Phenotypic flexibility in the city: A meta-analysis on variation

Authors: Jules Petit[1,2,#], Melanie Dammhahn[1,2]

Affiliations:

[1]Department of Behavioural Biology, University of Münster

[2]Joint Institute for Individualisation in a Changing Environment (JICE), University of Münster and Bielefeld University

[#] Corresponding author: jules.petit1@outlook.com (JP)

ORCID: Jules Petit (0009-0008-4061-8346); Melanie Dammhahn (0000-0003-0557-740X)

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Abstract

Among global changes urbanisation is distinctive because it entangles a variety of human-induced rapid environmental changes, such as habitat loss and fragmentation, temperature change, introduction of human food sources, and pollution. Urban environments are assumed to be heterogeneous and variable in space and time. A key feature of animals coping with high environmental variability ought to be phenotypic flexibility, i.e. the capacity of individuals to express reversible variation in labile traits. However, this “phenotypic flexibility hypothesis” has not been tested rigorously. Using a meta-analysis approach, we compiled available raw data of studies directly comparing urban and non-urban populations and estimated fixed and reversible individual variation. Across all taxa, fixed variation did not differ between non-urban and urban populations, although patterns emerged without birds. Reversible variation was marginally lower in urban populations compared to non-urban ones. The potential decrease of phenotypic flexibility in urban individuals could result from different responses of individual plasticity and predictability. Overall, the effects of urbanisation on phenotypic variation are not as generalisable as expected and may depend on the taxa, species and traits. Future studies should increase efforts to directly link temporal and spatial environmental variation at the individual level with individual plasticity and predictability responses.

Keywords: phenotypic plasticity, individual variation, fixed variation, reversible variation, phenotypic flexibility, urbanisation, environmental heterogeneity, meta-analysis

Introduction

Among global changes urbanisation is one particular and fascinating process to study as it reconstructs several human-induced rapid environmental changes (HIREC) within a single environment. Indeed, urbanisation engenders habitat changes via habitat loss and/or fragmentation, induces pollution of different sorts (e.g. light, air, sound), and creates local warming effects through heat islands (Sih *et al.* 2011). Together these environmental alterations generate a dynamic and complex system making cities a major multi-level selection agent (Szulkin *et al.* 2020). As cities are constantly expanding throughout the world at an unprecedent rate and strongly affect wildlife it is crucial to understand what facilitates and constrains individual's adjustment to urban environments. Many studies already reported shifts in average phenotypic responses between urban and non-urban populations in various phenotypic traits. For example, in behaviour, species thriving in cities are bolder, more exploratory and more active (Burkhard *et al.* 2024; for other traits see Capilla-Lasheras *et al.* 2022; Iglesias-Carrasco *et al.* 2020; O'Donnell & delBarco-Trillo 2020; Putman & Tippie 2020). Those changes can be driven by local adaptation (i.e. selection of the individuals) but since environmental modifications in the city happen at large scales and often faster pace than evolution it is most likely that high phenotypic plasticity (i.e. individuals' phenotypic adjustment) is also fundamental for city dwellers to be successful (Hendry *et al.* 2008).

