1　　## A global meta-analysis reveals higher variation in breeding

2　　## phenology in urban birds than in their non-urban neighbours

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22　**Author contributions**

23　PC-L, MJT, DR, AC and DMD conceived the study. PC-L, AS-T, CJB and DMD performed the

24　literature search. PC-L extracted effect sizes from suitable published papers. MJT validated

25　effect size extraction. PC-L and YH performed all statistical analysis with advice from AS-T.

26　PC-L wrote the first draft of the manuscript with input from MJT, AS-T, DR, AC and DMD. All

27　authors read and revised the manuscript.

28　**Data availability**

29　All R scripts and datasets needed to reproduce the analyses presented in this paper are

30　available at: https://github.com/PabloCapilla/meta-analysis_variation_urban. Should the

31　manuscript be accepted, a DOI to this data repository will be provided.

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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 species nor over a broad geographical range. Here, we conduct a meta-analysis of the avian literature to compare urban *versus* non-urban means and variation in 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 populations have higher phenotypic variation in laying date than non-urban populations. This result arises from differences between populations within breeding seasons, conceivably due to higher landscape heterogeneity in urban habitats. These findings reveal a novel effect of urbanisation on animal life-histories with potential implications for species adaptation to urban environments (which will require further investigation). Higher variation in phenology in birds subjected to urban disturbance could result from plastic responses to a heterogeneous environment, or from higher genetic variation in phenology, possibly linked to higher evolutionary potential.

Introduction

Humans have drastically changed environmental conditions on Earth, particularly since the invention of agriculture during the Neolithic Revolution. 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 habitats (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 (Hendry *et al.* 2017). Indeed, numerous studies have reported divergent phenotypes between urban and non-urban populations in phenological, morphological, behavioural and reproductive traits (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). Most studies in urban ecology and evolution to date have focused on urban effects on *mean* phenotypes, and no study has explicitly investigated how urbanisation affects phenotypic *variation*. 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 (Fusco 2001; Pavlicev *et al.* 2011): 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).

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 in heterogeneous urban environments. Findings

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84 from urban and non-urban meta-populations of the common ragweed (*Ambrosia artemisiifolia*)

85 are consistent with this prediction as inter-population variation in several fitness proxies was

86 greater in urban compared to non-urban environments (Gorton *et al.* 2018). A meta-analysis

87 of selection strength found weaker selection occurring in human-disturbed populations

88 (Fugère & Hendry 2018; note that this analysis did not specifically test the effect of

89 urbanisation on selection strength and only included one study directly associated with

90 urbanisation), which if extrapolated to the urban context, could lead to higher phenotypic

91 variation in urban populations compared to their non-urban counterparts. Overall, these

92 studies converge with the notion that urban populations could display higher levels of

93 phenotypic variation due to several eco-evolutionary processes. These findings also highlight

94 that the extent to which urbanisation might impact phenotypic variation likely depends on the

95 interplay between the temporal and spatial scale at which environmental conditions fluctuate

96 in the urban habitat, as well as on the species' longevity and dispersal ability (Thompson *et*

97 *al.* 2022).

98

99 The temporal scale at which differences in phenotypic variation between urban and non-urban

100 habitats manifest can help us evaluate their ecological causes, and is likely to determine the

101 eco-evolutionary implications of increased phenotypic variation in urban habitats (Thompson

102 *et al.* 2022). First, urban populations could display higher phenotypic variation than non-urban

103 populations within a given breeding season (i.e., intra-annual variation; as a result, for

104 example, of consistent differences in landscape heterogeneity between habitats; Pickett et al.

105 2017). Second, urban populations could display higher phenotypic variation than non-urban

106 populations due to larger yearly fluctuations in environmental conditions (i.e., inter-annual

107 variation; if, for example, urban populations are more sensitive to changes in weather), with

108 or without intra-annual differences in phenotypic variation between urban and non-urban

109 populations. In the latter scenario, similar levels of phenotypic variation would be exposed to

110 natural selection in short-lived species (e.g., annual species).

111

5

112   Urban environments have been referred to as spatially more heterogeneous than non-urban

113   habitats of the same geographical area (Pickett *et al.* 2017). High urban habitat heterogeneity

114   could increase phenotypic variation compared to adjacent non-urban habitats if, for example,

115   urban organisms change their phenotype according to local environmental conditions (e.g.,

116   through either developmental or later-life phenotypic plasticity). The empirical assessment of

117   this idea, however, largely depends on the scale at which urban habitat heterogeneity is

118   measured, the spatial scale at which the organism of interest operates and the heterogeneity

119   of the non-urban habitat of reference (Pickett *et al.* 2017; Uchida *et al.* 2021). For example, a

120   megacity could be spatially heterogeneous, containing a diverse array of habitats (e.g.,

121   multiple urban parks with different ecological conditions, a varying level of impervious surface,

122   etc.), and, thus, be overall vastly more heterogeneous than a neighboring non-urban habitat.

123   However, species could reduce the range of environmental conditions that they experience

124   through matching habitat choice (e.g., Muñoz et al. 2014), limiting the potential effect of urban

125   habitat heterogeneity on phenotypic variation. Therefore, measuring habitat heterogeneity at

126   different spatial scales will be paramount to understand the potential association between

127   habitat heterogeneity and increased phenotypic variation in urban areas.

128

129   Here, we investigate how urbanisation impacts mean phenotypic values and phenotypic

130   variation using a meta-analysis of 399 paired urban and non-urban comparisons of avian life-

131   history traits (laying date, clutch size and number of fledglings) published between 1958 and

132   2020 including 35 bird species (Figure 1). We use paired within species urban – non-urban

133   comparisons to investigate the following questions: i) Is urbanisation associated with shifts in

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

135   traits? iii) What is the temporal and spatial scale at which urbanisation correlates with changes

136   in phenotypic variation? Based on previous research (Chamberlain *et al.* 2009; Sepp *et al.*

137   2018), we predict that urban bird populations display on average earlier phenology, smaller

138   clutch size and lower number of fledglings than non-urban populations. We also predict

139   increased phenotypic variation in urban populations compared to non-urban populations for

6

140 all three traits examined (see above). We disentangle urban effects on phenotypic variation

141 across different temporal and spatial scales, suggesting an ecological mechanism for the

142 effects of urbanisation on avian phenotypic variation. This study provides, for the first time,

143 meta-analytical evidence that urban conditions can magnify phenotypic variation in phenology

144 and highlights the potential role of increased habitat heterogeneity in urban areas as an

145 ecological mechanism underlying this effect.

146

Material and methods

148 **Literature review**

149 We began our literature search by inspecting two published reviews on the impact of

150 urbanisation on avian biology (Chamberlain *et al.* 2009; Sepp *et al.* 2018). As we were

151 interested in how phenology and reproduction were affected by urbanisation, we identified

152 studies cited in Chamberlain *et al.* (2009) (n = 37) and Sepp *et al.* (2018) (n = 32) that could

153 contain either raw data, or mean and variance estimates for first clutch laying initiation

154 (hereafter laying date), clutch size and number of nestlings fledged per breeding attempt

155 (hereafter number of fledglings), for paired urban and non-urban populations (see details

156 below). Then, we performed four searches of the Web of Science Core Collection on the 27th

157 of October 2020 (databases covered: SCI-EXPANDED – 1900-present, SSCI – 1956-present,

158 A&HCI – 1975-present, BKCI-S – 2005-present, BKCI-SSH – 2005-present and ESCI – 2015-

159 present) to recover studies published since 1900 and including all languages and all document

160 types. We performed the following four searches on the Web of Science Core Collection: (**1**)

161 TS=("urban*" AND ("bird*" OR "aves" OR "avian" OR "ornithol*" OR "passerine*" OR

162 "passeriform*" OR "songbird*" OR *list of bird genera*) AND ("laying date" OR "lay date" OR

163 "first egg" OR "clutch size" OR "eggs laid" OR "number of eggs" OR "fledgling*" OR "fledging"

