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Author for correspondence:
Caroline Isaksson
e-mail: caroline.isaksson@biol.lu.se

Facing rising temperatures in urban environments: the role of phenological plasticity in an urban-dwelling passerine, *Parus major*

Paul Cuchot[1], Megan J. Thompson[1,2], Clotilde Biard[3], Marcel Eens[4], Tapio Eeva[5], Laura Gervais[6], Caroline Isaksson[7], Juan Carlos Senar[8], Celine Teplitsky[1,†] and Anne Charmantier[1,†]

[1]CEFE, 34090 Montpellier, France
[2]Département des Sciences Biologiques, UQAM, Montreal, Canada H3C 3P8
[3]Institut d'Écologie et des Sciences de l'Environnement de Paris, Sorbonne University, 94010 Paris, France
[4]Department of Biology, Ethology Group, University of Antwerp Research Group Behavioural Ecology and Ecophysiology, Wilrijk, 2610 Antwerp, Belgium
[5]Department of Biology, Turun Yliopisto, FI-20014 Turku, Finland
[6]CNRS, SETE, 09200 Moulis, France
[7]Department of Biology, Lund University Faculty of Science, Lund 223 62, Sweden
[8]Evolutionary and Behavioural Ecology Unit, Museo de Ciencias Naturales de Barcelona, 08019 Barcelona, Spain

PC, 0000-0002-6060-803X; MJT, 0000-0002-0279-5340; ME, 0000-0001-7538-3542; TE, 0000-0002-0395-1536; LG, 0000-0002-7636-4818; CI, 0000-0002-6889-1386; JCS, 0000-0001-9955-3892; CT, 0000-0001-9458-709X; AC, 0000-0002-0691-2647

The capacity for birds to adjust their breeding time to variation in spring temperature via plasticity is crucial for insectivorous passerines in temperate areas, particularly in a context of climate disruptions. Recent studies suggested that phenological plasticity varies in response to environmental change via urbanization. We investigated the effects of urbanization on laying date, its phenotypic plasticity in response to spring temperature, and the between-individual variation in laying date, using data from five long-term studies of European great tits, *Parus major*, in forest and urban areas. First, we compared laying phenology and its plasticity in response to spring temperature between urban and forest populations. We confirmed that birds lay eggs earlier in urban environments in four populations and revealed reduced phenological plasticity in more urbanized environments in two populations. Additionally, we demonstrated greater between-individual variation in laying date in two urban areas. Second, we focused on urban populations only, and showed that the proportion of impervious surface area had little effect on the laying date. Overall, urbanization was associated with earlier breeding and less plasticity, although the strength of these associations varied among cities, likely owing to variation in the intensity of urbanization, landscape connectivity and habitat composition.

1. Introduction

The extension of the urban matrix into rural areas is one of the major drivers of habitat and biodiversity loss [1,2]. Urbanization deeply alters both biotic and abiotic environmental conditions, resulting in warmer urban environments with more artificial surfaces and increased pollution levels [3]. Moreover, in urban environments, humans frequently introduce new animal and plant communities [1], which can alter the spatial and temporal distribution of resources [4,5], which in turn influences interactions both within and

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[†]Joint senior authors.

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between species [6] as well as evolutionary dynamics [7,8]. The effects of these changes on phenotypic differences between non-urban and urban populations have been extensively studied, revealing notable morphological, physiological and behavioural shifts [9,10]. While these studies highlight the impact of urbanization on average phenotypic values, notably via plasticity [11,12], another crucial consideration is how urbanization affects already existing plastic responses that allow organisms to adapt to fluctuating environments.

Several lines of reasoning suggest that individual phenotypic plasticity may differ between non-urban and urban populations [13]. The degree of adaptive plasticity to an environmental variable depends on the slope of the optimal phenotypic response to environmental change, environmental predictability [14] and the cost–benefit balance of plasticity [15]. Since the urban matrix offers multiple novel constraints for a wide range of urban dwellers, it is likely that all these aspects may be altered by urbanization, leading to changes in plastic responses [16]. Furthermore, a decrease in plasticity may be expected if individuals are not able to perceive the environmental cue or to express the optimal phenotype because of environmental constraints [17,18]. In line with this, a recent study has shown that the plasticity of emergence time in pollinators, which enables them to adjust to changes in plant flowering times, is reduced in urban environments, limiting their ability to keep pace with the earlier blooming of plants [19]. Despite the scarcity of examples, the impact of urban environments on plasticity may be far from anecdotal.

Phenological plasticity enables consumers to track the timing of their resources, contributing to the match between predators' energetic needs and the abundance of resources [20]. Given that phenological plasticity is a crucial adaptation to variation in annual temperature for many seasonal species [21,22] and a key mechanism for adapting to climate change [23], it is important to consider how urbanization might influence its expression. In urban environments, the reliability of phenological cues may be degraded owing to different novel cues, such as artificial light at night or sound pollution [24,25], resulting in maladaptive plastic responses and possibly evolution of decreased plasticity [13]. Costs of plasticity, despite being generally low, may be higher in stressful habitats [26], and thus contribute to lower plasticity in urban environments. Moreover, urban birds in poor conditions may not be able to breed early at warmer temperatures [27]. However, prey abundance is more evenly distributed over a longer period in urban environments owing to a greater variety of tree species [28–30], and it is also lower overall [31,32]. A broader and lower resource peak could reduce the cost of asynchrony with the food peak, enabling birds more flexibility with respect to temperature [20].