In this context of rapidly fluctuating environments, urban individuals will tend to face higher number of different environments within their lifetime compared to non-urban individuals. Individuals predisposed to show a larger range of phenotypic responses will be advantaged compared to individuals with a narrower range of responses. This range of reversible phenotypic transformation an individual expresses defines its phenotypic flexibility, one form of phenotypic plasticity (Piersma & Drent 2003). It should not be mistaken with the term behavioural flexibility used in cognitive studies for individuals' learning or innovative abilities (Audet & Lefebvre 2017; Sol *et al.* 2002). Phenotypic flexibility is the key mechanism to understand species adaptation to urban life (Kark *et al.* 2007; Lowry *et al.* 2013; Sih *et al.* 2011). The phenotypic flexibility hypothesis stipulates that phenotypic flexibility should increase when individuals live under high fluctuating conditions compared to conspecifics living under low fluctuating conditions (Fox *et al.* 2019; March-Salas *et al.* 2021; Matesanz *et al.* 2010; Nicotra *et al.* 2010; Pigliucci *et al.* 1996; Valladares *et al.* 2014). The high environmental dynamism present in the city often label urban habitats as more heterogenous environments when compared to natural ones (although a consensus is difficult to reach, see Thompson *et al.* 2022). Urban habitats typically show stark spatial heterogeneity with high variation regarding the type and densities of buildings, or the presence of remnant and natural areas over short distances (Cadenasso *et al.* 2007; Pickett *et al.* 2001). Cities are also characterised by high spatial and temporal temperature fluctuations, especially in their centres, due to less greenery boosting the urban heat island effect (Soltani & Sharifi 2017). Lastly, the availability of anthropogenic food sources is subject to higher fluctuation at a short temporal scale compared to natural food sources (Stofberg *et al.* 2019). Overall, the high environmental heterogeneity in urban environments is expected to increase the phenotypic flexibility of urban individuals in contrast to non-urban conspecifics. Surprisingly, only one study investigated such phenomena. Gervais *et al.* (2025) found that higher spatial heterogeneity (i.e. variance in impervious area) was surprisingly not associated with greater phenotypic flexibility for breath rate and exploration in a passerine bird species. Yet, even studies comparing solely phenotypic flexibility between urban and non-urban populations are scarce and produced mixed results reducing our abilities to understand the biological importance of reversible variation in the context of urbanisation (but see Dammhahn *et al.* 2020; Gervais *et al.* 2025).

Urban environmental heterogeneity is not only expected to affect within-individual phenotypic responses but also between-individual differences. As mention above, the multi-environmental axis of human disturbances present in the city creates an urban filter selecting specific individuals and reducing the number of urban living species (Piano *et al.* 2017). These strong selective processes are most likely reducing interspecific competition in species communities in the cities. Therefore, according to niche theory, a reduction of competition is expected to shape phenotypic variation by decreasing between-individual differences in the city as individuals do not need to specialise for specific resources to increase fitness (Svanbäck & Bolnick 2005). This change of the fixed individual variation has the potential to damper the abilities of populations to cope with future environmental conditions when individuals in a population show high phenotypic homogenisation (Bolnick *et al.* 2011; Forsman & Wennersten 2016). However, we still do not know whether fixed individual variation, like reversible variation, is constrained by urbanisation (but see Gervais *et al.* 2025 for one example).

Reversible and fixed individual variation can be estimated via variance decomposition, as commonly used in quantitative genetics or animal personality to estimate heritability or repeatability respectively (Falconer & Mackay 1996; Nakagawa & Schielzeth 2010; Réale *et al.* 2007). In short, it allows to estimate within-individual (reversible) and between-individual (fixed) variation for a trait of interest. Disentangling both variation components is a necessary and crucial step to understand their specific eco-evolutionary consequences in the context of urbanisation and explain how species adapt to urban life. Reversible variation informs us about an organism's fast adjustments, which are key to cope with rapid environmental changes, often so rapid that genetic changes are lagging (Hendry *et al.* 2008). Fixed variation arises from genetic or permanent environmental effects and is indicative of local adaptation and selective processes (Dingemanse & Wolf 2013; Lynch & Walsh 1998; Wilson *et al.* 2010). Although variance partitioning offers a unique opportunity to test the phenotypic flexibility hypothesis and isolate a fixed marker of selective processes under urbanisation, most urban ecology meta-analyses summarized results regarding mean or total phenotypic variation change, thus lumping together both between- and within-individual variation (morphology: Putman & Tippie 2020; Thompson *et al.* 2022, life-history: Capilla-Lasheras *et al.* 2022, behaviour: Burkhard *et al.* 2024, physiology: Iglesias-Carrasco *et al.* 2020). Hence, there is an evident gap in evidence synthesis to understand how urbanisation affect fixed and, most importantly, reversible phenotypic variation.

