

Phenotypic plasticity drives phenological changes in a Mediterranean blue tit population

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Abstract

Earlier phenology induced by climate change, such as the passerines' breeding time, is observed in many natural populations. Understanding the nature of such changes is key to predict the responses of wild populations to climate change. Genetic changes have been rarely investigated for laying date, though it has been shown to be heritable and under directional selection, suggesting that the trait could evolve. In a Corsican blue tit population, the birds' laying date has significantly advanced over 40 years, and we here determine whether this response is of plastic or evolutionary origin, by comparing the predictions of the breeder's and the Robertson-Price (STS) equations, to the observed genetic changes. We compare the results obtained for two fitness proxies (fledgling and recruitment success), using models accounting for their zero inflation. Because the trait appears heritable and under directional selection, the breeder's equation predicts that genetic changes could drive a significant part of the phenological change observed. We, however, found that fitness proxies and laying date are not genetically correlated. The STS, therefore, predicts no evolution of the breeding time, predicting correctly the absence of trend in breeding values. Our results also emphasize that when investigating selection on a plastic trait under fluctuating selection, part of the fitness-trait phenotypic covariance can be due to within individual covariance. In the case of repeated measurements, splitting within and between individual covariance can shift our perspective on the actual intensity of selection over multiple selection episodes, shedding light on the potential for the trait to evolve.

KEYWORDS

adaptation, animal model, breeder's equation, climate change, *Cyanistes caeruleus*, laying date, Robertson-Price equation

1 | INTRODUCTION

Human activities initiated fast and global climate changes (IPCC, 2014), impacting organisms' life cycles and biotic interactions (e.g. food webs, competition, Kharouba et al., 2018; Palumbi, 2001; Parmesan, 2006). These changes can generate selective pressures on a variety of traits, including morphology and phenology (Fugère & Hendry, 2018; Merilä, 2012). Populations may adapt to these changes

through phenotypic plasticity (Pigliucci, 2001; Stearns, 1989; e.g. Charmantier et al., 2008; Nicotra et al., 2010), or through microevolution (i.e. genetic changes, e.g. Gienapp et al., 2008; Hoffmann & Sgro, 2011; Merilä & Hendry, 2014; Teplitsky & Charmantier, 2019); and both can occur simultaneously (Bonnet, Morrissey, Morris, et al., 2019). These two mechanisms allow different responses to environmental changes and may be under different constraints (DeWitt et al., 1998; Hansen & Houle, 2004; Walsh & Blows, 2009).

Microevolution occurs through generations (Bell & Collins, 2008; Grant & Grant, 2006; Hairston et al., 2005), and requires additive genetic variation of the trait associated with heritable fitness variation. Phenotypic plasticity, defined as the phenotypic variability of a given genotype in different environmental conditions (DeWitt & Scheiner, 2004; Moran, 1992), may allow faster acclimation than microevolution (Diamond & Martin, 2016), but may reach its limits in new environmental conditions (Chevin & Hoffmann, 2017). Distinguishing these two mechanisms is, thus, essential, yet challenging, to predict evolution and persistence of wild populations (Diamond & Martin, 2016; Gienapp et al., 2008; Hendry, 2016; Hoffmann & Sgro, 2011; Matesanz et al., 2010; Merilä & Hendry, 2014).

Most predictions of responses to selection are based on the breeder's equation (BE hereafter; Lush, 1937; Walsh & Lynch, 2018 chap. 6), that is, the predicted change in the mean trait between two generations is equal to its heritability multiplied by the selection differential. Instead, the Robertson-Price equation (known as STS, for secondary theorem of selection, Frank, 2012; Morrissey et al., 2010; Price, 1970; Queller, 2017; Robertson, 1968; Walsh & Lynch, 2018 chaps. 6, 20) states that the expected evolutionary response of a trait corresponds to its genetic covariance with fitness. These two prediction methods are conceptually different, as the breeder's equation assumes a direct relationship between the trait value and fitness, at the phenotypic scale, while the STS only focuses on the additive genetic relationship between fitness and the trait (Lande & Arnold, 1983; Morrissey et al., 2010; Walsh & Lynch, 2018 chaps. 6, 20). In wild populations, selection is not directly applied on the trait value (as assumed in the breeder's equation) but is the result of complex, and not only directly causal, relationships between fitness and the trait of interest (Morrissey et al., 2010). The use of the STS targets, among the sources of relationships between the trait and fitness (e.g. genetic or environmental), only the one affecting genetic transmission to the next generation, and is, thus, more widely applicable to the context of wild populations.

In many studies, the expected microevolutionary responses based on predictions from the BE were not confirmed at the genetic level. These unexpected evolutionary stases could result from overestimated adaptive potential (e.g. unaccounted indirect genetic effects, or genetic correlations), inaccurate modelling and/or insufficient power (Merilä & Kruuk, 2001; Pujol et al., 2018). The predictions from the STS could alleviate many of these issues, and its use has been strongly advocated (e.g. Morrissey et al., 2010), yet it is still rarely applied (as it requires large data sets and complex statistical modelling). Predictions from the BE and STS have rarely been compared, although when they are, they sometimes converge (e.g. Bonnet et al., 2017), or diverge, with the BE predicting stronger responses to selection (e.g. Morrissey et al., 2012; O'Sullivan et al., 2019; Reed et al., 2016). Such comparisons could shed light on evolutionary mechanisms at play and for which we need more in depth understanding.

