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RESEARCH ARTICLE

How interacting anthropogenic pressures alter the plasticity of breeding time in two common songbirds

Paul Cuchot[1] ⓘ | Timothée Bonnet[2] | Olivier Dehorter[3] | Pierre-Yves Henry[3,4] |
Céline Teplitsky[1]

[1]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

[2]Centre d'Etudes Biologiques de Chizé UMR 7372, Université de la Rochelle-CNRS, Villiers-en-Bois, France

[3]Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

[4]Mécanismes adaptatifs et évolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Brunoy, France

Correspondence
Paul Cuchot
Email: paul.cuchot@gmail.com

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Abstract

1. Phenological adjustment is the first line of adaptive response of vertebrates when seasonality is disrupted by climate change. The prevailing response is to reproduce earlier in warmer springs, but habitat changes, such as forest degradation, are expected to affect phenological plasticity, for example, due to loss of reliability of environmental cues used by organisms to time reproduction.

2. Relying on a two-decade, country-level capture-based monitoring of common songbirds' reproduction, we investigated how habitat anthropization, here characterized by the rural–urban and forest–farmland gradients, affected the average phenology and plasticity to local temperature in two common species, the great tit *Parus major* and the blue tit *Cyanistes caeruleus*.

3. We built a hierarchical model that simultaneously estimated fledging phenology and its response to spring temperatures based on the changes in the proportion of juveniles captured over the breeding season.

4. Both species fledge earlier in warmer sites (blue tit: 2.94 days/°C, great tit: 3.83 days/°C), in warmer springs (blue tit: 2.49 days/°C, great tit: 2.75 days/°C) and in most urbanized habitats (4 days for blue tit and 2 days for great tit). The slope of the reaction norm of fledging phenology to spring temperature varied across sites in both species, but this variation was explained by habitat anthropization only in the deciduous forest specialist, the blue tit. In this species, the responses to spring temperature were shallower in agricultural landscapes and slightly steeper in more urban areas. Habitat anthropization did not explain variation in the slope of the reaction norm in the habitat-generalist species (great tit), for which mean fledgling phenology and plasticity were correlated (i.e., steeper response in later sites).

5. The effects of habitat change on phenological reaction norms provide another way through which combined environmental degradations may threaten populations' persistence, to an extent depending on species and on the changes in their prey phenology and abundance.

Pierre-Yves Henry and Céline Teplitsky should be considered as joint senior author.

1 | INTRODUCTION

In temperate regions, climate change increases the frequency of warm and early springs (Lee et al., 2023; Parmesan & Yohe, 2003; Walther et al., 2002) so that most animal species advance their reproductive period. In species that rely on highly seasonal food sources, matching phenological shifts in resource availability is crucial for breeding success (Durant et al., 2007; Post & Forchhammer, 2008; Visser & Both, 2005; Visser & Gienapp, 2019). Migratory bird species arrive earlier on their breeding grounds (Cotton, 2003; Inouye et al., 2000; Neate-Clegg & Tingley, 2023) and resident species breed earlier (Crick et al., 1997; Dunn & Winkler, 2010) in warm springs. A lack of adjustment can lead to a timing mismatch between prey and predators/consumers (Miller-Rushing et al., 2010; Visser et al., 1998), ultimately resulting in decreased breeding success for predators/consumer species (Husby et al., 2010; Visser & Gienapp, 2019).

Most seasonal species adjust their breeding phenology in response to temperature (McLean et al., 2022; Parmesan, 2006; Thackeray et al., 2016), and there is cumulative evidence that plasticity plays a significant role in contemporary adjustments of phenological timing in response to climate change (Bonnet et al., 2019; Canale & Henry, 2010; Charmantier & Gienapp, 2014). Theory predicts that the degree of adaptive plasticity in phenological responses to temperature depends on two main parameters: (1) the slope of the optimum phenological response to environmental change, which depends on the temperature-dependence of the timing of the peak in food abundance (Visser & Both, 2005) and (2) environmental predictability (Lande, 2014), that is, how well the pre-breeding environment predicts the timing of the peak of food abundance. Both can vary within species, according to local environmental conditions, and can differ among species according to their ecological requirements (Burger et al., 2012; Moussus et al., 2011; Visser et al., 2009), resulting in differences in phenological plasticity among populations and species. For example, the breeding phenology of blue and great tit populations inhabiting deciduous forests is more sensitive to temperature than in populations inhabiting mixed and evergreen forests (Bailey et al., 2022). This can be explained by lower peaks of caterpillar abundance in evergreen forests (Blondel et al., 1993), which may require a greater dietary flexibility of nestlings and reduce the reliance of breeding birds on caterpillars and corresponding temperature cues (Vatka et al., 2011). Moreover, habitats can modulate the effects of pre-breeding temperatures on breeding phenology, for instance by imposing energetic constraints that delay reproduction. For example, tree swallows *Tachycineta bicolor* breeding in higher densities display steeper responses to temperature than birds breeding in low-density habitats, likely because the latter are poor-quality habitats (Bourret et al., 2015). Differences in phenological

responses to environmental cues among species can also be strong (e.g., Radchuk et al., 2019), and these variations can at least partly be explained by ecological characteristics such as the degree of habitat or thermal specialization (Moussus et al., 2011).

