A global meta-analysis reveals higher life-history phenotypic variation in urban birds than in their non-urban neighbours

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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 from 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 revised the manuscript.

Data availability

All R scripts and datasets needed to reproduce the analyses presented in this paper are available at: https://github.com/PabloCapilla/meta-analysis_variation_urban.

Abstract

Cities pose a major ecological challenge for wildlife worldwide. Phenotypic variation, which can result from underlying genetic variation or plasticity, is an important metric to understand eco-evolutionary responses 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 avian literature to compare urban *versus* non-urban means and variances in breeding phenology (i.e., lay date) and reproductive effort (i.e., clutch size, number of fledglings). First, we show that urban populations reproduce earlier and have smaller broods than non-urban conspecifics. Second, we show that urban bird populations have higher phenotypic variation in laying date than non-urban populations. This result arises from differences in phenological variation between populations within breeding seasons, conceivably due to higher landscape heterogeneity in urban habitats. Higher variation in reproductive timing in birds subject to anthropogenic disturbance might be a consequence of plastic responses or higher genetic variation in phenology in urban populations. Our results reveal a novel effect of urbanisation on animal life-history traits with important implications for our understanding of how species adapt to urban environments.

Introduction

Humans have drastically changed environmental conditions on Earth (Hendry *et al.* 2017). The footprint of human activity is most pronounced in urban environments, where microclimatic conditions, biogeochemical cycles and sensory landscapes are considerably different from those in non-urban environments (Grimm *et al.* 2008). Perhaps not surprisingly, multiple shifts in animal and plant phenotypes have been associated with the novel conditions and selective pressures found in cities (Johnson & Munshi-South 2017; Lambert *et al.* 2020). Indeed, numerous studies have reported divergent phenotypes between urban and non-urban populations across the globe (e.g., Alberti *et al.* 2017; Diamond *et al.* 2018; Campbell-Staton *et al.* 2020; reviewed in Johnson & Munshi-South 2017; Lambert *et al.* 2020; Diamond & Martin 2021). The extent to which populations can adapt to urban environments could be partly associated with how urbanisation affects their phenotypic variation (Thompson *et al.* 2022). 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 can help us understand the potential for future phenotypic changes in urban environments and the eco-evolutionary implications of such changes (Thompson *et al.* 2022).

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 (Chamberlain *et al.* 2009; Vaugoyeau *et al.* 2016; Sepp *et al.* 2018; Putman & Tippie 2020; Sanders *et al.* 2021). However, no study to date has explicitly investigated how urbanisation affects phenotypic variation in reproductive traits at a global scale.

Recent single-species studies suggest that phenotypic variation could be affected by urbanisation (Caizergues *et al.* 2018; Gorton *et al.* 2018; Thompson *et al.* 2022). 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 could 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 (Gorton *et al.* 2018). A meta-analysis of selection strength found weaker selection occurring in human-disturbed populations (Fugère & Hendry 2018; although this study did not specifically test the effect of urbanisation on selection strength and only included one study directly associated with urbanisation), which if extrapolated to the urban context, 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 could display higher levels of phenotypic variation, due to several eco-evolutionary processes reviewed in (Thompson *et al.* 2022). These findings also highlight that the extent to which urbanisation may impact phenotypic variation likely depends on the interplay between the temporal and spatial scale at which environmental conditions fluctuate in the urban habitat, as well as on the species' longevity and dispersal ability (Thompson *et al.* 2022).

The temporal scale at which differences in phenotypic variation between urban and non-urban habitats manifest can help us evaluate their ecological causes, and is likely to determine the eco-evolutionary implications of increased phenotypic variation in urban habitats (Thompson *et al.* 2022). First, urban populations could display higher phenotypic variation than non-urban populations within a given breeding season (as a result, for example, of consistent differences in landscape heterogeneity between habitats; Pickett *et al.* 2017). Second, urban populations could display higher phenotypic variation than non-urban populations due to larger yearly fluctuations in environmental conditions (if, for

example, urban populations are less resilient to changes in weather conditions), with or without differences in phenotypic variation between urban and non-urban populations within a given season. In the latter scenario, similar levels of phenotypic variation would be exposed to natural selection in short-lived species (e.g., annual species).

Urban environments have been referred to as spatially more heterogeneous than non-urban habitats of the same geographical area (Pickett *et al.* 2017). Urban habitat heterogeneity could increase phenotypic variation compared to adjacent non-urban habitats if, for example, urban organisms change their phenotype according to local environmental conditions (e.g., through both developmental and later-life phenotypic plasticity). The empirical assessment of this idea, however, largely depends on the scale at which urban habitat heterogeneity is measured, the spatial scale at which the organism of interest operates and the heterogeneity of the non-urban habitat of reference (Pickett *et al.* 2017; Uchida *et al.* 2021). For example, a megacity may be spatially heterogeneous, containing a diverse array of habitats (e.g., multiple urban parks with different ecological conditions, a varying level of impervious surface, etc.), and, thus, be overall vastly more heterogeneous than a neighboring non-urban habitat. However, a given species of interest could reduce the range of environmental conditions that it experiences through matching habitat choice (e.g., (Muñoz *et al.* 2014)), limiting the potential effect of urban habitat heterogeneity on phenotypic variation. Therefore, measuring habitat heterogeneity at different spatial scales will be paramount to understand the potential association between habitat heterogeneity and increased phenotypic variation in urban areas.

Here, we investigate how urbanisation impacts mean phenotypic values and phenotypic variation using a meta-analysis of 409 paired urban and non-urban comparisons of avian life-history traits (laying date, clutch size and number of fledglings) published between 1958 and 2020 including 33 bird species (Figure 1). We use within species urban – non-urban comparisons to investigate the following questions: i) Is urbanisation associated with shifts in

mean life-history traits? ii) Is urbanisation associated with changes in variation in life-history traits? iii) What is the temporal and spatial scale at which urbanisation correlates with changes in phenotypic variation? Based on previous research (Chamberlain *et al.* 2009; Sepp *et al.* 2018), we predict that urban bird populations display on average earlier phenology, smaller clutch size and lower number of fledglings than non-urban populations. We also predict increased phenotypic variation in urban populations compared to non-urban populations for all three traits examined (see above; and reviewed in Thompson *et al.* 2022). Lastly, we disentangle urban effects on phenotypic variation across different temporal and spatial scales, suggesting an ecological mechanism for the effects of urbanisation on avian phenotypic variation. This study provides, for the first time, meta-analytical evidence that urban conditions can magnify phenotypic variation in avian life-history traits and highlights the potential role of increased habitat heterogeneity in urban areas as an ecological mechanism underlying this effect.

Material and methods

Literature review

We began our literature search by inspecting two published reviews on the impact of urbanisation on avian biology (Chamberlain *et al.* 2009; Sepp *et al.* 2018). 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 either data, or mean and variance estimates for first clutch laying initiation (hereafter laying date), clutch size and number of nestlings fledged per breeding attempt (hereafter number of fledglings), for paired 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 (see also acknowledgements). 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; Westgate 2019) 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: $SD = SE \times \sqrt{n}$. Mean and SD were extracted from data quartiles and medians in four effect sizes from two studies following Luo *et al.* (2016) and Shi *et al.* (2020). When available, we extracted estimates per breeding season (i.e., papers often reported mean, SD and n for urban and non-urban populations in multiple breeding seasons). 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 association between urbanisation and, mean and variation in 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 if they (i) compared geographically close (i.e., paired) urban and non-urban populations and (ii) reported laying date of the first clutches 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 if urban and non-urban populations had been sampled in the same breeding seasons.

Initially, our data set contained 427 paired urban – non-urban 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 data points). One effect size for laying date, 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 (Nakagawa & Schielzeth 2013), including in our dataset (Figure S2). Therefore, we imputed these 23 missing SD values based on linear regressions of log mean against log standard deviation (not including imputed values in our meta-analysis produced quantitatively very similar results; k = 386 comparisons not including imputed SD values). Our final data set included 409 comparisons between paired urban and non-urban populations from 33 bird species and 65 studies (Figure 1; refs.: Perrins 1965; Middleton 1979; Schmidt & Steinbach

1983; Dhondt *et al.* 1984; Eden 1985; Stout *et al.* 1998; Boal & Mannan 1999; Mcgowan 2001; Schoech & Bowman 2001; Solonen 2001; Antonov & Atanasova 2003; Rollinson & Jones 2003; Liven-Schulman *et al.* 2004; Millsap *et al.* 2004; Conway *et al.* 2006; Beck & Heinsohn 2006; Mennechez & Clergeau 2006; Isaksson & Andersson 2007; Kelleher & O'Halloran 2007; Pande *et al.* 2007; Schoech *et al.* 2007; Hinsley *et al.* 2008; Isaksson *et al.* 2008; Newhouse *et al.* 2008; Solonen & Ursin 2008; Ibáñez-Álamo & Soler 2010; Berardelli *et al.* 2010; Shustack & Rodewald 2011; Seress *et al.* 2012, 2018, 2020; Stracey & Robinson 2012; Cardilini *et al.* 2013; Brahmia *et al.* 2013; Morrissey *et al.* 2014; Solonen & Hildén 2014; Sumasgutner *et al.* 2014; Gahbauer *et al.* 2015; Glądalski *et al.* 2015, 2016a, b, 2017; Lin *et al.* 2015; Wawyrzyniak *et al.* 2015; Bailly *et al.* 2016; Minias 2016; Perlut *et al.* 2016; Lee *et al.* 2017; Meyrier *et al.* 2017; Biard *et al.* 2017; Pollock *et al.* 2017; Preiszner *et al.* 2017; Thornton *et al.* 2017; Capilla-Lasheras *et al.* 2017; Gryz & Krauze-Gryz 2018; Bobek *et al.* 2018; Caizergues *et al.* 2018; de Satgé *et al.* 2019; Hajdasz *et al.* 2019; Kettel *et al.* 2019; Rosenfield *et al.* 2019; Welch-Acosta *et al.* 2019; Jarrett *et al.* 2020; Luna *et al.* 2020; Partecke *et al.* 2020). Of these 409 comparisons, 151 corresponded to comparisons of (first clutch) laying date (N = 32 studies), 124 corresponded to comparisons of clutch size (N = 42 studies) and 134 were comparisons of number of fledglings (N = 44 studies) (Figure S3). 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).