Among the studied responses to the ongoing climate change (e.g. increased spring temperatures), earlier phenology is common in a wide diversity of species (Kharouba et al., 2018; Radchuk et al., 2019; Walther et al., 2002). Yet these phenological changes seem

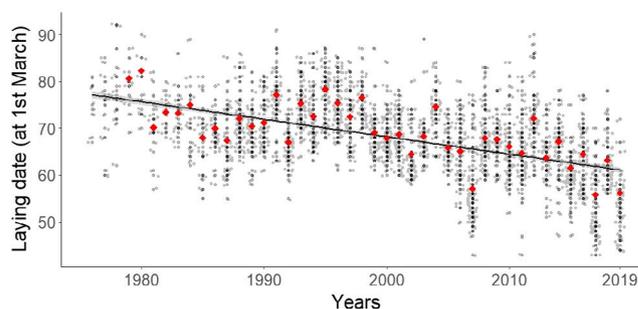


FIGURE 1 Phenotypic trend observed in laying date (1 = the 1st of March) since 1976 (sample size in TableS1). Annual averages are shown in red. The regression coefficient is -0.34 [$-0.46, -0.23$] (based on a Bayesian regression, with correction for annual and individual variances, for 100 000 iterations, thinning of 20, burning of 15 000)

to stem from plasticity rather than microevolution (Charmantier & Gienapp, 2014; Matesanz et al., 2010; Merilä & Hendry, 2014). This is puzzling, as selective pressures and heritability are non-negligible for many phenological traits, and an evolutionary response would be expected (Charmantier et al., 2006; Merilä & Kruuk, 2001; Pujol et al., 2018). Evolutionary responses have been rarely investigated, and even more rarely detected (Bonnet, Morrissey, & Kruuk, 2019; Kovach et al., 2012). The recent changes in laying date of insectivorous passerine birds, allowing them to track the phenology of their preys in a context of increasing spring temperature, is a well-studied example. Despite this trait being heritable (Postma, 2014, and supported by experimental set-ups, Verhagen et al., 2019) and submitted to strong selective pressures (e.g. Gienapp et al., 2006; Visser et al., 2015), so far, only plasticity was described as a driver of the birds' phenology shift (e.g. Charmantier & Gienapp, 2014).

We address these evolutionary and methodological questions using an intensively monitored population of blue tits (*Cyanistes caeruleus*, Passeriformes: Paridae). Their laying date significantly advanced over the past 44 years (about 14 days earlier, Figure 1), seemingly as an adaptation in response to the advancement of the density peak of their main food source for their chicks (the caterpillar *Tortrix viridana*, Lepidoptera: Tortricidae), following an increase in spring temperatures (Bonamour et al., 2019). Moreover, past studies described directional selection for earlier phenology (Porlier et al., 2012), genetic variation and plasticity for this trait (Bonamour et al., 2019; Charmantier et al., 2016; Delahaie et al., 2017; Porlier et al., 2012). It is, therefore, plausible that the observed phenotypic trend arises from microevolution or phenotypic plasticity (or both). To investigate the nature of this phenotypic change, we (1) analysed the phenotypic selection estimated with a fitness-trait regression over the whole data set, and further decomposed the phenotypic fitness-trait covariance into fitness-trait relationships arising from differences between individuals (inter-individual covariance) or from within individual variations (intra-individual covariance, i.e. residual fitness-trait covariance, Dingemanse et al., 2021). When multiple episodes of selection (here one per breeding period) are occurring for the same individuals, selection on the trait mean can

only emerge from the repeatable inter-individual fitness-trait covariation. In other words, genetic evolution throughout the study period is only expected if some individuals are consistently displaying a phenotype associated to high fitness. We (2) predicted the evolutionary response of laying date to selection using two distinct evolution models (BE and STS) to better understand the common discrepancy between expected and observed evolution in wild populations. As estimating fitness remains challenging (Hendry et al., 2018; Kingsolver & Diamond, 2011; Walsh & Lynch, 2018; Wolf & Wade, 2001), we implemented these two models for two fitness proxies. We were able to analyse how this influenced our selection measures, as the choice of the fitness component can be more or less representative of the selection applied to the trait of focus (Wolf & Wade, 2001). Our modelling also accounted for the fitness zero inflation (here with hurdle models, Bonnet, Morrissey, & Kruuk, 2019; Walsh & Lynch, 2018 chap. 29), which has not often been done, as it has been very difficult, until recently, to recombine parameters estimates from the process generating zeros and the Poisson process generating counts into a global model estimates. Finally, (3) we compared these predictions to the observed genetic trend as estimated by the trend in breeding values, as a noticeable change would support a genetic response of the trait (Hadfield et al., 2010; Pigeon et al., 2016).

2 | METHODS

2.1 | Study system

We studied a wild blue tit population in the Corsican forest of PIRIO (France, lat: 42.38, lon: 8.75) dominated by evergreen holm oaks (*Quercus ilex*, Fagales: Fagaceae, see Blondel et al., 2006 and Charmantier et al., 2016 for an extensive description of the population characteristics).

From 1976 to 2019, the team weekly monitored the nests boxes—provided in abundance—during the reproduction season, between April and June (67 boxes in 1976, 187 now, see Charmantier et al., 2016, for further details). Laying date was deduced from the number of laid eggs, as females lay one egg per day. The team captured and banded parents, and estimated their ages at the nest boxes, when chicks were at least 10 days old. The offspring were banded when 15 days old, and 1 week later, the number of chicks surviving (fledgling success) was estimated for each brood.

The mean population age is 2.29 years old. Dispersal is poorly known, and the recapture rate is estimated between 67% (males) and 86% (females, Bastianelli et al., 2021). Only first clutches were studied (second clutches represent less than 1% of breeding attempts, Marrot et al., 2015). Information on laying date, breeding success, and individual age was available for half of the monitored clutches and could be included in this study (between 1783 and 1132 individuals, Table 1 and Table S1). For many individuals, we only had one observation of laying date (49%, and females with laying date records for 2–4 years represent 45% of the data set).