Habitat anthropization, that is, human-induced modifications of habitats (mostly throughout conversion into agricultural lands and urbanization), can also alter bird phenology, and ultimately affect their phenological plasticity in response to temperature. Urbanization tends to advance breeding phenology in birds, with urban populations singing and laying eggs earlier than their rural conspecifics (Capilla-Lasheras et al., 2022; Møller et al., 2015). Chemical inputs and reduction in habitat heterogeneity caused by the intensification of agricultural practices may also disturb birds breeding phenology by modifying the phenology and abundance of their preferred prey (Stanton et al., 2018; Vickery et al., 2001). Overall, habitat anthropization could affect the phenological response of birds to temperature in at least three ways. First, anthropization effects on food abundance and seasonality may reduce the need to respond to temperature. The adaptive nature of plasticity relies on tracking the optimum breeding time, which is strongly defined by the peak of food abundance (Chevin & Lande, 2015). In anthropized habitats, the peak of prey abundance may spread over a longer period (Seress et al., 2018) making it poorly predictable. As a result, temperature would no longer be a relevant cue for the timing of prey emergence. Moreover, a broader resource peak would reduce the cost of asynchrony between the chick-rearing period and prey abundance, leaving birds less constrained by temperature (Visser & Gienapp, 2019). Second, birds also time their reproduction according to cues other than temperature (Chmura et al., 2020), which may be degraded in anthropized habitats (e.g., blurred information on invertebrate prey phenology and photoperiod change and loss of social cues), making the amount of available information poorer and less accurate. Third, trade-offs may arise between responding to challenges specific to anthropized habitats (e.g., pollution and low food quality) and responses to temperature (multidimensional plasticity; Westneat et al., 2019). Because breeding time depends on food availability (Perrins, 1970), plasticity can be shallower in lower-quality, stressful habitats (e.g., Bourret et al., 2015). However, the effects of anthropization, through urbanization and agriculture, on phenological plasticity in wild bird populations remain poorly studied (Kentie et al., 2018). There is an urgent need for investigating the effects of such human-induced changes on phenological responses to global warming as ongoing urban and agricultural expansions are causing unprecedented declines in wild bird populations (Reif & Vermouzek, 2019) possibly reducing the conditions for phenological adaptation.

The blue tit *Cyanistes caeruleus* and the great tit *Parus major* have been extensively used as models for research on climate-induced

predator–prey phenological mismatches (e.g., Biquet et al., 2022; Nussey et al., 2005). Both are temperate forest songbirds, and although very similar, these two species differ in their degree of habitat and diet specialization, with the blue tit being more specialized than the great tit (Moussus et al., 2011; Snow, 1954). Using these two species as models, we investigated how average fledging phenology and plasticity to local temperature varied along two anthropization gradients: the rural–urban gradient (indexed by Impervious Surface Area, hereafter imperviousness) and the forest–farmland gradient (indexed by Tree Density). We evaluated the effects of habitat composition at a landscape scale on breeding phenology and plasticity to local temperature using a nationwide (183 sites), long-term (21 years) ringing monitoring programme of common birds during the reproductive period across mainland France. Such monitoring programmes are ideal to investigate the consequences of habitat anthropization on bird breeding phenology as the spatial spread of ringing stations offers a representative coverage of both forest–farmland and rural–urban gradients (Figure S1.3). We developed an integrative modelling approach, based on the changes in the proportion of captured juveniles throughout the breeding seasons for each year and site, to infer breeding phenology from the peak of fledging (i.e., when chicks leave the nest).

We predicted that plasticity to local temperature varies among sampling sites and that habitat anthropization affects mean phenology (additive effects) and phenological plasticity (interactive effect). Plasticity of the blue tit was expected to be more affected by anthropization effects than for the great tit because of its dependence on more specific habitats and food resources. This could potentially alter the environmental cues that normally trigger breeding and/or provide a poor-quality environment, preventing the bird from achieving the necessary body condition for earlier breeding despite earlier warm conditions.

2 | MATERIALS AND METHODS

2.1 | Study species

The blue tit and the great tit are two hole-nesting passerines that have long been used as model to understand the ecology and evolution of breeding phenology in birds (Blondel, 2007; Bonamour, 2021; Visser et al., 1998). Both species are forest-dwelling passerines that rely on trees to nest and forage. Yet, the great tit has a broader ecological niche (generalist): It occupies urban and disturbed habitats more densely than the blue tit, whereas the blue tit is more specialized on deciduous forests (Gibb, 1954; Moussus et al., 2011; Snow, 1954; Solonen, 2001). They are supposed to synchronize their reproduction to match the peak of offspring food requirements with the peak of caterpillar abundance (Visser et al., 1998). Tits breed once to twice per year (with a higher prevalence for second broods in Great Tit; Jiguet et al., 2007) and start breeding during their first year. Females lay between 5 and 13 eggs per clutch (Gibb, 1950). In France, tits initiate breeding in March. Incubation and chick rearing

last around 35 days. Once fledged, young individuals are still fed by their parents for about 20 days (Gibb, 1950).

2.2 | Capture data

Capture data were collected by volunteer bird ringers from 2001 to 2021 following the French Constant Ringing Effort Site protocol (Robinson, 2023; more information at https://crbpo.mnhn.fr, section 'STOC Capture'). Capture sessions start early May (median 16 May, 95% range: 3 May–6 June) and end early July (6 July [19 June–24 July]), covering most of the incubation and chick-fledging periods. Median time between the first and last capture sessions was 49 days (95% range: 28 to 69 days). The number of capture sessions and locations of mist nets vary between sites but are held constant within each site among sessions and years. Per spring, on average, there are three capture sessions per site (95% range: three to six sessions). A capture session lasts from dawn to noon. Captured birds are identified to the species level, ringed with a unique numbered metal ring (or recorded as recapture if already ringed), sexed and aged based on plumage (juvenile for birds born during the ongoing breeding season, or adult if born in previous years; Svensson, 1992). The centre of all capture sites is precisely georeferenced. The median spatial coverage is 2 ha (95% range: 1.6–4.2 ha), and the median elevation is 91 m (95% range: 1–951 m). Several passerine species, including blue and great tits, are occasionally observed to form flocks after fledging. As flocks could have a biased age ratio (more juveniles), we conducted an assessment of the proportion of birds captured in flocks. Our findings indicate that the proportion of birds captured in flocks is relatively low (6%, Appendix S2).

We selected sites where data were collected during at least 3 consecutive years with at least three sessions per spring. We only included sessions lasting a minimum of 5 h. To secure parameter estimability at the level of sites, we only kept sites where at least three blue tits or three great tits were captured on average per year. Only one record per individual per day was used. After data selection according to these criteria, the final data set represented a total of 11,489 blue tits (7938 juveniles and 3551 adults) and 23,497 great tits (16,629 juveniles and 6868 adults) for 185 sites over a period of 21 years (Figure 1). On average, 9.9 blue tits and 19.2 great tits were captured per site and per year. Maps representing the numbers of mean captured individuals per year for each site and for both species are available in Appendix S9.