Using a combined approach of data re-analysis follow by a formal meta-analysis, we aim to test the predictions of the phenotypic flexibility and the phenotypic homogenisation hypotheses. We first summarised studies that have repeated individual measurements for both urban and non-urban populations for labile traits (i.e., behaviour, physiology, life-history, and morphology) and quantified within- and between-individual variation by performing variance decomposition on all available datasets. We tested whether habitat type (urban versus non-urban) explained differences for each phenotypic variance component. Specifically, we tested two predictions (i) within-individual variation is higher in urban compared to non-urban populations (i.e. indicating higher phenotypic flexibility) and (ii) between-individual variation is lower in urban compared to non-urban populations (i.e. indicating individual homogenisation). In addition, we tried to refine our estimates of 'true' within individual variation (individual predictability) by fitting population reaction norms in function of time (i.e. trial number) and sex as suggested by Stamps *et al.* (2012).

Materials and Methods

Literature review: Scoping and search term development

We first identified few studies fitting the two main requirements for the meta-analysis (e.g. urban versus non-urban populations comparisons, repeated measurement for labile traits). Using Google Scholar and the bibliography in these papers, we found thirteen suitable papers (Text S1). Based on these papers, we established a first keyword query (*Query 1*).

Query 1:

All Fields =“phenotypic plasticity” OR repeata OR consistenc*, “inter-individual” or flexibilit* or “individual plasticity” or “animal personality”) AND Topic = (urban* or rural*)*

Using *Query 1* in Web of Science with specific categories (Text S2), we extracted 2,864 papers (13.12.2022) and recovered all papers mentioned above except Møller & Tryjanowski (2014). In addition, we assessed the suitability of *Query 1* to yield relevant papers. We sorted the papers by author’s name and screened 1,000 papers using five categories: paper with non-wild animals, paper without repeated measurements, paper with urban or non-urban populations, paper with urban and non-urban populations, and paper of unknown category due to lack of methodological detail. From this categorisation, the hit rate was at 3.5%. To improve it and facilitate the screening process, exclusion keywords were added to the search. We made two groups: i) papers which were highly irrelevant using the strong exclusion criteria ‘paper with non-wild animals’ (n = 767) and, ii) papers which were highly relevant ‘paper with wild animals, studying urban or non-urban populations, and with repeated measurements for labile traits’ (n = 35).

For each group, we calculated the frequencies of the words used in the title and abstract separately using *R* packages *wordcloud* (Fellows 2018) and *wordcloud2* (Lang & Chien 2018). Six words were used repeatedly in the irrelevant paper group and never used in the relevant paper group (e.g., planning, water management, emission, policy, carbon, and child). We added them in the query as exclusion words. We also added important missing keywords such as “intra-individual”, “repeated disturbance”, “repeated exposure”, and “repeated trial”. We did not use “repeat*” because it added many irrelevant articles. Based on these refinements *Query 2* was developed.

Query 2:

TOPIC = "phenotypic plasticity" or repeata or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*" AND ABSTRACT = urban* or rural* NOT ABSTRACT = "planning" or "water management" or emission* or polic* or carbon* or child**

Query 2 yielded 1,509 papers in Web of Science with specific categories (Text S3) and retrieved the twelve original papers from the Google Scholar search (Møller & Tryjanowski 2014 was still missing) as well as the 35 papers from the 1,000 papers screening. Thus, Query 2 was more specific and effective to find relevant papers and was used for the literature search.