2.1.1 | Pedigree

The pedigree is based on social relationships observed at the nest, although extra-pair paternity is known to occur in this population, (leading to a conservative estimation of genetic parameters, Charmantier et al., 2004). All individuals with unknown ancestry are considered as unrelated (i.e. founder individuals). We attributed a dummy identity to unknown parents (i.e. uncaptured) with banded offspring (to keep all information on siblings, but some of the 489 dummy females and 239 dummy males might be attributed to parents already ringed and registered in the database). The pedigree is, therefore, composed of a maximum of 2587 different individuals, including 2050 founders. The maximum depth of the pruned pedigree is 16 generations (Appendix S2). The pedigree was built, fixed and pruned, using the *pedantics* package (Morrissey, 2018).

2.1.2 | Modelling phenology and fitness

We chose the laying date to approach the reproductive phenology of this blue tit population, at the scale of each breeding pair (i.e. hypothesizing that most individuals have similar incubation and chick growth periods). Laying dates (LD) are expressed using March 1 as reference (for which LD = 1).

We focused on two annual fecundity measures to estimate fitness (ignoring selection via survival costs, Bastianelli et al., 2021; Verhulst & Nilsson, 2008): the number of fledglings and the number of recruits for each clutch (which are poorly correlated, $R^2 = 0.09$, $F = 90.77$, $df = 1 \text{ \& } 1118$, $p < 0.0001$). The number of fledglings represents the female fecundity and parental quality until the chicks reach maturity (Marrot et al., 2018; McCleery et al., 2004; Sauve et al., 2019), at about 21 days for blue tits (Charmantier et al., 2016). Descendants were considered recruits if they had been recaptured in the studied area during the breeding period (though they were not always breeding in a nest box when caught, see also Appendix S3 for discussion on the sampling bias). The number of recruits thus integrates parental care after fledgling and the offspring ability to survive and becoming a breeder.

2.2 | Statistical analysis

2.2.1 | Estimating selection pressures

Because we were interested in selection potentially leading to a change of the average phenotype in the population, and because quadratic selection has been estimated to be very weak (Porlier et al., 2012), we only estimated directional selection gradients and differentials.

First, we calculated selection differentials (S_p) as the phenotypic covariance between laying date and relative fitness (W'), using a bivariate linear model for each fitness proxy. To correct for annual variations, fitness was divided by its annual population mean, and laying

TABLE 1 Variables description and results of animal models (see the variable distribution in Figure S2)

	Standardized laying date N = 1783 1976-2019 (Equation 2)	Fledglings N = 1177 1976-2019 (Equation 3)	Recruits N = 1132 1976-2018 (Equation 3)
	Binomial $\mu = 0.93, SD = 0.26$	Binomial $\mu = 0.27, SD = 0.45$	Poisson $\mu = 1.34, SD = 0.66$
Intercept	83.11 [49.94, 112.75] (81.55)	-3.56 [-4.80, -2.28] (-3.50)	1.30 [0.80, 2.03] (1.41)
Age	-0.45 [-0.51, -0.39] (-0.44)	0.17 [-0.67, 0.95] (0.11)	-0.05 [-0.55, 0.33] (-0.12)
Age ²	0.05 [0.05, 0.06] (0.05)	-0.03 [-0.19, 0.09] (-0.04)	0.02 [-0.06, 0.08] (0.02)
Year	-0.04 [-0.05, -0.03] (-0.04)	-	-
Additive genetic variance V_A	0.14 [0.04, 0.22] (0.13)	0.01 [0, 1.30] (0.36)	0.002 [0, 0.46] (0.13)
Covariance _A (B, P)	-	0.003 [0, 0.12] (0.04)	0.0002 [0, 0.03] (0.01)
Annual variance V_Y	0.30 [0.18, 0.46] (0.32)	0.0001 [-0.01, 0.01] (0.001)	-0.001 [-0.12, 0.1] (-0.001)
Covariance _Y (B, P)	-	1.45 [0.43, 3.20] (1.71)	0.20 [0.03, 0.55] (0.27)
Female identity V_I	0.001 [0, 0.15] (0.06)	-0.04 [-0.14, 0.04] (-0.05)	-0.14 [-0.5, 0.04] (-0.21)
Covariance _I (B, P)	-	0.01 [0, 1.91] (0.56)	0.002 [0, 0.49] (0.14)
Covariance _P (B, P)	-	0 [-0.02, 0.02] (0.001)	-0.0002 [-0.07, 0.09] (0.002)
Male effect V_M	0.0002 [0, 0.3] (0.01)	2.14 [0.86, 5.30] (2.75)	-0.16 [-0.52, 0.05] (-0.21)
Residual variance V_R	0.23 [0.21, 0.26] (0.23)	-	-
Phenotypic variance V_P	0.93 [0.80, 1.20]	Fixed to 1	fixed to 1
Heritability h^2	0.13 [0.03, 0.21] (0.13)	0.03 [0.02, 0.03] (0.03)	0.23 [0.10, 0.47] (0.26)
		3.14 [1.86, 6.30] (3.75)	1.44 [1.11, 2.1] (1.56)
		7.88 [7.29, 8.83] (8.07)	0.53 [0.37, 0.98] (0.61)
		0.002 [0, 0.3] (0.09)	0.001 [0, 0.25] (0.08)
		0.0004 [0, 0.2] (0.01)	0.0004 [0, 0.04] (0.01)

Note: The laying date was modelled using a univariate animal model. The two fitness proxies were described with bivariate animal models (their Binomial and Poisson parts considered as response variables); we indicate the covariance between the Binomial (B) and Poisson (P) processes. Posterior modes are given with their 95% confidence interval in brackets; the mean estimates are given in parenthesis. For fitness models, estimates are given on the latent scale and observed scale (grey cells). Fixed effect estimates with 95% confidence intervals excluding zero are indicated in bold.