In France, this research does not require an ethical approval. The authorization to capture and mark wild birds has been granted by the Ministry of Environment and by prefecture of the Ile-de-France to the Muséum National d'Histoire Naturelle for 5 years (on 19 February 2018 and prefectural decree #IDF-2017-11-29-001 on 29 November 2017 respectively), which delegated to the 'Centre de Recherches sur la Biologie des Populations d'Oiseaux' (https://crbpo.mnhn.fr) the organization of bird ringing in France, including granting licences to qualified volunteers for the Constant Ringing Effort Sites programme.

2.3 | Modelling fledging phenology with capture data

We aimed to infer fledging phenology, as a proxy of breeding phenology, from capture data using the progressive increase in the proportion of juveniles among captured birds throughout the breeding season (Figure 2). This model is based on the idea of Moussus et al. (2011) to derive phenology from changes in the proportion of juveniles, but we built an integrative model to estimate phenology and its plasticity in response to several environmental variables in a single framework. We modelled the probability for a captured individual to be a juvenile, for each species separately, in a Bayesian hierarchical framework using Markov Chain Monte Carlo sampling using the program JAGS (Plummer, 2003) via the R package *R2jags* (Su & Yajima, 2021).

The number of juveniles on day t, year j and site k, follows a binomial distribution (Equation 1) which is characterized by two parameters: the probability that a captured individual is a juvenile $p_{t,j,k}$ and the total number of captured individuals $Ntot_{t,j,k}$.
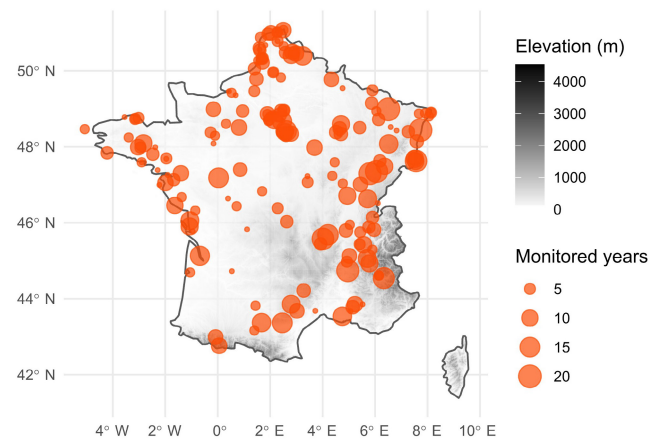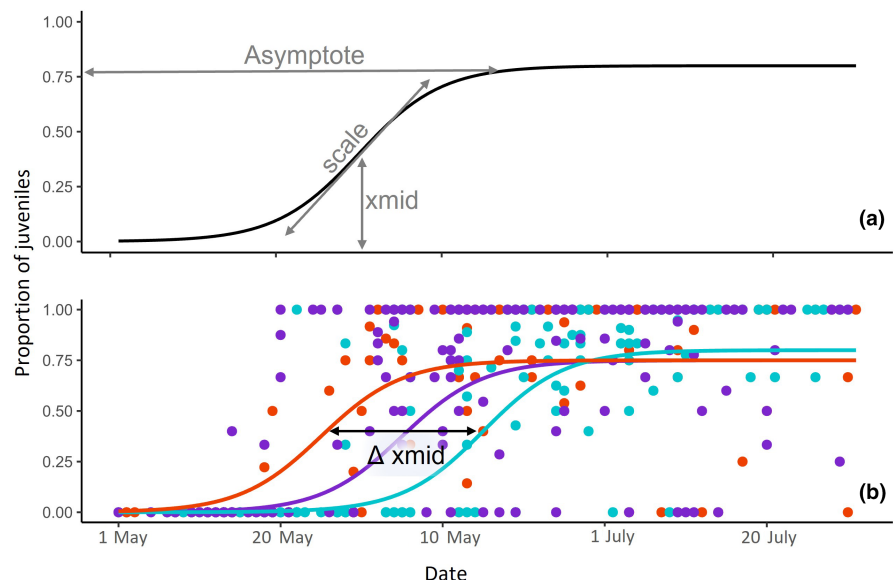

FIGURE 1 Location of Constant Ringing Effort Sites in France for the 2001–2021 period, and number of monitored years.

$$Njuv_{t,j,k} \sim Bin(p_{t,j,k}, Ntot_{t,j,k}). \quad (1)$$

Following Moussus et al. (2011), we assumed that during the breeding period (April to July), $p_{t,j,k}$ follows a sigmoid curve (Figure 2). We thus modelled p separately for each species with a 3-parameter function (Equation 2).

$$p_{t,j,k} = \frac{asymptote_{j,k}}{1+e^{\frac{xmid_{j,k}-t}{scale_{j,k}}}}. \quad (2)$$

The first parameter "asymptote" corresponds to the upper asymptote of the curve and describes the proportion of juveniles in the population at the end of the monitoring period. The second parameter "xmid" is the inflexion point of the curve. This parameter corresponds to the peak of juveniles fledging. The date for this inflexion point results from the timing of several processes: egg laying (i.e., breeding phenology), egg incubation, chick rearing, chick mortality in the nest and just after fledging (the few days when recently fledged juveniles remain in the close vicinity of their nest), and occurrence of seconds broods. We assumed that the duration of egg incubation and chick rearing remains the same and does not vary from year to year or site to site. We thus used "xmid" as a proxy for breeding phenology. We evaluated the reliability of using fledging as a proxy of breeding (egg laying) phenology by comparing the estimated breeding phenology with the observed average laying date in five populations of blue and great tits in southern France. Estimated and observed breeding phenology correlated very well (≥ 0.8, Appendix S4).

The last parameter, "scale", corresponds to a shape parameter and estimates the slope of the curve at the inflexion point. "Scale" can be interpreted as a measure of the synchrony of fledging. For instance, the more synchronous are egg-laying dates across pairs or sites, the higher the synchrony of chick fledging and the steeper the curve (high scale value). Conversely, the higher the difference in number of broods across pairs or sites, the shallower the curve. We checked that the different parameters of the sigmoid curve were

FIGURE 2 Modelling the pattern of temporal emergence of juveniles throughout a breeding period. (a) In early spring, the proportion of juveniles is 0: Juveniles are still in the egg or in the nest. A plateau is reached in June, when most chicks have fledged. (b) Examples of change in the proportion of juveniles of blue tits in France (102 capture sites) during the breeding season for 3 years (2009 in orange, 2010 in blue and 2011 in purple). Each dot represents a capture session at a site. Phenological changes between years are documented by the change in estimates of xmid.

uncorrelated or weakly correlated and therefore that the effects we model on a parameter are not incorrectly ascribed to another one (Appendix S13).