164 OR "reproductive success" OR "fitness")); (**2**) TS=("urban*" AND "bird" AND "laying date"); (**3**)

165 TS=("urban*" AND "bird" AND "clutch size"); (**4**) TS=("urban*" AND "bird" AND "fledglings").

166 The *list of avian genera* in the first search string consisted of a list of all avian genera and can

167 be found in Supplementary text D (see also acknowledgements). We complemented the

168 search on the Web of Science Core Collection by searching Scopus using search string '(1)'

169 above (Scopus field 'TITLE-ABS-KEY'). Both literature searches, on the Web of Science Core

170 Collection and Scopus, included studies published before the 27th of October 2020. We used

171 the literature search results in these two major search engines to assess the

172 comprehensiveness of our search (see Supplementary Text A for details). These searches

173 found 892, 71, 198, 167 (on the Web of Science Core Collection) and 735 (on Scopus) studies,

174 respectively, which we combined with the studies identified from Chamberlain *et al.* (2009)

175 and Sepp *et al.* (2018) to create a list of 2,132 (non-unique) studies (Figure S1). We then de-

176 duplicated this list using the R package 'revtools' (using exact matching of study titles in

177 function '*find_duplicates*', v0.4.1; Westgate 2019) and by manually inspecting all titles and

178 author lists. Our final list contained 1,166 unique studies (Figure S1), which we screened by

179 reading their title and abstract (this first screening step was made by PC-L, CJB and DMD). If

180 the title and/or abstract indicated that the paper could fit our requirements for data collection

181 (see below), we read the study fully, aiming to extract mean, standard deviation (SD) and

182 sample size (n) of our life-history traits of interest for urban and non-urban bird populations. If

183 SD was not available but authors provided SE, the former was calculated as: $SD = SE \times \sqrt{n}$.

184 Mean and SD were extracted from data quartiles and medians in four effect sizes from two

185 studies following (Luo *et al.* 2016; Shi *et al.* 2020). When available, we extracted estimates

186 per breeding season (i.e., papers sometimes reported mean, SD and n for urban and non-

187 urban populations in multiple breeding seasons). If a study reported incomplete information

188 for inclusion in our meta-analysis (e.g., mean was provided but not SD or SE), we contacted

189 the authors to ask for this missing information (a complete list of authors that provided

190 estimates can be found in the acknowledgements).

191

192 **Criteria for inclusion**

193 We were interested in investigating the effects of urbanisation on life-history traits, with an

194 interest in testing the association between urbanisation and, mean and variation in trait values.

195   Paired urban – non-urban designs, where an urban population is compared to an adjacent

196   non-urban population, are a powerful approach to identify the effects of urban living while

197   controlling for temporal and geographical variation, and large-scale genetic structure among

198   populations (Caizergues *et al.* 2021; Salmón *et al.* 2021). Therefore, we included studies if

199   they compared geographically close (i.e., paired) urban and non-urban populations and

200   reported laying date of the first clutches of the season, clutch size or number of fledglings for

201   the same breeding season across both habitats. When multiple populations were compared

202   along a gradient of urbanisation, we extracted estimates for the two populations at the

203   extremes of the gradient (i.e., most and least urbanised populations). When studies combined

204   estimates across several breeding seasons, we included them in our meta-analysis if urban

205   and non-urban populations had been sampled in the same breeding seasons. All effect sizes

206   were extracted by one author (PC-L). To validate data extraction, another author (MJT)

207   checked 15% of the studies included in the meta-analysis, comprising 55 effect sizes (17.80%

208   of the final data set; Supplementary Text B).

209

210   Initially, our dataset contained 443 paired urban – non-urban estimates from 40 bird species

211   and 74 studies. Of these, three observations were removed due to missing sample sizes, 26

212   observations were removed due to missing SD and 11 observations were removed because

213   their sample size was one (which precludes the calculation of mean and SD). Four

214   observations were removed because they reported a SD of zero (these indeed had very low

215   sample sizes: 3, 2, 7, 2 observations). Our final dataset included 399 comparisons between

216   paired urban – non-urban populations from 35 bird species and 68 studies (Figure 1; refs.:

217   Middleton 1979; Schmidt & Steinbach 1983; Dhondt *et al.* 1984; Eden 1985; Stout *et al.* 1998;

218   Boal & Mannan 1999; Mcgowan 2001; Schoech & Bowman 2001; Solonen 2001, 2014;

219   Antonov & Atanasova 2003; Rollinson & Jones 2003; Liven-Schulman *et al.* 2004; Millsap *et*

220   *al.* 2004; Sharma *et al.* 2004; Beck & Heinsohn 2006; Conway *et al.* 2006; Mennechez &

221   Clergeau 2006; Charter *et al.* 2007; Isaksson & Andersson 2007; Kelleher & O'Halloran 2007;

222   Schoech *et al.* 2007; Hinsley *et al.* 2008; Isaksson *et al.* 2008; Newhouse *et al.* 2008; Solonen

9

223   & Ursin 2008; Berardelli *et al.* 2010; Ibáñez-Álamo & Soler 2010; Shustack & Rodewald 2011;

224   Seress *et al.* 2012, 2018, 2020; Stracey & Robinson 2012; Brahmia *et al.* 2013; Cardilini *et al.*

225   2013; Morrissey *et al.* 2014; Sumasgutner *et al.* 2014; Gahbauer *et al.* 2015; Glądalski *et al.*

226   2015, 2016b, a, 2017, 2018; Lin *et al.* 2015; Wawyrzyniak *et al.* 2015; Bailly *et al.* 2016; Minias

227   2016; Perlut *et al.* 2016; Biard *et al.* 2017; Capilla-Lasheras *et al.* 2017; Kopij 2017; Lee *et al.*

228   2017; Pollock *et al.* 2017; Preiszner *et al.* 2017; Thornton *et al.* 2017; Bobek *et al.* 2018;

229   Caizergues *et al.* 2018; Gryz & Krauze-Gryz 2018; de Satgé *et al.* 2019; Hajdasz *et al.* 2019;

230   Kettel *et al.* 2019; Rosenfield *et al.* 2019; Welch-Acosta *et al.* 2019; Baldan & Ouyang 2020;

231   Evans & Gawlik 2020; Jarrett *et al.* 2020; Luna *et al.* 2020; Partecke *et al.* 2020). Of these 399

232   comparisons, 151 corresponded to comparisons of laying date (n = 32 studies), 119 were

233   comparisons of clutch size (n = 42 studies) and 129 were comparisons of number of fledglings

234   (n = 48 studies) (Figure S2). Last, there were 363 comparisons for single years (n = 47 studies)

235   and an additional 36 comparisons included estimates across multiple years (n = 21 studies).

236

237   **Meta-analytic effect sizes**

238   We standardised laying date across studies by coding it as the number of days after the 1st of

239   January (January 1st = 1). Mean laying date estimates across habitats always fell within the

240   same calendar year. For each of the three life-history traits, we computed the log response

241   ratio (lnRR) and the log coefficient of variation ratio (lnCVR) to investigate differences in mean

242   values and variability between urban and non-urban populations (Hedges *et al.* 1999;

243   Nakagawa *et al.* 2015; Senior *et al.* 2020). We calculated lnRR and lnCVR along with their

244   associated sampling variances (Nakagawa *et al.* 2015) using the R function '*escalc*' in the

245   'metafor' R package (v3.4.0; Viechtbauer 2010). Both lnRR and lnCVR were calculated so that

246   positive values meant higher estimates in urban populations compared to their non-urban

247   counterparts. Often mean and variance values are positively associated (e.g., Taylor's Law;

248   (Nakagawa & Schielzeth 2013; Cohen & Xu 2015). Therefore, we chose lnCVR over lnVR

249   (i.e., log total variation ratio; Nakagawa *et al.* 2015) as the former accounts for the mean–

250   variance relationship (Nakagawa *et al.* 2015; Senior *et al.* 2020). However, we carried out

10

251 sensitivity analysis using, among others, the log total variation ratio (section 'Sensitivity

252 analyses').