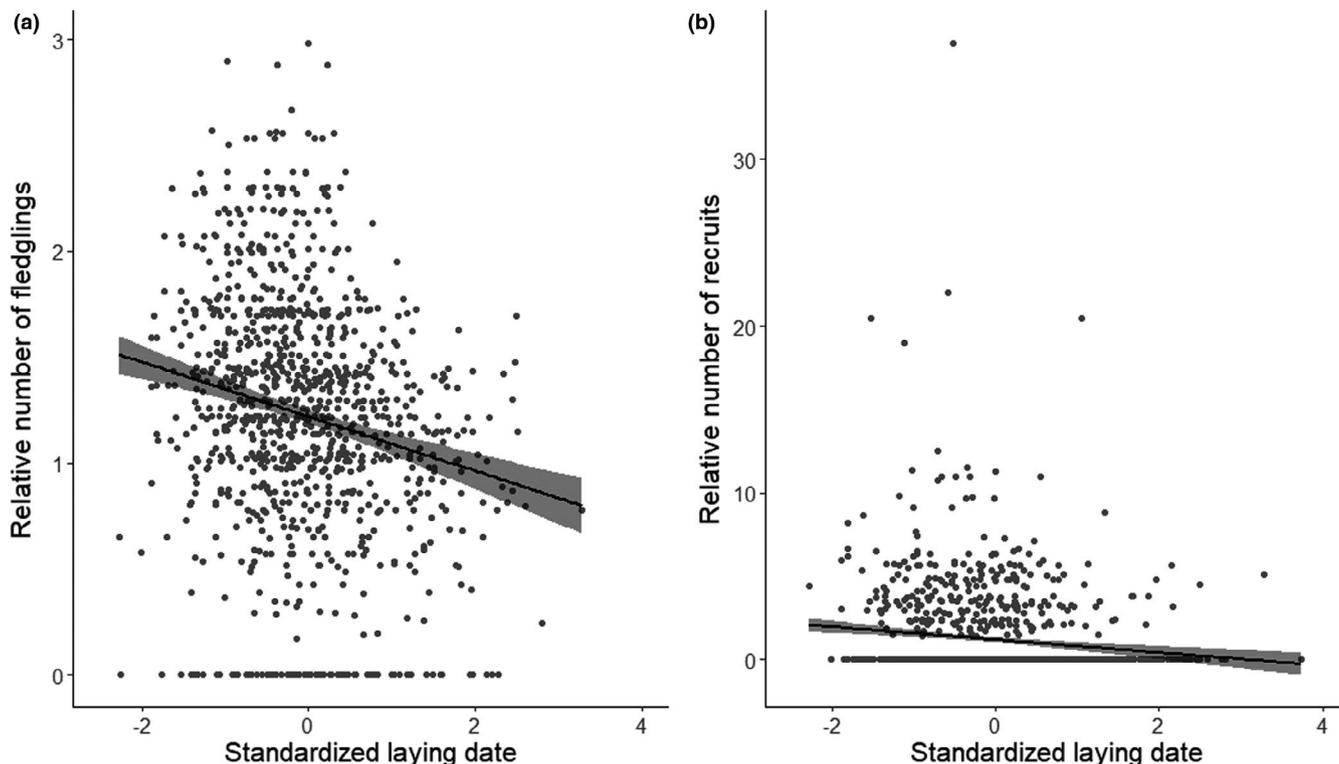


FIGURE 2 Linear regression of annual relative fitness and annually standardized laying date (standardized by annual mean and standard deviation), from which are derived selection gradients (β), with selective value approached by (a) the number of fledglings ($\beta = -0.12 [-0.16, -0.08]$), and (b) the number of recruits ($\beta = -0.33 [-0.48, -0.19]$)

date was centred at its annual mean (LD' , see Figure 2 for selection gradients). This standardization allows for the study of selection between breeding females within a given year. This covariance was further decomposed into inter- and intra- individual covariances, by including individual identity as a random effect (Dingemans et al., 2021), enabling to estimate the difference between individuals (on which selection can apply), while the residuals indicates how much is due to intra-individual differences (which depends on the individual's plasticity).

$$S_p = \sigma_I (LD', W') + \sigma_R (LD', W'). \quad (1)$$

We also estimated the selection gradient (β) over the entire data set (see Table S1 for sample sizes), based on a linear regression between laying date (centred by annual mean and divided by annual standard deviation) and the relative fitness proxy (W' , Hereford et al., 2004; Lande & Arnold, 1983; Wade & Kalisz, 1990).

$$\beta = \frac{1}{\bar{w}} \frac{dw}{dz}. \quad (2)$$

These models were implemented in the Bayesian framework, using the *MCMCglmm* package (Hadfield, 2019) and run for 1 000 000 iterations (thinning = 20, burning = 15 000).

2.2.2 | Estimating genetic variation with animal models

The additive genetic variation of each fitness proxy and laying date was estimated using univariate animal models (Kruuk et al., 2008, 2014; Wilson et al., 2010). Animal models are linear mixed models, that use the information on individuals' relatedness included in the population pedigree to estimate individual breeding values and their variance (Hadfield et al., 2010; Lynch & Walsh, 1998; Wilson et al., 2010).

Laying date

Beforehand, we checked there was no spatial phenotypic trends (as it could affect genetic parameters Marrot et al., 2015; Stopher et al., 2012) based on Mantel tests (results not shown) and decided not to consider clutch size as it is not genetically correlated with laying date in this population (Delahaie et al., 2017). For animal models, laying dates were centred by the population average and divided by the population standard deviation (LD_{ST}) to ensure the model's proper convergence with the chosen prior, while keeping the relative contribution of the variance components unaffected.