These three parameters were assumed to follow a normal distribution (Equations 3–5).

$$\text{xmid}_{j,k} \sim N(\mu_{\text{xmid}j,k}, \sigma_{\text{xmid}}), \tag{3}$$

$$\text{asymptote}_{j,k} \sim N(\mu_{\text{asymptote}j,k}, \sigma_{\text{asymptote}}), \tag{4}$$

$$\text{scale}_{j,k} \sim N(\mu_{\text{scale}j,k}, \sigma_{\text{scale}}), \tag{5}$$

where $\mu_{j,k}$ corresponding to the mean of the distribution and σ to the associated variance. For each of these three parameters (μ_{xmid}, $\mu_{\text{asymptote}}$ and μ_{scale}), we considered two random effects to account respectively for between-year and between-site variation. All priors were set to be weakly informative (Table S7.1). We ran this Bayesian hierarchical model with three chains of 35,000 iterations each and a burn-in of 10,000, and no thinning. The R code is available in Appendix S6. All parameters were considered to have converged when the R-hat value was below 1.1 (Brooks & Gelman, 1998). This criterion was verified to be satisfied for all estimates used for inferences in the Result section. A very limited number of parameters did not meet the convergence diagnostic (175 out of 8770; Appendix S12); all of these parameters were scale or asymptote parameters, that is, parameters that we do not use for statistical inference about phenological plasticity. To assess the robustness of our analysis, we iteratively ran the most complete model (Equation 7) three times (Appendix S11) and documented the results, checking that the parameters of interest remained unchanged. We relied on posterior distributions, their medians as point estimates and the associated 95% credible interval (extracted from the highest posterior density) to infer the statistical support for our predictions (i.e., departure of parameter estimates from 0).

2.4 | Temperature data

Temperature data for each site were extracted from the SAFRAN forecast model provided by the French meteorological agency (Quintana-Seguí et al., 2008). This model integrates data from meteorological stations and satellite monitoring to estimate climatic variations all over France, based on an 8-km grid.

The window of temperature driving the initiation of reproduction opens later in the season at higher latitudes. We relied on Bailey et al. (2022) to define the most likely 60-day time windows of highest plasticity for each studied site, with a central midpoint (in Julian days) calculated as $1.91 \times \text{latitude} - 10.76$. In our dataset, average latitude is 47.7, and 95% of the sites are located between 43.7 and 50.6. We then extracted the mean temperature within the defined window for each year and site, which finally allowed us to calculate local temperature anomaly (yearly site temperature minus mean site temperature over the period 2000–2022).

2.5 | Environmental data

The degree of habitat anthropization around each site was computed using high-resolution layers provided by the Territory service of the European Earth observation programme, Copernicus (https://land.copernicus.eu/pan-european/high-resolution-layers). Data are based on satellite images and combine optical and radar data to characterize Tree Density (European Environment Agency & European Environment Agency, 2020c) and Imperviousness (i.e., Impervious Surface Area, Corsini et al., 2021; European Environment Agency & European Environment Agency, 2020b; Szulkin et al., 2020) per 10-m pixel. For each site, we computed the mean Tree and Imperviousness density per $10\,\text{m}^2$ in a 1-km buffer using the *sf* R package (Pebesma, 2018). The size of the buffer was chosen according to the study of van Overveld et al. (2017), which showed that the spatial extent of families making excursions outside of their woodlot during the post-fledging period is equal to $1100\,\text{m} \pm (\text{SE} = 265$, range: 643–2374, $n = 6$) in blue tits and 666 m ($\text{SE} = 42$, range: 245–1898, $n = 64$) in great tits.

Because of capture constraints due to the use of mist nets, most capture sites are settled in shrublands, woodlands with dense understorey or reedbeds (Eglington et al., 2015). Although this implies that very few sites are qualified as 'dense urban' or 'open farmland' in the dataset, it reflects well the distribution of habitats in France: A visual assessment was conducted to determine the correspondence between available habitats across France, encompassing both anthropization gradients, and habitats across sites, as depicted in Figure S1.3, with the results indicating a relatively close correspondence.

A principal component analysis revealed that tree density is strongly and negatively associated with farmlands (calculated from Corine Land Cover) in the same buffer area (Figure 3). A decrease in *tree density* is therefore essentially compensated by an increase in farmland and conveys information about the degree of habitat anthropization through agriculture. Due to the collinearity between *tree density* and farmland coverages, only tree *density* was used in the models. *Imperviousness* was strongly correlated with the proportion of built-up pixels, also extracted from high-resolution layers provided by Copernicus (European Environment Agency & European Environment Agency, 2020a). This correlation justifies that we can interpret the effects of *imperviousness* as effects of habitat urbanization (see Appendix S1).

2.6 | Estimating reaction norms of fledging phenology to local temperature along anthropization gradients

In the first step, we modelled the "xmid" parameter, the proxy for breeding phenology, according to temperature only in order to