Literature review: The search

We performed the literature search in five databases (Web of Sciences collection, Scopus, ProQuest, EBSCOhost Open Dissertations, and OpenGrey) on the 10th of March 2023. The details of the search term used for each database can be found in Table S1. In total, we found 4,322 papers. We removed 1,150 duplicates using the software *Ryan* (Ouzzani *et al.* 2016) and double checked with a conservative string match script in *R* (v.4.4.0; R Core Team 2022) resulting in 3,172 papers. We performed three screening phases resulting in 113 papers. The first screening excluded all studies on humans, plants, domesticated or zoo animals, discarding 2,626 studies. The second and third screening excluded studies that did not have repeated measurements of labile traits for both urban and non-urban populations, discarding 409 and 25 studies respectively. The number of papers excluded for each screening phase is explained in Figure S1.

Dataset collection

To assess whether phenotypic flexibility (i.e. within-individual variation) differs between urban and non-urban populations, variance partitioning needed to be performed (for details see '*Variance partitioning*'). None of the 113 papers did the adequate partitioning as most studies were not focusing on phenotypic flexibility. Therefore, raw data was extracted if made open access or authors were contacted to obtain raw data or asked to run a specific *R*-script (Text S4 for contact procedure). After the final contacting phase and a deep data check, we collected data from 33 studies. Initially, the meta-dataset contained 111 paired urban–non-urban estimates from 23 species.

Data categorisation

Labile traits are defined as traits with the capacity to be reversibly expressed (Brommer 2013; Westneat *et al*. 2015). For behavioural, physiological, cognitive, and life history traits, we assumed an overall presence of reversible variation (i.e. phenotypic flexibility). However, morphological traits can be labile, such as body mass, or not, such as tarsus length in birds, which grows continuously without reversible change. We excluded all morphological traits that were not labile. To standardised across studies, we relabelled traits following functional definitions coming from key papers (Table S2).

The level of urbanisation can be assessed in multiple ways (Szulkin *et al*. 2020) and cities encompasses various types of habitats. To facilitate comparisons, we followed the classification into urban and non-urban habitats by the authors of the original studies. Urban habitats were referred as "urban", "stable urban", "dynamic urban", "city", "urban zone", and "suburban". Non-urban habitats were referred as "forest", "rural", "extra-urban", "pond", "crops", "country", "woodland", "agricultural", "lake", and "artificial reservoir". Although environmental heterogeneity exists within urban and non-urban habitats, we assume that within-habitat variation is smaller than between-habitat variation as all studies had clear macro-environmental changes associated with urban and non-urban areas (e.g. human presence, percentage of imperviousness).

Measurement intervals can affect repeatability estimates via temporal bias of phenotypic variation assessment. Short-interval measurements produce higher repeatability estimates than long-interval measurements (Araya-Ajoy *et al*. 2015; Bell *et al*. 2009). Particularly, high repeatability can occur when individuals are measured under different environmental conditions over a short period of time (e.g. low versus high predation risk; Araya-Ajoy *et al*. 2015, Dingemanse & Dochtermann 2013 for the pseudo-repeatability). Therefore, we classified measurement intervals for each trait into six categories (minute, day, hour, week, month, and year) based on the shortest interval. For example, if 3 tests were performed within 4 h over 7 days, we classified it as 'hour' interval.

The biological meaning of different measurement intervals depends on the species lifespan. Therefore, we created four temporal categories (very-short, short, medium, long) relating the measurement interval to one round of a breeding season. To illustrate for a bird species, repetitions made across two years (≥ two breeding seasons) would be considered a long interval. Repetitions made between the first and the second half of one breeding season would be considered medium whereas repetitions within a shorter period within one breeding season (e.g. one week) would be considered short. Repetitions over consecutive days would be considered very short.

Development (e.g. age class) can strongly affect phenotypic variation within a population (Sears 2014). To standardise comparisons and consider this potential effect, we subsetted datasets that had both, juvenile and adult, age classes. The category juvenile included age classes such as 'juvenile', 'larvae', 'chicks' or 'pupae'. The category adult included the age class named 'adult'.