We modelled laying date as:

$$LD_{ST} \sim bX + aZ_1 + cZ_2 + \varepsilon. \quad (3)$$

The design matrices X , Z_1 and Z_2 relate observations to the parameters. The parameter b contains the fixed effects and includes linear and quadratic effects of age, and a linear trend for year to avoid any biased temporal trend in breeding values (Postma & Charmantier, 2007). The parameter a contains the breeding values for females ('animal' effect), which are assumed to be normally distributed, such that $a \sim N(0, A \cdot V_A)$, where V_A is the additive genetic variance and A the relatedness matrix, based on the pedigree (Lynch & Walsh, 1998 chap. 26). Parameter c represents other random effects: we included the annual variations (V_Y), the female identity as a random factor (i.e. permanent environment, later referred to as V_I) to account for repeated measurements, we also tested for an effect of the breeding partner (V_M , Brommer & Rattiste, 2008; Germain et al., 2016). Finally, ϵ are the residuals (V_R). This model assumes that $LD_{ST} \sim N(bX, V_p)$, with phenotypic variance V_p .

This model was run for 1 020 000 iterations (thinning = 1000, burning = 20 000).

We could then extract predicted breeding values (a in Equation 3) from this model (Best Linear Unbiased Predictor 'BLUP', Hadfield et al., 2010; Kruuk et al., 2008; Lynch & Walsh, 1998 chap. 26; Walsh & Lynch, 2018 chap. 20), for 894 females, their cohort was inferred from their estimated age. We calculated the linear regression coefficient of breeding values for each iteration over time (using the gam function from the *mgcv* package), and we fitted time splines on the posterior distributions of the BLUPs to visualize any trend (Bonnet, Morrissey, Morris, et al., 2019; Pigeon et al., 2016, using the gam function of the *mgcv* package).

Fitness proxies

The two fitness proxies are counts, with a substantial zero inflation (see their distributions in Figure S2). Not accounting for data following a Poisson distribution (see the figure S5 of Bonnet, Morrissey, & Kruuk, 2019) or being zero-inflated can lead to uncalibrated confidence intervals (Perumean-Chaney et al., 2013). Modelling zero-inflated distribution requires implementing generalized linear animal models, that have been discussed recently (Bonnet, Morrissey, & Kruuk, 2019; Kruuk et al., 2014; Walsh & Lynch, 2018) but very rarely applied (e.g. de Villemereuil, Rutschmann, et al., 2019), fitness being usually modelled as following a Gaussian (e.g. Bonnet et al., 2017) or a Poisson distribution (e.g. Kruuk et al., 2014; Reed et al., 2016). One of the major impediments so far was the difficulty to recombine the Binomial and Poisson parts of the fitness, to obtain the overall models parameters on the observed scale (but see below).

We used a Hurdle model (Zuur et al., 2009 chap. 11, Equation 3) where the number of fledglings/recruits is decomposed into (1) a binomial process (logit link, W_{Binomial}), modelling the probability of failure and (2) a zero-truncated Poisson distribution modelling success, with the number of fledglings/recruits modelled as a count (log link, $W_{\text{zero-truncated Poisson}}$). A zero-inflated Poisson would have been best to account for different sources of null recruitment, for example our failure to capture all recruits, but these models were too complex to converge. In each case, we have:

$$\log(W_{\text{zero-truncated Poisson}}), \text{logit}(W_{\text{Binomial}}) \sim bX + aZ_1 + cZ_2 + \epsilon \quad (4)$$

with b = age and age², a = animal_q, c = year and permanent environment, and ϵ the residuals. We kept years only as a random effect, and we removed any male effect, for the model to properly converge.

The residual variance of the Binomial process is fixed to one, so the residual covariance between the Binomial and Poisson processes is null. These models were run for 5 030 000 iterations (thinning = 1000, burning = 30 000).

The genetic and phenotypic variances of each fitness proxy were back transformed to the observed scale (recombining the Binomial and Poisson parts of the fitness, to obtain the overall variances) using the *QGglimm* package (taking advantage of a newly developed method by Bonnet, Morrissey, de Villemereuil; based on Morrissey, 2015 and de Villemereuil et al., 2016, and including fixed effect in V_p , de Villemereuil, 2018, de Villemereuil et al., 2018). Because these extractions are very time-consuming, we only extracted the phenotypic and genetic covariances and variances. We restricted the number of iterations used to 300.

Heritabilities

Narrow-sense heritabilities were then calculated as the ratio of additive genetic variance and the sum of estimated components, including fixed effects, as discussed by de Villemereuil et al., 2018. We calculated the heritabilities of fitness proxies using the variances at the observed level, extracted with the *QGglimm* package.

2.2.3 | Predicting response to selection

The breeder's equation

This equation defines the predicted evolutionary response (R , in days) as the heritable part of the selection strength (Morrissey et al., 2010, Equation 5):

$$R = h^2 \times S_p \times \text{number of generations} \times \frac{1}{2} \quad (5)$$

where h^2 is heritability and S_p the selection differential. It is halved, because laying date is a sex limited trait and only females are hypothesized to respond (Caro et al., 2009; Lande, 1980). Multiplying by the number of generations (21 generations for a generation time of 2 years) gives the overall expected response during the study period (from 1976 to 2019 for fledglings, 2018 for recruits). This prediction is, therefore, particularly conservative, as generations normally overlap.

The Robertson-Price equation

Following the STS, the evolutionary response can be estimated by the genetic covariance between laying date and each fitness proxy (Morrissey et al., 2010; Walsh & Lynch, 2018 chap. 6), which was estimated using multivariate animal models. These models were run with all explanatory variables included in the previous fitness models (Equation 4), with the residual variance of the Binomial process fixed

to one (no residual covariance considered between the Binomial part and the other variables). We modelled the fitness proxies based on the same distribution described above (hurdle models). Again, the fitness proxies were not standardized, but we used the globally standardized laying date (LD_{ST}), to fit the prior range.