FIGURE 3 Principal component analysis plot of all 185 capture sites. *Imperviousness* and *tree density* are averaged in a 1-km buffer around each site and extracted from high-resolution layers. Farmlands is computed as the proportion of farmland area in a 1-km buffer and extracted from Corine Land Cover. Correlations between variables are described in Appendix S1.
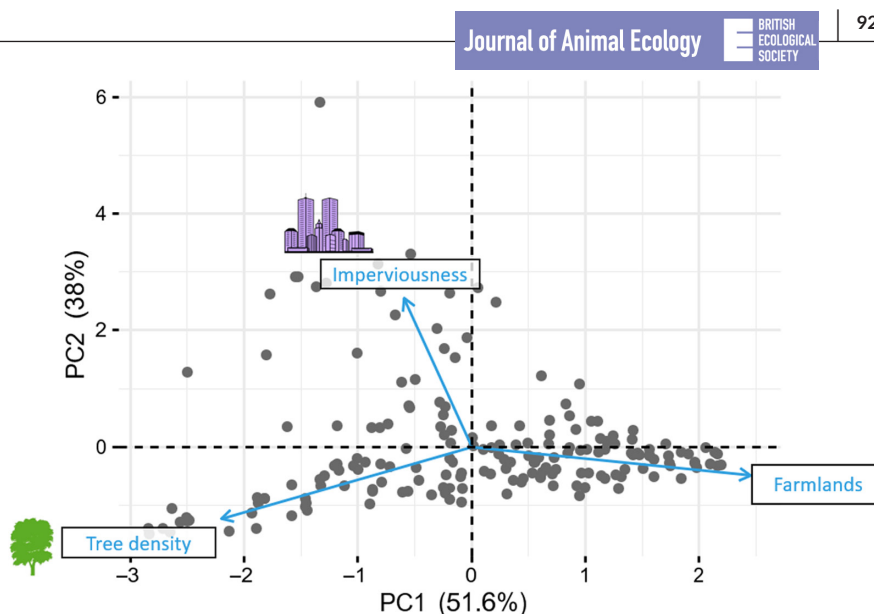
estimate phenological plasticity to temperature per site and per species (Equation 6). Models were similar for both species: To account for inter and intra-site variation in phenological response to temperature, we included both mean site temperature (calculated among the 2000–2022 period) and local temperature anomaly (spring temperature deviation from mean site temperature; Equation 6; van de Pol & Wright, 2009).

$$\mu_{xmidj,k} = (\alpha + \mu_{0k} + \mu_{0j}) + (\beta_1 + \mu_{1k}) \times \text{temperature anomaly}_{j,k} + \beta_2$$
$$\times \overline{\text{temperature}}_k + \beta_3 \times \text{temperature anomaly}_{j,k} \quad (6)$$
$$\times \overline{\text{temperature}}_k$$

where α corresponding to the between-site intercept (average phenology across sites), μ_{0k} to the random site intercept, μ_{0j} to the random year intercept, β_1 to the mean slope across sites, μ_{1k} to the random site slope and β_2 to the linear effect of mean site temperature. Site random slope and intercept were defined with a multinormal distribution, allowing us to explore the covariance between these parameters (Appendix S10).

In the second step, we added to the previous model (Equation 6) the habitat covariates necessary to test our predictions, that is, the effects of habitat anthropization on phenological plasticity to local temperature anomalies. This model (7) accounted for temperature effects as in model (6), but also integrated the fixed effects of *tree density*, *imperviousness*, their interaction with temperature anomaly, *and* an interaction between mean site temperature and temperature anomaly (Equation 7).

$$\mu_{xmidj,k} = \alpha + (\mu_{0k} + \mu_{0j}) + (\beta_1 + \mu_{1k}) \times \text{temperature anomaly}_{j,k} + \beta_2$$
$$\times \overline{\text{temperature}}_k + \beta_3 \times \overline{\text{temperature}}_k$$
$$\times \text{temperature anomaly}_{j,k} + \delta_1 \times \text{tree density}_k + \gamma_1 \quad (7)$$
$$\times \text{tree density}_k \times \text{temperature anomaly}_{j,k} + \delta_2$$
$$\times \text{imperviousness}_k + \gamma_2 \times \text{imperviousness}_k \times \text{temperature anomaly}_{j,k}.$$

We calculated the median and 95% credible intervals for each posterior distributions of the regression parameters β_1, β_2, β_3, δ, δ_2, γ_1 and γ_2.

3 | RESULTS

3.1 | Between-site variability in phenological plasticity

Juveniles of both species fledged earlier in warmer sites and years (i.e., in sites with higher average temperature and years with high temperature anomaly, Table 1). Average phenology varied strongly among sites in both species (Figure 4; Table 1). Responses to temperature anomaly also varied among sites (Figure 4; Table 1) with larger variance in slopes in great tits than in blue tits (Table 1). Mean fledging phenology differed by only 3 days between blue and great tit (1 June for blue tit and 29 May for great tit). The covariance between random intercepts μ_{0k} and random slopes μ_{1k} was negative for the great tit (but not for the blue tit; Table 1), implying that later breeding populations were more sensitive to local temperature anomaly. In both species, the response to local temperature anomaly appeared to be independent of mean temperature.

3.2 | Effects of habitat anthropization on phenology and its plasticity to temperature

Both species reproduced earlier in more impervious sites (Figure 5; Table 2; Figure S3.1). The slope of the reaction norm of phenology to temperature anomaly was significantly modified as *tree density* decreased in the blue tit only: the lower the tree density, the flatter the relationship to temperature anomaly (i.e., the lower the dependence; Figure 5; Table 2). Blue tit populations tended to be more sensitive to temperature anomaly when imperviousness was high (Figure 5; Table 2). Finally, neither tree density nor imperviousness explained variations in the slope of the reaction norm to temperature anomaly in great tit, suggesting that this species reacted in the same way, whatever the degree and the type of habitat anthropization.

	Blue tit		Great tit	
	Median	95% CI	Median	95% CI
Fixed effects				
Intercept	**151.24**	[149.72; 153.05]	**148.19**	[146.49; 149.83]
Mean temperature	**−2.94**	[−3.91; −1.97]	**−3.83**	[−4.7; −2.98]
Temperature anomaly	**−2.49**	[−3.64; −1.21]	**−2.75**	[−3.75; −1.63]
Temperature anomaly×mean temperature	−0.39	[−0.99; 0.26]	0.05	[−0.44; 0.53]
Random effects				
Site intercept variance	**4.66**	[3,68; 5.72]	**4.43**	[3.61; 5.3]
Site slope variance	**1.3**	[0,03; 3.01]	**1.46**	[0.45; 2.31]
Covariance (intercept, slope)	−0.6	[−5.58; 2.04]	**−2.9**	[−6.24; −0.01]