We aimed here to investigate how urbanization affects mean laying date, its phenotypic plasticity in response to spring temperature, and the degree of variability at the population level. To achieve this, we used five pairs of urban and forest European populations of great tits (*Parus major*), with at least a decade of monitoring data and repeated breeding records. We compared lay date timing and its plastic response to temperature (i) between urban and forest populations and (ii) along an urbanization gradient within each urban population. Assessing between-individual variation in plastic responses is often challenging, as it requires a sufficient number of repeated measurements per individual [33]. As a result, population-level studies are commonly used as an alternative approach. While they do not directly capture individual variability, methods such as individual mean centring can help disentangle individual responses from overall population patterns, providing valuable insights into phenotypic plasticity [34]. In line with previous findings in a variety of bird species [35], we predicted earlier average breeding timing in urban populations and in more urbanized habitats within the city, compared with forest populations and less urbanized habitats within the city. Urban cues related to, for example, the urban heat island effect and artificial light can modify the ability to reliably predict future environmental conditions, which can lead to lower environmental sensitivity in urban tits. We hence predicted lower plasticity in lay date in urban populations and in more urbanized habitats within the city than in forests and less urbanized habitats across urban gradients. We also aimed to examine whether individuals in urban populations vary more in their average lay date timing than their conspecifics in forest populations, as found in bird species globally [35,36].

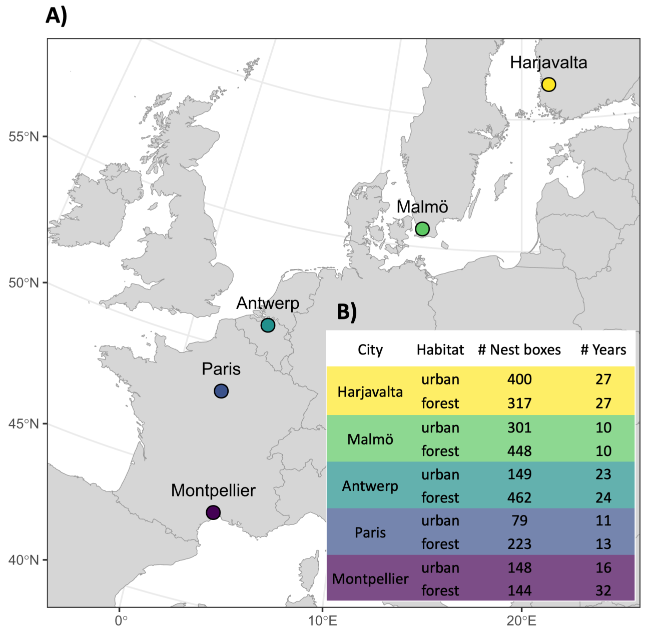
2. Material and methods

(a) Study areas and monitoring

We gathered data on urban and non-urban (hereafter 'forest') great tit populations from long-term monitoring programmes that track nest box occupancy, reproduction timing and breeding success of individuals. We compiled data from five study systems across Europe (figure 1): Montpellier (France; coordinates: 43.602° N, 3.879° E), Paris (France; 48.851° N, 2.343° E), Antwerp (Belgium; 51.210° N, 4.410° E), Malmö (Sweden; 55.600° N, 13.010° E) and Harjavalta (Finland; 61.320° N, 22.130° E). Each study system included data from both an urban and a non-urban population and spanned a monitoring period of at least 10 years. Overall, the dataset included a total of 2677 nest boxes (1077 in urban environments and 1600 in non-urban ones; table 1).

Laying dates were observed or estimated by visiting nest boxes once a week during the breeding season, starting mid-March. If nest boxes were not monitored on the day the first egg was laid, the laying date was estimated on the assumption that one egg was laid per day. We only considered the laying dates of first clutches, excluding second and replacement clutches [37,38]. First clutches were defined as the initial clutch laid by a female within a breeding season, occurring within 30 days of the earliest lay date for the focal species in a given year and sampling location [39,40]. This 30 day cut-off ensures that second and replacement clutches are not used when the first clutch is missed [39]. We included clutches of females with unknown identity, i.e. uncaptured individuals, assigning dummy identities to these females.

Parents were captured inside their breeding nest box when chicks were between 10 and 15 days old. The dataset includes a total of 12 609 laying dates, with 4934 in urban environments and 7675 in forest ones (table 1). Numbers of breeding repetitions per individual and population are shown in electronic supplementary material, table S1.



City	Habitat	# Nest boxes	# Years
Harjavalta	urban	400	27
	forest	317	27
Malmö	urban	301	10
	forest	448	10
Antwerp	urban	149	23
	forest	462	24
Paris	urban	79	11
	forest	223	13
Montpellier	urban	148	16
	forest	144	32

Figure 1. (A) Map of Europe showing locations of the five study systems. Each study system comprises two populations, one in an urban environment and the other in a non-urban environment (defined as 'forest' in table). (B) Table with the number of nest boxes and monitored years per population.