Meta-analytic 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 (Hedges *et al.* 1999; Nakagawa *et al.* 2015; Senior *et al.* 2020). We calculated lnRR and lnCVR along with their associated

sampling variances (Nakagawa *et al.* 2015) using the R function '*escalc*' in the 'metafor' R package (v2.5-57; Viechtbauer 2010). Both lnRR and lnCVR were calculated 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 values at the same time (e.g., Taylor's Law; Nakagawa & Schielzeth 2013; Cohen & Xu 2015), as was observed in our data (Figure S2). Therefore, we chose lnCVR over lnVR (i.e., log total variation ratio; Nakagawa *et al.* 2015) as the former is designed to account for the mean–variance relationship (Nakagawa *et al.* 2015; Senior *et al.* 2020). However, we also show results for the log total variation ratio in Figure S5.

Quantifying habitat heterogeneity and urban index

We calculated habitat heterogeneity from the 3CS LC (Copernicus Climate Change Service Land Cover) and the ESA-CCI LC (European Space Agency-Climate Change Initiative Land Cover) land cover products ("ESA. Land Cover CCI Product User Guide" 2017; "ESA. 3CS Land Cover Product User Guide" 2020). These datasets provide methodologically consistent land cover per year and gridded maps from 1992 to 2019, with a global coverage and a spatial resolution of circa 300 m per pixel (0.002778° or 10 arcseconds). Each pixel in the products is classified as one of the 22 land cover categories defined by the UN-FAO-LCCS (United Nations Food and Agriculture Organization Land Cover Classification System) ("ESA. Land Cover CCI Product User Guide" 2017; "ESA. 3CS Land Cover Product User Guide" 2020). From those studies included in our main meta-analysis, we extracted the coordinates of their urban and non-urban populations (N = 30 studies with coordinates provided for urban and non-urban populations). Then, we sampled the landscape of every study by extracting the number of pixels belonging to each land cover category around each urban and non-urban location (i.e., within a circular buffer around each location). The extraction was performed for several buffer radii from 250 m to 5000 m in intervals of 250 m. Landscape heterogeneity was calculated as the effective number of land covers present in each buffer and computed as the exponential of the Shannon-Wiener diversity index (i.e.,

Hill's numbers for $q = 1$) (Hill 1973; Chao *et al.* 2014), resulting into a measure that not only accounts for the absolute richness of land cover categories but also weights in the relative abundance of each category. Urban index was calculated as the proportion of each buffer area categorized as an 'urban' land cover type. Land cover data were processed and analysed using R (v.4.0.3; R Core Team 2021). Geospatial vectorial operations were conducted utilising the 'sf' R package (v.1.0-7; Pebesma 2018) while raster extraction were performed with the 'raster' R package (v.3.5-15; Hijmans 2020). All geospatial analyses were performed in the WSG 1984 projected Coordinate Reference Systems, EPSG: 6326. We could retrieve location information for 250 urban *versus* non-urban comparisons for laying date, clutch size and number of fledglings, from 12 species ad 30 studies between 1992 and 2017 (land cover data were not available before 1992; see above).

Meta-analyses and random effects

We handled the data sets, ran all analyses and produced visualisations using R (v.4.0.3; R Core Team 2021). To evaluate the overall effect of urbanisation on avian life-history traits, we fitted phylogenetic multilevel (intercept-only) meta-analyses for each response term (i.e., lnRR and lnCVR) combining the three life-history traits (i.e., laying date, clutch size and number of fledglings). Both meta-analytic models estimated four 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 term. We estimated total heterogeneity (I^2) and the proportion of variation explained by each random term in our meta-analytic (intercept-only) models following (Nakagawa & Santos 2012; Senior *et al.* 2016) and as implemented in the R function '*i2_ml'* ('orchaRd' R package v.0.0.0.9000; Nakagawa *et al.* 2020).

Phylogenies

Phylogenetic trees were extracted from the Open Tree of Life (Hinchliff *et al.* 2015; Rees & Cranston 2017), 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 (Grafen 1989) and generated a phylogenetic correlation matrix to include in our phylogenetic meta-analytic models (Figure 1). We assessed the phylogenetic signal in our meta-analysis based on the proportion of variation explained by the phylogeny (i.e., $I^2_{phylogeny}$; e.g., Cinar *et al.* 2022).

Modelling heterogeneous variances and correlations among traits

Laying date, clutch size and number of fledglings are often correlated in bird species (Rowe *et al.* 1994; Dunn & Møller 2014). To assess whether urbanisation is associated with correlated responses across life-history traits and the robustness of our results to the existence of these correlations, we built trivariate meta-analytic models of lnRR and lnCVR 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 residual 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)

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

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

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

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

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

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

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_y provides the deviation from the overall mean associated with the yth 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_a^2, the variance of the phylogenetic effect, and A, a l by l matrix of distances between species calculated from a phylogenetic tree (details above). h_w captures among species variation not explained by the phylogenetic effect and follows a normal distribution around 0 and variance σ_h^2.

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 these trivariate meta-analytic models in the 'metafor' R package (v2.5-57; Viechtbauer 2010) using maximum likelihood and compared model AIC (Akaike information criterion; Burnham *et al.* 2011). 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 zero covariances:

$\sigma^2_{t-LD} = \sigma^2_{t-CS} = \sigma^2_{t-NF}$; 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- 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 (Thompson *et al.* 2022). To disentangle processes operating at these two temporal scales, 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 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:

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

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

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).

Assessing the effect of urbanisation and habitat heterogeneity on differences in phenotypic variation between habitats

Using the subset of studies which allowed quantification of urban index in urban and non-urban populations (see above), we first verified that urban index was indeed higher for urban populations than for non-urban populations. We compared urban index in urban and non-urban populations at different spatial scales via linear models. Then, to assess whether the increase in phenotypic variation in urban habitats was predicted by habitat heterogeneity and/or urban index, we ran an additional meta-regression to explain differences in phenotypic variation between urban and non-urban populations (i.e., lnCVR), where the difference in habitat heterogeneity and urban index between urban and non-urban populations were included as continuous moderators. This meta-regression included 250 urban – non-urban comparisons from 12 species and 30 studies (i.e., the subset of observations after 1992 for which geolocations were available).

Publication bias

We assessed the evidence for the existence of two types of publication biases, small-study and time-lag effects, following the recommendation in Nakagawa *et al.* (2022). We ran four additional multilevel meta-analytic models, two for lnRR and two lnCVR. Each of these models for lnRR and lnCVR included as a new moderator either the square-root of the inverse of the effective sample size or the mean-centered year of study publication (Trikalinos & Ioannidis 2005; Nakagawa *et al.* 2022). The amount of variation explained by these moderators (i.e., $R^2_{marginal}$) was calculated using the R function 'r*2_ml'* ('orchaRd' R package v.0.0.0.9000; Nakagawa *et al.* 2020). The statistical significance of these two moderators provides evidence for the existence of small-study and time-lag effects, respectively (Nakagawa *et al.* 2022).

Results

i) Is urbanisation associated with shifts in mean life-history avian traits?

Assessing the overall effect of urbanisation on phenotypic means across the three studied life-history traits, we found that urban populations tended to have overall lower mean values than their non-urban counterparts: life-history traits in urban habitats had, on average, 4.30% lower values than in non-urban habitats (lnRR mean estimate [95% Confidence Interval] = -0.044 [-0.103,0.015]; I^2_{total} = 98.6%; Figure S4; Table S1). 28.8% of the heterogeneity in lnRR was explained by phylogenetic and species-specific effects ($I^2_{phylogeny}$ = 4.3%; $I^2_{species\ ID}$ = 24.5%; Table S1), while 4.8% of heterogeneity was explained by consistent differences among studies (Table S1). Further analysis calculating urban effects per trait and 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 produce fewer fledglings per clutch than non-urban populations (lnRR [95% CI] = -0.075 [-0.183, 0.034]; Figure 2a; Figure S5a). 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 much earlier laying date in urban populations also reported more similar clutch size and number of fledglings between habitats (Figure 3a & 3b). Likewise, studies reporting large differences in clutch size between urban and non-urban populations also reported large differences between habitats in number of fledglings (Figure 3c; see 'Study ID (correlations)' in Table S3; i.e., correlations among studies in the values of lnRR for each trait).

ii) Is urbanisation associated with changes in variation in avian life-history traits?

