# Agriculture alters the ancestral phenological plasticity to spring warmth in a forest specialist, but not in its generalist sister species

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# Abstract

Phenological adjustment is the first line of adaptive response of vertebrates when ancestral seasonality is disrupted by climate change. The prevailing response is to reproduce earlier in warmer springs, but habitat changes, such as conversion of ancestral (pre-human) habitats into cities and agricultural lands, are expected to affect phenological plasticity, for example due to loss of reliability of environmental cues used by organisms to time reproduction. Relying on two-decade, country level capture-based monitoring of common songbirds' reproduction, we investigated how the conversion of forest habitat into agricultural lands, and into artificialized surfaces affected the deviation of average phenology and plasticity to local temperature from its presumed ancestral state, i.e., in non-urbanized forests. For this, 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. 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 reaction norm of fledging phenology to spring temperature varied across sites in both species, but this variation was explained by ancestral habitat only in the deciduous forest specialist, the blue tit. In this species, the responses to spring temperature were shallower in agricultural landscapes. The ancestral reaction norm is preserved in the habitat-generalist species (great tit), as well as along the urbanization gradient and was correlated to mean fledgling phenology (i.e., steeper response in later sites). The effects of habitat change on ancestral adaptive reaction norms provide another way through which combined environmental degradations may threaten populations persistence, to an extent depending on species and changes in their prey phenology and abundance.

# Introduction

In temperate regions, climate change increases the frequency of warm and early springs (Walther et al., 2002; Parmesan & Yohe, 2003; Lee et al., 2023), so that animals need to advance their reproductive period to match phenological shifts in resource availability (Visser & Both, 2005; Visser & Gienapp, 2019). Migratory bird species arrive earlier on their breeding grounds (Inouye et al., 2000; Cotton, 2003; 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 preys and predators/consumers ("trophic mismatch hypothesis", Durant et al., 2007; Miller-Rushing et al., 2010; Stenseth & Mysterud, 2002; Visser et al., 1998), ultimately resulting in decreased breeding success for predators/consumer species (Husby et al., 2010; Visser & Gienapp, 2019; Visser et al., 2021).

Most seasonal species adjust their breeding phenology in response to temperature (Thackeray et al., 2016; McLean et al., 2022) and there is ample evidence that plasticity is the prevailing mechanism in studied vertebrate models (Gienapp et al., 2006; Charmantier et al., 2008; Canale & Henry, 2010; Charmantier & Gienapp, 2014; Charmantier et al., 2016). 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), i.e., 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 (Visser et al., 2009; Moussus et al., 2011), resulting in differences in phenological plasticity among populations and species. For example, blue and great tit populations inhabiting deciduous forests are more sensitive to temperature in terms of their breeding phenology than 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. 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, i.e., human-induced modifications of an ancestral environment (e.g., through urbanization, conversion into agricultural lands, etc.) can also alter bird phenology and ultimately affect their plasticity in response to temperature. Urbanization affects breeding phenology in birds with urban populations laying and singing earlier than their rural conspecifics (Møller et al., 2015; Capilla-Lasheras et al., 2022). Chemical inputs and reduction of habitat heterogeneity caused by the intensification of agricultural practices may also disturb birds breeding phenology by modifying prey phenology and abundance (Vickery et al., 2001; Britschgi et al., 2006; Stanton et al., 2018). Human-induced habitat alterations could also affect the phenological response of birds to temperature. First, in human-altered habitats, the peak of prey abundance may spread over a longer period (Seress et al., 2018). A broad, flat seasonal peak of prey is poorly predictable, making temperature an irrelevant cue for prey emergence. Moreover, a broader resource peak would reduce the cost of asynchrony, leaving birds less constrained by temperature (Visser & Gienapp, 2019). Second, cues other than temperature may be degraded in anthropized habitats (e.g., blurred information on invertebrate prey phenology and photoperiod change), making the amount of available information poorer and less accurate. Third, anthropized habitats may represent lower-quality habitats, leading to lower plasticity levels (Bourret et al., 2015). However, the effects of anthropization, through urbanization and agriculture, on phenological plasticity in wild bird populations remains 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 growing urban and agricultural expansions are causing unprecedented declines in wild bird populations (Donald et al., 2001; Reif & Vermouzek, 2019; Rigal et al., 2023) and possibly reducing the conditions for phenological adaptation.