Variance partitioning

The two main objectives of the meta-analysis were to assess whether within- and between-individual variation change under urbanisation. For all traits, we partitioned the variance using linear mixed effects models (LMMs) to estimate both variance components. All models were run on continuous or count data using Gaussian error distribution to facilitate the comparison between the estimates. It is accepted that count data can be analysed using Gaussian error distribution as estimates remain unbiased although residual heterogeneity might occur (Schielzeth *et al.* 2020; Zuur *et al.* 2009). Therefore, we verified homogeneity of residuals for all our models via the function *check_model()* from the *performance* package (Lüdecke *et al.* 2021). Based on model validation, we ensured that models estimated properly the overall total phenotypic variation and the mean (Text S5). We would like to stress that, here, models are used solely as a tool to calculate descriptive statistics such as overall average, inter-group variance (e.g. individual identity) and inter-observation variance (e.g. residuals). We did not perform any model selection as the only goal of these models was to estimate the variance. We used only untransformed data and excluded composite variables from PCAs because we were interested to estimate the raw amount of variance change. Any transformation could change the relationships among variances (Emerson 1991). Fitting count data in Gaussian statistic without transformation maintains the variance-mean relationship which we resolved by using logarithm coefficient variance ratio (lnCVR) estimates in the meta-analysis (see below 'Meta-analytic effect size'), as suggested by Senior *et al.* (2020).

The variance partitioning was based on the following steps. First, we ran 'intercept-only' LMMs (IO-LMM) with individual identity as random intercept. Second, we ran 'adjusted' LMMs (AD-LMM) with trial number and sex (if available) as fixed factors as well as other fixed factors when the authors mentioned that they improved the model fit significantly. IO-LMMs were used to perform basic variance partitioning and verify that the mean estimation from the LMMs were aligned with the classical mean estimation approach (Text S5). IO-LMMs were also used for sensitivity analyses AD-LMMs were used to control for variation arising from experimental or natural causes (De Villemereuil *et al.* 2018). AD-LMMs compute more ecologically accurate variance partitioning which we used for the effect size in the main meta-analytic models. We did not include interactions, quadratic effects and more than three fixed effects as their variance estimation becomes difficult using a frequentist approach. For both model types, Maximum Likelihood method was used to estimate all variance components simultaneously making variance estimates more comparable between models (by avoiding differential variance estimations when fixed factors are included) and targeting better the true variance parameter value (Bryk & Raudenbush 1992; Searle *et al.* 1992). In all models, between-individual variation was approximated via the variance hold by the variable "ID_individual" (i.e. between-individual variance). Within-individual variation was approximated using the residual variance (i.e. within-individual variance). Usually, in meta-analysis, authors extract estimates based on descriptive statistics rather than using a variance partitioning approach. Therefore, we also extracted the mean and total variance with the basic function "mean()" and "var()" in *R* (v.4.4.0; R Core Team 2022) for each urban and non-urban dataset separately. We checked that the mean and total variance estimates from our models did not deviate > 5% compared to the basic estimation method (Text S5). We considered that 5% deviation is an adequate threshold to validate how the models accomplish a solid estimation. After excluding observations with inappropriate deviation (Table S3), on average for the IO-LMM, the overall ‘mean’ divergence was 0.46% with a maximum positive divergence of 4.20% and a maximum negative divergence of 4.89%. The overall ‘variance’ divergence was 2.08% with a maximum positive divergence of 3.82% and a maximum negative divergence of 5.36%. For the AD-LMM, the overall ‘variance’ divergence was -1.36% with a maximum positive divergence of 5.87% and a maximum negative divergence of 5.81%. We did not calculate the divergence for the ‘mean’ since the inclusion of fixed factors deviated the model intercept from the ‘true’ mean.