The coefficient of phenotypic variation in urban populations was, on average, 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 S6 and Table S1). Only 6.0% of the heterogeneity in lnCVR was explained by phylogenetic and species-specific effects ($I^2_{phylogeny}$ = 3.0%; $I^2_{species\ ID}$ = 3.0%; Table S1), while consistent differences between studies explained no heterogeneity in lnCVR ($I^2_{study\ ID}$ = 0.0%; Table S1). A subsequent model of lnCVR separating urban effects on phenotypic variation per trait and accounting for potential covariation across the three investigated traits in the response to urbanisation (see Methods and Table S4) revealed that the overall effect of urbanisation on life-history trait variation was driven by urban populations having a more variable phenology than their non-urban counterparts (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). Although the 95% confidence intervals overlapped zero, the direction of the mean effects for clutch size and number of fledglings also reflected higher phenotypic variation in urban populations compared to non-urban populations (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 (Figure 3; 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 total variation (i.e., lnVR; Nakagawa *et al.* 2015) instead of the coefficient of variation (i.e., lnCVR; Figure S5).

iii) What is the temporal and spatial scale at which urbanisation affects phenotypic variation?

Differences in phenotypic variation in laying date between the urban and non-urban habitat arose from differences in variation within breeding seasons rather than between breeding seasons (Table 1). While laying dates in urban populations were 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 strong difference between urban and non-urban populations (lnCVR intercept mean [95% CI] = 0.007 [-0.133, 0.147]; Table 1). 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; however, the estimated lnCVR in both models showed large differences: the mean lnCVR within breeding seasons was more than 27 times larger than mean lnCVR among breeding seasons (Table 1).

Furthermore, to assess whether urbanisation and/or habitat heterogeneity could explain increased phenotypic variation in urban bird populations, we investigated the extent to which our quantification of urban index and habitat heterogeneity predicted differences in phenotypic variation across habitats. First, we confirmed that the urban populations included in our meta-analysis were indeed exposed to higher levels of urbanisation than paired non-urban populations (urban index in urban population ± SE = 0.641 ± 0.006; urban index in non-urban population ± SE = 0.018 ± 0.006; at a spatial scale of 2000 m in both cases for

reference; Figure 4a). Including the difference in urban index and habitat heterogeneity between paired urban and non-urban populations revealed that the more heterogeneous the urban habitat was, the larger the phenotypic variation in this habitat compared to the non-urban habitat; this effect was particularly strong at medium-large spatial scales (Figure 4c). Differences in urban index between populations did not strongly explain variation in lnCVR (Figure 4b).

iv) Assessment of publication bias

We found little evidence for the existence of small-study or time-lag biases in our data set. Small-study effects and time-lag effects were not detected in our multilevel meta-analytic models of lnRR (slope estimate for the square-root of the inverse of the effective sample size [95% CI] = -0.024 [-0.187, 0.138], $R^2_{margnal}$ = 0.05%; slope estimate for year of publication [95% CI] = -0.001 [-0.003, 0.002], $R^2_{margnal}$ = 0.05%). Small-study effects and time-lag effects were not detected either in our multilevel meta-analytic models of lnCVR (slope estimate for the square-root of the inverse of the effective sample size [95% CI] = 0.292 [-0.122, 0.705], $R^2_{margnal}$ = 1.92%; slope estimate for year of publication [95% CI] = 0.001 [-0.004, 0.006], $R^2_{margnal}$ = 0.11%). Overall, these findings suggest that our results do not suffer from publications bias (Nakagawa *et al.* 2022).

Discussion

We compiled a global dataset of avian life-history traits for paired urban and non-urban populations of the same species to assess how urban living is related to changes in mean phenotypic values and variances of breeding phenology, reproductive effort, and reproductive success. A phylogenetically multilevel meta-analysis of this dataset confirms a well-documented effect of urbanisation on mean phenotypes: urban bird populations laid earlier and smaller clutches than their non-urban counterparts. This model, however, also reveals correlated responses to urbanisation across life-history traits: e.g., the earlier the

laying date in urban populations, the smaller the difference in clutch sizes between habitats. Our study goes a step further than previous meta-analyses in urban ecology by explicitly investigating how urbanisation could impact phenotypic variation. Our findings highlight that urbanisation is not only associated with lower mean phenotypes, but also with increases in phenotypic variation. Investigating the temporal and spatial scale at which increases in urban phenotypic variation arise revealed hints at the ecological causes and evolutionary consequences of increased phenotypic variation in urban bird populations.

Urbanisation has been associated with shifts in mean phenotypic values across a wide range of organisms (Alberti *et al.* 2017; Merckx *et al.* 2018; Santangelo *et al.* 2022), including birds, which show smaller body sizes and generally lower life-history trait values in urban habitats (Chamberlain *et al.* 2009; Sepp *et al.* 2018; Thompson *et al.* 2022). Our analyses expand the spatial, temporal and phylogenetic coverage of previous meta-analyses of the avian literature (Chamberlain *et al.* 2009; Sepp *et al.* 2018), and agree on their findings. Our results indicate that urban bird populations lay their eggs earlier and produce smaller clutches, which results in a lower number of surviving nestling, than their non-urban neighbouring populations. It should be noted, however, that our lnRR analysis indicates a high heterogeneity. This finding indicates large variation among studies in how urbanisation associates with changes in mean phenotypes and suggests that additional ecological traits (e.g., diet or migratory strategy) may also affect how populations respond to urbanisation. Our results also indicate that the mean response to urbanisation is correlated among traits. Interestingly, we found that earlier laying dates in urban populations were associated with smaller differences in clutch size and number of surviving nestlings between habitats. Clutch size decreases with later laying date in several bird species (Rowe *et al.* 1994; Dunn & Møller 2014), and these two traits (i.e., laying date and clutch size) are often hypothesized to co-evolve because of a strong negative genetic correlation (Garant *et al.* 2008). All else being equal, urban conditions triggering an earlier onset of reproduction (e.g., light pollution (Dominoni *et al.* 2013) or increase resource availability during winter (Schoech *et al.* 2004))

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 in spring (Seress *et al.* 2018, 2020)). The extent to which mean phenotypic shifts represent adaptive responses to urbanisation in birds, either via genetic changes or plasticity, or are maladaptive, is mostly unknown (Lambert *et al.* 2020; see Santangelo *et al.* (2022) for evidence of adaptive phenotypic shifts in urban plants). Our results, however, underscore that phenotypic shifts in urban populations are widespread and that the response to urbanisation of associated life-history traits should be investigated together.

Urbanisation has been recently hypothesised to increase phenotypic variation (Thompson *et al.* 2022) and, indeed, higher variation in the morphological traits of urban great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) has been recently reported (Thompson *et al.* 2022). Our findings greatly expand the evidence for this emerging hypothesis showing that urbanisation is overall associated with increases in variation in laying dates across a wide range of bird species. Previous studies have suggested that city characteristics, such as warmer temperatures in early spring due to the urban heat island effect, could allow birds to lay more clutches per season (Yeh & Price 2004; Schoech *et al.* 2008), with thereby longer breeding seasons and hence higher phenotypic variation in urban laying dates (a similar result has also been reported in Lepidoptera (Merckx *et al.* 2021)). This effect, however, does not necessarily explain our results as our meta-analysis only included first clutch laying dates per season. As such, our findings indicate that urban bird populations display more variation in the onset of reproduction than their non-urban neighbours regardless of the total number of clutches laid in urban and non-urban habitats.

Higher phenotypic variation in urban than in non-urban populations within breeding seasons could be explained by at least two different evolutionary mechanisms, which could act in isolation or in combination: differences in the underlaying additive genetic variance in laying

date, whereby urban birds have a wider range of genotypes for laying date; and / or differences in habitat heterogeneity influencing plasticity in laying date, whereby urban areas have larger environmental variation than non-urban habitat (Shochat *et al.* 2006; Heisler & Brazel 2018; Strubbe *et al.* 2020; Thompson *et al.* 2022). No study to date has investigated whether urban birds show higher additive genetic variance than non-urban populations. However, genetic analyses of European great tits in urban and non-urban habitats generally suggest small differences in the magnitude of genetic variation between habitats (Björklund *et al.* 2010; Caizergues *et al.* 2021; Salmón *et al.* 2021). This is, perhaps, not surprising given the high mobility of birds and the fact that gene flow between urban and non-urban bird populations likely occurs at a large spatial scale (Salmón *et al.* 2021). Interestingly, some studies have reported weaker selection for laying dates in urban areas than in non-urban habitats, suggesting relaxed selection on phenology in urban birds (Caizergues *et al.* 2018; Branston *et al.* 2021), which could increase the amount of phenotypic variation in phenology (Caizergues *et al.* 2018). Assessing differences in phenotypic variation between urban and non-urban populations of less mobile species will be important to evaluate how biological traits (e.g., dispersal ability) determine the evolutionary impact of urban ecological conditions. Previous work in mammal and amphibian species with lower dispersal ability than birds suggests a comparable level of (genetic) variation between urban and non-urban habitats (Fusco *et al.* 2021; Richardson *et al.* 2021).