Using the blue tit (*Cyanistes caeruleus*) and the great tit (*Parus major*), two forest species that have been used as models for research on climate-induced predator-prey phenological mismatches (e.g., Biquet et al., 2022; Nussey et al., 2005), we investigated how the conversion of forest habitats into agricultural lands (forest cover), and into artificialized surfaces (ground imperviousness) affected the deviation of average phenology and plasticity to local temperature from its presumed ancestral state, i.e., in non-urbanized forests. 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 program of common birds during the reproductive period across mainland France. Such monitoring programs are ideal to investigate the consequences of habitat anthropization on bird breeding phenology as the different ringing stations are spread across most habitats. We considered two gradients of habitat degradation: loss of ancestral habitat, assessed by forest density (both species being primarily forest birds), and artificialization, estimated by the degree of ground imperviousness. 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 varied among sampling sites and whether habitat anthropization had an effect on phenology (additive effects) and its response to temperature (interactive effect). We expected phenological plasticity to be more variable and more habitat dependent in the deciduous forest specialist (the blue tit) than in the more generalist species (the great tit).

# Materials and methods

## 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 (Visser et al., 1998; Blondel, 2007; Charmantier et al., 2016; Bonamour, 2021). 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; Snow, 1954; Solonen, 2001; Moussus et al., 2011). They synchronize their reproduction to match the peak of offspring food requirements with the peak of caterpillar abundance (Visser et al. 1998, 2006, Marciniak et al. 2007). Tits breed once to twice per year and start breeding during their first year. Females lay between 5 and 13 eggs per clutch (Gibb., 1950; A. P. Møller et al., 2014). 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 (Verhulst, 1995).

## Capture data

Capture data were collected by volunteer bird ringers from 2001 to 2021 following the French Constant ringing Effort Site protocol (Julliard & Jiguet, 2002). Capture sessions start early May (median May 16th, 95% range: May 3rd – June 7th) and end early July (July 7th [June 19th – July 24th]), covering most of the incubation and chick fledging periods. 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: 3 to 6 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). Mist-netting of birds is most efficient in habitats with a low canopy (since mist-nets capture up to 3-to-4 m above the ground). Most CES sites are thus settled in shrublands, woodlands with dense understory, or reedbeds (Eglington et al., 2015). The center of all CES sites is precisely georeferenced. The median spatial coverage is 2 ha (95% range: 1.6 – 4.2 ha), and the median elevation is 91m (95% range: 1m – 951m).

We selected sites where data were collected during at least 3 consecutive years with at least 3 sessions per spring. We only included sessions lasting a minimum of 5 hours. To secure parameter estimability at site-level, we only kept sites where at least 3 blue tits or 3 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 11489 blue tits (7938 juveniles and 3551 adults) and 23497 great tits (16629 juveniles and 6868 adults) for 185 sites over a period of 22 years (Figure 1). On average 9.91 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.

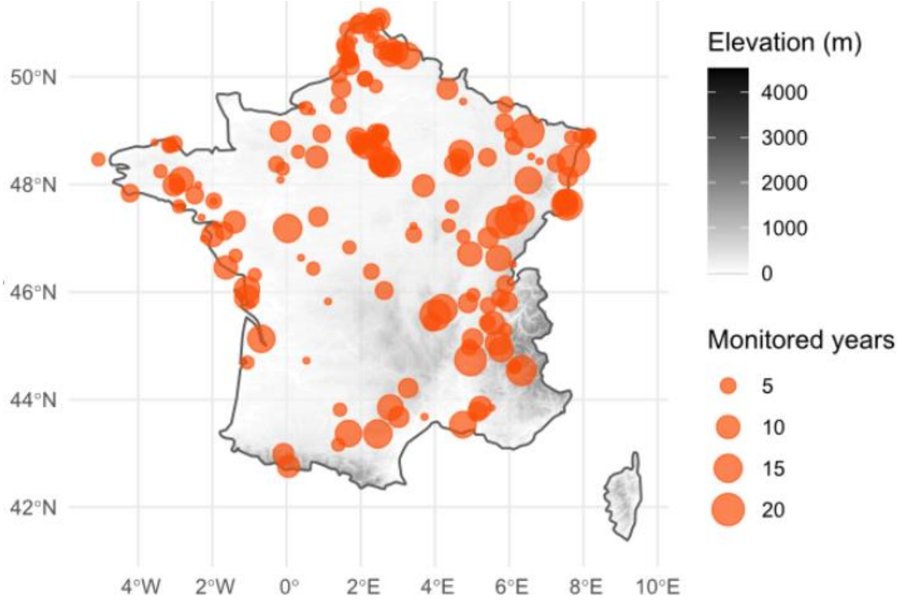

*Figure 1: Location of constant ringing effort sites in France for the 2001 - 2021 period and their number of monitored years.*

## 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 of the proportion of juveniles among captured birds throughout the breeding season (Figure 2). We modeled the probability for a captured individual to be a juvenile for each species separately in a Bayesian hierarchical framework using Markov Chain Monte Carlo 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 (eq.1) which is characterized by 2 parameters: the probability that a captured individual is a juvenile $p_{t,j,k}$ and the total number of captured individuals $Ntot_{t,j,k}$.