Meta-analytic effect size

For all variance estimates that were validated, we calculated the log coefficient of variation ratio (lnCVR) to investigate differences in the variability between urban and non-urban populations (Nakagawa *et al.* 2015; Senior *et al.* 2020). Mean and variance values are often positively associated (e.g. Taylor’s Law; Cohen & Xu 2015). Therefore, we chose lnCVR over lnVR as we did not mitigate the mean-variance relationship using log-transformation on the count data. We calculated lnCVR for between- and within-individual variation separately for both IO-LMMs and AD-LMMs with their associated sampling variance. To do so, we used the variance components, ID_individual and residuals, from the LMMs and the intercept from the basic *R* function *mean()* in R (v.4.4.0; R Core Team, 2022). We used the script from Nakagawa *et al.* (2015) as the package metafor (v.4.6-0; Viechtbauer 2010) do not apply the mean-variance relationship correction for lnCVR sampling variance. Positive lnCVR values meant higher estimates for urban populations compared to non-urban ones. Although our variance components were estimated with repeated measurements, we used the original sample size of the study for the calculation of the lnCVR to follow the most conservative approach. Using two sample size variants weighted for the number of repeated measurement did not change our findings (analyses not reported).

Final dataset

In total, 33 and 27 paired urban–non-urban estimates were discarded for IO-LMMs and AD-LMMs respectively due to poor model fit or inability to calculate lnCVR (Text S5 for procedure and Table S3, Table S4 for summary of the deletion).

The final meta-dataset – comprising IO- and AD-LMMs together – included 89 paired urban–non-urban estimates from 22 species and 31 studies (Figure 1; Bar-Ziv *et al.* 2023; Batabyal *et al.* 2017; Batabyal & Thaker 2019; Biondi *et al.* 2022; Dominoni *et al.* 2020, 2015; Garitano-Zavala *et al.* 2022; Hardman & Dalesman 2018; Harten *et al.* 2021; Heppner *et al.* 2023; Huang *et al.* 2020; Jakubas *et al.* 2020; Kaiser *et al.* 2018, 2019, 2020; Kozlovsky *et al.* 2017; Mazza *et al.* 2020; Mazza & Guenther 2021; Ouyang *et al.* 2019; Papp *et al.* 2015; Prasher *et al.* 2019; Smit *et al.* 2024; Solaro & Sarasola 2019; Stansell *et al.* 2022; Tabh *et al.* 2022; Thompson *et al.* 2018; Tüzün *et al.* 2017; Vardi & Berger-Tal 2022; Vincze *et al.* 2016; J. Petit & M. Dammhahn, unpublished data; R. Rimbach & M. Dammhahn, unpublished data). Of these 89 comparisons, 61 corresponded to comparisons of behavioural traits (20 studies), 12 were comparisons of cognitive traits (7 studies), 5 were comparisons of physiological traits (4 studies), 11 were comparisons of morphological traits (9 studies). Last, within the 61 behavioural traits, 15 corresponded to comparisons of boldness (11 studies), 32 corresponded to comparisons of activity/exploration (11 studies), 8 corresponded to comparisons of aggression (3 studies), 1 corresponded to neophilia (1 study), 3 corresponded to neophobia (3 studies) and 2 corresponded to foraging (2 studies). For IO-LMMs only, the dataset included 78 paired urban–non-urban estimates from 20 species and 27 studies. Of these 78 comparisons, 56 corresponded to comparisons of behavioural trait (20 studies), 10 corresponded to cognitive traits (7 studies), 3 were comparisons of physiological trait (2 studies), 9 were comparisons of morphological traits (7 studies). Last, within the 56 behavioural traits, 15 corresponded to comparisons of boldness (11 studies), 28 corresponded to comparisons of activity/exploration (11 studies), 8 corresponded to comparisons of aggression (3 studies), 1 corresponded to neophilia (1 study), 2 corresponded to neophobia (2 studies), and 2 corresponded to foraging (2 studies). For AD-LMMs only, the dataset included 84 paired urban–non-urban estimates from 21 species and 29 studies (list reference here). Of these 84 comparisons, 58 corresponded to comparisons of behavioural trait (19 studies), 10 were comparisons of cognitive trait (6 studies), 11 were comparisons of morphological traits (9 studies) and 5 were comparisons of physiological trait (4 studies). Last, within the 58 behavioural traits, 31 corresponded to comparisons of activity/exploration (10 studies), 8 corresponded to comparisons of aggression (3 studies) and 13 corresponded to comparisons of boldness (10 studies), 1 corresponded to neophilia (1 study), 3 corresponded to neophobia (3 studies), and 2 corresponded to foraging (2 studies).