Habitat complexity differs between urban and non-urban habitats (Arnfield 2003; Pickett *et al.* 2017). 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. Several ecological mechanisms could mediate this effect. Urban environments are characterised by an array of microhabitats with varying levels of human pressure, exotic plant species and resource availability. Thus, the intensity and timing of the environmental cues that birds use to time their reproduction could vary at a small local scale, increasing phenotypic variation in phenology in the presence of plasticity.

The existence of plastic responses to urban habitat heterogeneity, which our results might indicate, do not preclude selection from acting on urban bird populations. First, plasticity is an important mechanism of adaptation, sometimes aligned in direction with adaptative genetic changes (De Lisle *et al.* 2022), and indeed often involved in adaptation to urban environments (Halfwerk *et al.* 2019; Campbell-Staton *et al.* 2021). Second, plastic responses can aid adaptation to urban conditions in the presence of genetic-by-environment interactions by increasing the amount of genetic variation available for natural selection (Via & Lande 1985). Addressing which evolutionary mechanisms cause the observed increase in phenotypic variation in urban bird populations is beyond the scope of this study and we acknowledge that these arguments are largely speculative at this point. However, our findings highlight that eco-evolutionary processes may largely differ between urban and non-urban bird populations and generate new avenues for future research in urban ecology and evolution.

In agreement with our initial predictions, habitat heterogeneity was associated with the magnitude of the difference in phenotypic variation between urban and non-urban bird populations. However, we acknowledge that this analysis has a number of limitations and that the results require cautious interpretation. First, only a subset of published studies provided locations (i.e., coordinates) for their urban and non-urban study populations (30 out of 65 published papers). When study site coordinates were provided, only one pair of coordinates per study location were provided, making impossible to accurately assess the actual area over which a given breeding population was studied. Additionally, it is common in urban eco-evolutionary studies to monitor several populations within one single city. However, in most studies, spatial information was provided at the scale of the whole city (e.g., a single set of coordinates), preventing the accurate quantification of habitat heterogeneity for every sub-population within a given urban habitat. These limitations highlight that the ability to perform global meta-analyses on the effects of urban habitat heterogeneity on phenotypic variation would be greatly improved if individual studies in

urban ecology provided accurate coordinates of the location of their study populations (where ethical to do so). Reporting such information would allow future research synthesis to quantify phenotypic variation within urban habitats (e.g., across different sub-populations in the same city) as well as between urban and non-urban habitats.

Taken together, our results show that urbanisation is associated not only with changes of mean phenotypic values, but also with increases in the amount of phenotypic variation that avian populations display. Our analyses also highlight a temporal and spatial mechanism that could generate such differences in phenotypic variation between urban and non-urban habitats. We show that urban avian populations have a 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) suggesting that the ecological conditions that generate such differences are constant across multiple years. Our coupled spatial analysis indicates habitat heterogeneity and plastic responses as potential eco-evolutionary mechanisms generating these results. The eco-evolutionary implications of higher phenotypic variation in urban environments will likely vary among species (Thompson *et al.* 2022) and our findings highlight the need for detailed investigation of these consequences. To this end, long-term studies of individually marked individuals in replicated paired urban and non-urban environments could be particularly fruitful to unravel whether differences in phenotypic variation between urban and non-urban populations are caused by differences in underlaying genetic variation and/or plastic responses to the urban environment.

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Competing interests

The authors declare no competing interests.

References

Alberti, M., Correa, C., Marzluff, J.M., Hendry, A.P., Palkovacs, E.P., Gotanda, K.M., *et al.* (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl. Acad. Sci. U. S. A.*, 114, 8951–8956.

Antonov, A. & Atanasova, D.Y. (2003). Small-scale differences in the breeding ecology of urban and rural Magpies Pica pica. *Ornis Fenn.*, 80, 21–30.

Arnfield, A.J. (2003). Two decades of urban climate research: A review of turbulence, exchanges of energy and water, and the urban heat island. *Int. J. Climatol.*, 23, 1–26.

Bailly, J., Scheifler, R., Berthe, S., Clément-Demange, V.A., Leblond, M., Pasteur, B., *et al.* (2016). From eggs to fledging: Negative impact of urban habitat on reproduction in two tit species. *J. Ornithol.*, 157, 377–392.

Beck, N.R. & Heinsohn, R. (2006). Group composition and reproductive success of cooperatively breeding white-winged choughs (Corcorax melanorhamphos) in urban and non-urban habitat. *Austral Ecol.*, 31, 588–596.

Berardelli, D., Desmond, M.J. & Murray, L. (2010). Reproductive success of burrowing owls in urban and grassland habitats in southern New Mexico. *Wilson J. Ornithol.*, 122, 51–59.

Biard, C., Brischoux, F., Meillère, A., Michaud, B., Nivière, M., Ruault, S., *et al.* (2017). Growing in cities: An urban penalty for wild birds? A study of phenotypic differences between urban and rural great tit chicks (Parus major). *Front. Ecol. Evol.*, 5, 79.

Björklund, M., Ruiz, I. & Senar, J.C. (2010). Genetic differentiation in the urban habitat: the great tits (Parus major) of the parks of Barcelona city. *Biol. J. Linn. Soc.*, 99, 9–19.

Boal, C.W. & Mannan, R.. W. (1999). Comparative Breeding Ecology of Cooper's Hawks in Urban and Exurban Areas of Southeastern Arizona. *J. Wildl. Manage.*, 63, 77–84.

Bobek, O., Gal, A., Saltz, D. & Motro, U. (2018). Effect of nest-site microclimatic conditions on nesting success in the Lesser Kestrel Falco naumanni. *Bird Study*, 65, 444–450.

Brahmia, Z., Scheifler, R., Crini, N., Maas, S., Giraudoux, P. & Benyacoub, S. (2013). Breeding performance of blue tits (Cyanistes cæruleus ultramarinus) in

relation to lead pollution and nest failure rates in rural, intermediate, and urban sites in Algeria. *Environ. Pollut.*, 174, 171–178.

Branston, C.J., Capilla, P., Christopher, L., Griffiths, K., White, S. & Dominoni, D.M. (2021). Urbanisation weakens selection on the timing of breeding and clutch size in blue tits but not in great tits. *Behav. Ecol. Sociobiol.*, 75, 155.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.*, 65, 23–35.

Caizergues, A.E., Charmantier, A. & Grégoire, A. (2018). Urban versus forest ecotypes are not explained by divergent reproductive selection. *Proc. R. Soc. B*, 285, 20180261.

Caizergues, A.E., Le Luyer, J., Grégoire, A., Szulkin, M., Senar, J., Charmantier, A., *et al.* (2021). Epigenetics and the city: non-parallel DNA methylation modifications across pairs of urban-rural Great tit populations. *Evol. Appl.*, 15, 149–165.

Campbell-Staton, S.C., Velotta, J.P. & Winchell, K.M. (2021). Selection on adaptive and maladaptive gene expression plasticity during thermal adaptation to urban heat islands. *Nat. Commun.*, 12, 6195.

Campbell-Staton, S.C., Winchell, K.M., Rochette, N.C., Fredette, J., Maayan, I., Schweizer, R.M., *et al.* (2020). Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol.*, 4, 652–658.

Capilla-Lasheras, P., Dominoni, D.M., Babayan, S.A., O'Shaughnessy, P.J., Mladenova, M., Woodford, L., *et al.* (2017). Elevated Immune Gene Expression Is Associated with Poor Reproductive Success of Urban Blue Tits. *Front. Ecol. Evol.*, 5, 64.

Cardilini, A.P.A., Weston, M.A., Nimmo, D.G., Dann, P. & Sherman, C.D.H. (2013). Surviving in sprawling suburbs: Suburban environments represent high quality breeding habitat for a widespread shorebird. *Landsc. Urban Plan.*, 115, 72–80.

Chamberlain, D.E., Cannon, A.R., Toms, M.P. & Leech, D.I. (2009). Avian productivity in urban landscapes□: a review and meta-analysis. *Ibis*, 151, 1–18.

Chao, A., Chiu, C. & Jost, L. (2014). Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. *Annu. Rev. Ecol. Evol. Syst.*, 45, 297–324.

Cinar, O., Nakagawa, S. & Viechtbauer, W. (2022). Phylogenetic multilevel meta-analysis: A simulation study on the importance of modeling the phylogeny. *Methods Ecol. Evol.*, 13, 383–395.

Cohen, J.E. & Xu, M. (2015). Random sampling of skewed distributions implies Taylor's power law of fluctuation scaling. *Proc. Natl. Acad. Sci.*, 112, 7749–7754.