Table 1. Number of observed laying dates (first clutches only) and females, average calendar date for the first egg laid, and average distance between urban and forest populations. The average distance was calculated between each forest nest box and the central location of the urban nest boxes to avoid zero distances which could occur when forest nest boxes are arranged in a circular pattern around the city.

city	habitat	no. lay dates	no. females	average laying date	distance city–forest (m)
Harjavalta	urban	1269	1241	8 May	7164
	forest	1652	1584	10 May	
Malmö	urban	657	492	29 April	29 932
	forest	876	737	29 April	
Antwerp	urban	1822	1134	7 April	9590
	forest	3672	2475	12 April	
Paris	urban	254	215	2 April	66 850
	forest	678	517	8 April	
Montpellier	urban	932	780	7 April	17 886
	forest	797	638	10 April	

(b) Environmental data

(i) Temperature

Temperature data (in °C) were obtained from the E-OBS Gridded Dataset v. 26 with a resolution of 0.1° (11 × 11 km). The gridded dataset uses blended weather time series from the European-wide weather station network of the European Climate Assessment & Dataset project (ECA&D). Blended time series use data from nearby weather and synoptic stations to extend existing weather station time series and fill in gaps [41]. Full documentation explaining blending and quality control methods can be found on the ECA&D website (https://www.ecad.eu/). For each of the ten populations, we extracted the mean daily temperature for all years for which we had laying dates. The definitions of the temperature metrics are detailed in 'Statistical analysis' (§2c).

(ii) Impervious surface area

Impervious surface area (ISA) around each nest box was computed using high-resolution raster data provided by the European Earth observation programme Copernicus (https://www.copernicus.eu). Data were based on satellite images and combined optical and radar data to characterize imperviousness density (i.e. ISA, resolution 10 m [42]). ISA includes all sealed non-natural surfaces (e.g. roads, sidewalks, buildings), and correlates with several urban metrics, including increased temperature via the heat island effect [43], increased sound and light pollution, and decreases in tree cover [44]. ISA is increasingly used to quantify urbanization and is especially useful when examining urbanization effects at broad scales, given data are available across large spatial and temporal extents [45]. We computed the proportion of ISA in a 100 m radius around each nest box (range = 0–1, where 1 is all ISA), which corresponds to the literature-based estimates of parental foraging area while feeding nestlings in blue and great tits in both non-urban [46–48] and urban areas [46,49]. Further, lay date responses of great tits to environmental variation at small spatial scales have previously been documented in a woodland population (75 m [50]; <50 m [51]). For these reasons, and since the proportion of ISA at 100 m and 1000 m scales is correlated in these datasets (see also [45]), we did not examine impacts of urbanization at larger spatial scales. Urban populations of tits were monitored at nest boxes close to city centres and tended to have a higher proportion of ISA (mean (s.d.) = 0.37 (0.31)), whereas forest populations of tits were monitored at nest boxes located outside cities and had a lower proportion of ISA (mean (s.d.) = 0.01 (0.04)). Cities varied among each other in how urbanized they were: Paris was most urbanized (ISA mean (s.d.) = 0.63 (0.25)), Montpellier and Harjavalta were less urbanized (ISA mean (s.d.) = 0.46 (0.40) and 0.42 (0.31), respectively) and Antwerp and Malmö were the least urbanized (ISA mean (s.d.) = 0.27 (0.21) and 0.28 (0.21), respectively). See also electronic supplementary material, figure S1 in appendix S2 for ISA distributions of each city.

(c) Statistical analysis

We performed all analyses using R v. 4.2.1 [52]. Differences in population variance and phenotypic plasticity of laying date in response to spring temperature between forest and urban populations and along the urbanization gradient were explored using hierarchical Bayesian linear mixed models with Gaussian error structures (*brms* R package [53]). We ran these models with four chains of 15 000 iterations each and a burn-in of 5000. Convergence was confirmed for all parameters when the $\hat{R}$ value was below 1.1 [54]. This criterion was met for all estimates used in Results (§3).

(i) Defining temperature windows

Average spring temperatures are known to affect breeding time in passerines in general [55] and great tits in particular [56]. Experimental evidence suggests a direct effect of average temperatures on breeding time [57,58], although, in the wild, mean temperature can also be an integrative factor representing other environmental conditions, such as food resources. Determining the time window of average temperature that best explains variation in average laying date for each population is usually done using a sliding window approach [59]. However, these analyses can require long-term datasets (>20 years; [60]). Because monitoring of several populations was shorter than 20 years (see figure 1B), a sliding window comparison was associated with a high risk of bias. We thus made the hypothesis of a similar window for each pair of urban and forest populations. This hypothesis was confirmed by running a sliding window analysis for the urban populations with the longest monitoring and comparing them with their forest counterparts (Antwerp and Harjavalta; see electronic supplementary material, appendix S6).

To obtain the city-specific windows, we relied on the results from the study by Bailey *et al*. [56], which assessed the temperature windows best predicting the annual population mean laying date in 67 tit populations across Europe. For Montpellier, Antwerp and Harjavalta, we used the windows found by Bailey *et al.* for the forest populations. For Paris and Malmö, the windows were not directly available from that study. However, Bailey *et al.* had shown that across populations, the midpoint of the window strongly depends on latitude ([56], figure 2) and that the duration was assumed to be 56 days (the intercept of the model comparing windows among populations is given in Bailey *et al.* ([56], tbl. S2). We used this relationship to predict the midpoint date and duration of the window for Paris and Harjavalta. After defining the windows, we computed the average daily temperature over each period for all combinations of city, habitat and year. Note that the windows are the same for a given pair of forest and city populations, but the average temperature may differ, as average temperatures are based on E-OBS temperature data (electronic supplementary material, figure S3).