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

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 modeled $p$ separately for each species with a 3-parameter function (eq.2).

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

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 inflection point of the curve. This parameter corresponds to the peak of juveniles fledging. The date for this inflection point results from the timing of several processes: egg laying (i.e., breeding phenology), eggs 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. 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 ( $\geq 0.8$, Appendix S4).

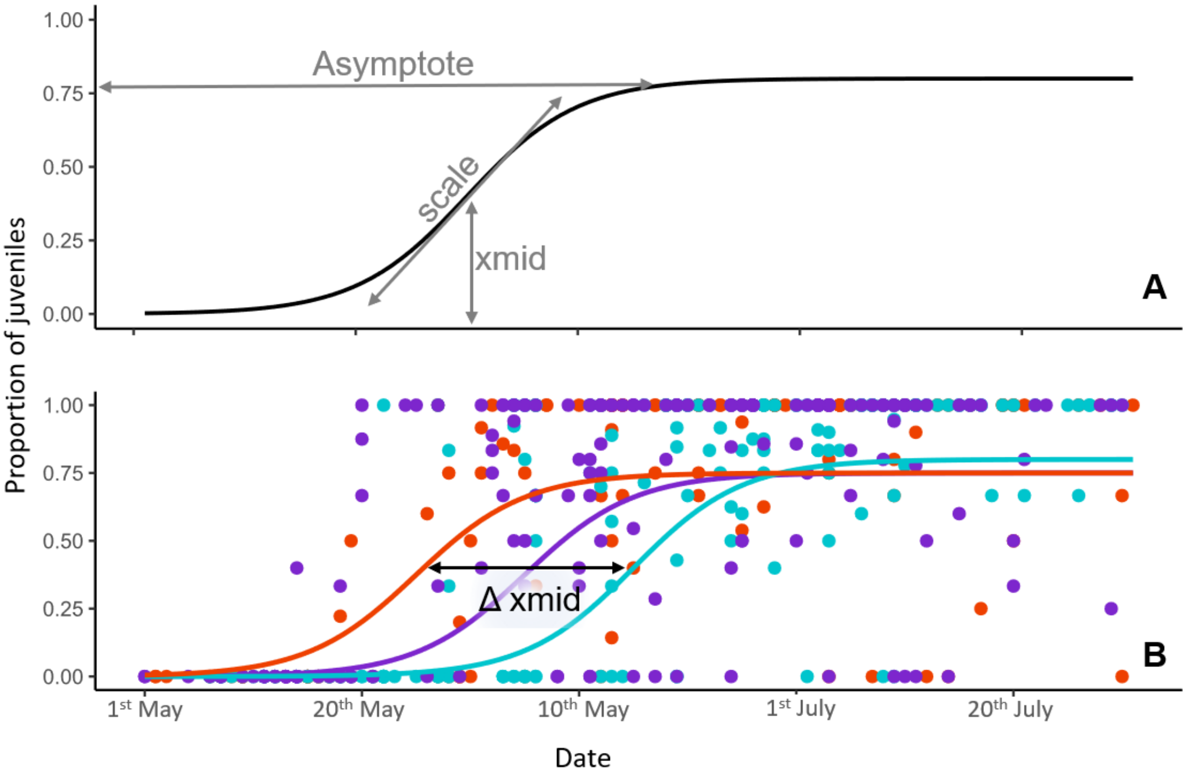

*Figure 2 : Modelling the pattern of temporal emergence of juveniles throughout a breeding period. A) In early spring the proportion of juveniles is 0: juveniles are still in the egg or in the nest. A plateau is reached in June, when most chicks have fledged. B) Examples of change of the proportion of 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.*

The last parameter, *scale,* corresponds to a shape parameter and estimates the slope of the curve at the inflection 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.