Conway, C.J., Garcia, V., Smith, M.D., Ellis, L.A. & Whitney, J.L. (2006). Comparative demography of Burrowing Owls in agricultural and urban landscapes in southeastern Washington. *J. F. Ornithol.*, 77, 280–290.

Dhondt, A.A., Eyckerman, R., Moermans, R. & Hublé, J. (1984). Habitat and laying date of Great and Blue Tit Parus major and P. caeruleus. *Ibis*, 126, 388–397.

Diamond, S.E., Chick, L.D., Perez, A., Strickler, S.A. & Martin, R.A. (2018). Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities. *Proc. R. Soc. B*, 285, 20180036.

Diamond, S.E. & Martin, R.A. (2021). Evolution in Cities. *Annu. Rev. Ecol. Evol. Syst.*, 52, 519–540.

Dominoni, D., Quetting, M. & Partecke, J. (2013). Artificial light at night advances avian reproductive physiology. *Proc. R. Soc. B*, 280, 20123017.

Dunn, P.O. & Møller, A.P. (2014). Changes in breeding phenology and population size of birds. *J. Anim. Ecol.*, 83, 729–739.

Eden, S.F. (1985). The comparative breeding biology of magpies Pica pica in an urban and a rural habitat (Aves: Corvidae). *J. Zool.*, 205, 325–334.

ESA. 3CS Land Cover Product User Guide. (2020).

ESA. Land Cover CCI Product User Guide. (2017).

Fugère, V. & Hendry, A.P. (2018). Human influences on the strength of phenotypic selection. *Proc. Natl. Acad. Sci. U. S. A.*, 115, 10070–10075.

Fusco, N.A., Pehek, E. & Munshi-South, J. (2021). Urbanization reduces gene flow but not genetic diversity of stream salamander populations in the New York City metropolitan area. *Evol. Appl.*, 14, 99–116.

Gahbauer, M.A., Bird, D.M., Clark, K.E., French, T., Brauning, D.W. & McMorris, F.A. (2015). Productivity, mortality, and management of urban peregrine falcons in northeastern North America. *J. Wildl. Manage.*, 79, 10–19.

Garant, D., Hadfield, J.D., Kruuk, L.E.B. & Sheldon, B.C. (2008). Stability of genetic

variance and covariance for reproductive characters in the face of climate change in a wild bird population. *Mol. Ecol.*, 17, 179–188.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., *et al.* (2015). Inter-annual and inter-habitat variation in breeding performance of blue tits (Cyanistes caeruleus) in central Poland. *Ornis Fenn.*, 92, 34–42.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., *et al.* (2016a). Effects of extreme thermal conditions on plasticity in breeding phenology and double-broodedness of Great Tits and Blue Tits in central Poland in 2013 and 2014. *Int. J. Biometeorol.*, 60, 1795–1800.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., *et al.* (2016b). Effects of nest characteristics on reproductive performance in Blue Tits Cyanistes caeruleus and Great Tits Parus major. *Avian Biol. Res.*, 9, 37–43.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., *et al.* (2017). Differences in the breeding success of blue tits Cyanistes caeruleus between a forest and an urban area: A long-term study. *Acta Ornithol.*, 52, 59–68.

Gorton, A.J., Moeller, D.A. & Tiffin, P. (2018). Little plant, big city: A test of adaptation to urban environments in common ragweed (Ambrosia artemisiifolia). *Proc. R. Soc. B*, 285, 20180968.

Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. London*, 326, 119–157.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., *et al.* (2008). Global change and the ecology of cities. *Science, 319, 756-760.*

Gryz, J. & Krauze-Gryz, D. (2018). Influence of habitat urbanisation on time of breeding and productivity of tawny Owl (Strix aluco). *Polish J. Ecol.*, 66, 153–161.

Hajdasz, A.C., Otter, K.A., Baldwin, L.K. & Reudink, M.W. (2019). Caterpillar phenology predicts differences in timing of mountain chickadee breeding in urban and rural habitats. *Urban Ecosyst.*, 22, 1113–1122.

Halfwerk, W., Blaas, M., Kramer, L., Hijner, N., Trillo, P.A., Bernal, X.E., *et al.* (2019). Adaptive changes in sexual signalling in response to urbanization. *Nat. Ecol. Evol.*, 3, 374–380.

Hedges, L., Gurevitch, J. & Curtis, P. (1999). The Meta-Analysis of Response Ratios

in Experimental Ecology. *Ecology*, 80, 1150–1156.

Heisler, J.M. & Brazel, A.J. (2018). The urban physical environment: temperature and urban heat islands. In: *Urban Ecosystem Ecology* (eds. Aitkenhead-Petersn, J. & Volder, A.). American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, pp. 29–56.

Hendry, A.P., Gotanda, K.M. & Svensson, E.I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philos. Trans. R. Soc. B*, 372, 20160028.

Hijmans, R.J. (2020). raster: Geographic Data Analysis and Modeling.

Hill, M.O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, 54, 427–432.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M., *et al.* (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci. U. S. A.*, 112, 12764–12769.

Hinsley, S.A., Hill, R.A., Bellamy, P.E., Harrison, N.M., Speakman, J.R., Wilson, A.K., *et al.* (2008). Effects of structural and functional habitat gaps on breeding woodland birds: Working harder for less. *Landsc. Ecol.*, 23, 615–626.

Ibáñez-Álamo, J.D. & Soler, M. (2010). Does urbanization affect selective pressures and life-history strategies in the common blackbird (Turdus merula L.)? *Biol. J. Linn. Soc.*, 101, 759–766.

Isaksson, C. & Andersson, S. (2007). Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. *J. Avian Biol.*, 38, 564–572.

Isaksson, C., Johansson, A. & Andersson, S. (2008). Egg yolk carotenoids in relation to habitat and reproductive investment in the great tit Parus major. *Physiol. Biochem. Zool.*, 81, 112–118.

Jarrett, C., Powell, L.L., McDevitt, H., Helm, B. & Welch, A.J. (2020). Bitter fruits of hard labour: diet metabarcoding and telemetry reveal that urban songbirds travel further for lower-quality food. *Oecologia*, 193, 377–388.

Johnson, M.T.J. & Munshi-South, J. (2017). Evolution of life in urban environments. *Science*, 358, eaam8327.

Kelleher, K.M. & O'Halloran, J. (2007). Influence of nesting habitat on breeding Song Thrushes Turdus philomelos. *Bird Study*, 54, 221–229.

Kettel, E.F., Gentle, L.K., Yarnell, R.W. & Quinn, J.L. (2019). Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes.

Urban Ecosyst., 22, 117–125.

Lambert, M.R., Brans, K.I., Des Roches, S., Donihue, C.M. & Diamond, S.E. (2020). Adaptive Evolution in Cities: Progress and Misconceptions. *Trends Ecol. Evol.*, 36, 239–257.

Lee, S., Lee, H., Jablonski, P.G., Choe, J.C. & Husby, M. (2017). Microbial abundance on the eggs of a passerine bird and related fitness consequences between urban and rural habitats. *PLoS One*, 12, e0185411.

Lin, W.L., Lin, S.M., Lin, J.W., Wang, Y. & Tseng, H.Y. (2015). Breeding performance of Crested Goshawk Accipiter trivirgatus in urban and rural environments of Taiwan. *Bird Study*, 62, 177–184.

De Lisle, S.P., Mäenpää, M.I. & Svensson, E.I. (2022). Phenotypic plasticity is aligned with phenological adaptation on both micro- and macroevolutionary timescales. *Ecol. Lett.*, 00, 1–12.

Liven-Schulman, I., Leshem, Y., Alon, D. & Yom-Tov, Y. (2004). Causes of population declines of the Lesser Kestrel Falco naumanni in Israel. *Ibis*, 146, 145–152.

Luna, Á., Palma, A., Sanz-Aguilar, A., Tella, J.L. & Carrete, M. (2020). Sex, personality and conspecific density influence natal dispersal with lifetime fitness consequences in urban and rural burrowing owls. *PLoS One*, 15, 1–17.

Luo, D., Wan, X., Liu, J. & Tong, T. (2016). Optimally estimating the sample mean from the sample size, median, mid-range, and/or mid-quartile range. *Stat. Methods Med. Res.*, 27, 1785–1805.

Mcgowan, K.J. (2001). Avian Ecology and Conservation in an Urbanizing World. In: *Avian Ecology and Conservation in an Urbanizing World* (eds. Marzluff, J.M., Bowman, R. & Donelly, R.). Kluwer Academic Press, New York, pp. 365–381.

Mennechez, G. & Clergeau, P. (2006). Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica*, 30, 182–191.

Merckx, T., Nielsen, M.E., Heliölä, J., Kuussaari, M., Pettersson, L.B., Pöyry, J., *et al.* (2021). Urbanization extends flight phenology and leads to local adaptation of seasonal plasticity in Lepidoptera. *Proc. Natl. Acad. Sci.*, 118, e2106006118.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D., *et al.* (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*, 558, 113–116.