(ii) Urban versus forest average laying date and its plastic response to temperature

We first assessed, for each study system separately, the additive and interactive effects of spring temperature (see ‘Defining temperature windows’ (§2c(i))) and habitat (set as a categorical variable, either urban or forest) on laying date in order to estimate how population responses and individual plasticity to temperature differ between habitats. Each linear mixed model included year and female identity as random intercepts in equation (2.1). A heterogeneous variance structure was fitted on the female ID to estimate different between-female variance in laying date per habitat category (also known as a heterogeneous variance model; Gianola []). Because of power limitations, we could not fit individual slopes in the models (models including random slopes were unable to estimate the among-individual variation in temperature responses; see electronic supplementary material, appendix S7). Therefore, as recommended by van de Pol & Wright [34], we separated within-subject from between-subject effects using within-subject centring to assess population-level responses and average individual plasticity. To do so, we fitted respectively as fixed effects mean individual temperature $\overline{\mathrm{temp}}_i$ (average of the temperature during the window experienced by an individual across its breeding events) and temperature anomaly (i.e. individual yearly temperature deviation from its mean temperature temp_{jk}), which involves subtracting the individual mean temperature from the annual temperature observation.

$$\begin{aligned}\mathrm{Layingdate}_{ijk} = {} & \alpha + (\mu_{0i} + \mu_{0j}) + \beta_{\mathrm{B}} * \overline{\mathrm{temp}}_i + \beta_{\mathrm{W}} * (\mathrm{temp}_{jk} - \overline{\mathrm{temp}}_i) + \delta * \mathrm{habitat}_{ik} \\ & + \gamma_{\mathrm{B}} * \overline{\mathrm{temp}}_i * \mathrm{habitat}_{ik} + \gamma_{\mathrm{W}} * (\mathrm{temp}_{jk} - \overline{\mathrm{temp}}_i) * \mathrm{habitat}_{ik} + \varepsilon_{ij},\end{aligned} \tag{2.1}$$

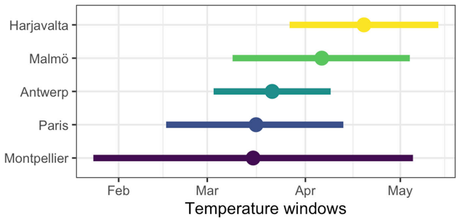


Figure 2. Temperature windows were defined for each forest–urban study system. Different windows between urban and forest populations of the same study system were not considered. Harjavalta, Antwerp and Montpellier windows were taken from Bailey *et al*. [56]. The Paris and Malmö windows were calculated based on the relationship between the geographical location and the centre of the window, established in the study by Bailey *et al*. [56] (1.49 × latitude + 0.92 × longitude).

where Layingdate_{ijk} is the laying date of individual i in year j and in habitat k (city or forest), α is the mean laying date of the population, μ_{0i} the female identity random intercept (grouped per habitat category), μ_{0j} the year random intercept, β_B the between-individual response to spring temperature of laying date of the study system (includes both the forest and urban populations), β_W the within-individual response to the temperature of laying date, δ the additive effect of habitat type, γ_B the effect of habitat category on between-individual response to spring temperature, and γ_W the effect of habitat category on within-individual response (plasticity) to spring temperature. ε_{ij} corresponds to the residual error term. Because differences in study duration could influence estimates of plasticity and between-individual variance, we repeated the analyses using only data from the overlapping years between the urban and forest populations in Montpellier (2008–2023). The resulting estimates were consistent with those from the full dataset (electronic supplementary material, appendix S8). Similar results were previously reported by Thompson *et al.* [45], who also found no effect of study duration on these estimates.

Because the number of individuals with repeated measures was low in Paris and Harjavalta, we ran additional analyses restricted to individuals with repeated observations and a simulation study to evaluate the robustness of our results. We simulated laying dates using the fixed and random effects estimated from the empirical models while preserving the original data structure (numbers of individuals, repeats, habitats and years), and then refitted the same model to each simulated dataset. Each set of parameters was run 100 times (electronic supplementary material, appendix S9).

For the comparison of between-individual variance in laying date (variance among random female intercepts), we calculated logarithms of the ratio of variances,

$$\text{lnVR} = \ln(\sigma^2_\text{urban}/\sigma^2_\text{forest}), \tag{2.2}$$

which were considered non-significant when the 95% credible interval overlapped zero. Higher variances (i.e. between-individual variance) in urban habitats have a positive lnVR.