These three parameters were assumed to follow a normal distribution (eq. 3-5).

$$xmid_{j,k} N\left(\mu_{xmid\,j,k}, \sigma_{xmid}\right) \tag{3}$$

$$asymptote_{j,k} N\left(\mu_{asymptote\,j,k}, \sigma_{asymptote}\right) \tag{4}$$

$$scale_{j,k} N\left(\mu_{scale\,j,k}, \sigma_{scale}\right) \tag{5}$$

with $\mu_{j,k}$ corresponding to the mean of the distribution and σ to the associated variance. For each of these three parameters ($\mu_{xmid}$, $\mu_{asymptote}$ and $\mu_{scale}$), we considered two random effects to account respectively for between-year and between-site variation. All priors have been set to be flat (Table S7.1). We ran this Bayesian hierarchical model with three chains of 35000 iterations each and a burn-in of 10000, and no thinning. The Gelman-Rubin convergence diagnostics (Brooks & Gelman, 1998) were satisfied (i.e. < 1.1) for all parameter estimates used for inference in the Results section. We rely 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).

## Temperature data

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

## Environmental data

Because of their associated food availability and their positives effects on their reproductive success (Keller & Van Noordwijk, 1994; Naef-Daenzer et al., 2001; Lambrechts et al., 2004), non-artificialized dense forests are considered as optimal and ancestral habitats for blue and great tits (Amininasab et al., 2016). The proportion of ancestral habitat (i.e., non-artificialized forests) surrounding each site was computed using high-resolution layers provided by the Territory service of the European Earth observation program, Copernicus (https://land.copernicus.eu/pan-european/high-resolution-layers). Data are based on satellite images and combine optical and radar data to characterize forest density (i.e., percentage of tree cover, European Environment Agency & European Environment Agency, 2020b; Corsini et al., 2023) and ground imperviousness (i.e., percentage of waterproofed ground; e.g. roads, buildings, European Environment Agency & European Environment Agency, 2020a; Szulkin et al., 2020; Corsini et al., 2021) per 10-m pixel. For each site, we computed the mean value of both variables 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-fledgling period is equal to 1100 m ± (SE = 265, range: 643–2374, n= 6) in blue tits and 666 m (SE = 42, range: 245–1898, n = 64) in great tits.

A principal component analysis revealed that forest density is strongly, negatively associated with crop surface area (calculated from Corine Land Cover) in the same buffer area (Figure 3). A decrease in forest density is therefore essentially compensated by an increase of farmland, and conveys information about the degree of habitat anthropization through agriculture. Due to the strong collinearity between forest and farmland cover, only forest cover was used in the models.

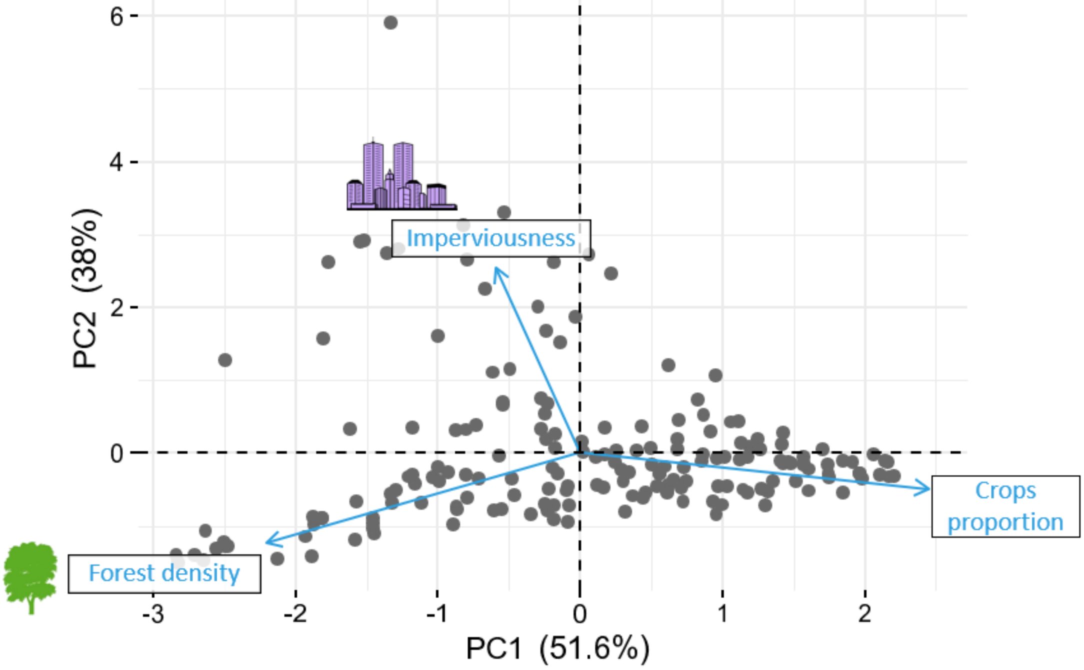

*Figure 3: Principal component analysis (PCA) plot of all 185 capture sites. Imperviousness (also known as ground-waterproofing) and forest density are averaged in a 1-km buffer around each site and extracted from high resolution layers. Crops proportion is computed in a 1-km buffer too and extracted from Corine Land Cover. Correlations between variables are described in Appendix 1.*