Meyrier, E., Jenni, L., Bötsch, Y., Strebel, S., Erne, B. & Tablado, Z. (2017). Happy

to breed in the city? Urban food resources limit reproductive output in Western Jackdaws. *Ecol. Evol.*, 7, 1363–1374.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol. Evol.*, 7, 1476–1481.

Middleton, A. (1979). Influence of Age and Habitat on Reproduction by the American Goldfinch. *Ecology*, 60, 418–432.

Millsap, B., Breen, T., McConnell, E., Steffer, T., Phillips, L., Douglass, N., *et al.* (2004). Comparative Fecundity and Survival of Bald Eagles Fledged from Suburban and Rural Natal Areas in Florida. *J. Wildl. Manage.*, 68, 1018–1031.

Minias, P. (2016). Reproduction and survival in the city: Which fitness components drive urban colonization in a reed-nesting waterbird? *Curr. Zool.*, 62, 79–87.

Morrissey, C.A., Stanton, D.W.G., Tyler, C.R., Pereira, M.G., Newton, J., Durance, I., *et al.* (2014). Developmental impairment in eurasian dipper nestlings exposed to urban stream pollutants. *Environ. Toxicol. Chem.*, 33, 1315–1323.

Muñoz, M.M., Stimola, M.A., Algar, A.C., Conover, A., Rodriguez, A.J., Landestoy, M.A., *et al.* (2014). Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proc. R. Soc. B*, 281, 20132433.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., *et al.* (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods Ecol. Evol.*, 13, 4–21.

Nakagawa, S., Lagisz, M., O'Dea, R.E., Rutkowska, J., Yang, Y., Noble, D.W.A., *et al.* (2021). The orchard plot: Cultivating a forest plot for use in ecology, evolution, and beyond. *Res. Synth. Methods*, 12, 4–12.

Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., *et al.* (2015). Meta-analysis of variation: Ecological and evolutionary applications and beyond. *Methods Ecol. Evol.*, 6, 143–152.

Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evol. Ecol.*, 26, 1253–1274.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4, 133–142.

Newhouse, M.J., Marra, P.P. & Johnson, L.S. (2008). Reproductive Success of House Wrens in Suburban and Rural Landscapes. *Wilson J. Ornithol.*, 120, 99–104.

OpenTreeOfLife, Redelings, R., Reyes, L.L.S., Cranston, K.A., Allman, J., Holder, M.T., *et al.* (2019). Open Tree of Life Synthetic Tree.

Pande, S., Pawashe, A., Mahajan, M.N., Joglekar, C. & Mahabal, A. (2007). Effect of food and habitat on breeding success in Spotted Owlets (Athene brama) nesting in villages and rural landscapes in India. *J. Raptor Res.*, 41, 26–34.

Partecke, J., Hegyi, G., Fitze, P.S., Gasparini, J. & Schwabl, H. (2020). Maternal effects and urbanization: Variation of yolk androgens and immunoglobulin in city and forest blackbirds. *Ecol. Evol.*, 10, 2213–2224.

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *R J.*, 10, 439–446.

Perlut, N.G., Bonter, D.N., Ellis, J.C. & Friar, M.S. (2016). Roof-Top Nesting in a Declining Population of Herring Gulls (Larus argentatus) in Portland, Maine, USA. *Waterbirds*, 39, 68–73.

Perrins, C.M. (1965). Population Fluctuations and Clutch-Size in the Great Tit. *J. Anim. Ecol.*, 34, 601–647.

Pickett, S.T.A., Cadenasso, M.L., Rosi-Marshall, E.J., Belt, K.T., Groffman, P.M., Grove, J.M., *et al.* (2017). Dynamic heterogeneity: a framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosyst.*, 20, 1–14.

Pollock, C.J., Capilla-Lasheras, P., McGill, R.A.R., Helm, B. & Dominoni, D.M. (2017). Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling blue tits (Cyanistes caeruleus). *Sci. Rep.*, 7, 5014.

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A., *et al.* (2017). Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Anim. Cogn.*, 20, 53–63.

Putman, B.J. & Tippie, Z.A. (2020). Big City Living: A Global Meta-Analysis Reveals Positive Impact of Urbanization on Body Size in Lizards. *Front. Ecol. Evol.*, 8, 580745.

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rees, J.A. & Cranston, K. (2017). Automated assembly of a reference taxonomy for phylogenetic data synthesis. *Biodivers. Data J.*, 5, e12581.

Richardson, J.L., Michaelides, S., Combs, M., Djan, M., Bisch, L., Barrett, K., *et al.*

(2021). Dispersal ability predicts spatial genetic structure in native mammals persisting across an urbanization gradient. *Evol. Appl.*, 14, 163–177.

Rollinson, D.J. & Jones, D.N. (2003). Variation in breeding parameters of the Australian magpie Gymnorhina tibicen in suburban and rural environments. *Urban Ecosyst.*, 6, 257–269.

Rosenfield, R.N., Hardin, M.G., Taylor, J., Sobolik, L.E. & Frater, P.N. (2019). Nesting density and dispersal movements between urban and rural habitats of cooper's Hawks (Accipiter cooperii) in Wisconsin: Are these source or sink habitats? *Am. Midl. Nat.*, 182, 36–51.

Rowe, L., Ludwig, D. & Schluter, D. (1994). Time, condition, and the seasonal decline of avian clutch size. *Am. Nat.*, 143, 698–772.

Salmón, P., Jacobs, A., Ahrén, D., Biard, C., Dingemanse, N.J., Dominoni, D.M., *et al.* (2021). Continent-wide genomic signatures of adaptation to urbanisation in a songbird across Europe. *Nat. Commun.*, 12, 2983.

Sanders, D., Frago, E., Kehoe, R., Patterson, C. & Gaston, K.J. (2021). Impacts of Artificial Light at Night on Biological Timings. *Nat. Ecol. Evol.*, 5, 74–81.

Santangelo, J.S., Ness, R.W., Cohan, B., Fitzpatrick, C.R., Innes, S.G., Koch, S., *et al.* (2022). Global urban environmental change drives adaptation in white clover. *Science*, 375, 1275–1281.

de Satgé, J., Strubbe, D., Elst, J., De Laet, J., Adriaensen, F. & Matthysen, E. (2019). Urbanisation lowers great tit Parus major breeding success at multiple spatial scales. *J. Avian Biol.*, e02108.

Schmidt, V.K.-H. & Steinbach, J. (1983). Niedriger Bruterfolg der Kohlmeise (Parus major) in städtischen Parks und Friedhöfen. *J. für Ornithol.*, 124, 81–83.

Schoech, S.J. & Bowman, R. (2001). Variation in the timing of breeding between suburban and wildland Florida Scrub-Jays: Do physiologic measures reflect different environments? In: *Avian Ecology and Conservation in an Urbanizing World* (eds. Marzluff, J.M., Bowman, R. & Donelly, R.). Kluwer Academic Press, New York, pp. 289–306.

Schoech, S.J., Bowman, R., Bridge, E.S. & Boughton, R.K. (2007). Baseline and acute levels of corticosterone in Florida Scrub-Jays (Aphelocoma coerulescens): Effects of food supplementation, suburban habitat, and year. *Gen. Comp. Endocrinol.*, 154, 150–160.

Schoech, S.J., Bowman, R. & Reynolds, S.J. (2004). Food supplementation and

possible mechanisms underlying early breeding in the Florida Scrub-Jay (Aphelocoma coerulescens). *Horm. Behav.*, 46, 565–573.

Schoech, S.J., Bridge, E.S., Boughton, R.K., Reynolds, S.J., Atwell, J.W. & Bowman, R. (2008). Food supplementation: A tool to increase reproductive output? A case study in the threatened Florida Scrub-Jay. *Biol. Conserv.*, 141, 162–173.

Senior, A.M., Grueber, C.E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E.S.A., *et al.* (2016). Heterogeneity in ecological and evolutionary meta- analyses: its magnitude and implications. *Ecology*, 97, 3293–3299.

Senior, A.M., Viechtbauer, W. & Nakagawa, S. (2020). Revisiting and expanding the meta-analysis of variation: The log coefficient of variation ratio. *Res. Synth. Methods*, 11, 553–567.

Sepp, T., McGraw, K.J., Kaasik, A. & Giraudeau, M. (2018). A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? *Glob. Chang. Biol.*, 24, 1452–1469.

Seress, G., Bókony, V., Pipoly, I., Szép, T., Nagy, K. & Liker, A. (2012). Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. *J. Avian Biol.*, 43, 403–414.

Seress, G., Hammer, T., Bókony, V., Vincze, E., Preiszner, B., Pipoly, I., *et al.* (2018). Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. *Ecol. Appl.*, 28, 1143–1156.

Seress, G., Sándor, K., Evans, K.L. & Liker, A. (2020). Food availability limits avian reproduction in the city: An experimental study on great tits Parus major. *J. Anim. Ecol.*, 89, 1570–1580.

Shi, J., Luo, D., Weng, H., Zeng, X., Lin, L., Chu, H., *et al.* (2020). Optimally estimating the sample standard deviation from the five-number summary. *Res. Synth. Methods*, 11, 641–654.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.*, 21, 186–191.