253

254 **Quantifying habitat heterogeneity and urban index**

255 We calculated habitat heterogeneity from the 3CS LC (Copernicus Climate Change Service

256 Land Cover) and the ESA-CCI LC (European Space Agency-Climate Change Initiative Land

257 Cover) land cover products (ESA. Land Cover CCI Product User Guide 2017; ESA. 3CS Land

258 Cover Product User Guide 2020). These datasets provide methodologically consistent land

259 cover per year and gridded maps from 1992 to 2019, with a global coverage and a spatial

260 resolution of circa 300 m per pixel (0.002778° or 10 arcseconds). Each pixel in the products

261 is classified as one of the 22 land cover categories defined by the UN-FAO-LCCS (United

262 Nations Food and Agriculture Organization Land Cover Classification System). From a subset

263 of studies included in our main meta-analysis, we could extract the coordinates of their urban

264 and non-urban populations (26 studies out of 68 provided accurate coordinates of their urban

265 and non-urban populations). Then, we sampled the landscape of every study by extracting the

266 number of pixels belonging to each land cover category around each urban and non-urban

267 location (i.e., within a circular buffer around each location). The extraction was performed for

268 several buffer radii from 250 m to 5000 m in intervals of 250 m. Landscape heterogeneity was

269 calculated as the effective number of land covers present in each buffer and computed as the

270 exponential of the Shannon-Wiener diversity index (i.e., Hill's numbers for $q = 1$) (Hill 1973;

271 Chao *et al.* 2014), resulting into a measure that not only accounts for the absolute richness of

272 land cover categories but also weights in the relative abundance of each category. An urban

273 index was calculated as the proportion of each buffer area categorized as an 'urban' land

274 cover type. Land cover data were processed and analysed using R (v.4.2.0; R Core Team

275 2022). Geospatial vectorial operations were conducted utilising the 'sf' R package (v.1.0-7;

276 Pebesma 2018) while raster extractions were performed with the 'raster' R package (v.3.5-15;

277 Hijmans 2020). All geospatial analyses were performed in the WSG 1984 projected

278 Coordinate Reference Systems, EPSG: 6326. Additionally, we calculated the distance

279 between each urban and non-urban pair of populations using the function '*pointDistance*' in

280 the R package 'raster'. We could retrieve location information for 232 urban *versus* non-urban

281 comparisons for laying date, clutch size and number of fledglings, from 11 species and 26

282 studies between 1992 and 2017 (land cover data were not available before 1992; see above).

283

284 **Meta-analyses**

285 We handled the datasets, ran all analyses and produced visualisations using R (v.4.2.0; R

286 Core Team 2022). To evaluate the effect of urbanisation on bird life-history traits, we fitted

287 phylogenetic multilevel (intercept-only) meta-analyses for each response term (i.e., lnRR

288 [Model 1] and lnCVR [Model 3]; Table 1) combining the three life-history traits (i.e., laying date,

289 clutch size and number of fledglings; we also fitted models that separated variation between

290 these traits; see below; Table 1). Both meta-analytic models estimated four random intercept

291 effects, publication identity (i.e., among-study variation), population identity (i.e., in several

292 cases, we found multiple studies from the same urban - non-urban populations pairs),

293 phylogeny (more details below), species identity (i.e., among-species variation not explained

294 by phylogeny), and an observation ID term. For the intercept-only models, we estimated total

295 heterogeneity (I^2) following Nakagawa & Santos (2012) and Senior et al. (2016b) as

296 implemented in the R function '*i2_ml*' ('orchaRd' R package v.0.0.0.9000; Nakagawa et al.

297 2021).

298

299 **Phylogenies**

300 Phylogenetic trees were extracted from the Open Tree of Life (Hinchliff *et al.* 2015; Rees &

301 Cranston 2017), using the interface provided by the R package 'rotl' (v3.0.12; Michonneau *et*

302 *al.* 2016; OpenTreeOfLife *et al.* 2019). We calculated tree branch length (Grafen 1989) and

303 generated a phylogenetic correlation matrix to include in all our phylogenetic multilevel meta-

304 analytic models (Figure 1). We assessed the phylogenetic signal in our meta-analysis based

305 on the proportion of variation explained by the phylogeny ($I^2_{phylogeny}$; Cinar et al. 2022).

306

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 to test 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 observation ID variances (i.e., one observation ID 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-effects 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)

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

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

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

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

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

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

13

331   Where y_i is the statistic of interest (lnRR or lnCVR) for the ith effect size ($i = 1,2,3,...,k$; where

332   k is the number of the effect sizes included in the analysis - i.e., number of urban – non-urban

333   paired comparisons). 'LD', 'CS', 'NF' refer to overall means (μ), variances (σ²) and correlations

334   (ρ) involving effect sizes for laying date ('LD'), clutch size ('CS') and number of fledglings

335   ('NF'). ε_i is the observation ID deviation for the ith observation, which is assumed to follow a

336   normal distribution with mean zero and variance $\sigma^2_{\varepsilon-LD}, \sigma^2_{\varepsilon-CS}, \sigma^2_{\varepsilon-NF}$ for laying date, clutch size

337   and number of fledglings, respectively. τ_{t-LD}, τ_{t-CS}, and τ_{t-NF} are the deviations from the

338   mean associated with the tth study and trait ('LD', 'CS', or 'NF'), each following a multivariate

339   normal distribution with mean of zero and variance-covariance structure detailed in Equation

340   5 (p provides the correlations between τ_{t-LD}, τ_{t-CS}, and τ_{t-NF}). v_y provides the deviation from

341   the overall mean associated with the yth population (Equation 4). a_l is the phylogenetic effect

342   for the lth species, which follows a normal distribution with mean equal to zero and variance-

343   covariance structure given by σ^2_a, the variance of the phylogenetic effect, and A, a l by l matrix

344   of distances between species calculated from a phylogenetic tree (Equation 5; details above).

345   h_w captures among species variation not explained by the phylogenetic effect and follows a

346   normal distribution around zero and variance σ^2_h (Equation 6).

347

348   We compared models with different constraints in the parameters of the variance-covariance

349   structure in Equation 3 to assess the strength of evidence for heterogeneous variances and

350   correlations among traits (see results in Tables S2 and S4). We fitted these trivariate meta-

351   analytic models in the 'metafor' R package ('*rma.mv*' function; v3.4.0; Viechtbauer 2010) using

352   maximum likelihood and compared models using AIC (Akaike Information Criterion; Burnham

353   et al. 2011). We then calculated a ΔAIC value for each model (i.e., the difference in AIC

354   between a given model and the model with the lowest AIC) and used this value to assess the

355   strength of evidence for a given variance-covariance structure. We fitted models with the

356   following constraints in the variance-covariance structure:

357   (i)   Single variance across traits and zero covariances:

358 $\sigma_{t-LD}^2 = \sigma_{t-CS}^2 = \sigma_{t-NF}^2$; and all $p = 0$

359 (ii) Compound symmetric variance-covariance matrix:

360 $\sigma_{t-LD}^2 = \sigma_{t-CS}^2 = \sigma_{t-NF}^2$; and $p_{LD-CS} = p_{LD-NF} = p_{CS-NF}$

361 (iii) Heteroscedastic compound symmetric variance-covariance matrix:

362 $\sigma_{t-LD}^2, \sigma_{t-CS}^2$ and σ_{t-NF}^2 can vary freely but $p_{LD-CS} = p_{LD-NF} = p_{CS-NF}$

363 (iv) Diagonal variance-covariance matrix:

364 $\sigma_{t-LD}^2, \sigma_{t-CS}^2$ and σ_{t-NF}^2 can vary freely but all $p = 0$

365 (v) Unstructured variance-covariance matrix

366 $\sigma_{t-LD}^2, \sigma_{t-CS}^2, \sigma_{t-NF}^2, p_{LD-CS}, p_{LD-NF}$ and p_{CS-NF} can vary freely