## Estimating reaction norms of fledging phenology to temperature

We modeled the $xmid$ parameter, the proxy for breeding phenology, according to temperature in order to estimate phenological plasticity to temperature (eq. 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 1990-2022 period) and local temperature anomaly (spring temperature deviation from mean site temperature; eq. 6, van de Pol & Wright, 2009).

$$\mu_{xmid\,j,k} = \left(\alpha + \mu_{0k} + \mu_{0j}\right) + (\beta_1 + \mu_{1k}) * temp\ anom_{j,k} + \beta_2 * \overline{temp}_k \tag{6}$$

with $\alpha$ corresponding to the between-site intercept (average phenology across sites), $u_{0k}$ to the random site intercept, $u_{0j}$ to the random year intercept, $\beta_1$ to the mean slope across sites, $u_{1k}$ to the random site slope and $\beta_2$ to the linear effect of mean site temperature.

To evaluate the effects of habitat anthropization on phenological plasticity to local temperature anomalies, we designed a model that integrated the fixed effects of *forest density*, *imperviousness*, their interaction with *temperature anomaly* plus an interaction between mean site temperature and *temperature anomaly* (eq. 7).

$$\begin{aligned} \mu_{xmid\,j,k} = \alpha + \left(\mu_{0k} + \mu_{0j}\right) + (\beta_1 + \mu_{1k}) * temperature\ anomaly_{j,k} + \beta_2 \\ * \overline{temperature}_k + \beta_3 * \overline{temperature}_k * temperature\ anomaly_{j,k} \\ + \delta_1 * forest\ density_k + \gamma_1 * forest\ density_k \\ * temperature\ anomaly_{j,k} + \delta_2 * imperviousness_k + \gamma_2 \\ * imperviousness_k * temperature\ anomaly_{j,k} \end{aligned} \tag{7}$$

We calculated the median and 95% credible intervals for each posterior distributions of the regression parameters $\beta_1$, $\beta_2$, $\beta_3$, $\delta$, $\delta_2$, $\gamma_1$ and $\gamma_2$.

# Results

## 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 differs by only three days between blue and great tit (June 1st for blue tit and May

29th for great tit). The covariance between random intercepts $\mu_{0k}$ and random slopes $\mu_{1k}$ was negative for great tits (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.

*Table 1: Median and 95% credible intervals of posterior distributions for the estimates of the fledging phenology models (eq. 6). Residual variance in mean breeding phenology (intercept) between sites – after accounting for the effect of mean site temperature - corresponds to sigma_int, and between-site variance in phenological response to local temperature anomaly (slope) corresponds to sigma_slope. Covariance between random slopes and random intercepts corresponds to Cov_slope_int.*

| | **Blue tit** | | **Great tit** | |
|---|---|---|---|---|
| | Median | 95% CI | Median | 95% CI |
| 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] |
| sigma_int | **4.66** | [3,68 ; 5.72] | **4.43** | [3.61 ; 5.3] |
| sigma_slope | **1.3** | [0,03 ; 3.01] | **1.46** | [0.45 ; 2.31] |
| Cov_slope_int | -0.6 | [-5.58 ; 2.04] | **-2.9** | [-6.24 ; -0.01] |