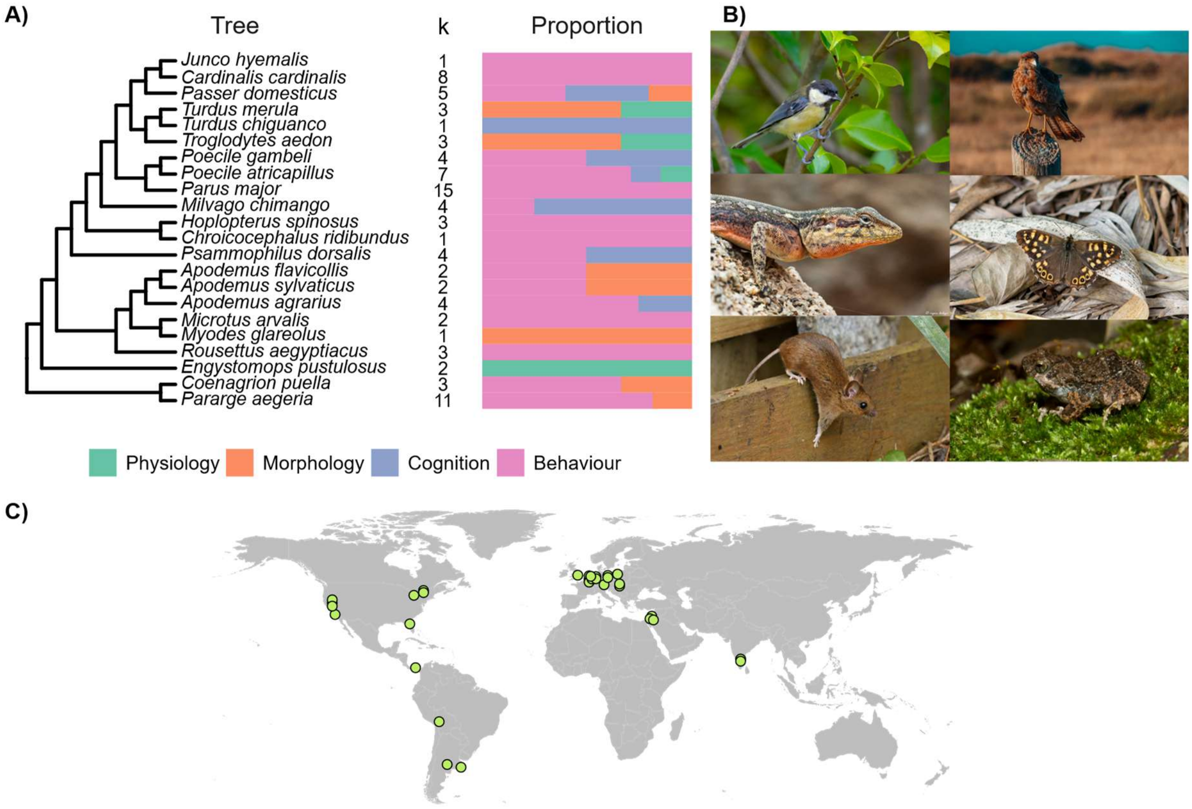

Figure 1. Phylogenetic and geographical portrayal of the meta-analysis data set. A) Phylogenetic tree of the 22 species included in the meta-analysis with the number of effect sizes (k = urban–non-urban comparisons) included per species (the numbers may vary if IO-LMMs or AD-LMMs are meta-analysed, see 'Final dataset') and the proportion of comparisons for each phenotypic trait type. B) Pictures of species included in the meta-analysis representing the five major taxa. Left to right from top to bottom: *Parus major*, *Milvago chimango*, *Psammophilus dorsali*, *Pararge aegeria*, *Apodemus sylvaticus*, and *Engystomops pustulosus*. All images were extracted from www.flickr.com (Authors: Nicolas Venner, Gonzalo Arias, Vipin Baliga, Nicolas Venner, Tim Worfolk, Brian Gratwicke) in accord with their copyright (Text S6). C) Global map (excluding Antarctica) showing the location of each study included in the meta-analysis. Each point represents the urban location of the urban–non-urban pair.

Phylogenies

We used the Open Tree of life (Hinchliff *et al.* 2015; Rees & Cranston 2017) and the interface provided by the *R* package *rotl* (v.3.1.0; Michonneau *et al.* 2016; OpenTreeOfLife *et al.* 2019) to calculate the phylogenetic trees. We estimated tree branch length using Grafen's method (Grafen 1989) and generated a phylogenetic correlation matrix to include in all our multilevel meta-analytic models. We assessed the phylogenetic signal based on the proportion of variation explained by phylogeny (Cinar *et al.* 2022).

Meta-analysis

We evaluated the effect of urbanisation on phenotypic flexibility of labile traits running phylogenetic multilevel (intercept-only) meta-analysis for each response term (Model 1 and Model 3, Table 1). We also fitted models that separate labile traits into four principal trait types: behaviour, physiology, morphology, and cognition (Model 2 and Model 4, Table 1). One recent study found that different phenotypic traits might show different change across the variance partition (Gervais *et al.