367

368 **Within- and between-breeding season differences in phenology and life-history traits**

369 Urban and non-urban populations may differ in both within- and between-breeding season

370 variation in life-history traits. However, differences in variation for these two temporal scales

371 are likely generated by contrasting ecological and evolutionary processes. To disentangle

372 processes operating at these two temporal scales, we performed additional meta-analyses

373 including i) urban – non-urban comparisons within breeding seasons (k = 363 comparisons

374 from 47 studies in the original dataset with effect sizes per year; Model 5) and ii) urban – non-

375 urban comparisons between breeding seasons (i.e., combining all within-breeding season

376 estimates from a study; k = 36 comparisons present in the original data set, plus 67 additional

377 comparison calculated from within-breeding season estimates; see below). When a given

378 study reported estimates across multiple breeding seasons, we calculated between-breeding

379 season mean and variance as:

380

381 $$\bar{x}_{among-season} = \sum_{i=1}^{g} \bar{x}_i \frac{n_i}{N}; where, N = \sum_{i=1}^{g} n_i \text{ (Equation 7)}$$

382

383 $$S_{among-season}^2 = \sum_{i=1}^{g} \frac{n_i}{N} s_i^2 + \sum_{i=1}^{g} \frac{n_i}{N} \left(\bar{x}_i - \bar{x}_{among-season}\right)^2 \text{ (Equation 8)}$$

384

15

385   Where, $\bar{x}_{among-season}$ and $S^2_{among-season}$ are mean and variance across multiple breeding

386   seasons. g is the total number of breeding seasons reported by a given study; $\bar{x}_i$, s^2_i, n_i, are

387   mean, variance and sample size for each breeding season i. $\bar{x}_{among-season}$ for a given study

388   is, therefore, the weighted average across breeding seasons (Equation 7); whereas

389    $S^2_{among-season}$ for a given study is the weighted sum of within-season variances (first term in

390   Equation 8) and between-season mean variances (second term in Equation 8).

391

392   **Assessing the effect of urbanisation and habitat heterogeneity on differences in**

393   **phenotypic variation between habitats**

394   We investigated the spatial drivers of differences in phenotypic variation between urban and

395   non-urban populations using the subset of studies which allowed the quantification of an urban

396   index in urban and non-urban populations (see above). We first verified that the urban index

397   was indeed higher for urban than for non-urban populations. We compared the urban index in

398   urban and non-urban populations at different spatial scales via linear models, with the

399   difference in urban index between population as the response variable and an intercept term.

400   Then, to assess whether the increase in phenotypic variation in urban habitats was predicted

401   by habitat heterogeneity and/or urban index, we ran an additional meta-regression to explain

402   differences in phenotypic variation between urban and non-urban populations (i.e., lnCVR),

403   where the difference in habitat heterogeneity and urban index between urban and non-urban

404   populations were included as continuous moderators. This meta-regression included 232

405   urban – non-urban comparisons from 11 species and 26 studies (i.e., the subset of

406   observations after 1992 for which geolocations were available).

407

408   **Sensitivity analyses**

409   We assessed the robustness of our results with several complementary analyses. First, we

410   re-ran the trivariate lnRR model (Model 2; Table 1) using Hedges' g (Hedges 1981) with

411   heteroscedastic population variances as the response variable (Table 1; Model 8; i.e., 'SMDH',

16

412   calculated using the R function '*escalc*' in the 'metafor' R package (v3.4.0; Viechtbauer 2010)).

413   In addition, we assessed the robustness of the lnCVR results by re-running the trivariate

414   lnCVR model (Model 4; Table 1) using lnVR as the response variable (i.e., the logarithm of

415   the total variation ration; Nakagawa et al. 2015; Model 9; Table 1). Last, we used an alternative

416   approach that directly models the log of the phenotypic standard deviation (lnSD) to assess

417   differences in phenotypic variation between urban and non-urban populations (Eq. 18 in

418   Nakagawa et al. (2015); Model 10; Table 1). We followed the model specification shown in

419   Senior et al. (2016a), in short:

420

421 $$lnSD_j = \beta_0 + \beta_1 Habitat_j + \beta_2 ln\overline{Mean}_j + \tau_{i[j]} + v_y + a_l + h_w \text{ (Equation 9)}$$

422

423   Where β_0 is the overall intercept, β_1 is the habitat effect on lnSD (i.e., a β_1 statistically different

424   from zero would indicate that urban and non-urban populations differ in their phenotypic

425   variation) and β_2 is the slope of the regression of (log) mean values against (log) standard

426   deviations, which is explicitly modelled. v_y, a_l and h_w are as per Equation 1. $\tau_{i[j]}$ is the random

427   effect for the *j*th effect size in the *i*th study. Within each study effect sizes across habitats are

428   assumed to be correlated; this correlation is calculated by the model (Senior *et al.* 2016a). We

429   applied the model in Equation 9 for each trait independently (i.e., three univariate models, one

430   per trait).

431

432   **Publication bias**

433   We assessed the evidence for the existence of two types of publication biases, small-study

434   and decline effects (time-lag effects), following Nakagawa et al. (2022). For that, we ran four

435   additional uni-moderator multilevel meta-analytic models, two for lnRR and two lnCVR. Each

436   of these models included as a single moderator either the square-root of the inverse of the

437   effective sample size or the mean-centered year of study publication (Trikalinos & Ioannidis

438   2005; Nakagawa *et al.* 2022). The variation explained by these moderators (i.e., $R^2_{marginal}$) was

439   calculated using the R function 'r2_ml' ('orchaRd' R package v.0.0.0.9000; Nakagawa et al.

440   2021).

441

Results

443   After systematically inspecting 1,166 studies published between 1958 and 2020 (Figure S1),

444   our meta-analysis included 399 urban – non-urban comparisons for three bird life-history traits:

445   laying date (k = 151 effect sizes, n = 32 studies), clutch size (k = 119 effect sizes, n = 42

446   studies) and number of fledglings (k = 129 effect sizes, n = 48 studies) (Figure 1). This dataset

447   included 35 bird species, with most studies located in the northern hemisphere (Figure 1c).

448

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

450   We found that urban populations tended to have, on average, 3.6% lower mean values than

451   their non-urban counterparts, but note that the 95% confidence interval (hereafter 'CI') for this

452   estimate overlapped zero (Model 1: lnRR mean estimate [95% CI] = -0.035 [-0.076,0.005];

453   Figure S3; Table S1). Total heterogeneity was high (I^2_{total} = 97.8%), with 17.2% of it explained

454   by phylogenetic and species-specific effects combined ($I^2_{phylogeny}$ = 1.7%; $I^2_{species\ ID}$ = 15.5%),

455   while 8.4% was explained by differences among studies (Table S1). Further analyses

456   calculating urban effects per trait and accounting for potential covariation in the response to

457   urbanisation across the three focal traits (i.e., using a model with an unstructured variance-

458   covariance matrix; see Methods and Table S2) confirmed that urban populations had indeed

459   lower mean values in every life-history trait: urban populations laid their eggs earlier (Model 2:

460   lnRR [95% CI] = -0.048 [-0.084, -0.012]; Figure 2a), laid smaller clutches (Model 2: lnRR [95%

461   CI] = -0.066 [-0.107, -0.025]; Figure 2a), and tended to produce fewer fledglings per clutch

462   than non-urban populations (Model 2: lnRR [95% CI] = -0.070 [-0.171, 0.032]; Figure 2a). This

463   meta-analytic model estimated different random effect intercepts per trait and allowed for

464   correlations across traits (Model 2; see Methods for details). This model revealed correlations

465   in the response to urbanisation across traits: studies reporting earlier laying date in urban

466   populations also reported more similar clutch size and number of fledglings between

467   populations (i.e., negative correlations between lnRR for laying dates and clutch size; Figure

468   3a & 3b). Likewise, studies reporting large differences in clutch size between urban and non-

469   urban populations also reported large differences between both habitats in number of

470   fledglings (Figure 3c; see 'Study ID (correlations)' in Table S3; i.e., correlations among studies

471   in the values of lnRR for each trait).