(iii) Effect of impervious surface area within urban populations

To investigate smaller-scale effects of urbanization, we explored the interactive effect on the laying date of local ISA at the nest box level and temperature. This analysis was restricted to breeding events occurring in the urban populations. We fitted as fixed effects the mean individual temperature, $\overline{\text{temp}}_i$, and temperature anomaly. We fitted a model for each city that included the interaction between temperature variables (mean and anomaly) and ISA, with year and female identity as random intercepts,

$$\begin{aligned}\text{Layingdate}_{ij} = {} & \alpha + (\mu_{0i} + \mu_{0j}) + \beta_\text{B} * \overline{\text{temp}}_i + \beta_\text{W} * (\text{temp}_j - \overline{\text{temp}_i}) + \varphi * \text{ISA} \\ & + \gamma_\text{B} * \overline{\text{temp}}_i * \text{ISA} + \gamma_\text{W} * (\text{temp}_j - \overline{\text{temp}_i}) * \text{ISA} + \varepsilon_{ij},\end{aligned} \tag{2.3}$$

where φcorresponds to the additive effect of ISA on laying date,γ_B the effect of ISA on between-individual response to spring temperature, and γ_W the effect of ISA on within-individual response (plasticity). ISA was mean-centred per population.

3. Results

(a) Earlier breeding in urban habitats at the population level

In four out of the five study systems, we found that urban populations laid earlier than their forest counterparts, with average differences ranging from 2.16 to 4.82 days: Montpellier −3.31 days, Paris −2.93, Antwerp −4.82 and Harjavalta −2.16 (table 2; electronic supplementary material, appendix S4: figure S4 and table S2). Note that the difference in phenology was weakest in Malmö, which is also the city with the lowest ISA (electronic supplementary material, figure S1). Within all five urban populations, we did not find an earlier laying date in more urbanized areas (higher value of ISA; electronic supplementary material, table S6).

(b) Phenotypic plasticity in laying date in response to temperature

Individual plastic responses of laying date to spring temperature anomalies (β_W) ranged from −1.72 to −3.66 d °C^{-1}. This is similar to the range of between-individual responses to average experimental temperature (β_B), which ranged from −1.86 to

Table 2. Fixed effects median and 95% confidence interval of posterior distributions from Bayesian mixed models of great tit laying date in response to individual mean temperature, individual temperature anomaly, habitat (‘urban’ being the reference category), and interactions between habitat and, respectively, mean temperature and temperature anomaly. Year and female ID were considered as random intercepts. For the female ID random intercept, the models provided one estimate per category of habitat. Differences between forest and urban random intercepts were estimated using the natural logarithm of the ratio of variance (lnVR, see ‘Statistical analysis’ (§2c)). Temperatures correspond to the average daily mean temperature over a window estimated by Bailey *et al*. [56] (see figure 2). Each row represents one model. A positive lnVR indicates that individuals are more variable in laying dates in the urban populations than in the forest ones. Bold terms correspond to fixed effects for which the 95% posterior distributions do not cross zero.

	fixed effect											
	intercept		**mean temperature**		**temperature anomaly**		**habitat**		**mean temperature * habitat (forest)**		**temperature anomaly * habitat (forest)**	
	median	**95% CI**	**median**	**95% CI**	**median**	**95% CI**	**median**	**95% CI**	**median**	**95% CI**	**median**	**95% CI**
Harjavalta	140.54	[137.48,143.57]	**−2.65**	[−3.30,−1.99]	**−1.72**	[−3.38,−0.08]	**3.34**	[1.52,5.13]	−0.26	[−0.64,0.13]	−1.49	[−3.23,0.25]
Malmö	135.21	[129.10,141.00]	**−2.50**	[−3.40,−1.56]	**−1.97**	[−3.16,−0.78]	−0.88	[−4.40,2.71]	0.02	[−0.55,0.58]	−0.16	[−1.38,1.03]
Antwerp	121.53	[115.65,127.57]	**−3.18**	[−3.97,−2.39]	**−3.66**	[−4.42,−2.90]	**8.57**	[5.78,11.33]	**−0.51**	[−0.88,−0.13]	0.05	[−0.23,0.34]
Paris	109.87	[96.15,121.41]	**−1.86**	[−3.09,−0.39]	**−2.01**	[−3.23,−0.61]	**12.68**	[5.05,19.93]	**−1.17**	[−1.99,−0.29]	**−1.63**	[−2.56,−0.69]
Montpellier	120.51	[99.02,141.01]	**−2.33**	[−4.25,−0.32]	**−3.06**	[−5.24,−0.80]	**20.36**	[8.30,32.40]	**−1.61**	[−2.73,−0.49]	**−2.24**	[−3.95,−0.54]

	random effect (s.d.)						**lnVR**		**residual**	
	year		**female ID, forest (intercept)**		**female ID, urban (intercept)**					
	median	**95% CI**	**median**	**95% CI**	**median**	**95% CI**	**median**	**95% CI**	**median**	**95% CI**
Harjavalta	1.75	[1.31,2.44]	2.89	[0.66,3.80]	4.11	[2.96,4.83]	**0.72**	[0.38,3.06]	4.22	[3.50,5.06]
Malmö	1.63	[0.96,3.18]	2.08	[0.17,3.27]	3.09	[1.73,4.14]	0.80	[−0.07,5.52]	5.66	[5.10,6.12]
Antwerp	2.69	[2.05,3.70]	3.66	[3.41,3.90]	4.23	[3.91,4.56]	**0.29**	[0.10,0.48]	4.40	[4.27,4.54]
Paris	3.25	[2.13,5.75]	3.94	[3.28,4.52]	4.67	[3.84,5.52]	0.34	[−0.07,0.75]	3.98	[3.54,4.45]
Montpellier	4.42	[3.40,6.02]	3.01	[2.06,3.75]	5.46	[4.81,6.06]	**1.19**	[0.76,1.86]	5.26	[4.87,5.69]

-3.18 d °C^{-1}. The CIs of β_W and β_B largely overlapped, confirming that changes in laying date are due to females plastically laying overall earlier when spring temperatures were warmer (table 2; figure 3A). In Paris and Harjavalta, where the number of individuals with repeated measurements is low, both the analyses based on individuals with more than one observation and the simulations showed that within-individual effects could still be detected under limited sampling, although we remain cautious about the weight these two study areas carry in our overall conclusions regarding individual plasticity patterns (electronic supplementary material, appendix S9).

