A global meta-analysis reveals more variable life histories in urban birds compared to their non-urban neighbours

Authors:

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Abstract.

Cities pose a major ecological challenge for wildlife worldwide. Phenotypic variation is a pivotal metric to predict evolutionary potential in response to environmental change. Recent work suggests that urban populations might have higher levels of phenotypic variation than non-urban counterparts. This prediction, however, has never been tested across taxa nor over a broad geographical range. Here, we conduct a meta-analysis of the urban avian literature to compare urban *versus* non-urban means and variances for phenology and reproductive performance. First, we show that urban birds reproduce earlier and have smaller broods than non-urban ones. Second, we demonstrate that urban populations have a more variable phenology than non-urban populations. Our analyses reveal that the latter pattern arises from differences in phenological variation between individuals within breeding seasons, likely because of higher heterogeneity in the urban study areas. These findings suggest that the opportunity for selection on phenology may be stronger in urban bird populations and that the patterns of phenotypic variation in urban and non-urban avian populations may consistently differ.

Introduction

Humans have drastically changed the environmental conditions on Earth[1]. The footprint of human activity is most pronounced in urban environments, where microclimatic conditions, biogeochemical cycles and the sensory landscape are considerably different to those in non-urban environments[2]. Perhaps not surprisingly, animals and plants are changing their phenotypes in response to the novel conditions and selective pressures found in cities[3,4] and, indeed, numerous studies have reported contrasting phenotypes between urban and non-urban populations across the globe (e.g.[5–7]; reviewed in[3,4,8]). The extent to which populations can adapt to urban living will partly depend on how urbanisation affects phenotypic variation[9]. Phenotypic variation is tightly linked to eco-evolutionary processes: it is an essential condition for current selection, it results from past selection pressures, and it depends on gene flow and phenotypic plasticity. As such, assessing how urbanisation affects phenotypic variation is essential to understand the evolutionary drivers of and potential for phenotypic change in urban environments.

Urban evolutionary ecologists have traditionally focused on differences in mean trait values between urban and non-urban populations, typically finding altered phenology, morphology, behaviour and reproductive performance in urban populations (or populations exposed to urban-like factors) compared to non-urban counterparts[10–14]. However, no study to date has explicitly investigated how urbanisation affects phenotypic variation at a global scale (see[15] for a study of changes in fitness variation in response to human-related activities).

Recent single-species studies suggest that phenotypic variation may be affected by urbanisation[9,16]. For example, in species with limited dispersal ability (i.e., whose dispersal occurs at a smaller scale than the scale at which the urban habitat varies), adaptation to local conditions may increase phenotypic variation within the urban matrix. Findings from urban and non-urban meta-populations of the common ragweed (*Ambrosia artemisiifolia*) are consistent with this prediction as inter-population variation in several fitness proxies was

greater in urban environments compared to non-urban environments[16]. A recent meta-analysis of selection strength found weaker selection occurring in human-disturbed populations[15], which could lead to higher phenotypic variation in urban populations compared to their non-urban counterparts. Overall, these studies converge with the notion that urban populations may display higher levels of phenotypic variation (reviewed in[9]). These findings also highlight that the extent to which urbanisation may impact phenotypic variation is likely to depend on the interplay between the spatial and temporal scale at which environmental conditions fluctuate in the urban habitat, and the species' dispersal ability and longevity[9].

Here, we investigate how urbanisation impacts mean phenotypic values and phenotypic variation using a meta-analysis of 409 urban – non-urban comparisons of avian life-history traits (laying dates, clutch size and number of fledglings) published between 1958 and 2020 including 33 bird species (Figure 1). Specifically, we ask the following questions: i) does urbanisation affect mean life-history avian phenotypes? ii) does urbanisation impact variation in avian life-history traits? iii) what is the temporal and spatial scale at which urbanisation affects phenotypic variation? Based on previous research[10,13], we predict that urban bird populations display earlier phenology and are less productive than non-urban populations. We also predict increased phenotypic variation in urban populations compared to non-urban populations (see above; and reviewed in[9]). Lastly, we disentangle urban effects on phenotypic variation across different temporal and spatial scales, suggesting an ecological cause for the effects of urbanisation on avian phenotypic variation.