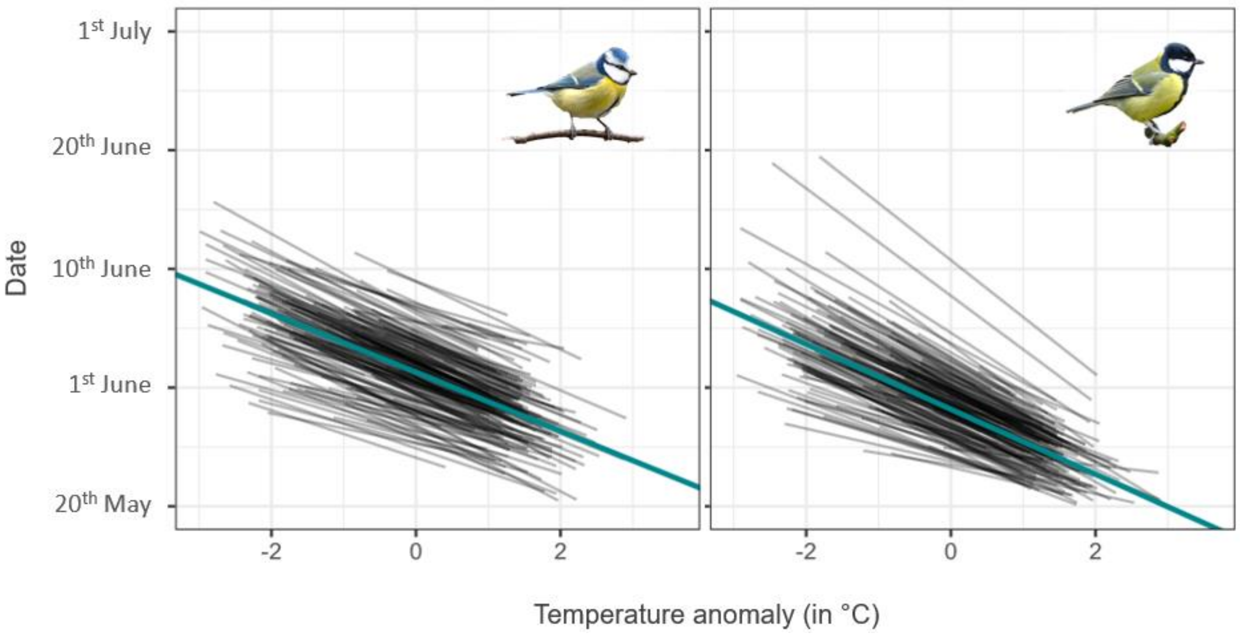

*Figure 4 : Site specific responses of breeding phenology (xmid) to local temperature anomaly. Each grey line represents the estimated phenological response to temperature for a single site, based on the posterior median for parameters in equation (6). The thicker turquoise line represents the predicted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

## Effects of habitat anthropization on phenology and its plasticity to temperature

Both species reproduce 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 by the loss of forest cover (i.e., when moving from the ancestral forest habitat to agricultural landscapes) in blue tits: the lower the forest cover, the flatter the relationship to temperature anomaly (i.e., the lower the dependence; Figure 5; Table 2). Phenological response to local temperature anomaly were similar between most anthropized and ancestral habitats (i.e., non-forest) for both species (Figure 5). Blue tit populations located in average forest sites, tended to be more sensitive to temperature anomaly when artificialization was higher (Figure 5, Table 2). Finally, neither forest cover nor imperviousness explain variations in the slope of the reaction norm to temperature anomaly in great tit, suggesting that this species reacts in the same way, whatever the degree and the type of habitat anthropization.

*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 (eq. 6).*

| | Blue tit | | Great tit | |
|---|---|---|---|---|
| | Median | 95% CI | Median | 95% CI |
| 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] |
| Forest 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] |
| Forest density * temperature anomomaly | **-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] |
| sigma_int | **4.71** | [3.7 ; 5.8] | **4.41** | [3.61 ; 5.26] |
| sigma_slope | **0.87** | [0.04 ; 2.35] | **1.5** | [0.71 ; 2.33] |
| Cov_slope_int | -1.13 | [-6.36 ; 0.96] | **-3.05** | [-6.36 ; -0.33] |

