seen in older females (“treatment \times age class”: $\chi^2 = 3.55$, $df = 1$, $p = .059$). Yet, this did not result in a significant age-dependent experimental hatch date effect in laying date ($\chi^2 = 2.23$, $df = 1$, $p = .14$). Remarkably, no age-specific hatch date effects were found within the larger descriptive dataset (see Table S1), neither in timing of arrival (“hatch date \times age class”: $\chi^2 = 0.31$, $df = 1$, $p = .58$; “hatch date \times age class \times year”: $\chi^2 = 12.68$, $df = 4$, $p = .12$) nor in female egg-laying dates (“hatch date \times age class”: $\chi^2 = 0.003$, $df = 1$, $p = .95$; Table S1).

4 | DISCUSSION

To improve our understanding of organisms' ability to adjust complex life cycles to climate change, we investigated if an ontogenetic effect

of hatch date in avian long-distance migrants causally affects timing of spring migration and egg laying during adulthood. Pied flycatcher spring arrival dates were positively correlated with the natural variation in hatch dates in three of the 5 years considered. If a photoperiodic cue during hatch date underlies these correlations, then we expected that an experimental delay in hatch date would also become visible as a delay in timing in years with positive correlations: i.e. in 2010–2011 and 2014 for spring arrival. Consistent with this, we found that experimentally delayed chicks arrived considerable later in 2010 (and a bit in 2011). However, in 2014, there was a discrepancy between experimental and natural hatch date effects. We also found inconsistent results for effects on female laying date: year-specific treatment effects were present after a delay, but surprisingly, no effect of natural hatch date variation occurred. Our findings therefore imply that different mechanisms contributed to the observed hatch date effects on timing during adulthood, rather than a single ontogenetic (possibly photoperiodic) hatch date effect—as proposed by Both (2010)—being responsible for experimental and hatch date effects in both our datasets.

Our study experimentally tested the role of ontogeny in migratory and reproductive timing. However, positive timing trait correlations as observed may also result from genetic inheritance of timing traits. Indeed, heritability of female laying dates measured over a prolonged period is considerable ($h^2 = 0.33$; Visser et al., 2015) in pied flycatchers (but see Both, 2010; Both & Visser, 2001). Therefore, we propose that positive hatch date correlations with arrival dates in 3 years, but the general lack of effects in female egg laying and two arrival years, rather arises from fluctuations in the extent of plasticity in timing traits. We hypothesize that variation in time schedules is prevalent at departure from the wintering grounds, but this variation can be obscured if migration conditions are unfavorable, and thereby disrupt the correlation between African departure and arrival at the breeding grounds (e.g. in 2012, 2013). Similarly, birds may plastically adjust the interval between arrival and egg laying to spring temperatures (Both & Visser, 2001), and thereby alter the expression of genetic variation in laying dates. Relatively weak correlations between arrival and egg laying dates in females (e.g. 2013: $\beta = 0.33$, descriptive dataset) may indicate such additional plasticity in specific years. Our previous study on consistency and repeatability of spring timing traits supports this idea of fluctuating plasticity; which was stronger in females than in males of our population (Both et al., 2016).

The extent of plasticity likely differs between and within populations. For example, in Finland, pied flycatchers showed changes in arrival dates and little “apparent plasticity” in egg laying dates, mainly because temperatures during their spring migration became more favourable, while temperatures at the breeding sites did not change (Ahola et al., 2004). Similarly, subsets of birds may respond differently. A meta-analysis of migratory songbirds revealed that timing of migration in early individuals was more affected by climatic variation compared to individuals on later passage (Tøttrup et al., 2010). Because years and areas vary in environmental circumstances, plasticity to these conditions may affect correlations between hatch date and later timing traits, and also affects the likelihood of genetic variation being expressed. Plasticity to fluctuating environmental conditions may even be so strong that this leads to delayed breeding within a population,