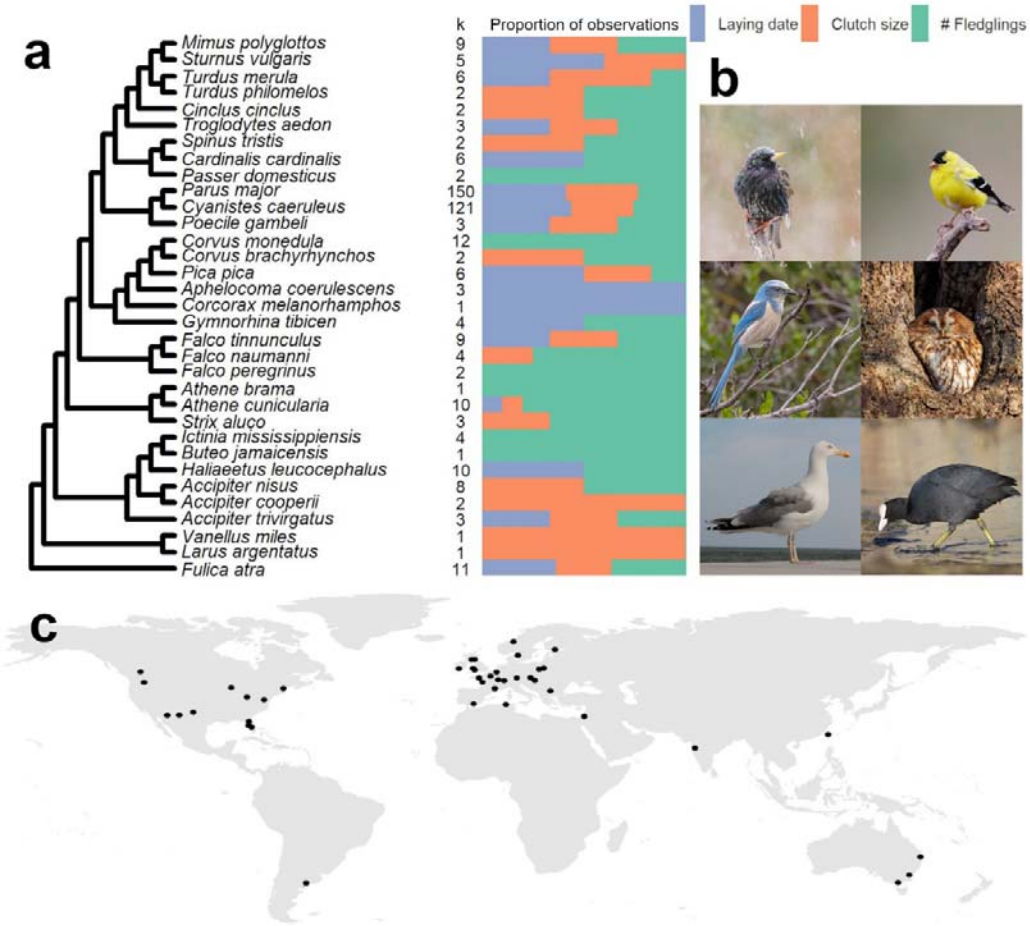

Figure 1. Phylogenetic and geographical breadth of the meta-analytic data. (a) Phylogenetic tree of the 33 avian species included in the meta-analysis along with the number of effect sizes (i.e., urban – non-urban comparisons) included per species ('k'; which may encompass multiple years of study from the same publication) and the proportion of observations for each life-history trait (purple: Laying date; orange: Clutch size; Green: Number of fledglings). (**b**) Our meta-analysis included a broad range of species, as examples, left to right from top to bottom: *Sturnus vulgaris*, *Spinus tristis*, *Aphelocoma coerulescens*, *Strix aluco*, *Larus argentatus* and *Fulica atra*. All images are copyright free (CC - Public Domain Mark 1.0. Authors: Shenandoah National Park [first two images], Mike Carlo/U.S. Fish & Wildlife Service, Raini Svensson, Vanzan and Ekaterina Chernetsova) and were extracted from www.flickr.com. (**c**) Global map (excluding Antarctica) showing the location of each study included in the meta-analysis. Each point represents one study in which one or more urban – non-urban pairs of populations were sampled across a varying number of years.

Results & Discussion

After systematically inspecting 940 studies published between 1958 and 2020 (see Methods), our meta-analysis included 409 urban – non-urban comparisons for three life-history traits: laying date (151 effect sizes from 32 studies), clutch size (124 effect sizes from 42 studies) and number of fledglings (134 effect sizes from 44 studies) (Figure 1, S1 & S2). To test whether urban populations reproduce earlier, have smaller clutches, fewer nestlings survive to fledging, and display more variation in these life-history traits compared to non-urban conspecifics, we meta-analysed log response ratios (lnRR[17]) and log coefficient of variation ratios (lnCVR[18,19]) accounting for phylogenetic effects[20]. These effect sizes were used to compare means and coefficients of variation of urban *versus* non-urban populations, and are widely used in evidence synthesis in ecology and evolution[18,21,22]. In the context of this meta-analysis, positive values of lnRR and lnCVR indicate higher mean values and higher variation, respectively, in urban populations compared to non-urban populations (and *vice versa*; see Methods).

Combining data across the three studied life-history traits, urban populations had overall lower mean values than their non-urban counterparts (lnRR mean estimate [95% Confidence Interval] = -0.050 [-0.096, -0.004]; I^2_{total} = 98.6%; Figure S4; Table S1). Further analysis accounting for potential covariation across the three investigated traits in the response to urbanisation (i.e., using a model with an unstructured variance-covariance matrix; see Methods and Table S2) confirmed that urban populations had lower mean values in every life-history trait: urban populations laid their eggs earlier (lnRR [95% CI] = -0.056 [-0.084, -0.028]; Figure 2a), laid smaller clutches (lnRR [95% CI] = -0.075 [-0.109, -0.040]; Figure 2a), and tended to fledge fewer nestlings per clutch than non-urban populations (lnRR [95% CI] = -0.075 [-0.183, 0.034]; Figure 2a – but note that the 95% CI overlaps zero in this case, seemingly due to more variation in lnRR for fledgling number than for clutch size, see Figure S6a). This meta-analytic model estimated different random effect intercepts per trait and allowed for correlations across traits (see Methods for details). This model revealed strong

correlations in the response to urbanisation across traits: studies reporting large differences in laying dates between urban and non-urban populations also reported small differences between habitats in clutch size and number of fledglings (see 'Study ID (correlations)' in Table S3; i.e., correlations among studies in the values of lnRR for each trait).