We found steeper between-individual responses to spring temperature (β_B) in forest populations compared with their urban counterparts for three out of the five study systems. Population response was 1.16 times steeper in forest than in urban populations (calculated from table 2: $\delta_{\text{Bplast}} = (0.51 + 3.18)/3.18$) for Antwerp, 1.62 in Paris ($\delta_{\text{Bplast}} = (1.17 + 1.86)/1.86$) and 1.69 in Montpellier ($\delta_{\text{Bplast}} = (1.61 + 2.33)/2.33$).

We detected a difference in within-individual plasticity (β_W) in Montpellier and Paris, with the response to individual temperature deviation being 1.73 times stronger in the forest population than in the urban one (Montpellier: $\delta_{\text{Wplast}} = (2.24 + 3.06)/3.06$), Paris: 1.81 $\delta_{\text{Wplast}} = (1.63 + 2.01)/2.01$).

We found no effect of the proportion of ISA on laying date response to spring temperature, at either population or individual level, when examining the impact of urbanization within urban populations (electronic supplementary material, table S6; figure 3B).

(c) Between-individual variance in average laying date

Generally, birds from urban populations exhibit greater variance in laying dates than those from forest populations (lnVR > 0; table 2; electronic supplementary material, figure S5). In Malmö and Paris, support for this trend was very weak (lnVR distribution crossed zero).

4. Discussion

In this study, we examined variation in laying phenology and its plasticity to spring temperatures in great tits, comparing urban and forest populations as well as analysing patterns along urbanization gradients. Our results confirm previous findings that birds lay earlier both when exposed to warmer spring temperatures and in urban compared with forest habitats, at the population level. We found evidence of reduced average individual plasticity in response to temperature in urban habitats for two study systems: Montpellier and Paris. Our results also suggest that between-individual variation in laying date is higher in some urban areas compared with nearby forests.

(a) Urbanization and laying date

Great tits reproduced earlier in each urban population when compared with their forest counterparts. This result was expected as shown repeatedly in birds [61,62], including great tits [63,64]. Earlier avian breeding in urban environments can be partially explained by the heat island effect, which raises minimum temperatures owing to heat retention by built surfaces and reduced vegetation. Our study uniquely investigates both the additive and interactive effects of temperature and urbanization on laying date. By including both variables in the same model, we were able to begin disentangling their effects. Although we accounted for temperature using E-OBS data, this may not fully capture fine-scale urban heat island effects, and future studies should record ambient temperature at the core of the birds' territories. In the Montpellier, Paris and Malmö populations, the two habitats were remote enough that the annual average temperature differed between forest and habitat windows (table 1; electronic supplementary material, figure S3). In Montpellier and Paris, urban birds laid earlier than forest birds after controlling for broad-scale temperature, suggesting that other urban factors might also influence breeding phenology. Among these, artificial light at night in highly urbanized environments can affect birds by causing an over-estimation of photoperiod length [65] and by increasing foraging time [66], which might improve pre-breeding body condition. Moreover, urban environments are often associated with voluntary or involuntary anthropogenic food provisioning during winter, which is known to advance the breeding phenology of birds by enabling them to attain the body condition required for reproduction [67]. For example, faecal metabarcoding in forest blue tits (*Cyanistes caeruleus*) prior to the breeding season revealed that higher supplementary food consumption was associated with a 5 day advancement in breeding phenology [68]. Importantly, urban effects such as artificial light and supplementary feeding can vary within cities across the species distribution. This variation, e.g. in light spectra across replicated cities, could be exploited to further decipher the specific role of artificial light at night versus other drivers of earlier bird phenology (e.g. [69]). Interestingly, within urban populations, females laying in more urbanized conditions, those with higher ISA, did not lay earlier, confirming that the phenological shift associated with urbanization is observable at a broader scale only.

(b) Urbanization and phenological plasticity

Aligned with our predictions, we found evidence for reduced temperature plasticity of laying date, although this evidence was strong only in two of the five urban populations: Montpellier and Paris. Note that these two cities had the highest ISA values (electronic supplementary material, figure S1). Several factors may explain lower phenological plasticity in more urban habitats [70]. First, environmental cues necessary for the onset of laying behaviour, such as resource abundance, might be poorer in