472

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

474   The coefficient of phenotypic variation in urban populations was, on average, 4.4% higher than

475   in non-urban populations, but note that the 95%CI for this estimate overlapped zero (Model 3:

476   lnCVR mean estimate [95% CI] = 0.043 [-0.092, 0.178]; I^2_{total} = 74.3%; Figure S5 and Table

477   S1). 9.1% of the heterogeneity in lnCVR was explained by phylogenetic and species-specific

478   effects combined ($I^2_{phylogeny}$ = 5.8%; $I^2_{species\ ID}$ = 3.3%), while differences between studies

479   explained no heterogeneity in lnCVR ($I^2_{study\ ID}$ = 0.0%; Table S1). A subsequent model of

480   lnCVR separating urban effects on phenotypic variation per trait and accounting for potential

481   covariation across the three investigated traits in the response to urbanisation (see Methods

482   and Table S4) revealed that the overall effect of urbanisation on life-history trait variation was

483   driven by urban populations having a more variable phenology than their non-urban

484   counterparts (Model 4: lnCVR mean for laying date [95% CI] = 0.176 [0.084, 0.268], i.e., 19.2%

485   more variation, on average, in laying date in urban than non-urban populations). Although the

486   95%CIs overlapped zero, the direction of the average effects for clutch size and number of

487   fledglings also reflected higher phenotypic variation in urban compared to non-urban

488   populations (Model 4: lnCVR mean estimates [95% CI]: clutch size = 0.055 [-0.051, 0.160],

489   number of fledglings = 0.037 [-0.096, 0.171]; Figure 2b). We did not find evidence for

490   correlations in lnCVR between the three life-history traits (Figure 3; the model including

491   correlations among traits scored more than 1.08 AIC points below the top model, which only

492   included independent Study ID random intercepts per trait [Model 4]; Table S4; Table S5).

493

19

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 populations arose from differences in variation within breeding seasons (i.e., intra-annual) rather than between breeding seasons (i.e., inter-annual; Table 2). While laying dates in urban populations were more variable than in non-urban populations within breeding seasons (Model 5: lnCVR mean estimate [95% CI] = 0.177 [0.078, 0.281]; Table 2), a subsequent meta-analytic model isolating effects on phenotypic variation arising from between breeding season fluctuations revealed no difference between urban and non-urban populations (Model 6: lnCVR intercept mean [95% CI] = 0.074 [-0.014, 0.161]; Table 2). 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 lnCVR estimates were very different between these models: the mean lnCVR within breeding seasons was more than 2.4 times larger than the mean lnCVR among breeding seasons (Table 2).

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 populations. First, we confirmed that the urban populations included in our meta-analysis showed higher levels of urbanisation than paired non-urban populations regardless of the spatial scale used (urban index in urban population ± SE = 0.669 ± 0.047; urban index in non-urban population ± SE = 0.021 ± 0.007; 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 as a moderator in a meta-regression 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). Urban and non-

522   urban populations in each studied pair were located at a mean distance of 65.4 km (median =

523   33.1 km; range = [2.4 km, 625.1 km]; n = 26 geo-referenced studies).

524

525   **iv) Sensitivity analyses and assessment of publication bias**

526   In line with our main analysis of lnRR (Table S3), using SMDH as the effect size provided

527   negative estimates (i.e., lower phenotypic means in urban populations) for laying dates (SMDH

528   mean estimate [95% CI] = -0.298 [-0.634, 0.039]), clutch size (SMDH mean estimate [95% CI]

529   = -0.145 [-0.420, 0.130]) and number of fledglings (SMDH mean estimate [95% CI] = -0.022

530   [-0.298, 0.254]) (Model 8 in Table 1). Uncertainty around mean SMDH estimates was high and

531   the 95%Cis overlapped zero. Analysing lnVR instead of lnCVR provided further evidence for

532   increased phenotypic variation in urban populations, particularly for phenology (Model 9 in

533   Table 1): the mean lnVR estimate for laying date was positive and statistically different from

534   zero (lnVR mean estimate for laying date [95% CI] = 0.158 [0.069, 0.247]). As in our lnCVR,

535   lnVR mean estimates for clutch size and number of fledglings were close to zero (lnVR mean

536   estimate for clutch size [95% CI] = -0.012 [-0.110, 0.056]; lnVR mean estimate for number of

537   fledglings [95% CI] = -0.034 [-0.120, 0.052]). Additionally, the arm-based model of lnSD for

538   laying date (Model 10 in Table 1) revealed a positive 'urban' effect on lnSD: urban populations

539   had lnSD values 0.197 higher than non-urban populations (i.e., β_1 in Equation 9; 95%CI =

540   [0.122, 0.272]). Laying date (log) mean phenotypic values were positively correlated with lnSD

541   (i.e., β_2 in Equation 9; estimate [95%CI] = 0.416 [0.068, 0.764]). The arm-based models of

542   clutch size and number of fledglings confirmed correlations between lnMean and lnSD (β_2 in

543   Equation 9 for clutch size, estimate [95%CI] = 0.326 [0.070, 0.582]; for number of fledglings,

544   estimate [95%CI] = 0.231 [0.155, 0.307]), but did not provide evidence for urban effects on

545   phenotypic variation in clutch size or number of fledglings (β_1 in Equation 9 for clutch size,

546   estimate [95%CI] = 0.020 [-0.079, 0.119]; for number of fledglings, estimate [95%CI] = -0.017

547   [-0.099, 0.065]). We did not find evidence of publication bias in lnRR or lnCVR (Supplementary

548   Text C).

21

Discussion

550   We compiled a global dataset of bird life-history traits for paired urban and non-urban

551   populations of the same species to assess how urban living is related to changes in phenotypic

552   means and variation for breeding phenology, reproductive effort, and reproductive success. A

553   phylogenetically controlled multilevel meta-analysis of this dataset confirms a well-

554   documented effect of urbanisation on mean phenotypes: urban bird populations lay earlier and

555   smaller clutches than their non-urban counterparts. This model, however, also reveals

556   correlated responses to urbanisation across life-history traits: e.g., the earlier the laying date

557   in urban populations, the smaller the difference in clutch sizes between habitats. Our study

558   goes a step further than previous meta-analyses in urban ecology by explicitly investigating

559   how urbanisation could impact phenotypic variation. Our findings highlight that urbanisation is

560   associated with both a decrease in mean phenotypes, and an increase phenotypic variation.

561   Investigating the temporal and spatial scale at which urban phenotypic variation increases

562   revealed hints at the ecological causes and evolutionary consequences.