These results indicate that urban bird populations overall lay their eggs earlier and produce smaller clutches, which results in a lower number of surviving fledglings than their non-urban neighbouring populations. These findings are largely in agreement with previous meta-analyses investigating the effects of urbanisation on mean avian life-histories[10,13], whose conclusions we have confirmed using a larger dataset with higher spatial, temporal and phylogenetic coverage. Additionally, our results suggest the mean response to urbanisation is correlated among traits. Interestingly, we found that earlier laying dates in urban populations compared to non-urban populations were associated with smaller differences in clutch size and number of surviving nestlings between habitats (after accounting for mean differences among traits between habitats). Clutch size decreases with laying date in multiple bird species[23], and these two traits are often hypothesized to co-evolve because of a strong negative genetic correlation[24]. All else being equal, urban conditions that advance the onset of reproduction (e.g., light pollution[25]) could indirectly increase clutch size and, therefore, reduce differences in reproductive output (clutch size and, possibly, number of fledglings) between urban and non-urban populations that arise via other mechanisms (e.g., resource limitation[26,27]).

When combining data across the three studied life-history traits, the coefficient of phenotypic variation in urban populations was 8.0% higher than in non-urban populations (lnCVR mean estimate [95% CI] = 0.077 [-0.032, 0.186]; I^2_{total} = 71.9%; Figure S5 and Table S1; note that the 95% CI overlapped zero). A subsequent model of lnCVR accounting for potential covariation across the three investigated traits in the response to urbanisation (see Methods and Table S4) revealed that this trend was mainly driven by urban populations having a

more variable phenology (lnCVR mean for laying date [95% CI] = 0.193 [0.107, 0.279], i.e., 21.9% more variation, on average, in laying date in urban than non-urban populations). Urban and non-urban populations did not statistically differ in the amount of phenotypic variation in clutch size or number of fledglings (i.e., 95% CIs overlapped zero; the direction of the effect reflected higher phenotypic variation in urban populations for both traits; Figure 2b) (lnCVR mean estimates [95% CI]: clutch size = 0.052 [-0.046, 0.149], number of fledglings = 0.064 [-0.071, 0.198]). We did not find evidence for the existence of correlations among life-history traits in their lnCVR (models including correlations among traits scored more than 1.57 AIC points below the top model, which only included independent random intercepts per trait; Table S4). Differences in phenotypic variation between habitats were quantitatively very similar when we meta-analysed the amount of variation (i.e., lnVR[18]) instead of the coefficient of variation (i.e., lnCVR; Figure S6).