TABLE 1 Median and 95% credible intervals of posterior distributions for the estimates of the fledging phenology models (Equation 6). Variance estimates are reported for the Random effects section.
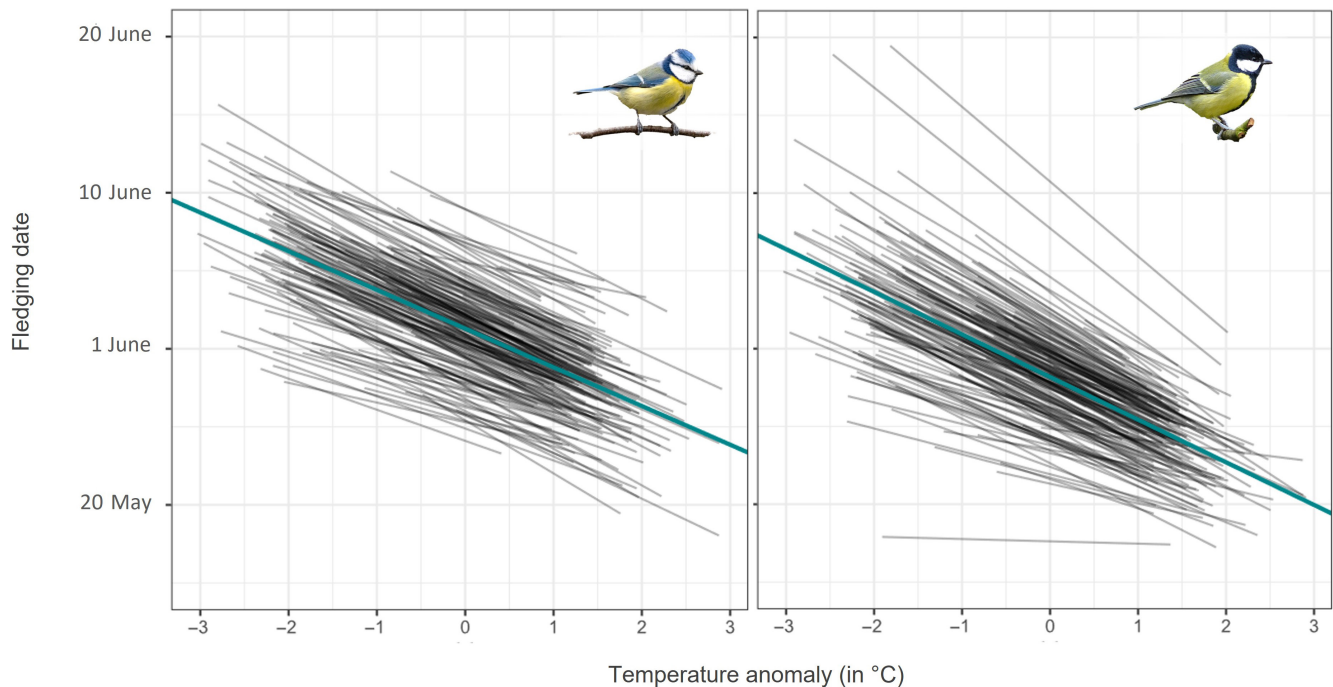
Note: Terms in bold correspond to distributions for which the confidence interval does not overlap zero.

FIGURE 4 Site-specific responses of fledging phenology (xmid) to local temperature anomaly. Each grey line represents the estimated phenological response to temperature for a single site, based on the posterior median for parameters in Equation (6). The thicker turquoise line represents the predicted mean response to temperature anomaly across all sites.

4 | DISCUSSION

Both tit species reproduced earlier in warmer springs. Phenological plasticity of tits to spring temperature is already well established (Bailey et al., 2022; Bonamour et al., 2019; Charmantier et al., 2008; Phillimore et al., 2016; Shutt et al., 2019; Visser et al., 2009). The advancement of reproduction in warm years is a global phenotypic response, known from many other taxa of seasonal vertebrates (McLean et al., 2022; Thackeray et al., 2016),

phenological plasticity playing a major role in the adaptive responses to climate change (Biquet et al., 2022; Charmantier et al., 2008; Radchuk et al., 2019). Interestingly, the slopes for the responses to mean site temperature and to temperature anomaly were very similar (Table 1), suggesting that differences in fledging phenology across sites could be explained to a large extent by plasticity (Phillimore et al., 2016). Across habitats, the slope of the reaction norm to temperature ranged from −3.62 to −0.9 days/°C in the blue tit and from −4.81 to −0.16 days/°C in the great tit, with
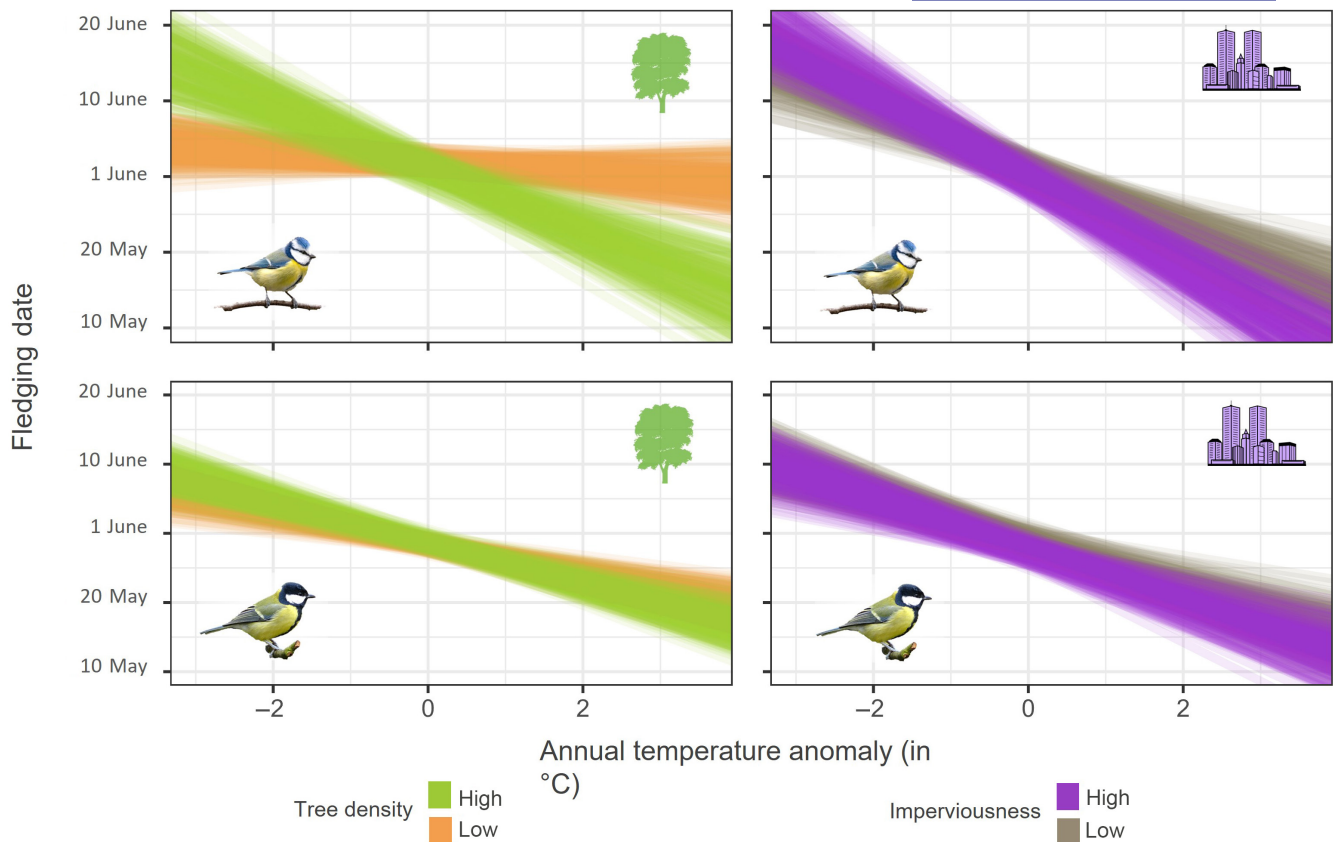
FIGURE 5 Effects of both *tree density* (left panels) and *imperviousness* (right panels) on blue tits (upper panels) and great tits (lower panels) phenological response to local temperature anomaly. Each line corresponds to a projection of the model with parameter values sampled from the 0.10–0.90 posterior distributions. For both environmental factors, 'High' and 'Low' correspond, respectively, to their 0.1 and 0.9 quantiles across all capture sites.