Shustack, D.P. & Rodewald, A.D. (2011). Nest predation reduces benefits to early clutch initiation in northern cardinals Cardinalis cardinalis. *J. Avian Biol.*, 42, 204–209.

Solonen, T. (2001). Breeding of the Great Tit and Blue Tit in urban and rural habitats in Southern Finland. *Ornis Fenn.*, 78, 49–60.

Solonen, T. & Hildén, M. (2014). Breeding phenology in Great and Blue Tits (Parus spp.): Are urban populations more resistant to climate change than rural ones? *Ornis Fenn.*, 91, 209–219.

Solonen, T. & Ursin, K.A. (2008). Breeding of Tawny Owls Strix aluco in rural and urban habitats in southern Finland. *Bird Study*, 55, 216–221.

Stout, W.E., Anderson, R.K. & Papp, J.M. (1998). Urban, suburban and rural red-tailed hawk nesting habitat and populations in southeast Wisconsin. *J. Raptor Res.*, 32, 221–228.

Stracey, C.M. & Robinson, S.K. (2012). Are urban habitats ecological traps for a native songbird? Season-long productivity, apparent survival, and site fidelity in urban and rural habitats. *J. Avian Biol.*, 43, 50–60.

Strubbe, D., Salleh Hudin, N., Teyssier, A., Vantieghem, P., Aerts, J. & Lens, L. (2020). Phenotypic signatures of urbanization are scale-dependent: A multi-trait study on a classic urban exploiter. *Landsc. Urban Plan.*, 197, 103767.

Sumasgutner, P., Nemeth, E., Tebb, G., Krenn, H.W. & Gamauf, A. (2014). Hard times in the city-attractive nest sites but insufficient food supply lead to low reproduction rates in a bird of prey. *Front. Zool.*, 34, 17–31.

Thompson, M.J., Capilla-Lasheras, P., Dominoni, D.M., Réale, D. & Charmantier, A. (2022). Phenotypic variation in urban environments: mechanisms and implications. *Trends Ecol. Evol.*, 37, 171–182.

Thornton, M., Todd, I. & Roos, S. (2017). Breeding Success and Productivity of Urban and Rural Eurasian Sparrowhawks Accipiter nisus in Scotland. *Ecoscience*, 24, 115–116.

Trikalinos, T. & Ioannidis, J.P.A. (2005). Assessing the evolution of effect sizes over time. In: *Publication Bias in Meta-Analysis* (eds. Rothstein, H., Sutton, A. & Borenstein, M.). John Wiley, Chichester, pp. 241–259.

Uchida, K., Blakey, R. V., Burger, J.R., Cooper, D.S., Niesner, C.A. & Blumstein, D.T. (2021). Urban Biodiversity and the Importance of Scale. *Trends Ecol. Evol.*, 36, 123–131.

Vaugoyeau, M., Adriaensen, F., Artemyev, A., Bańbura, J., Barba, E., Biard, C., *et al.* (2016). Interspecific variation in the relationship between clutch size, laying date and intensity of urbanization in four species of hole-nesting birds. *Ecol. Evol.*, 6, 5907–5920.

Via, S. & Lande, R. (1985). Genotype-Environment Interaction and the Evolution of

Phenotypic Plasticity. *Evolution*, 39, 505–522.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor. *J. Stat. Softw.*, 36, 1–48.

Wawyrzyniak, J., Kaliński, A., Glądalski, M., Bańbura, M., Markowski, M., Skwarska, J., *et al.* (2015). Long-Term Variation in Laying Date and Clutch Size of the Great Tit Parus major in Central Poland: A Comparison between Urban Parkland and Deciduous Forest. *Ardeola*, 62, 311–322.

Welch-Acosta, B.C., Skipper, B.R. & Boal, C.W. (2019). Comparative breeding ecology of Mississippi Kites in urban and exurban areas of West Texas. *J. F. Ornithol.*, 90, 248–257.

Westgate, M.J. (2019). revtools: An R package to support article screening for evidence synthesis. *Res. Synth. Methods*, 10, 606–614.

Yeh, P.J. & Price, T.D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *Am. Nat.*, 164, 531–542.

Tables

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 date, clutch size and number of fledglings per clutch were meta-analysed to assess differences in variation between urban and non-urban populations within and among 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]***	0.052 [-0.046, 0.149]	0.064 [-0.071, 0.198]	409
Within breeding season	***0.193*** ***[0.094, 0.292]***	0.024 [-0.110, 0.158]	0.149 [-0.025, 0.322]	376
Among breeding seasons	0.007 [-0.133, 0.147]	0.077 [-0.034, 0.189]	0.011 [-0.136, 0.158]	101

Figures

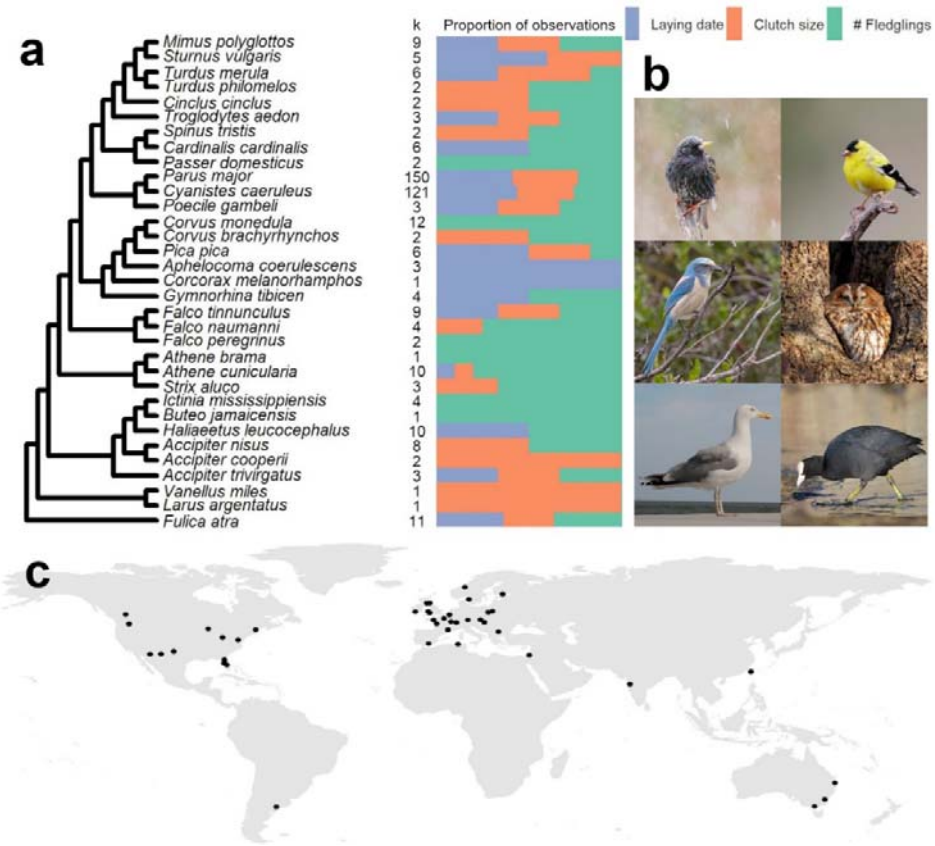

Figure 1. Phylogenetic and geographical breadth of the meta-analytic data. (a) Phylogenetic tree of the 33 avian species included in the meta-analysis along with the number of effect sizes (i.e., urban – non-urban comparisons) included per species ('k'; which may encompass multiple years of study from 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 area

in which one or more urban – non-urban pairs of populations were sampled across a varying number of years.