563

564   Urbanisation has been associated with shifts in mean phenotypic values across a many

565   organisms (Alberti *et al.* 2017; Merckx *et al.* 2018; Santangelo *et al.* 2022), including birds,

566   which generally show smaller body sizes and lower life-history trait values in urban habitats

567   (Chamberlain *et al.* 2009; Sepp *et al.* 2018; Thompson *et al.* 2022). Our analyses expand the

568   spatial, temporal and phylogenetic coverage of previous meta-analyses of the avian literature

569   (Chamberlain *et al.* 2009; Sepp *et al.* 2018), and agree on their findings. Our results indicate

570   that urban bird populations lay their eggs earlier and produce smaller clutches, which results

571   in a lower number of surviving nestlings, than their non-urban neighbouring populations. Note,

572   that our analysis indicates a high total heterogeneity in lnRR (I^2_{total} = 97.8%). This finding

573   indicates large variation (e.g., among studies and species) in how urbanisation associates with

574   changes in mean phenotypes and suggests that additional ecological traits (e.g., diet or

575   migratory strategy) may also affect how populations respond to urbanisation. Our results also

22

576   indicate that the mean response to urbanisation is correlated among traits. Interestingly, we

577   found that the earlier the laying dates were in urban *versus* non-urban populations, the smaller

578   the difference in clutch size and in number of surviving nestlings between habitats. Many bird

579   species show a negative phenotypic and genetic correlation between clutch size and lay date

580   (Rowe *et al.* 1994; Sheldon *et al.* 2003; Dunn & Møller 2014), and these two traits are often

581   hypothesized to co-evolve (Garant *et al.* 2008). All else being equal, urban conditions

582   triggering an earlier onset of reproduction (because of e.g., light pollution (Dominoni *et al.*

583   2013) or increased resource availability during winter (Schoech *et al.* 2004)) could indirectly

584   increase clutch size and, therefore, reduce differences in reproductive output between urban

585   and non-urban populations that arise via other mechanisms (e.g., resource limitation in spring;

586   Seress *et al.* 2018, 2020). The extent to which mean phenotypic shifts represent adaptive

587   responses to urbanisation in birds, either via genetic changes or plasticity, or are maladaptive,

588   is mostly unknown (Lambert *et al.* 2020; Branston *et al.* 2021; Caizergues *et al.* 2022;

589   Santangelo *et al.* 2022). Our results, however, highlight that phenotypic shifts in urban

590   populations are widespread and that the response to urbanisation of associated life-history

591   traits should be investigated together.

592

593   Urbanisation has been recently hypothesised to increase phenotypic variation and, indeed,

594   higher variation in morphological traits of urban great tits (*Parus major*) and blue tits (*Cyanistes*

595   *caeruleus*) has been recently reported (Thompson *et al.* 2022). Our findings greatly expand

596   the evidence for this emerging hypothesis showing that urbanisation is overall associated with

597   increases in variation in laying date across many bird species. Previous studies have

598   suggested that city characteristics, such as warmer temperatures in early spring due to the

599   urban heat island effect, could allow birds to lay more clutches per season (Yeh & Price 2004;

600   Schoech *et al.* 2008), with thereby longer breeding seasons and hence higher phenotypic

601   variation in urban laying dates (a similar result has also been reported in Lepidoptera; Merckx

602   *et al.* 2021). This effect, however, does not necessarily explain our results as our meta-

603   analysis only included first clutch laying dates per season. As such, our findings indicate that

23

604 urban bird populations display more variation in the *onset* of reproduction than their non-urban

605 neighbours.

606

607 Higher phenotypic variation in urban than in non-urban populations within breeding seasons

608 could be explained by at least two, non-exclusive, eco-evolutionary mechanisms: differences

609 in the underlying additive genetic variance in laying date, whereby urban birds have a wider

610 range of breeding values for laying date; and / or differences in habitat heterogeneity

611 influencing plasticity in laying date, whereby urban areas have larger environmental variation

612 than non-urban habitats (Shochat *et al.* 2006; Heisler & Brazel 2018; Strubbe *et al.* 2020;

613 Thompson *et al.* 2022). No study to date has investigated whether urban birds show higher

614 additive genetic variance than non-urban populations. However, genetic analyses of European

615 great tits in urban and non-urban habitats generally suggest small differences in the magnitude

616 of genetic variation between habitats (Björklund et al. 2010; Caizergues et al. 2021; Salmón

617 et al. 2021). This is, perhaps, not surprising given the high mobility of birds and the fact that

618 gene flow between urban and non-urban bird populations likely occurs at a large spatial scale

619 (Salmón *et al.* 2021). Interestingly, some studies have reported weaker selection for laying

620 date in urban areas than in non-urban habitats, suggesting relaxed selection on phenology in

621 urban birds (Caizergues *et al.* 2018; Branston *et al.* 2021), which could increase genetic

622 variation in phenology. Assessing differences in phenotypic variation between urban and non-

623 urban populations of less mobile species will be important to evaluate how biological traits

624 (e.g., dispersal ability) determine the evolutionary impact of urban ecological conditions. To

625 this end, previous work in mammal and amphibian species that have a lower dispersal ability

626 than birds suggests a similar level of (genetic) variation between urban and non-urban habitats

627 (Fusco *et al.* 2021; Richardson *et al.* 2021).

628

629 Habitat complexity differs between urban and non-urban habitats (Arnfield 2003; Pickett *et al.*

630 2017). Our analyses indicate that differences in urban *versus* non-urban habitat heterogeneity

631 could indeed help to explain the observed pattern of increased phenotypic variation in urban

24

632   populations. Several ecological mechanisms could mediate this effect. Urban environments

633   are characterised by an array of microhabitats with varying levels of human pressure, exotic

634   plant species and resource availability. Thus, the intensity and timing of the environmental

635   cues that birds use to time their reproduction could vary at a small local scale, increasing

636   phenotypic variation in phenology in the presence of plasticity. The existence of plastic

637   responses to urban habitat heterogeneity, which our results might indicate, do not preclude

638   selection from acting on urban bird populations. First, plasticity is an important mechanism of

639   adaptation, sometimes aligned in direction with adaptative genetic changes (De Lisle *et al.*

640   2022), and indeed is often involved in adaptation to urban environments (Halfwerk *et al.* 2019;

641   Campbell-Staton *et al.* 2021). Second, plastic responses can aid adaptation to urban

642   conditions in the presence of genetic-by-environment interactions by increasing genetic

643   variation available for natural selection (Via & Lande 1985). Addressing which evolutionary

644   mechanisms cause the observed increase in phenotypic variation in urban bird populations is

645   beyond the scope of this study and we acknowledge that these arguments are largely

646   speculative at this point. However, our findings highlight that eco-evolutionary processes could

647   largely differ between urban and non-urban bird populations and generate new avenues for

648   future research in urban ecology and evolution.

649

650   In agreement with our initial predictions, habitat heterogeneity was associated with the

651   magnitude of the difference in phenotypic variation between urban and non-urban bird

652   populations. However, we acknowledge that this analysis has several limitations and that the

653   results require cautious interpretation. First, only a subset of published studies provided

654   coordinates for their urban and non-urban study populations (30 out of 65 published papers).

655   When study site coordinates were provided, only one pair of coordinates per study location

656   was provided, preventing an accurate assessment of the actual area over which a given

657   breeding population was studied. Additionally, it is common in urban eco-evolutionary studies

658   to monitor several populations within one single city. However, in most studies, spatial

659   information was provided at the scale of the whole city (e.g., a single set of coordinates),

25

660   preventing the accurate quantification of habitat heterogeneity for every sub-population within

661   a given urban habitat. These limitations highlight that the ability to perform global meta-

662   analyses on the effects of urban habitat heterogeneity on phenotypic variation would be greatly

663   improved if individual studies in urban ecology provided accurate coordinates of the location

664   of their study populations. Reporting such information would allow future research synthesis

665   to quantify phenotypic variation within urban populations (e.g., across different sub-

666   populations in the same city) and between urban and non-urban populations.

667

668   Taken together, our results show that urbanisation is associated with both a decrease in mean

669   phenotypic values and increasing phenotypic variation in bird populations. Our analyses also

670   highlight a temporal and spatial mechanism that could generate such differences in phenotypic

671   variation between urban and non-urban habitats. We show that urban bird populations have a

672   more variable phenology than non-urban conspecifics within breeding seasons (i.e.,

673   differences in phenology across habitats are seemingly not due to between-year fluctuations)

674   suggesting that the ecological conditions that generate such differences are constant across

675   multiple years. Our coupled spatial analysis indicates habitat heterogeneity and plastic

676   responses as potential eco-evolutionary drivers generating these results. The eco-

677   evolutionary implications of higher phenotypic variation in urban environments will likely vary

678   among species (Thompson *et al.* 2022) and our findings highlight the need for detailed

679   investigation of these consequences. To this end, long-term studies of individually marked

680   organisms in replicated paired urban and non-urban environments could be particularly fruitful

681   to unravel whether differences in phenotypic variation between urban and non-urban

682   populations are caused by differences in underlying genetic variation and/or plastic responses

683   to the urban environment.