TABLE 2 Median and 95% credible intervals of posterior distributions for the estimates of the fledging phenology models, which include forest density and *imperviousness* effects and their interaction with temperature anomaly (Equation 6). The posterior distributions are graphically represented in Appendix S5.

	Blue tit		Great tit	
	Median	**95% CI**	**Median**	**95% CI**
Fixed effects				
Intercept	**151.13**	[149.54; 152.97]	**148.22**	[146.54; 149.81]
Mean temperature	**−2.96**	[−3.91; −1.97]	**−3.66**	[−4.56; −2.79]
Temperature anomaly	**−2.37**	[−3.5; −1.04]	**−2.75**	[−3.76; −1.62]
Temperature anomaly × mean temperature	−0.35	[−0.9; 0.24]	0.06	[−0.46; 0.59]
Tree density	−0.23	[−1.16; 0.65]	0.11	[−0.67; 0.9]
Imperviousness	−0.91	[−1.96; 0.12]	**−0.96**	[−1.86; −0.12]
Tree density × temperature anomaly	**−0.91**	[−1.51; −0.35]	−0.29	[−0.78; 0.22]
Imperviousness × temperature anomaly	**−1.12**	[−1.77; −0.47]	−0.19	[−0.73; 0.35]
Random effects				
Site intercept variance	**4.71**	[3.7; 5.8]	**4.41**	[3.61; 5.26]
Site slope variance	**0.87**	[0.04; 2.35]	**1.5**	[0.71; 2.33]
Covariance (intercept, slope)	−1.13	[−6.36; 0.96]	**−3.05**	[−6.36; −0.33]

Note: Terms in bold correspond to distributions for which the confidence interval does not overlap zero.

the steeper slopes in most forested habitats. In previous studies of the same species, the estimated slopes ranged from −7 to −2 days/°C (Bailey et al., 2022; Bonamour et al., 2019; Matthysen et al., 2011). Altogether, our results are in line with previous studies in forest habitats but reveal shallower reaction norms at some sites. Hence the fact that the majority of plasticity estimates are coming from long-term monitoring programmes mainly located in favourable environments for tits, that is, forest-dominated habitats (Bailey et al., 2022; Culina et al., 2021) is likely to bias our perception towards steep phenological reaction norms. Our results thus highlight the importance of documenting plasticity over a much broader and representative range of habitats (Appendix S1).

The slopes of reaction norms were identical across habitats for the habitat-generalist species (the great tit). In turn, forest conversion into farmland altered the phenological reaction norm of the deciduous forest specialist (the blue tit). This shallower plasticity in farmland-dominated habitats could be explained by four different hypotheses, the first three in relation to the ecology of plasticity, the fourth to our methodological approach.

First, the availability of cues about when to breed may be limited (blurred) in farmland landscapes compared with forests. Temperature conveys direct information about when to breed (Visser et al., 2009), but the predictive value of temperature for optimal timing may be lost in farmland area, leading blue tits to use alternative cues to time their reproduction, such as social cues from conspecifics or cues from food availability (Chmura et al., 2020). The reduction in plasticity with the loss of forest cover, in the blue tit but not in the great tit, suggests that the phenology of the blue tit may be more determined by diet composition or social cues (the species the most tied to forest and with the most restricted diet). Second, blue tits dwelling in poorly forested areas may have weaker body condition, or higher stress, at the onset of the breeding period, limiting their ability to breed early in warmer years (Verhulst & Nilsson, 2008). As resources are limited for insectivorous species in farmlands (Boatman et al., 2004; Potts, 1987), female blue tits may not reach the necessary body condition to breed earlier despite earlier warm conditions (Thomas et al., 2001). This hypothesis, emphasizing the direct role of food availability and body condition is in line with the fact that the more generalist species (great tit) maintained a constant reaction norm to temperature along the whole forest–farmland gradient. Third, lower plasticity in farmlands could be an adaptive response if the food peaks are broader (Stanton et al., 2018; Vickery et al., 2001). If prey are more diversified, and their abundances are spread over a longer time period, the risk of trophic phenological mismatch is reduced, alleviating the selective pressure on the timing of egg laying. At sites with the poorest habitat quality, it could then be more (selectively) important to reduce breeding synchronization among conspecifics to minimize intra-specific competition. However, the fact that farmland had no effect on the plasticity of the great tit strongly reduces support for this interpretation. Even if the great tit has a broader diet, a large diet overlap is expected among the two tits. This overlap makes it unlikely that the phenology of the main prey is temperature-driven for the generalist species but not for the specialist one.