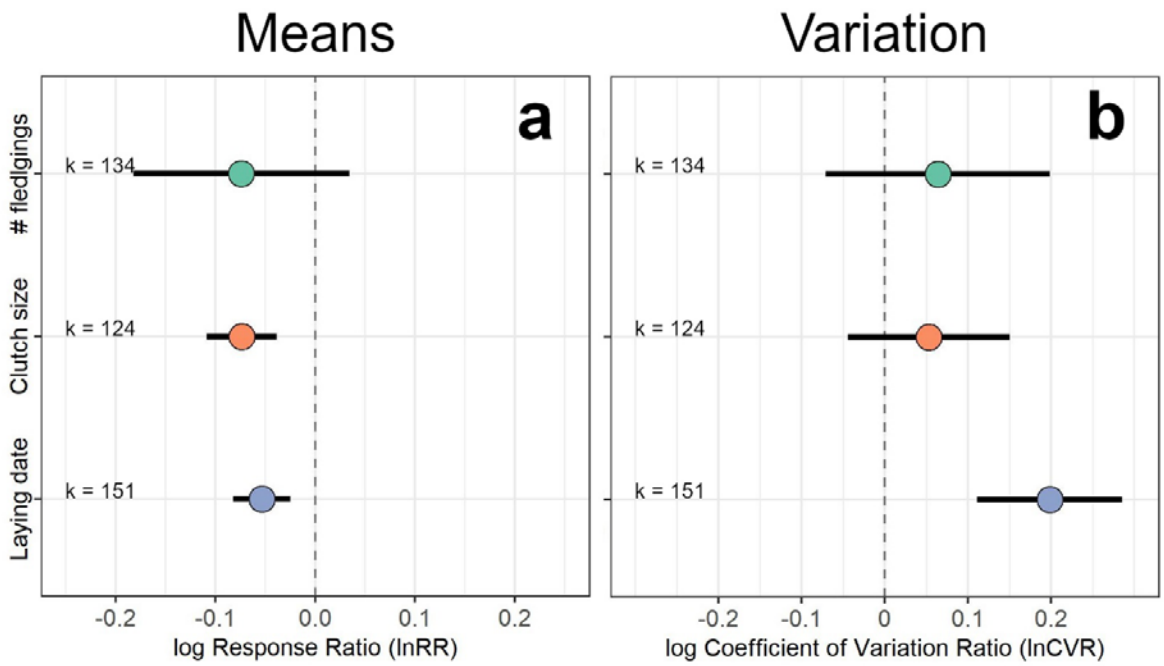

Figure 2. Urban populations have earlier phenology, lower reproductive output and more variable life-history traits than non-urban populations. (**a**) Urban populations laid earlier and had smaller clutches, producing fewer fledglings, than their paired non-urban populations (illustrated by negative lnRR estimates). (**b**) Our meta-analysis revealed that variation in life-history traits was higher in urban populations compared to non-urban counterparts, with a marked difference between habitats in laying dates (illustrated by positive estimates of lnCVR). Model estimates for (**a**) lnRR and (**b**) lnCVR are shown along with their 95% confidence intervals per trait as calculated by our meta-analytic models accounting for correlated responses to urbanisation among traits (see Table S3 & Table S5 for full model outputs and Figure S4 and S5 for overall meta-analyses of lnRR and lnCVR). Raw data and model estimates are presented in Figure S6. 'k' provides the number of urban – non-urban comparisons.

Higher phenotypic variation in phenology in urban compared to non-urban avian populations might indicate that the opportunity for selection to act on phenological traits is stronger in urban populations[28]. However, the actual evolutionary implications of this finding are likely to depend on the interplay between the temporal scale at which urbanisation affects phenotypic variation and the longevity of a given species[9]. Phenotypic variation in phenology could be increased in urban bird populations by at least two temporal mechanisms acting alone or simultaneously. First, urban populations could display higher variation in phenology within a given breeding season as a result of increased spatial heterogeneity in urban habitats[29]. Second, urban populations could display higher variation in phenology due to larger yearly fluctuations in environmental conditions, with or without differences in phenotypic variation between urban and non-urban populations within a given breeding season. In this latter scenario, natural selection in short-lived species, whose individuals mostly breed one single year, may not act on different phenotypic variation between urban and non-urban habitats.

Additional analyses attending to the temporal source of differences in phenotypic variation for laying date between urban and non-urban populations demonstrated that these arose from differences in variation within breeding seasons rather than being the result of more variation in phenology between breeding seasons (Table 1). While laying date in urban populations was more variable than in non-urban populations within breeding seasons (lnCVR mean estimate [95% CI] = 0.193 [0.094, 0.292]; Table 1), a subsequent meta-analytic model isolating effects on phenotypic variation arising from between breeding season fluctuations revealed no statistical difference between urban and non-urban populations (lnCVR intercept mean [95% CI] = 0.007 [-0.133, 0.147]; Table 1). While the sample size for this latter meta-analysis was almost four times smaller than for the meta-analysis of within breeding season differences in variation, the estimated lnCVR in both models showed large differences: mean lnCVR within breeding seasons was more than 27 times larger than mean lnCVR among breeding seasons.

Higher phenotypic variation in urban than in non-urban populations within breeding seasons can be explained by at least two different processes: i) differences in the additive genetic variance in laying dates, whereby urban birds have a wider range of genotypes for laying dates, or ii) differences in habitat heterogeneity influencing plasticity in laying dates, whereby urban areas have larger environmental variation than non-urban habitat[30–32]. While environmental conditions are often found to be different between urban and non-urban habitats[33], and this is likely to impact patterns of phenotypic variation[7,34], the role of habitat heterogeneity in shaping differences in phenotypic variation between urban and non-urban avian populations has received little attention[29,31]. Our analyses indicate that differences in urban *versus* non-urban habitat heterogeneity could indeed contribute to explain the observed pattern of increased phenotypic variation in urban populations. Using a subset of studies that reported the approximated location of their urban and non-urban populations, we quantified habitat heterogeneity and assessed whether urban populations were exposed to a more heterogeneous habitat than non-urban populations[29], and whether the increase in phenotypic variation in urban habitats was predicted by urban habitat heterogeneity. These additional meta-analyses, although limited by intrinsic features of the data set (see Supplementary text 1) showed that, in our data set, urban habitats were spatially more heterogeneous than non-urban habitats[29] (Figure 3a) and that urban habitat heterogeneity was associated with higher phenotypic variation in urban bird populations compared to their non-urban counterparts, especially at large spatial scales (Figure 3b; see Supplementary text 1 for full details and discussion of the limitations of this complementary analysis). Our findings do not suffer from common publications biases, small-study effects or time-lag effects (Supplementary text 2).