684

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695

Competing interests

696

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698

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1093   **Tables**

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1095   **Table 1. Description of meta-models.** Model IDs are given sequentially from 1 to 10 to

1096   facilitate understanding of methods and results. 'Data' refers to whether a given model

1097   contained data for all traits of interest ('All traits') or models were fitted per trait. Moderator

1098   'Trait' is a 3-level factor with levels 'Laying date', 'Clutch size' and 'Number of fledglings'.

1099   'Equations' provide references to the Equations described in the methods section, whereas

1100   'Details' gives a brief description of each model Model ID and references to output tables and

1101   figures.

| Model ID	Response	Data	Moderators	Equations	Details
1	lnRR	All traits	Intercept	-	Overall meta-analysis. Univariate. Table S1. Figure S3.
2	lnRR	All traits	Trait	Equation 1	Effect per trait. Trivariate. Tables S2, S3. Figure 2, 3, S4.
3	lnCVR	All traits	Intercept	-	Overall meta-analysis Univariate. Table S1. Figure S5.
4	lnCVR	All traits	Trait	Equation 1	Effects per trait. Trivariate. Table 2, S4, S5. Figure 2, 3, S4.
5	lnCVR	All traits	Trait	Equation 1	Comparison of intra-annual phenotypic variation. Table 2.
6	lnCVR	All traits	Trait	Equation 1, 7, 8	Comparison of inter-annual phenotypic. Table 2.
7	lnCVR	All traits	Trait + Difference in urbanisation + Difference in habitat heterogeneity	Equation 1 (with additional moderators)	Trivariate. Fitted for different spatial scales. Figure 4.
8	SDHM	All traits	Trait	Equation 1	Similar structure as Model 2.
9	lnVR	All traits	Trait	Equation 1	Similar structure as Model 4.
10	lnSD	Each trait individually	Intercept + Habitat + lnMean	Equation 9	Armed-based model (Senior *et al*. 2016a).

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Table 2. 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 ('intra-annual') and among ('inter-annual') 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. See Table 1 for a description of model IDs.

Temporal scale	lnCVR estimate [95% CI]			k
	Laying date	**Clutch size**	**Number of fledglings**	
Overall [Model 4]	*0.176* *[0.084, 0.268]*	0.055 [-0.051, 0.160]	0.037 [-0.096, 0.171]	399
Intra-annual [Model 5]	*0.177* *[0.078, 0.282]*	0.015 [-0.122, 0.152]	0.116 [-0.059, 0.291]	363
Inter-annual [Model 6]	0.074 [-0.014, 0.161]	0.096 [-0.019, 0.211]	-0.006 [-0.147, 0.135]	103
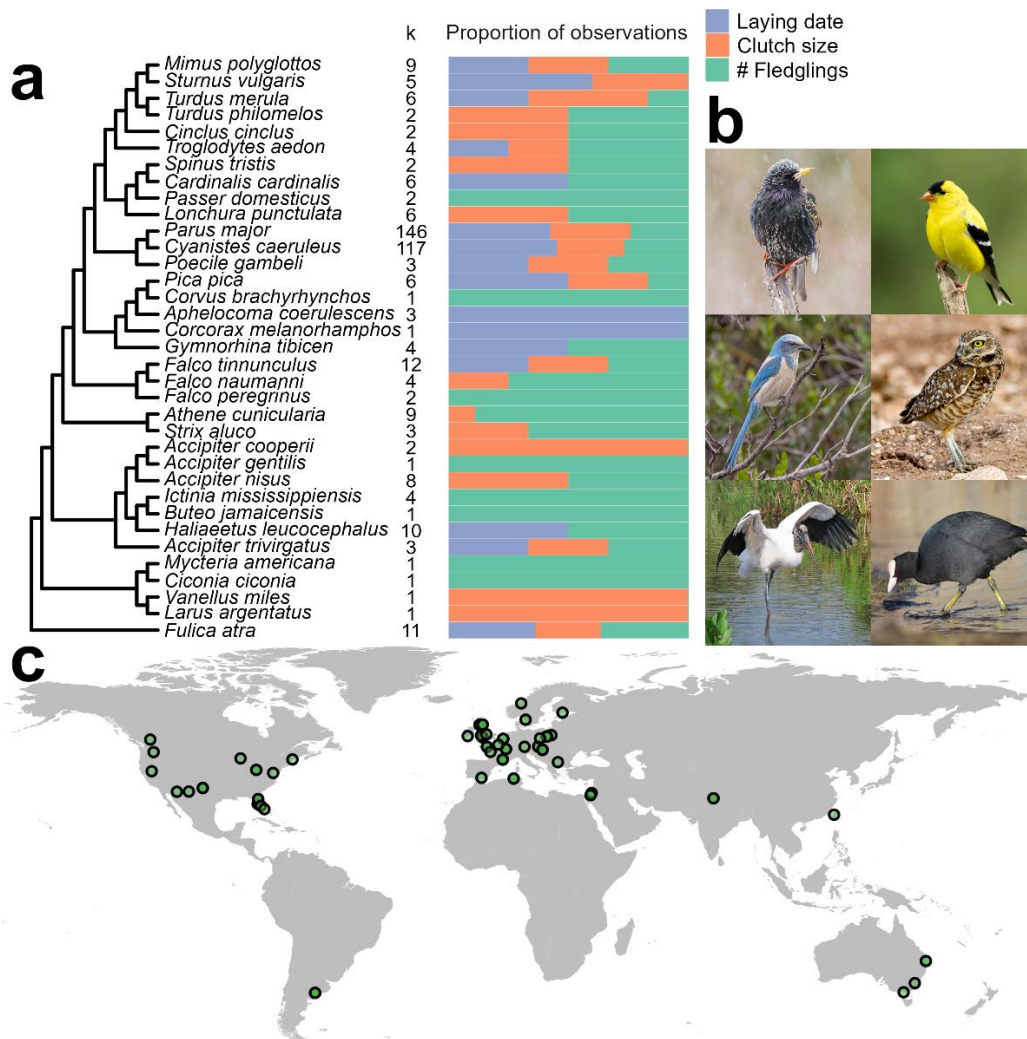
Figures

Figure 1. Phylogenetic and geographical breadth of the meta-analytic data. (a) Phylogenetic tree of the 35 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*, *Athene cunicularia*, *Mycteria americana* 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, Jennifer Soos, Susan Young 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.
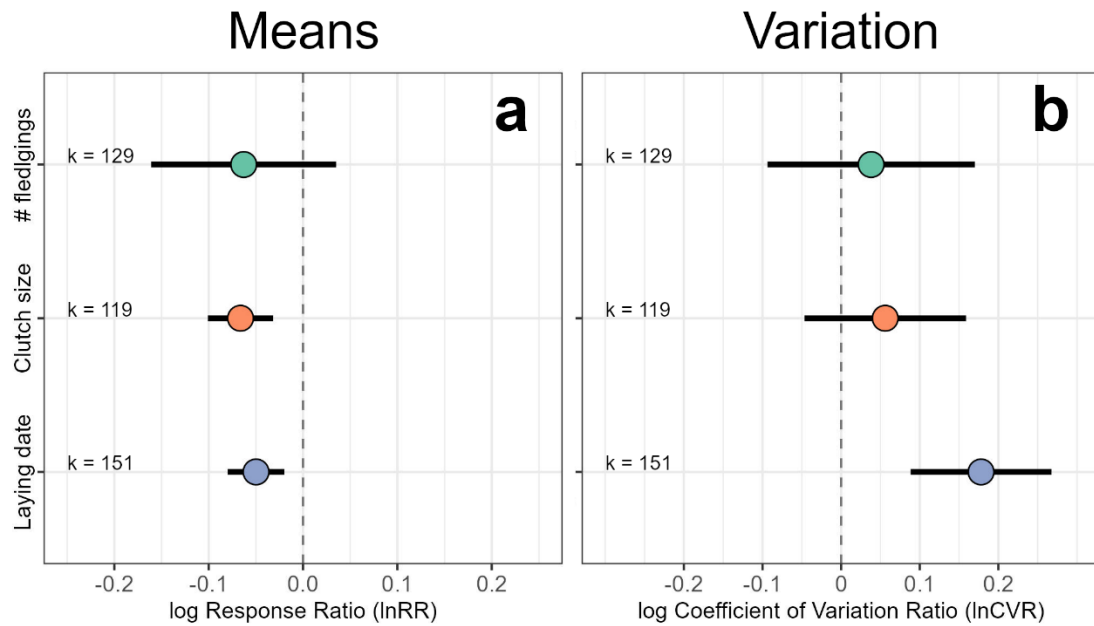
Figure 2. Urban populations have earlier phenology, lower reproductive output and more variable life-history traits than non-urban populations. (**a**) Urban populations laid earlier and had smaller clutches, producing fewer fledglings, than their paired non-urban populations (illustrated by negative lnRR estimates; Model 2). (**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 populations in laying date (illustrated by positive estimates of lnCVR; Model 4). Model estimates for (**a**) lnRR and (**b**) lnCVR are shown along with their 95% confidence intervals per trait as calculated by our phylogenetic multilevel meta-analytic models accounting for correlated responses to urbanisation among traits (see Table S3 & Table S5 for full model outputs and Figure S3 and S5 for overall meta-analyses of lnRR and lnCVR). Raw data and model estimates are presented in Figure S4. 'k' provides the number of urban – non-urban comparisons.