Fourth, our estimates of phenology are derived from the capture of juveniles, not from the direct monitoring of laying date. Hence, the plasticity of juvenile phenology in farmlands may be different from egg-laying date plasticity because of (i) lower capture probabilities of juveniles if individuals fledging early also disperse sooner and further (Nilsson & Smith, 1985), or (ii) increased pre- and post-fledging mortality of early hatched in warmer spring. Explaining lower plasticity in farmlands can result from selection for earlier breeding (higher survival of chicks from early clutches) in cold springs, and selection for later breeding in warm springs. Such pattern would be opposite to those described in forest habitat (Bonamour et al., 2019), but cannot be excluded if some agricultural practices such as the timing of the application of chemicals like pesticides or fertilizers affect chicks' survival depending on their hatching time. Overall, agricultural practices can impact tits even though they do not breed inside the crops. For example, exposure to an insecticide decreased the body mass of tit chicks born in sprayed hedges (Odderskaer & Sell, 1993). Insecticide exposure also reduced the reproductive success (number of fledglings) of tits reproducing in conventional orchards (Bouvier et al., 2005). While studies are lacking, pesticides may alter resource availability and phenology, or directly affect tits capacity to assimilate environmental signals in the timing of their physiological preparation to reproduce (Marlatt et al., 2022).

We detected earlier breeding phenology with increased *imperviousness*, in line with previous studies showing that urban birds tend to breed earlier than their rural counterparts (Caizergues et al., 2018; Capilla-Lasheras et al., 2022; Najmanová & Adamík, 2009). Our results (up to 2 days earlier for blue tits and 4 days earlier for great tits when comparing the most and least impervious sites, Figure S3.1) are in the range of what was previously observed: 4 to 7 days of lag between songbirds' populations located in more rural area versus in cities (Najmanová & Adamík, 2009). A common explanation for earlier breeding is that springs occur earlier in cities due to the urban heat island effect (Yeh & Price, 2004). However, such an effect might be hard to detect with our data because of the large spatial resolution of SAFRAN meteorological model (8 km × 8 km). Environmental factors other than higher temperature can further explain earlier breeding in more urbanized areas. Artificial light may affect phenology (Dominoni et al., 2020; Senzaki et al., 2020), especially through indirect effects (Partecke et al., 2006) that may enhance reproductive activity, for example, by allowing increased foraging time in diurnal animals (Deviche & Davies, 2013; Titulaer et al., 2012), or by altering the perception of photoperiod length (Bentley et al., 1998). Artificial food provisioning (bird feeding) could also advance phenology (Harrison et al., 2010; Møller et al., 2018) in more urbanized populations by facilitating the earlier reach of nutritional thresholds and/or the sequestration of potentially limiting, nutrients required for reproduction (e.g., calcium: Reynolds et al., 2004; protein: Schoech et al., 2004). Interactions between temperature and these putative environmental factors may induce multidimensional plasticity, potentially explaining the slightly increased phenological plasticity in more urbanized sites for blue tits as the evolution of reaction

norm in urban environments is unlikely. Because, at our study sites, urbanization tended to occur more in forested areas than in farmlands (Figure 3), and because tits populations are known to be highly connected (Lemoine et al., 2016; Spurgin et al., 2019), gene flow between rural and urban environments would be expected to hinder the evolution of locally adapted reaction norms (Lenormand, 2002).

Altogether, understanding the (mal)adaptive nature of these multivariate phenological responses and their causal relationship will require in-depth understanding of the variations of species diets, prey availability and predictability of prey phenology along the forest–farmland and the rural–urban gradients, the two main gradients of habitat anthropization. We investigated fledging phenology in the blue and great tits because they are common research models in ecology and evolution of phenotypic plasticity, due to their high abundance, widespread distribution and ease to study in artificial nest-box populations (Blondel et al., 2006). However, there is a need to broaden the ecological and evolutionary diversity of studied seasonal species (Youngflesh et al., 2023), a challenge that our modelling framework could contribute to tackle. Our model can be applied to a much wider range of species than hole-nesting species, provided that juvenile emergence is unimodal and can be documented by the age structure of repeated samples of individuals throughout the reproductive season. Such a design is common in standardized monitoring schemes of songbirds by capture, covering tens of species at continental scale over decadal time (Robinson, 2023). Future studies applying our approach to multispecies dataset will increase the robustness and generality of our understanding of the range and limits of plastic compensation of global environmental changes by seasonal organisms.

AUTHOR CONTRIBUTIONS

Paul Cuchot led the formal analysis and writing of the original draft. Paul Cuchot, Céline Teplitsky and Pierre-Yves Henry shared conceptualization, planning the analysis and editing drafts. Olivier Dehorter provided the data, and Timothée Bonnet helped with the analysis. All authors commented on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

Data are available via the Zenodo Repository: https://doi.org/10.5281/zenodo.10658859.

STATEMENT OF INCLUSION

Our study is based on a nationwide citizen science programme, assembling data provided by volunteers, wildlife authorities and non-governmental conservation organizations. The main results have been shared with the volunteers but they did not receive the manuscript before submission. If published, a post on the CRBPO's blog will inform the community of the scientific content and key messages.

ORCID

Paul Cuchot https://orcid.org/0000-0002-6060-803X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Environmental variables.

Appendix S2. Proportion of individuals captured in flocks.

Appendix S3. Urbanization effect on fledgling timing.

Appendix S4. Reliability of using fledging as a proxy of breeding (egg-laying) phenology.

Appendix S5. Posterior distributions.

Appendix S6. R code.

Appendix S7. Priors.