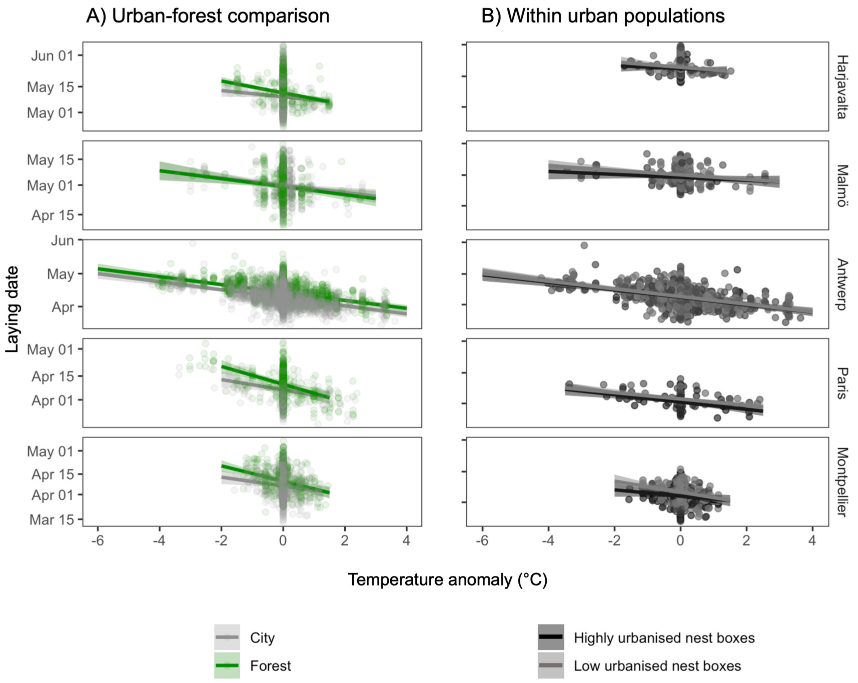


Figure 3. Differences in laying date plasticity in response to temperature: (A) between urban and forest populations (see table 2 for model outputs) and (B) within urban populations along an urbanization gradient (see electronic supplementary material, table S6 for model outputs). For the urban–forest comparison, we ran one model per study system and included the habitat (city or forest) as a fixed effect, in interaction with both mean temperature and temperature anomaly. For the within-urban-population comparison, we ran one model per urban population and included a fine-scale measure of urbanization (at the nest box level) as a fixed effect, in interaction with both mean temperature and temperature anomaly. Urbanization categories for (B) were defined according to the least and most urbanized nest boxes per city. The accumulation of zero values for temperature anomalies corresponds to individuals with only one recorded breeding event. Cities are ordered in descending latitudinal position.

urban environments because of increased evergreen and exotic tree species [71,72]. Also, birds use social cues, i.e. information transmitted by conspecifics, to exchange signals about optimal timing for breeding, which helps them synchronize egg-laying with resource availability [55]. In noisy urban environments, however, these social exchanges may be disrupted [73], potentially reducing their ability to adjust reproductive timing in response to environmental changes. Second, urban birds may already breed as early as local conditions permit, so their ability to advance laying dates in warmer years may be limited, leading to lower plasticity. Consistent with this idea, a recent experimental study reported that great tits exposed to artificial light at night, which advances the laying phenology, exhibited reduced temperature plasticity [65]. Another possibility is that urban birds could have lower plasticity because of nonlinear reaction norms, i.e. forest birds would also display shallower plasticity if they were exposed to the same temperature as city birds. This pattern has at least been shown once in a subalpine plant [74], but seems to be uncommon in birds and very limited in great tits [75]. Third, the lower but also broader resource peaks in urban environments for temperate insectivorous birds (e.g. blue tits and great tits, see [28–30]) may lead to reduced plasticity. This, in turn, likely reduces the selection pressure on temperature plasticity, which could result in reduced plasticity as a way to minimize the costs of maintaining it.

(c) Between-individual variance in laying date

We found higher between-individual laying date variance in three urban populations, Montpellier, Antwerp and Harjavalta, when comparing with their forest counterparts. Thompson *et al.* [36] suggested some hypotheses that could explain greater individual differences in urban populations. First, increased habitat heterogeneity in urban environments, because of higher levels of patchiness, fragmentation and tree species diversity, could lead to more diverse expression of phenotypic traits (e.g. through plasticity; [76]). We found that greater between-individual variance tended to associate with increased variation of ISA (electronic supplementary material, appendix S2; Montpellier ISA standard deviation = 0.40, Paris = 0.25, Harjavalta = 0.31), which may suggest that urban breeding territories that contain variable habitat types (e.g. trees versus concrete) have the highest laying diversity. Examining tree diversity or composition in urban breeding territories, specifically, could potentially explain higher individual differences in lay date. For example, non-native tree species can have delayed phenology compared with native trees in urban areas of Malmö, Sweden [31]. Since tits can partially rely on phenological cues from trees to adjust their lay date timing [77], linking phenological diversity at multiple trophic levels in urban areas in the future may be especially conducive. Second, if cities act as sinks for the surrounding populations, i.e. because they have lower survival and/or breeding output, we might expect consistent dispersal into cities to drive greater genetic diversity and a more diverse expression of phenotypic traits such as laying date across individuals. In the Montpellier populations, where we also observed the strongest tendencies for higher urban phenological variation, there is evidence for such source–sink dynamics, as we have previously described lower reproductive output and lower juvenile survival in city compared with forest great tits [78–80] and some weak urban-related genetic structure [81].