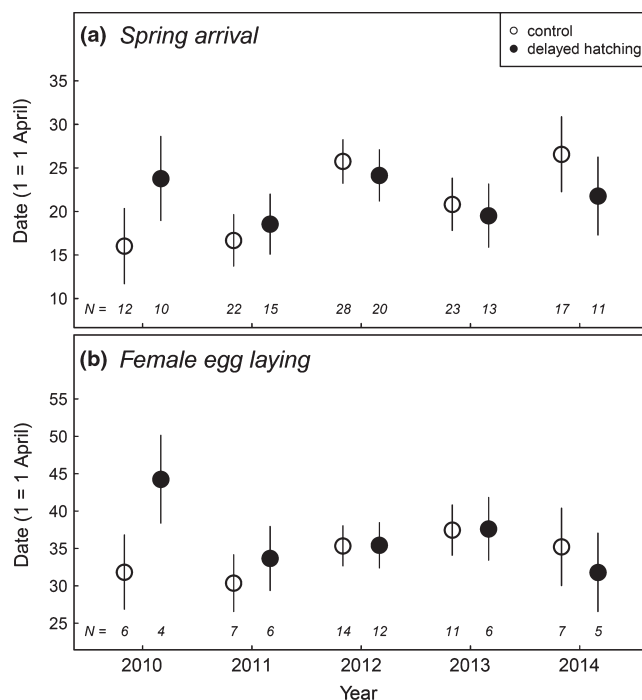


FIGURE 2 Timing of spring arrival (a) and female egg laying (b) of pied flycatchers that received a control treatment or an additional hatching delay of 6–7 days as chicks in 2009–2011. The effect of a delayed hatch date on timing during adulthood (2010–2014) varied among years, with clearly later spring arrival and egg laying dates in 2010. Shown are means and 95%-confidence intervals for the effect of “year \times treatment” on timing. Timing estimates were inferred from linear mixed models (with individual as random intercept) that also included “true age,” “original hatch date” (i.e. observed hatch date minus achieved experimental shift in hatch days) and, in case of spring arrival, “sex”

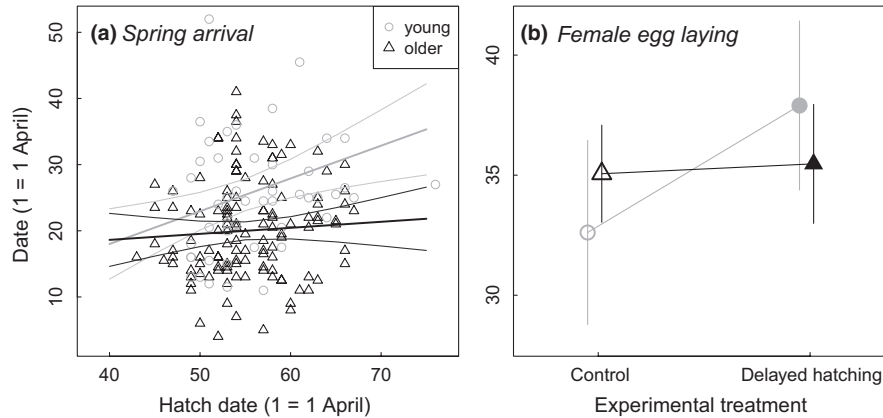


FIGURE 3 Timing of spring arrival (a) and female egg laying (b) was later for young pied flycatchers recruiting in their first year (symbol: circle) if they were born later in the season. When birds were older (symbol: triangle), the impact of early-life experimental hatch date variation (incl. shift) on arrival timing (a) or the experimental delay in hatching on timing of female egg laying (b) disappeared. Lines indicate the estimated means and 95%-confidence intervals for the hatch date or treatment interactions with "age class" in a linear mixed model with "individual" as random intercept, "year," "sex" (only for spring arrival) and "original hatch date" (only for egg laying)

despite the presence of strong heritability and fecundity selection for early laying (Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017). Thus, although phenotypic plasticity is often seen as a solution to track climatic variation in migration and reproductive decisions (e.g. Phillimore et al., 2016), it may also oppose or slow down life-cycle adjustments (Visser, 2008).

The large experimental delay effect on timing traits in 2010 shows that environmental effects are not always masking genetic expression, but can operate in the same direction. The early-life environmental effect likely is a temporal rather than a permanent effect since the experimental hatching delays resulted in later migration and egg laying in first-year birds, but effects were not evident in older birds (Figure 3). Experienced migrants are likely more capable than young birds to optimally perform their migrations (Newton, 2008), and have more time to compensate early-life effects.

Based on the year-to-year fluctuations in visibility of date effects in the descriptive dataset (Figure 1) we would expect that the power to detect experimental effects in first-year birds was high in 2011, reasonable in 2010, but very low in 2012. Yet, the experimental effect was largely driven by chicks recruiting in 2010 (Figure 2). Although our treatments yield an effective difference of 5.7 hatch days among control and delayed recruits, and did not influence overall recruitment rate, there were differences in the age at which birds recruited into our population. The fraction of 1-year-old recruits from our experiment differed among years: 44% of all first-year birds recruited in 2010 ($n = 27$), 24% ($n = 15$) in 2011, and 32% ($n = 20$) in 2012. The age-specific effect is thus mostly determined by the cohort born in 2009. This means that our ability to detect effects was different in all 3 years; either due to a limited number of first-year recruits (i.e. 2011) or because of year-to-year fluctuations in visibility of trait variation (i.e. being poor in 2012). It is therefore unclear if the early-life effect is always induced but sometimes masked or arises in specific birth years only.