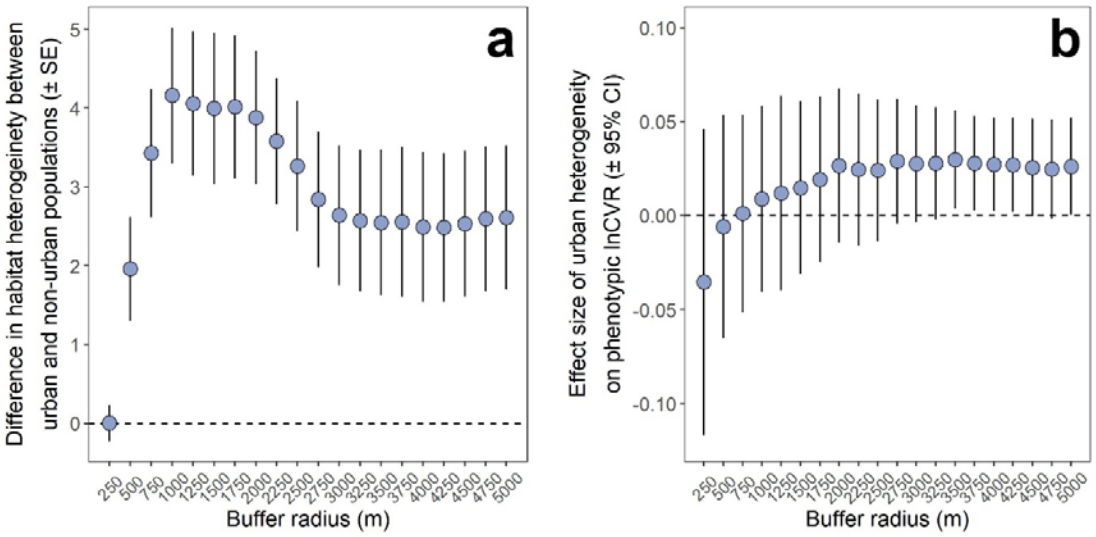

Figure 3. Urban heterogeneity effects on the difference in variation between urban and non-urban bird populations (i.e., lnCVR). (a) Habitat heterogeneity was higher in urban populations than in non-urban populations across most spatial scales (e.g., different buffer sizes). (**b**) The higher the difference in habitat heterogeneity between urban and non-urban populations, the higher the difference in phenotypic variation between urban and non-urban populations tended to be (i.e., positive effect of urban heterogeneity on lnCVR); particularly at a relatively large spatial scale (e.g., buffer radius larger than 2000 m). Points represent (**a**) mean difference in habitat heterogeneity between urban and non-urban populations (± SE), and (**b**) the effect size of urban habitat heterogeneity on the difference in phenotypic variation across habitats (i.e., mean lnCVR and its 95% confidence interval). 'Buffer radius' refers to the radius of a circular area centred at each study location and over which habitat heterogeneity was calculated (see Supplementary text 1 for more details).

Table 1. Differences in variation (lnCVR) in life-history traits between urban and non-urban populations at different temporal scales. Urban – non-urban differences in variation (lnCVR) in laying dates, clutch size and number of fledglings per clutch were meta-analysed to assess differences in variation between urban and non-urban populations within and between breeding seasons (e.g., different temporal scales). lnCVR estimates represent meta-analytic model intercepts following the model structure presented in Table S5; positive values indicate higher variation in urban populations than in non-urban populations and *vice versa*. 'CI' = confidence interval; 'k' = sample size. Terms in italic bold highlight lnCVR estimates whose 95%CIs do not overlap zero.

Temporal scale	lnCVR estimate [95% CI]			k
	Laying date	Clutch size	Number of fledglings	
Overall	***0.193 [0.107, 0.279]***	0.0518 [-0.046, 0.149]	0.0635 [-0.071, 0.198]	409
Within breeding season	***0.193 [0.094, 0.292]***	0.024 [-0.110, 0.158]	0.149 [-0.028, 0.322]	376
Between breeding seasons	0.007 [-0.133, 0.147]	0.0774 [-0.034, 0.189]	0.011 [-0.136, 0.158]	101

Conclusion

Taken together, our results show that urbanisation impacts not only the mean phenotype of avian populations but also the amount of phenotypic variation that these populations display. Our results also highlight a temporal and spatial mechanism that could generate such differences in phenotypic variation among urban and non-urban habitats. That urban avian populations have more variable phenology than non-urban conspecifics within breeding seasons (i.e., differences in phenology across habitats are seemingly not due to between-year fluctuations) suggests that the opportunity for selection could be consistently higher in urban environments than in non-urban environments, even for species in which most individuals reproduce in a single breeding season only.

Why do urban populations display higher phenotypic variation that their non-urban neighbours? Our analyses reveal this pattern and shed light on the temporal and spatial scale at which it occurs but do not explain how it is generated. One possibility that our spatial analysis highlights is that high environmental heterogeneity in urban habitats[32] might allow for plastic responses to microhabitat conditions, thereby increasing the amount of phenotypic variation in urban bird populations[16]. Alternatively, higher phenological variation in urban environments could be a consequence of relaxed selection in this habitat[35] or gene flow from non-urban to urban habitats[36]. Weaker selection for early laying in urban habitats has been found in at least one bird species[35], which coupled with the high dispersal ability of birds, could increase the amount of phenotypic variation in phenology. The ecological and evolutionary implications of higher phenotypic variation in urban environments will likely vary among species[9] and our findings highlight the need for detailed investigation of these consequences. To this end, long-term studies of individually marked individuals in paired urban and non-urban environments could be particularly fruitful.