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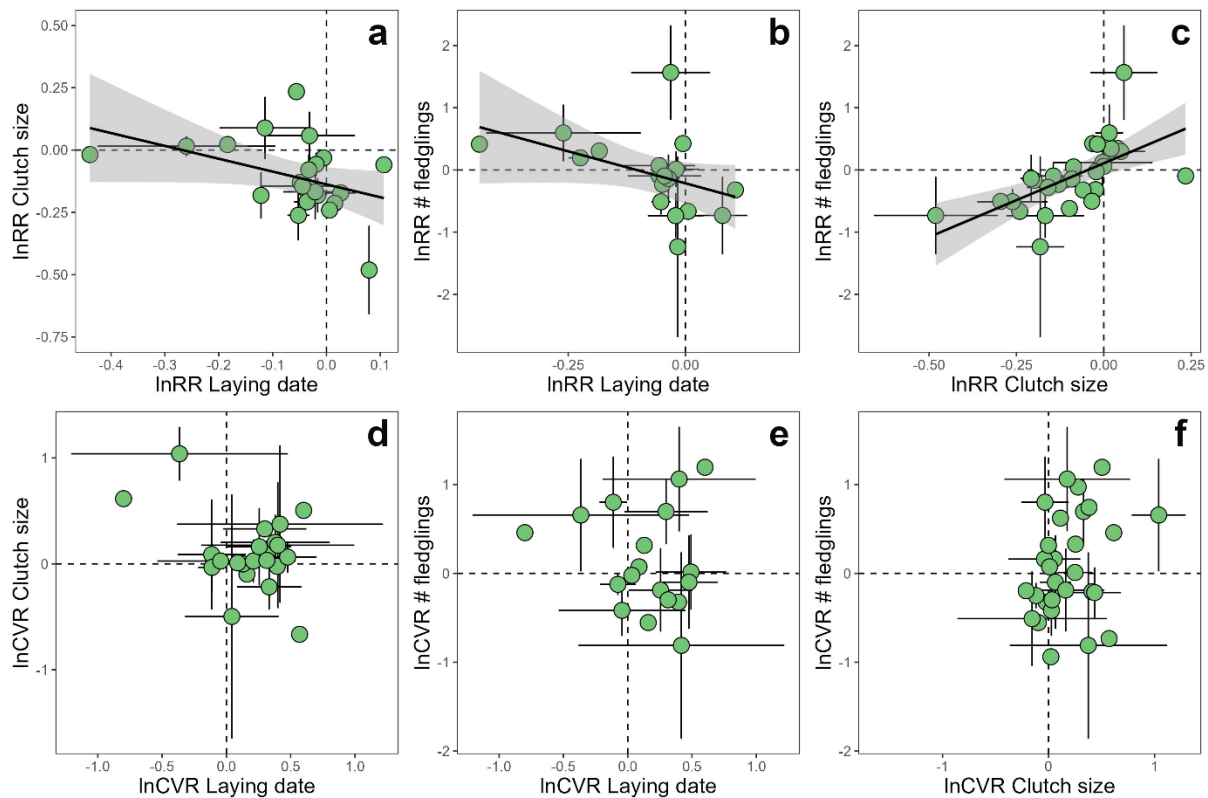
**Figure 3. Life-history traits show a correlated response to urbanisation.** Our meta-analysis investigated correlated responses to urbanisation across the three studied life-history traits, and revealed strong correlations in log response ratio (lnRR) but not log coefficient of variation ratio (lnCVR). (**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), leading to a negative correlation between lnRR for these two traits. (**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; Table S3; Model 2). (**d** - **f**) We found no strong statistical evidence for models including correlations across traits in how urbanisation affected phenotypic variation (Table S4, 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 raw 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 (Model 2; Table S3).
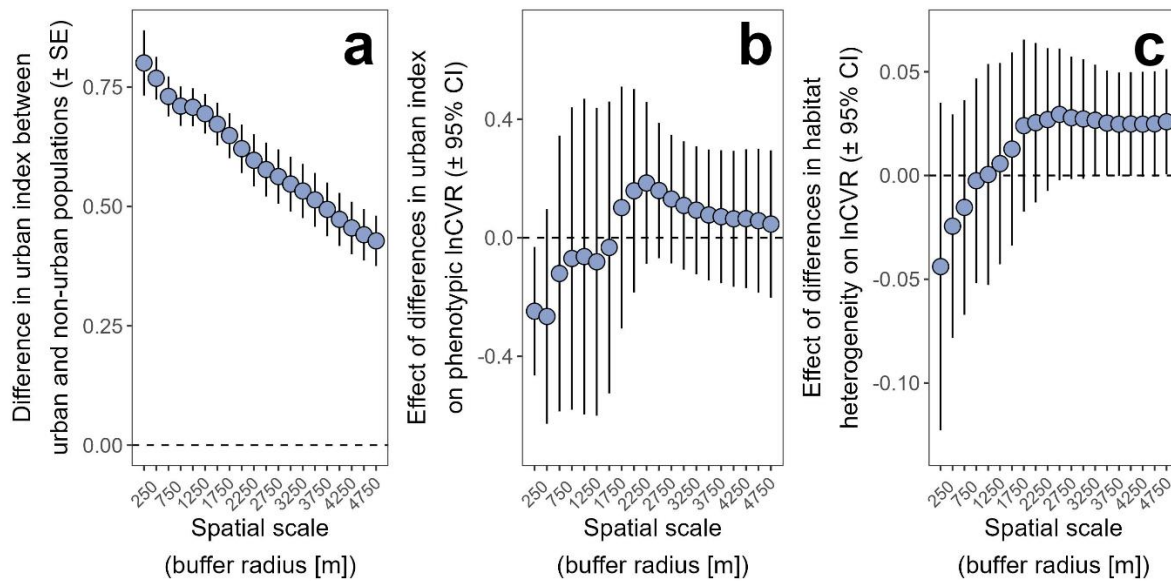
Figure 4. Effects of habitat heterogeneity on the difference in phenotypic variation between urban and non-urban bird populations (i.e., lnCVR). (**a**) After quantifying urban index and habitat heterogeneity, we verified that urban populations had higher urban index (i.e., the proportion of landcover at a given spatial scale categorised as 'urban' [see methods]). The y axis represents the difference in urban index between urban and non-urban populations. The positive values observed for all comparisons represent that urban populations had 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. 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. 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.

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