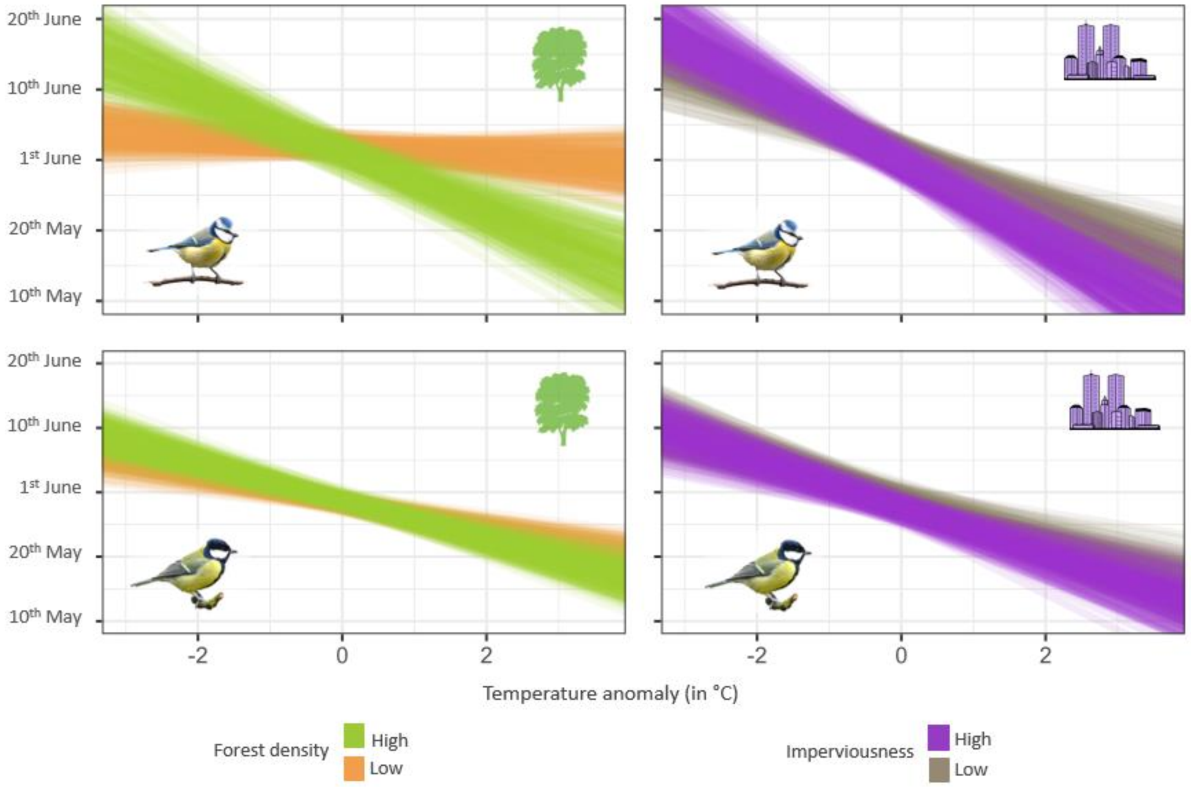

*Figure 5: Effects of both forest density and imperviousness on blue and great tits phenological response to local temperature anomaly. Each line corresponds to a projection of the model with parameters values sampled from the 0.10-0.90 posterior distributions. For both environmental factors," High" and" Low" correspond respectively to their 0.1 and 0.9 quantile across all capture sites.*

## Discussion

Both tit species reproduced earlier in warmer springs. This phenological response of tits to climate warming is already well established (Charmantier et al., 2008; Visser et al., 2009; Phillimore et al., 2016; Bonamour et al., 2019; Shutt et al., 2019; Bailey et al., 2022), and had been proved to be essentially mediated by plastic phenotypic adjustments (Charmantier et al., 2008; Biquet et al., 2022). The advancement of reproduction in warm years is a global phenotypic response, known from many other taxa of seasonal vertebrates (Thackeray et al., 2016; McLean et al., 2022). Nonetheless, our study is the first to establish that this relationship holds over a large variety of habitats (i.e., at country-level). Across study sites, the slope of the reaction norm to temperature ranged from -3.62 to -0.9 day/°C in blue tit (95% range: -3.29 to -1.58) and from -4.81 to -0.16 day/°C in great tit (95% range: -3.68 to -1.50). In most the cited studies on tits, the estimated slope ranged from -4 to -2.5 day/°C. But none of these studies estimated a plasticity close to 0 (i.e., absence of phenotypic response to temperature anomalies). This finding suggests that phenological plasticity varies more across sites, and habitats, than suggested by existing publications. This potentially biased perception of the variability of phenological reaction norms is likely explainable by the fact that the majority of long-term, nest-box based, monitoring programs are located are mainly located in favourable environments for tits, i.e., forest-dominated habitats (Lambrechts et al., 2010; Culina et al., 2021; Bailey et al., 2022).

Interestingly, the response to mean site temperature and to temperature anomaly was 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). If fledging phenology had advanced more in response to the mean site temperature than expected given our estimate of plasticity, we could have suggested that the observed phenological changes were consistent with a response to selection for earlier fledging date, as it is the case in some tits populations (Van Noordwijk et al., 1995; Gienapp et al., 2006; Marrot et al., 2017).