It remains an open question what exactly has caused the ontogenetic delay effect that resulted in later migration and egg laying

in first-year experimental birds. Can this still be a photoperiodic effect? Photoacceleration is known to allow faster development in late-hatched migrants born under shorter day lengths and thereby guarantees a timely onset of autumn migration (as in Coppack et al., 2001). However, in our Dutch population, flycatchers have an early breeding phenology and therefore chicks born late in the season experience longer days than early born chicks (see Figure S1). Explaining our results by day length changes will thus require a photo-delay effect on spring migration. One may, however, argue that absence of a day length effect by photoacceleration in early breeding populations allows for the expression of inherited timing traits, and thus lead to a positive correlation between birth date and migration timing. While on the other hand, photoacceleration in birds born after the longest day may obscure expression of inherited timing traits in Northern populations or even has caused inverted trait-correlations (Both, 2010). In our study, we used experimentally delayed hatching as a method to study the causal effect of hatch date on timing, whereas we did not directly tested changes in photoperiod or the effect of an advance in hatch dates. Laboratory studies are needed to unravel if populations differ fundamentally in their cue-responses to photoperiod.

Alternatively, the positive environmental effect of delayed hatching in our population may originate from other factors that change seasonally over time and covary with date. An obvious candidate is caterpillar availability, as an important diet component, that showed seasonal variations during ontogeny. Despite differences in timing and height of the caterpillar peak in the experimental years, there was no strong support that seasonal declines in food altered chick fledging weights, fledging numbers or their overall recruitment rates (Burger, 2014). Effects of food limitation may potentially still influence timing in other ways, e.g. by affecting the quality of feathers (Jenni & Winkler, 1994), immune function or competitive ability, and thereby alter the migration departure, speed and/or subsequently arrival in the next breeding season. However, within our own dataset,

post hoc analyses did not reveal additional effects of food supply on arrival date ($\chi^2 = 1.73$, $df = 1$, $p = .19$) or female laying date ($\chi^2 = 2.23$, $df = 1$, $p = .14$), neither did food supply replace treatment effects (i.e. "year \times food": $\chi^2 = 1.97$, $df = 4$, $p = .74$ in arrival; $\chi^2 = 1.42$, $df = 4$, $p = .84$ in female laying).

It will depend on the specific mechanism underlying the experimental effect of hatch date, whether earlier laying can also promote earlier time schedules of offspring. Over the last three decades laying dates of pied flycatchers have been advancing by about 10 days, and this likely has been accompanied by a similar advance in spring migration dates (Both, 2010; Visser et al., 2015). The question is whether the (poorly understood) environmental effect of hatch date on young birds could be responsible for this advance, without an evolutionary change for earlier genotypes? If we assume that the individual time schedule is partly caused by genetic and partly by environmental conditions, individuals that arrive in warm years may advance the hatch dates and thereby the arrival schedule of their young. However, through this mechanism only first-year birds must progressively advance (but often do not breed, Both et al., 2017), and if this process would be true and continues, young females would arrive and breed earlier than older females. This would lead to an increasing delay in arrival from the first to the second year of breeding, whereas our data on arrival show that first-year females still arrive later than older females (Both et al., 2016). Hence, we consider is more plausible that when conditions are good, this simply increases the chance that genetic trait variation is expressed, while poor conditions either obscure trait variation or operate in the same direction.

In summary, we have experimentally demonstrated that early-life environmental effects around hatching can result in considerable delays in time schedules of long-distance migrants later in life, as studied in a free-living population of pied flycatchers. This was only visible in their first year and when environmental circumstances allow such an effect to be expressed. The discrepancy between experimental and naturally occurring hatch date effects as found in our study implies that variation in offspring phenology is not caused by parental egg-laying date and hatch date per se, but that such effects are likely a combination of inherited timing traits and environmental factors that can covary with parental egg-laying date. Our study highlights the importance of performing experiments across several years in the field, as this helps to judge the relevance of mechanisms that influence trait variation, expression and adaptive significance in their natural, but complex environments. Strong support for year-specific expression of hatch date and delay effects on time schedules implies that trait-variation can be easily obscured, and probably explains the lack of hatch effects on female egg laying. This masking of (likely) genetic variation, particularly in egg laying of females, might thereby slow-down life-cycle adjustments in our population, if genetic changes are required to further advance breeding dates in response to climate change (Visser, 2008). This contrasts with the proposed hypothesis of Both (2010) that earlier laying in parents promotes rapid transmission towards earlier phenotypes via a causal (photoperiodic) hatch date effect.

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AUTHORS' CONTRIBUTIONS

C.Bo and C.Bu designed the experiment; C.Bo, C.Bu and J.O. collected the data; J.O. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data that support this manuscript are available at the Dryad Digital Repository <https://doi.org/10.5061/dryad.d0cp4> (Ouwehand, Burger, & Both, 2017).

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SUPPORTING INFORMATION

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