Methods

Literature review

We began our literature search by inspecting two published reviews on the impact of urbanisation on avian biology[10,13]. As we were mainly interested in how phenology and reproduction were affected by urbanisation, we identified papers cited in Chamberlain *et al*. (2009) (N = 37) and Sepp *et al*. (2018) (N = 32) that could contain estimates for egg laying dates (hereafter laying dates), clutch size and number of nestlings fledged per breeding attempt (hereafter number of fledglings) for urban and non-urban populations. Then, we performed four searches of the Web of Science Core Collection on the 27th of October 2020 (databases covered: SCI-EXPANDED – 1900-present, SSCI – 1956-present, A&HCI – 1975-present, BKCI-S – 2005-present, BKCI-SSH – 2005-present and ESCI – 2015-present) to recover studies published since 1900 and including all languages and all document types. We performed the following four searches: (**1**) TS=("urban*" AND ("bird*" OR "aves" OR "avian" OR "ornithol*" OR "passerine*" OR "passeriform*" OR "songbird*" OR *list of bird genera*) AND ("laying date" OR "lay date" OR "first egg" OR "clutch size" OR "eggs laid" OR "number of eggs" OR "fledgling*" OR "fledging" OR "reproductive success" OR "fitness")); (**2**) TS=("urban*" AND "bird" AND "laying date"); (**3**) TS=("urban*" AND "bird" AND "clutch size"); (**4**) TS=("urban*" AND "bird" AND "fledglings"). The *list of avian genera* in the first search string consisted of a list of all avian genera and can be found in Supplementary text 3 (this search string was created by Antje Girndt – see acknowledgments). Searches 2-4 were contained within search 1; however, they were not restricted to avian genera, hence potentially capturing additional references that did not mention the scientific name of the study species. These searches found 892, 71, 198 and 167 studies, respectively, which we combined with the studies identified from Chamberlain *et al*. (2009) and Sepp *et al*. (2018) to create a list of 1,397 studies (Figure S1). We then de-duplicated this list using the R package 'revtools' (using exact matching of study titles in function '*find_duplicates*'; v0.4.1[37]) and by manually inspecting all study titles and author lists. Our final list contained 940 unique

studies (Figure S1). We screened each study by reading their title and abstract. If the title and/or abstract indicated that the paper could fit our requirements for data collection (see below), we read the study fully, aiming to extract mean, standard deviation (SD) and sample size (n) of our life-history traits of interest for urban and non-urban bird populations. If SD was not available but authors provided SE, the former was calculated as: $SD = SE \times \sqrt{n}$. When available, we extracted estimates per year (i.e., papers often reported mean, SD and n for urban and non-urban populations in multiple years of study). If a study reported incomplete information for inclusion in our meta-analysis (e.g., mean was provided but not SD or SE), we contacted the authors to ask for this missing information (a complete list of authors that provided estimates can be found in the acknowledgments).

Criteria for inclusion

We were interested in investigating the effects of urbanisation on life-history traits, with a particular interest in testing the effects of urbanisation on variation and mean trait values. Paired urban - non-urban designs, where an urban population is compared to a non-urban adjacent population are a powerful approach to identify the effects of urban living while controlling for temporal and geographical variation, as well as large-scale genetic structure among populations. Therefore, we included studies as long as they (i) compared geographically close (i.e., paired) urban and non-urban populations and (ii) reported laying dates of the first clutch of the season, clutch size or number of nestlings for the same breeding season across both habitats. When multiple populations were compared along a gradient of urbanisation, we extracted estimates for the two populations at the extremes of the gradient (i.e. most urban and least urban populations). When studies combined estimates across several breeding seasons, we included them in our meta-analysis as long as urban and non-urban populations had been sampled in the same breeding seasons. We found variation in the way that authors reported our three traits of interest. For example, ‘egg laying date’ often referred to the date on which clutches were completed, but sometimes this value indicated the laying date of the first egg of the clutch. Sometimes authors did not

specify if by 'laying dates' they referred to clutch completion dates or first egg laying dates. We always tried to extract information on the number of fledglings considering all breeding attempts regardless of whether none or some nestlings survived in a given attempt. However, studies sometimes reported number of fledglings across habitats considering only successful broods (i.e., those that fledged at least one nestling). Although there may be subtle methodological differences among some of the studies included in our data set, among-study variation is not likely to bias results since our effect sizes (see below) consist of within-study comparisons where the methods were the same for urban and non-urban populations.

Initially, our data set contained 427 urban – non-urban paired estimates from 33 bird species and 65 studies. Of these, three observations were removed due to missing sample sizes, and 11 observations were removed because their sample size was one (which precludes the calculation of a mean and their SD). Four observations were removed because they reported a SD of zero (these indeed had very low sample sizes: 3, 2, 7, 2 observations). One effect size for laying dates, nine effect sizes for clutch size and 13 effect sizes for number of fledglings from five studies contained missing SD data. Mean and SD are often strongly correlated[38], including in our dataset (Figure S3). Therefore, we imputed the 23 missing SD values based on linear regressions of log mean against log standard deviation. Our final data set included 409 comparisons between urban and non-urban populations from 65 published papers and 33 bird species (Figure 1; refs. [26,27,35,39–100]). Of these 409 comparisons, 151 corresponded to comparisons of laying dates (N = 32 studies), 124 corresponded to comparisons of clutch size (N = 42 studies) and 134 were comparisons of number of fledglings (N = 44 studies). Last, there were a total of 376 comparisons for single years (N = 47 studies) and an additional 33 comparisons included estimates across multiple years of study (N = 18 studies).