Despite the observed phenological variations across sites, the reaction norm of breeding phenology to temperature appeared largely conserved: it was similar in both species, identical across habitats for the generalist great tit, and maintained along the gradient of habitat urbanization for the blue tit. Only forest conversion into farmlands altered the phenological reaction norm of the deciduous forest specialist (the blue tit). A decrease in plasticity when shifting to farmland landscapes can be explained by a change in the abundance invertebrate preys (Vickery et al., 2001; Britschgi et al., 2006; Stanton et al., 2018). For example, a flatter peak of invertebrate prey abundance may require an increased dietary flexibility, decreasing the birds dependence on “ancestral preys” and their associated temperature cues during the breeding season (Vatka et al., 2011). Following the same rationale, Bailey *et al.* (2022) explained the weaker plasticity of tits in evergreen and mixed forests by the fact that they relied on a broader resource peak in these habitats, which reduced the cost of the trophic phenological mismatch during chick rearing, and then made birds less constrained by spring temperature. Moreover, they predicted that more specialist species, which occupy habitats with a narrow resource peak, should show stronger phenological plasticity. This applies to our results: the most specialist species (blue tit) had a stronger response to temperature anomalies than the generalist species (great tit) but only in its ancestral habitat. In the same environmental context (farmlands *vs* forests), Bourret et al. (2015) showed in the tree swallow *(Tachycineta bicolor)* that phenological plasticity was steeper in high density colonies, here populations benefitting from the highest prey abundances (Hussell, 2003). Further research is needed to determine whether such differences in phenological plasticity along the agricultural-artificial gradient are due to changes in resource abundance and phenology, or whether other factors associated with agricultural practices may affect the integration of environmental cues by birds.

We detected earlier breeding phenology in more artificialized sites, in line with previous studies showing that urban birds tend to breed earlier than their rural counterparts (Beck & Heinsohn, 2006; Najmanová & Adamík, 2009; Caizergues et al., 2018; Capilla-Lasheras et al., 2022). Our results (up to 2 days earlier for blue tits and 4 days earlier for great tits when comparing most anthropized and most ancestral sites, Figure S3.1), are in the range of what was previously observed: 4 to 7 days of lag across different songbirds' populations located in cities *vs* in more rural areas (Najmanová & Adamík, 2009). A common explanation for this trend is that springs occur earlier in cities due to the urban heat island effect (Yeh & Price, 2004; Schoech et al., 2008). However, very few sites were located in core urban areas (Figure S1.1), so the heat island effect is unlikely to have a strong impact on breeding phenology across the studied sites. Urbanization may have other effects on breeding phenology, beyond the higher temperatures usually associated to it, such as artificial light and food availability. Several studies suggested that artificial lights can advance bird phenology (Dominoni et al., 2020; Kempenaers et al., 2010; Senzaki et al., 2020). While direct effects of artificial lights on bird reproductive physiology have not been detected (Partecke et al., 2006), indirect effects may enhance reproductive activity, for example by allowing increased foraging time in diurnal animals (Deviche & Davies, 2013; Titulaer et al., 2012). Artificial food provisioning (bird tables) could also explain advanced phenology (Bourgault et al., 2009; Harrison et al., 2010; Schoech et al., 2008; Vafidis et al., 2016) 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).

Despite earlier breeding in more artificialized areas, the ancestral reaction norm of breeding phenology to temperature anomalies remained unchanged along the gradient of artificialization: blue and great tits adjusted their breeding time to temperature nearly identically in artificialized areas as in core forest (Figure 5). This reaction norm conservatism can be explained by the fact that, although prey abundance is lower in urban areas (lower peak), prey emergences remain synchronized by temperature (Seress et al., 2018). Furthermore, at least in our study design, artificialization tended to occur more in forested areas than in farmlands (Figure 3). It implies that populations from anthropized sites, were indeed surrounded by forest populations (exhibiting the ancestral reaction norm). Since urbanized environments are often ecological traps for passerines (Björklund et al., 2010; Zuñiga-Palacios et al., 2021),  we can also assume that forest population act as demographic sources, providing recruits for sinks in artificialized areas. Such an asymmetrical gene flow from ancestral, forest areas towards artificialized areas is expected to prevent the evolution of locally adapted reaction norms (Lenormand, 2002). This proximity of forest source populations to sinks in artificialized areas could explain that the reaction norm is conserved along the artificialization gradient for both species.

In summary, we showed apparent conservatism of phenological plasticity to local temperature across two gradients of habitat anthropization in two forest songbird species. It suggests that the ancestral reaction norm to temperature remained adaptive – or at least neutral – in most habitats. Only agriculture altered the phenological response to spring warmth in the forest-specialist species. Understanding the causal relationship of alteration of the reaction norm in farmlands will require further knowledge about prey availability, predictability and species diets along the forest-farmland gradient. We investigated 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). But, they have peculiar ecological requirements, usually tied to trees, as other secondary hole-nesting species. We need to broaden the ecological and evolutionary diversity of studied seasonal species (Youngflesh et al., 2023). Our modelling framework allows investigating the plasticity of breeding phenology in any 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 et al., 2014; Ahrestani et al., 2017; Morrison et al., 2022). 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 (DeWitt et al., 1998).

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## Author contributions

Paul Cuchot led 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.

## Conflicts of interests

The authors declare no competing interests.

## Data availability

We confirm that, should the manuscript be accepted, the data supporting the results will be archived in Dryad.