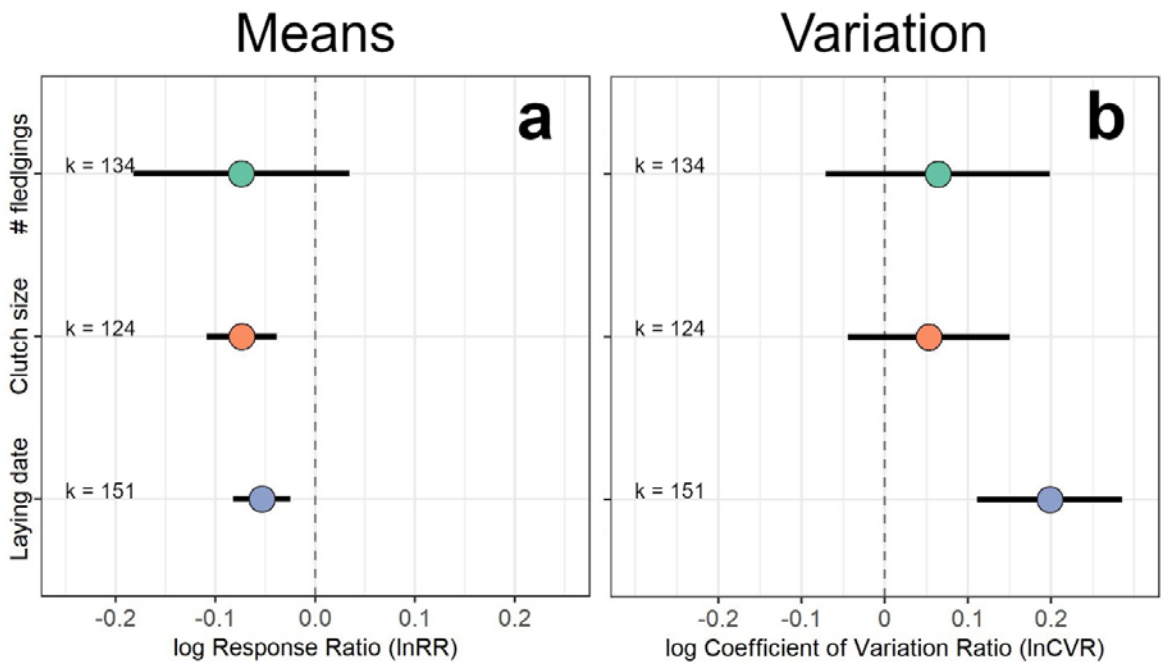

Figure 2. Urban populations have earlier phenology, lower reproductive output and more variable life-history traits than non-urban populations. (**a**) Urban populations laid earlier and had smaller clutches, producing fewer fledglings, than their paired non-urban populations (illustrated by negative 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 date (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 S6 for overall meta-analyses of lnRR and lnCVR). Number of studies included for laying date, clutch size and number of fledglings were 32, 42 and 44 studies respectively. Raw data and model estimates are presented in Figure S5. 'k' provides the number of urban – non-urban comparisons.

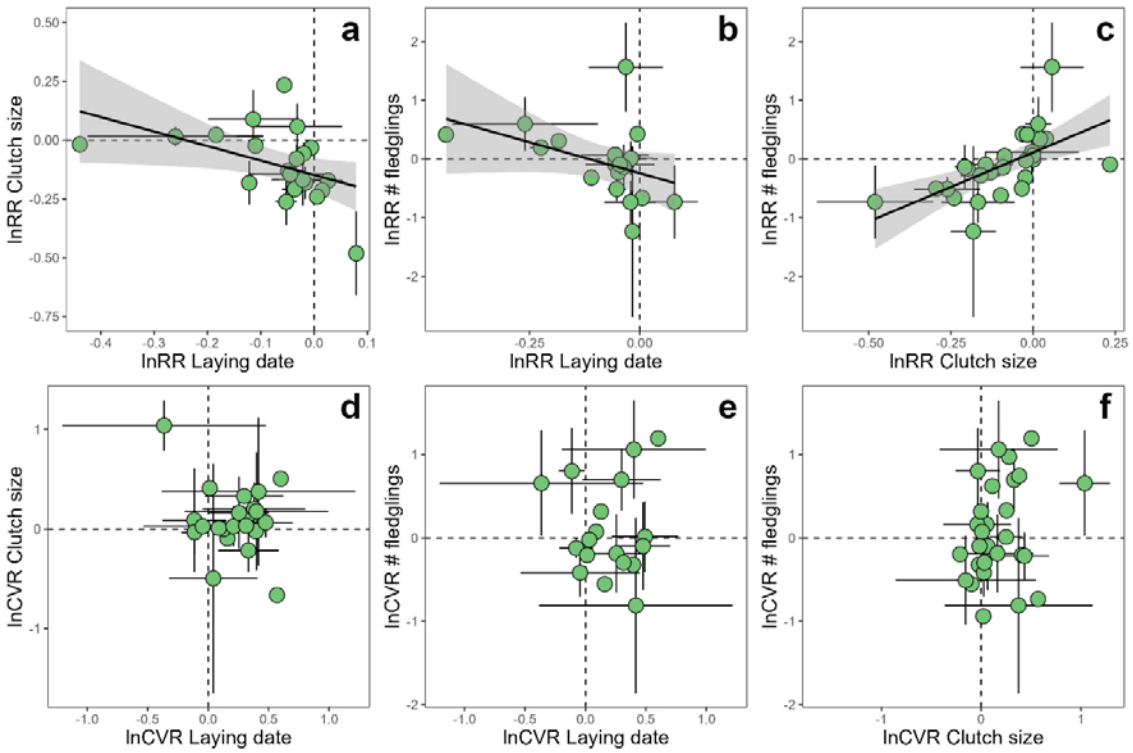

Figure 3. Avian life-history traits show a correlated response to urbanisation. Our meta-analysis allowed us to investigate correlated responses to urbanisation across the three studied life-history traits (laying date, clutch size, number of fledgelings), and revealed strong correlations in log response ratio (lnRR) but not log coefficient of variation ratio (lnCVR). (**a**) Earlier laying dates in urban populations compared to non-urban counterparts (i.e., negative values in the x axis) were associated with no differences in clutch size across habitats (i.e., y axis values close to zero), defining a negative correlation between lnRR for laying dates and clutch size. (**b**) A similar pattern was found between lnRR for laying dates and number of fledglings, while (**c**) lnRR for clutch size and number of fledglings were positively correlated (Table S2). (**d** - **f**) We found no statistical evidence for models including correlations across traits in how urbanisation affected phenotypic variation (Table S5): (**d**) differences between habitats in phenotypic variation in laying dates were not associated with differences between habitats in phenotypic variation in clutch size or (**e**) number of fledglings; and (**f**) differences between habitats in variation in clutch size were not associated with differences between habitats in variation in number of fledglings. Points represent mean

values per study ± SE. Regression lines (mean ± SE) in **a** - **c** were fitted using linear regressions to illustrate the correlation revealed by our trivariate meta-analysis (Table S3).

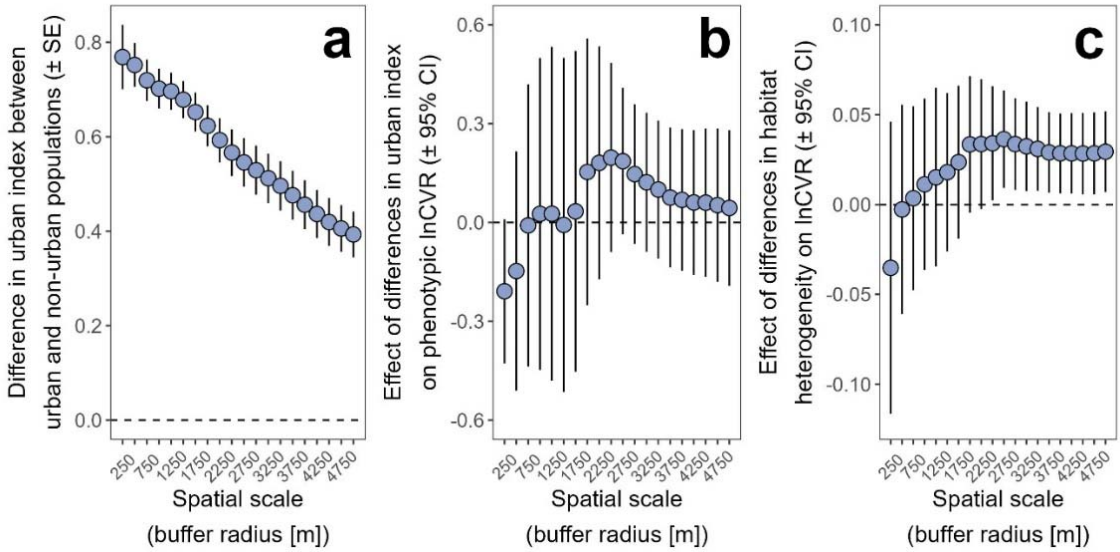

Figure 4. Effects of habitat heterogeneity on the difference in phenotypic variation between urban and non-urban bird populations (i.e., lnCVR). (**a**) After quantifying urban index and habitat heterogeneity, we verified that urban populations had higher urban index (i.e., the proportion of landcover at a given spatial scale categorised as 'urban' [see methods]), which was indeed the case. The y axis represents the difference in urban index between urban and non-urban populations, with positive values representing urban populations with higher urban index than their non-urban neighbours. (**b**) Differences in urban index between urban and non-urban populations did not predict the magnitude of the difference in phenotypic variation between populations (i.e., lnCVR). This figure shows the estimated effect of differences in urban index between populations on lnCVR. Significant positive values indicate that the higher the difference in urban index between urban and non-urban populations, the higher the lnCVR value (i.e., larger values of phenotypic variation in urban populations compared to non-urban counterparts). (**c**) Differences in habitat heterogeneity between urban and non-urban populations did positively predict the magnitude of the difference in phenotypic variation between populations (i.e., lnCVR), particularly at large spatial scales. This figure shows the estimated effect of differences in habitat heterogeneity on lnCVR at different spatial scales. Significant positive values indicate that the higher the difference in habitat heterogeneity between urban and non-urban

populations, the higher the lnCVR value (i.e., larger values of phenotypic variation in urban populations compared to non-urban counterparts). Points represent mean model estimates ± SE in **a**, and mean model estimates ± 95% confidence intervals (95%CI) in **b** and **c**. 'Spatial scale' refers to the radius of a circular area centred at each study location and over which urban index and habitat heterogeneity was calculated.