These models followed the same hypotheses than the previous animal models described for each response variable, written as:

$$(LD_{ST}, \log(W_{\text{zero-truncated Poisson}}), \text{logit}(W_{\text{Binomial}})) \sim bX + aZ_1 + cZ_2 + \varepsilon \quad (6)$$

with $b = \text{age}$ and age^2 , $a = \text{animal}_{\varphi}$, $c = \text{year}$ and permanent environment, and ε the residuals.

Then, we considered the overall expected response (R , in days):

$$R = \sigma_A(LD_{ST}, W)_{\text{observed scale}} \times \text{number of generations} \times \frac{1}{2} \times \text{sd}_{LD} \quad (7)$$

We halved the response, as LD is a female trait (the genetic covariance between LD and fitness would be null for half of the population; Bonnet, Morrissey, Morris, et al., 2019). As the laying date was standardized, we multiplied R by its standard deviation to express the response in the number of days.

We ran these models for 5 030 000 iterations (thinning = 1000, burning = 30 000). Fitness variances and its covariances with LD on the observed scale were obtained using the *QGglmm* package (see above). We could fuse the Binomial and Poisson parts of the fitness proxies to estimate overall values of phenotypic and genetic covariances with LD.

We performed a posterior predictive check (sampling response vectors based on the model and parameters posteriors, comparing them to the actual response) to compare bivariate models for both fitness proxies, showing better predictions when fitness was modelled using a Hurdle model than by a Gaussian distribution (Figure S6).

2.2.4 | Bayesian models parameters

All animal models presented above were run using the *MCMCglmm* package (Hadfield, 2019). All models were run with a weakly informative parameter expanded prior ($V = 1$ $\text{nu} = 1$, $\text{alpha.mu} = 0$, $\text{alpha.V} = 1$), not to impose any values for the variables. This prior fits the range of both standardized LD and fitness proxies on latent scale: it is consistent to prior expectations, since variances on the latent scale of the hurdle Poisson are expected to be low and the laying date was standardized to a variance of 1. We explored an informative and another uninformative prior, confirming our confidence in the current results, as genetic estimates did not depend on the choice of prior. We aimed for a minimum effective sample size of 1000 iterations.

We checked model convergence both visually and using the *heidel.diag* function (from the *coda* package). All estimates are posterior modes, given with their 95% confidence interval (CI).

3 | RESULTS

3.1 | Traits variation

The average laying date is $67.66 \pm \text{SD } 8.07$ days (i.e. approximately May 7), and it strongly advanced during the study period (Figure 1, $13.94 [-18.86, -9.43]$ days earlier than in 1976). Its strong variance is mostly explained by annual effects (30% [0.22, 0.44] of its phenotypic variance, Table 1, and Figure 1 for an illustration of LD annual variation) and female individual variance ($V_I + V_A = 20\%$ [0.14, 0.24]), while weakly influenced by males identity ($V_M < 1\%$ [0, 0.3]). Laying date also varies with age: the youngest and oldest females lay eggs later. The additive genetic variance of the laying date represents 13% [0.03, 0.21] of the phenotypic variance (Table 1, Figure S5). The permanent environment only explains a small amount of the variance ($V_I < 1\%$).

The average number of recruits is $0.30 \pm \text{SD } 0.64$ (Table 1) and the average number of fledglings is $4.05 \pm \text{SD } 2.69$ (including zero, and both proxies show zero inflation, see Figure S2). Yearly and residual variations contributed most to phenotypic variance of fitness proxies (Table 1). The genetic variance of fitness components is very small (Table 1, Figures S3 and S5). Heritabilities of all fitness components are weak (Table 1, given on both latent and observed scales for comparison; their posterior distribution can be found in Figures S3 and S4).

3.2 | Selection measures

Based on both fitness proxies, we detected significant negative selection (Figure 2). Selection differentials and gradients are stronger for recruits ($\beta = -0.33 [-0.48, -0.19]$; $S_p = -1.72 [-2.47, -0.99]$), than for fledglings ($\beta = -0.12 [-0.16, -0.08]$; $S_p = -0.53 [-0.74, -0.31]$).

The covariance between laying date and relative number of recruits results from both inter-individual covariances ($\sigma_{(LD, \text{Recruits})_{\text{Individuals}}} = -0.90 [-1.60, -0.12]$), that is, some individuals consistently laying earlier had more recruits, and from intra-individual covariances ($\sigma_{(LD, \text{Recruits})_{\text{Residuals}}} = -0.89 [-1.60, -0.16]$), that is, in years where a focal individual bred earlier, it also enjoyed higher fitness.

In contrast, the covariance between laying date and the number of fledging only emerges from intra-individual variances ($\sigma_{(LD, \text{Fledglings})_{\text{Residuals}}} = -0.35 [-0.59, -0.10]$, $\sigma_{(LD, \text{Fledglings})_{\text{Individuals}}} = -0.21 [-0.48, 0.10]$).

3.3 | Predicted and observed evolutionary responses

The breeder's equation predicts a significant negative evolutionary response per generation when using the most commonly used fitness proxy, that is, the number of recruits. It predicts an advance of -2.25 days $[-4.52, -0.40]$ over the studied period. If the selection

differential (S_p) is based on the number of fledglings, the predicted response to selection is significant but lower (-0.77 [$-1.31, -0.08$], Figures 3 and 4).