Coding of effect sizes

Laying date data was standardised across studies by coding it as days after January 1. In every case, mean laying date estimates across habitats fell within the same calendar year. For each of these three life-history traits we computed the log response ratio (lnRR) and the log coefficient of variation ratio (lnCVR) to investigate differences in mean values and variability between urban and non-urban populations[18,19]. We calculated lnRR and lnCVR along with their associated sampling variances[18] using the R function '*escalc*' in the 'metafor' R package (v2.5-57; Viechtbauer 2010). Both lnRR and lnCVR were coded in a way that positive values meant higher estimates in urban populations compared to their non-urban counterparts. Urban and non-urban populations can differ in mean and variance levels at the same time (e.g., Taylor's Law[38,102]), as observed in our data (Figure S3). Therefore, we chose lnCVR over lnVR (i.e., log total variation ratio[18]) as the former is designed to account for the mean–variance relationship[18,19]. We handled the data set, ran all analyses and produced visualisations using R v.4.0.3 [103].

Meta-analyses and random effects

To evaluate the effects of urbanisation on avian life-history traits, we fitted phylogenetic multilevel (intercept-only) meta-analyses for each response term (i.e. lnCVR or lnRR) combining all three life-history traits (i.e. laying date, clutch size and number of fledglings). All These meta-analytic models estimated five random intercept effects: publication identity (i.e., among-study variation), population identity, phylogeny (more details below) and species identity (i.e., among-species variation not explained by phylogeny), as well as a residual variance and/or within-study variation. We estimated total heterogeneity (I^2) and the proportion of variation explained by each random term in our meta-analytic (intercept-only) models following [21,104] and as implemented in the R function '*i2_ml'* ('metafor' R package v2.5-57[101]).

Modelling heterogeneous variances and correlations among traits

Laying date, clutch size and number of fledglings are often correlated in bird species[23]. To assess the robustness of our results to the existence of these correlations in our data set, we built meta-analytic models that allowed us to simultaneously estimate trait-specific means (i.e., one intercept for each trait – Equation 1), trait-specific residual variances (i.e., one 'observation identity' variance for each trait – Equation 1 & Equation 2) and trait-specific among-study variances and correlation among traits (Equation 1 & Equation 3). Including the random-effect terms detailed above, our model with heterogeneous variances and among-study correlations among traits can be written as: (we have omitted the term associated with sampling variance for simplicity – see Nakagawa et al. (2015) for more details)

$$y_i = \begin{bmatrix}\mu_{LD}\\ \mu_{CS}\\ \mu_{NF}\end{bmatrix} + \begin{bmatrix}\varepsilon_{i-LD}\\ \varepsilon_{i-CS}\\ \varepsilon_{i-NF}\end{bmatrix} + \begin{bmatrix}\tau_{t-LD}\\ \tau_{t-CS}\\ \tau_{t-NF}\end{bmatrix} + v_a + a_l + h_w \text{ (Equation 1)}$$

$$\begin{matrix}\varepsilon_{i-LD}\\ \varepsilon_{i-CS}\\ \varepsilon_{i-NF}\end{matrix} \sim N\left(\begin{bmatrix}0\\0\\0\end{bmatrix}, \begin{bmatrix}\sigma^2_{\varepsilon-LD}\\ \sigma^2_{\varepsilon-CS}\\ \sigma^2_{\varepsilon-NF}\end{bmatrix}\right) \text{ (Equation 2)}$$

$$\begin{matrix}\tau_{t-LD}\\ \tau_{t-CS}\\ \tau_{t-NF}\end{matrix} \sim N\left(\begin{bmatrix}0\\0\\0\end{bmatrix}, \begin{bmatrix}\sigma^2_{t-LD} & p_{LD-CS}\,\sigma_{t-LD}\,\sigma_{t-CS} & p_{LD-NF}\,\sigma_{t-LD}\,\sigma_{t-NF}\\ & \sigma^2_{t-CS} & p_{CS-NF}\,\sigma_{t-CS}\,\sigma_{t-NF}\\ & & \sigma^2_{t-NF}\end{bmatrix}\right) \text{ (Equation 3)}$$

$$v_a \sim N(0, \sigma^2_v) \text{ (Equation 4)}$$

$$a_l \sim N(0, A\sigma^2_a) \text{ (Equation 5)}$$

$$h_w \sim N(0, \sigma^2_h) \text{ (Equation 6)}$$

Where y_i is the statistic of interest (lnRR or lnCVR) for the ith effect size ($i = 1,2,3,\ldots,k$; where k is the number of the effect sizes included in the analysis - i.e., number of urban – non-urban paired comparisons). 'LD', 'CS', 'NF' refer to overall means (μ), variances (σ) and correlations (ρ) involving effect sizes for laying date ('LD'), clutch size ('CS') and number of fledglings ('NF'). ε_i is the residual deviation for the ith observation, which is assumed to follow a normal distribution with mean 0 and variance $\sigma^2_{\varepsilon-LD}$, $\sigma^2_{\varepsilon-CS}$, $\sigma^2_{\varepsilon-NF}$ for laying date, clutch size and number of fledglings, respectively. τ_{t-LD}, τ_{t-CS}, and τ_{t-NF} are the deviations from the mean associated with the tth study and trait ('LD', 'CS', or 'NF'), each following a multivariate normal distribution with mean of 0 and variance-covariance structure detailed in Equation 5 (p provides the correlations between τ_{t-LD}, τ_{t-CS}, and τ_{t-NF}). v_a provides the deviation from the overall mean associated with the ath population. a_l is the phylogenetic effect for the lth species, which follows a normal distribution with mean equal to 0 and variance-covariance structure given by σ^2_a, the variance of the phylogenetic effect, and A, a l by l matrix of distances between species calculated from a phylogenetic tree (more details below). h_w captures among species variation not explained by the phylogenetic effect and follows a normal distribution around 0 and variance σ^2_h.