(d) Support across city replicates

Most of the results presented here, although of the same sign and similar magnitude, showed some variation across the five cities. City-specific results can be explained by the fact that urban characteristics are themselves variable. For instance, we observed a tendency for lower average individual plasticity in urban populations in two of the five study systems, Montpellier and Paris. Among the studied cities, Montpellier and Paris have the most urbanized populations (see ISA distribution in electronic supplementary material, figure S1). Urbanization can vary not only in terms of the proportion of concrete but also in factors that may independently affect the breeding phenology of great tits, such as variation in artificial light, noise and chemical pollution. Moreover, connectivity between urban and forest populations may influence the strength of the observed patterns (reduced temperature plasticity and earlier breeding in urban environments). Indeed, connected populations would exhibit increased gene flow, reducing genetic differentiation between urban and forest populations. Cuchot *et al*. [70] showed that, along a suburban–rural gradient with relatively moderate levels of urbanization, indicative of good connectivity between populations, earlier fledging dates were indeed observed in more urbanized environments, but temperature plasticity did not differ between the most and least urbanized sites. In this study, we use forest and urban paired populations of great tits located across a wide latitudinal range (from 43.602 to 61.320° N), and some studies suggest that populations in higher latitudes exhibit lower plasticity to temperature (in tree swallows [82]; in great tits [83]). Interestingly, we observed a similar pattern in our study, with the Malmö and Harjavalta forest populations exhibiting the lowest plasticity. However, this trend is only evident in the forest populations (table 2). This suggests that latitude may influence temperature plasticity differently in urban and forest populations, with urbanization potentially mitigating the effects of latitude on temperature plasticity. We did not have enough power to formally test this result, but future studies should investigate a larger sample of replicated locations to explore how latitude and urbanization interact to shape plasticity across various environmental contexts, as this could reveal important patterns for understanding species' adaptability to climate change.

5. Conclusion

Our results confirm that urbanization alters the great tit phenological distribution by advancing laying date and increasing its variability in urban compared with forest birds. We also demonstrate that urbanization and temperature both advance breeding phenology and that some urban populations are less plastic than their forest conspecifics in their phenological response to interannual variation in temperature. We encourage further studies to explore these questions using finer-scale temperature data across urbanization gradients and within the birds' territories, which are so far lacking. It also remains to be determined whether breeding earlier and displaying reduced phenology plasticity in the city are adaptive responses of urban birds. In the future, determining how optimal lay date timing and variation [84,85] may be differentially impacted by temperature in urban and forest areas could facilitate predictions on how climate change will impact phenological fitness in environments with varying levels of human disturbance. Specifically, evaluating the ability of urban populations to plastically track their phenological optimum will importantly inform on the stability of populations and communities in cities under projected climate change scenarios [86].

Ethics. Harjavalta: Captures were performed under ringing permits delivered by the Finnish Museum of Natural History (1991–2007: 5976/434/87, 24/4342/92, 11/57/22/97, 17/57/13/2002) and Center for Economic Development, Transport and the Environment (2008–2024: LOS-2007-L-1001–254, VARELY/959/07.01/2012, VARELY/3622/2017, VARELY/8346/2022). Paris: This work conforms to European and French regulations regarding the use and ethical treatment of wild animals of protected species for scientific research (authorizations nos DRIEE-2012-31à38, 2019-DRIEE-IF/033 and /046, ethical approval no. APAFIS#19941-2019032516275025v5, bird ringing licence no. 1454 and Personal Project no. 537 from CRBPO, National Museum of Natural History MNHN). Montpellier: Captures were performed under personal ringing permits delivered by the CRBPO to A.C. (ringing permit no. 1907), Samuel Perret (no. 16368) and Arnaud Grégoire (no. 1904). All experimental protocols described were reviewed by the Ethics Committee for Animal Experimentation no. 036 (Languedoc Roussillon CEEA-LR) and approved on 12 December 2012, 5 June 2018, 11 October 2021 and 9 July 2024. Malmö: Captures were performed under personal ringing permits delivered by the Swedish Natural History Museum to C.I. (ringing permit no. 0681). Ethical approval was granted by the Malmö/Lund Ethical Board (nos M454.12:1 (2013–2016), M108-16 (2016–2021), 5.8.18-04500/2021 (2021–2023)). Antwerp: The work was performed in accordance with Belgian and Flemish laws regarding animal welfare and adhered to the ASAB/ABS guidelines for the use of animals in behavioural research and teaching. The Royal Belgian Institute of Natural Sciences (KBIN) provided ringing licences for M.E. and Erik Matthysen as well as their collaborators.

Data accessibility. All data and codes can be found in Zenodo [87]. Supplementary material is available online [88].

Declaration of AI use. AI-assisted technologies, namely DeepL and ChatGPT, were used with human oversight in the writing process to improve the manuscript's readability and language.

Authors' contributions. P.C.: conceptualization, formal analysis, methodology, visualization, writing—original draft; M.J.T.: data curation, methodology, validation, writing—review and editing; C.B.: data curation, validation, writing—review and editing; M.E.: data curation, validation, writing—review and editing; T.E.: data curation, validation, writing—review and editing; L.G.: methodology, software, validation, writing—review and editing; C.I.: data curation, validation, writing—review and editing; J.C.S.: validation, writing—review and editing; C.T.: conceptualization, data curation, funding acquisition, methodology, supervision, writing—review and editing; A.C.: conceptualization, data curation, funding acquisition, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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