The Robertson-Price equation predicted no significant response to selection over the studied period ($STS_{\text{Recruits}} = -0.14$ [$-0.29, 0.03$] and $STS_{\text{Fledglings}} = -0.07$ [$-2.24, 0.64$], Figure 3 and Figure S5), as there is no significant genetic covariance between the laying date and any of the two fitness proxies (Figure 3, Tables S2 and S3).

As described before, this population has been laying earlier and earlier for the last four decades. This phenotypic advance of 14 days is 7–14 times larger than the predictions reported above. This suggests the observed phenotypic change is at mainly of plastic origin. In line with this, we detected no temporal trend in estimated breeding values, suggesting there was no genetic change over the study

period (Figure 4; the iteration regression coefficient is null [$-0.002, 0.002$]).

4 | DISCUSSION

While there is a growing interest in organisms' potential to adapt to climate change (e.g. Radchuk et al., 2019), fewer studies have focused on the nature of observed phenotypic changes (but see Bonnet, Morrissey, Morris, et al., 2019; Bonnet et al., 2017; Sauve et al., 2019). In line with previous studies investigating the nature of trends in phenology (Charmantier et al., 2008; Charmantier & Gienapp, 2014; Gienapp et al., 2008), we found that, in this blue tit population, the trend for earlier laying date can be explained by plasticity alone.

As a first step to understand the underlying mechanisms of this change in breeding time, we estimated its evolutionary potential and detected a significant heritability. It is consistent with previous estimations in this population ($h^2 = 0.13$ [$0.06, 0.2$], Delahaie et al., 2017) and for laying date in general (usually around $h^2 = 0.20$, Postma, 2014).

We then found a global phenotypic selection for earlier breeding. The estimated strength of selection using recruits as the fitness proxy corresponds to previous estimates in this blue tit population (de Villemereuil et al., 2020; Porlier et al. had estimated $\beta = -0.25 \pm 0.09$, in 2012). It also matches results in other passerines (e.g. Gienapp et al., 2006; Sheldon et al., 2003; Visser et al., 2015; and more generally for life-history traits, Kingsolver et al., 2012). When approximating fitness with the number of fledglings, the selection gradient is lower and corresponds to what Marrot et al. (2018) have found in another blue tit population ($\beta = -0.05 \pm 0.01$).

This change of selection strength with the proxy of fitness is intriguing: selection through fledgling success is rather weak, and represents half of the strength of selection through recruitment success. Variations of selection strength using different fitness

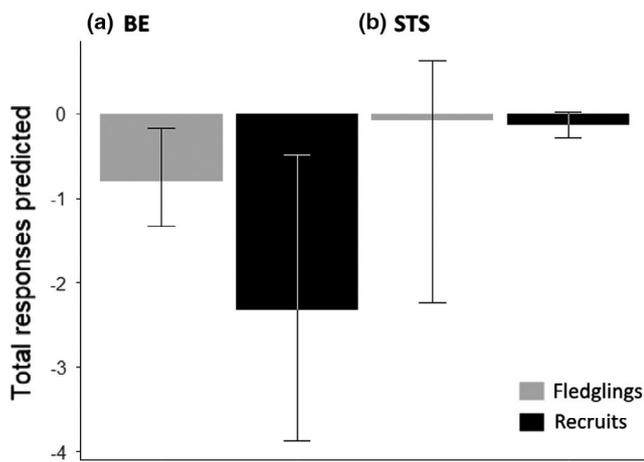


FIGURE 3 Evolutionary responses predicted by (a) the breeder's ($R = h^2 S$, Equation 5) and (b) the Robertson-Price ($STS, R = \sigma_A (LD_{ST}, W)$, Equation 6) equations for the two fitness proxies (values are given in the main text, we show posterior modes and 95% confidence intervals; see Figure S5, for their posterior distribution)

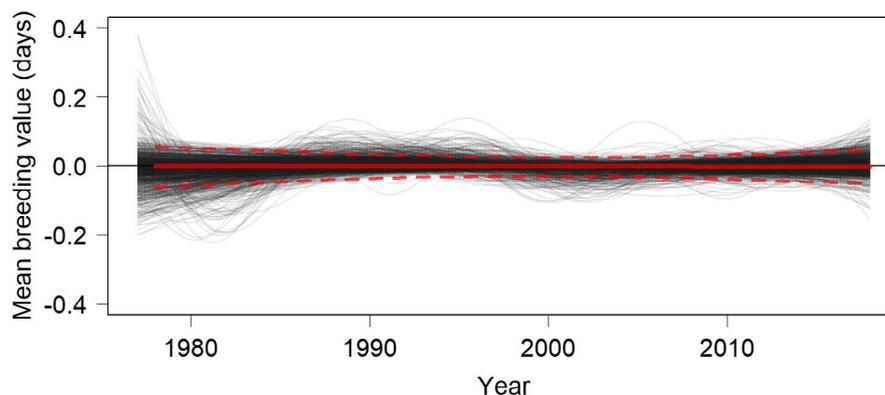


FIGURE 4 Temporal trend in estimated breeding values averaged by cohorts (measured in standard deviation). Cohorts with lower sample size (see Table S1) show more variability in genetic estimates. The regression of predicted breeding values over year is represented by the red lines (posterior mode as the continuous line, with its 95% CI as thin dashed lines; the overall regression coefficient is estimated to be 0.0003 [$-0.001, 0.001$]). Each black line is the estimated breeding value trend from a posterior sample (using a nonlinear smoothing function)

proxies have been reported (e.g. Gamelon et al., 2018; Vatka et al., 2020) but remain poorly investigated for bird phenology. Charmantier et al. (2006) found some similar results on mute swans (*Cygnus olor*, stronger selection via recruitment than hatching success for laying date, based on annual selection gradients). However, results may vary with species, for example, in the hihi (*Notiomystis cincta*), optimal laying date was strongly influenced by selection through offspring survival before fledging: the very low predation rate in this species may explain the importance of survival before fledging, relying mainly on parents feeding abilities (de Villemereuil, Schielzeth, et al. (2019). Recruitment success has been shown to be a better predictor of individual long-term genetic contributions to the population (Brommer et al., 2004; Reid et al., 2019). Still it contains more than parental fitness, as the recruitment probability is influenced by the offspring's own traits and quality (Thomson & Hadfield, 2017; Walsh & Lynch, 2018 chap. 29; Wolf & Wade, 2001). The stronger selection estimation via the number of recruits might represent later (or cumulative) selective episodes. While the high fledging success for early laying is assumed to be related to the parents' ability to synchronize their breeding time with the peak of prey abundance (Visser et al., 2015), the positive influence of early laying on the descendants' probability to recruit remains to be investigated, for example through their over-winter survival (Vatka et al., 2020).