We compared models with different constraints in the parameters of the variance-covariance structure in Equation 3 to assess the strength of evidence for heterogeneous variances and correlations among traits. We fitted the meta-analytic models in the 'metafor' R package (v2.5-57; Viechtbauer 2010) using maximum likelihood and compared model AIC (Akaike information criterion[105]). We then calculated a ΔAIC value for each model (i.e., the difference in AIC between a given model and the model with lowest AIC) and used this value to assess the strength of evidence for a given variance-covariance structure. We fitted models with the following constraints in the variance-covariance structure:

(i) Single variance across traits and no correlations:

$\sigma^2_{t-LD} = \sigma^2_{t-CS} = \sigma^2_{t-NF}$; and all $p = 0$

(ii) Compound symmetric variance-covariance matrix:

$\sigma^2_{t-LD} = \sigma^2_{t-CS} = \sigma^2_{t-NF}$; and $p_{LD-CS} = p_{LD-NF} = p_{CS-NF}$

(iii) Heteroscedastic compound symmetric variance-covariance matrix:

$\sigma^2_{t-LD}, \sigma^2_{t-CS}$ and σ^2_{t-NF} can vary freely but $p_{LD-CS} = p_{LD-NF} = p_{CS-NF}$

(iv) Diagonal variance-covariance matrix:

$\sigma^2_{t-LD}, \sigma^2_{t-CS}$ and σ^2_{t-NF} can vary freely but all $p = 0$

(v) Unstructured variance-covariance matrix

$\sigma^2_{t-LD}, \sigma^2_{t-CS}$ and σ^2_{t-NF} can vary freely, as well as p_{LD-CS}, p_{LD-NF} and p_{CS-NF} (i.e. correlation among traits).

Within- and between-breeding season differences in phenology and life-history traits between urban and non-urban population

Urban and non-urban populations may differ in both within-breeding season and between-breeding season variation in phenology and life-history traits. However, differences in variation for these two temporal scales are likely generated by contrasting ecological and evolutionary processes[9]. To disentangle processes operating at these two temporal scales that generate differences in phenotypic variation between urban and non-urban populations, we performed additional meta-analyses including 1) urban – non-urban comparisons within breeding seasons (k = 376 comparisons in the original data set) and 2) urban – non-urban comparisons between breeding seasons (i.e., combining all within-breeding season estimates from a given study; k = 33 between-breeding season comparisons present in the original data set, plus 68 additional comparison calculated from within-breeding season estimates; see below). When a given study reported estimates across multiple breeding seasons, we calculated between-breeding season mean and variance as:

$$\bar{x}_{among-season} = \sum_{i=1}^{g} \bar{x}_i \frac{n_i}{N}; where, N = \sum_{i=1}^{g} n_i \quad \text{(Equation 10)}$$

$$S^2_{among-season} = \sum_{i=1}^{g} n_i s_i^2 + \sum_{i=1}^{g} n_i \left(\bar{x}_i - \bar{x}_{among-season}\right)^2 \text{ (Equation 11)}$$

Where, $\bar{x}_{among-season}$ and $S^2_{among-season}$ are mean and variance across multiple breeding seasons. g is the total number of breeding seasons reported by a given study; $\bar{x}_i$, s_i^2, n_i, are mean, variance and sample size for each breeding season i. $\bar{x}_{among-season}$ for a given study is, therefore, the weighted average across breeding seasons (Equation 10); whereas $S^2_{among-season}$ for a given study is the weighted sum of within-season variances (first term in equation 11) and between-season mean variances (second term in Equation 11).

Phylogenies

Phylogenetic trees were extracted from the Open Tree of Life [106,107], using the interface provided by the R package 'rotl' (v3.0.10; Michonneau et al. 2016, OpenTreeOfLife et al. 2019). We calculated tree branch length [110] and generated a phylogenetic correlation matrix to include in our (comparative) meta-analytic models (Figure 1). We assessed phylogenetic signal in our meta-analysis based on the proportion of variation explained by the phylogeny (i.e. $I^2_{phylogeny}$; e.g., [22]).

Publication bias

We assessed the existence of two types of publication biases, small-study and time-lag effects, following the recommendation in [106]. We ran our meta-models for lnRR and lnCVR including two new moderators: 1) the square-root of the inverse of the effective sample size and 2) the year of study publication (mean-centered)[111,112]. The statistical significance of these two moderators provides evidence for the existence of small-study effects and time-lag effects, respectively [112]. In order to assess the effect of the existence of small-study effect in our estimates of lnRR and lnCVR, we ran additional lnRR and lnCVR meta-regressions

including the inverse of the effective sample size as a moderator to estimate adjusted lnRR and lnCVR intercepts for laying dates, clutch size and number of fledglings[106].

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Author contributions

PC-L, MJT, DR, AC and DMD conceived the study. PC-L, AS-T, CJB and DMD performed the literature search and PC-L extracted effect sizes from suitable published papers. PC-L and YH performed all statistical analysis with advice form AS-T. PC-L wrote the first draft of the manuscript with input from MJT, AS-T, DR, AC and DMD. All authors read and commented the manuscript.

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