We found strong divergences between the predictions of the breeder's equation, which predicts a greater change for recruits than for fledglings, and those of the STS, predicting no evolutionary changes, with the latter being supported by the absence of trends in the breeding values. We expected the STS to predict more accurately microevolution in the wild than the BE (Morrissey et al., 2010, although the predictions from both models sometimes concur, for example Pigeon et al., 2016; Reed et al., 2016), as the breeder's equation makes several hypotheses often invalid in the wild. It assumes the trait to be the target of selection, and not simply correlated to another selected trait, as it was developed in animal and plant breeding where the breeder applies consistent selection directly on the trait. Because the BE does not directly consider the genetic relationship between the trait and fitness (Morrissey et al., 2010; Walsh & Lynch, 2018 chap. 6), the hypothesis of causality of the trait on fitness is important. This assumption is violated here: the intra-individual covariance represents a large part of the phenotypic covariance between laying date and fitness (for both indices), that is, the fitness-trait relationship arises mainly from environmental effects. In turn, the STS considers that the trait responds to selection because it covaries genetically with fitness. It makes no hypothesis on the fitness-trait causality, which is difficult to assess in the wild (Frank, 2012; Walsh & Lynch, 2018 chap. 6). Based on the STS and two fitness proxies, we, therefore, predicted no response to selection on laying date. This is in line with most studies in wild populations showing very weak or null genetic variance for fitness (Hoffmann et al., 2016; McCleery et al., 2004; Teplitsky et al., 2009; Walsh & Lynch, 2018; Wheelwright et al., 2014), suggesting that evolutionary responses could be generally low or difficult to detect

at least at the annual scale, as this finding has been challenged by a study evaluating the genetic variance for lifetime fitness (Bonnet et al. in press).

Intra-individual fitness-trait covariances are to be expected when working on annual fitness and multiple reproductive events per individual (Dingemanse et al., 2021). These covariances could be due to environmental variations, for instance, years where the birds' are in good condition can lead them to both lay earlier and enjoy higher fecundity (Price et al., 1988; Gienapp et al., 2006; Walsh & Lynch, 2018 chap. 20). Such environmental covariations between laying date and reproductive success are likely not contributing to selection on the mean laying date among individuals and thus cannot result in changes at the genetic level.

In this population, these covariations could also result from the plastic response of the blue tits (Bonamour et al., 2019) tracking a fluctuating optimum in a changing environment (as supported by the findings of de Villemereuil et al., 2020). As the environment might highly differ between the reproductive events experienced by a same individual, the covariance between laying date and reproductive success will depend on the plasticity level of individuals (i.e. their ability to track the optimum phenotype). In that sense, intra-individual variations can be interpreted in terms of selection on the laying date individual-level plasticity.

Most studied natural populations of birds also showed a plasticity-induced phenotypic response to climate changes (Charmantier & Gienapp, 2014; Gienapp et al., 2008; Nussey et al., 2005; Renner & Zohner, 2018; Sauve et al., 2019). Plasticity enables individuals to track environmental variation, which can have important consequences for phenological traits. In this population, as we show here, plasticity seems sufficient to track environmental changes (although laying earlier could still be better). This is also supported by the weak and stable delay between the annual caterpillar density peak and the birds' annual mean laying date (the average annual delay is $2 \pm SD 7.7$ days; the caterpillar peak is estimated as the mass of caterpillar frass collected during a given time period, allowing estimation of caterpillar abundance throughout the season, see Blondel et al., 2006).

Whether the plastic response of phenological traits would be sufficient on a longer time scale remains unknown (Radchuk et al., 2019; Teplitsky & Charmantier, 2019). The plasticity of laying date has been selected in a given range of environments, and the ongoing global changes could cause selection on phenotypic plasticity for a broader range of environmental variations (including pressures favouring the development of response to multiple cues, Bonamour, 2019; Chevin et al., 2015; Diamond & Martin, 2016). Plasticity reaction norms can become maladaptive if the environmental change increases (Chevin & Hoffmann, 2017, e.g. through increasing frequency of extreme climatic events), affecting both laying date, as shown in our studied system (Bonamour et al., 2019), and selection pressures, like in another closely related blue tit population (Marrot et al., 2018). Such offset will impact populations and ecosystems (Renner & Zohner, 2018; Visser & Gienapp, 2019). Beyond phenotypic plasticity buffering evolution, understanding the interplay

between evolution of trait means and their plasticity will become increasingly important (e.g. Hendry, 2016).

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CONFLICT OF INTEREST

We declare that we have no competing interests.

AUTHOR CONTRIBUTIONS

C.T. designed the research. C.T., C.F. and S.B. (and many other contributors) collected field data. J.B. and P. de V. conducted statistical analyses. J.B., S.B., P. de V. and C.T., wrote the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13950>.

DATA AVAILABILITY STATEMENT

The phenotypic data and the pedigree information used in this article are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jh9w0vtcg>

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