* 2025). Thus, we ran a model exclusively on behavioural traits since it had an appropriate sample size for the category boldness, aggression, and activity/exploration (Model 5, Table 1). Since a large part of heterogeneity was still unexplained among our effect size, we tested whether the relationship of the meta-phenotypic traits and urbanisation differed among *a priori* selected moderators. We fitted a 'full' model that included each of the following predictors: taxa, category for test interval in relation to lifespan, provenance of data (whether wild animals are measured in the wild, in the lab, or both), and the number of random and fixed factors used in the LMM to partition the variance (Model 6 and Model 7, Table 1)

All meta-analytic models estimated four random intercept effects, publication identity (i.e. among-study variation), phylogeny (see 'phylogenies' section), species identity (i.e. among-species variation not explained by phylogeny), and an observation ID term (residuals). All models were fitted assuming compound symmetry variance structure. For all models, we estimated total heterogeneity (I^2) following Nakagawa & Santos (2012) and Senior *et al.* (2016) using the *R* function *i2_ml* (*orchaRd R* package v.2.0; Nakagawa *et al.* 2021). We considered I^2 values around 25%, 50%, and 75% as low, moderate, and high heterogeneity respectively (Higgins *et al.* 2003). We performed all analysis and produced visualisations using *R* (v.4.4.0; R Core Team 2022) and the code available in the paper of Capilla-Lasheras *et al.* (2022; https://doi.org/10.5281/zenodo.7010687).

Sensitivity analysis

We assessed the robustness of our results with two complementary analyses. First, we re-ran the same models as model 1 to 5 using lnCVR calculated from the variance component of IO-LMMs (Model 8 to 12, Table 1). Second, since bird taxa represented 62% of our effect sizes, we re-ran the phylogenetic multilevel (intercept-only) meta-analyses (Model 1 and 3, Table 1) only on birds (Model 13 and 14, Table 1) and excluding all bird species (Model 15 and 16, Table 1). We did not re-run models using lnVR because of the strong mean-variance relationship present in our study due to the count data.

Publication bias

We assessed small-study bias and decline effects (time-lag effects), following Nakagawa *et al.* (2022) method and the examples from Capilla-Lasheras *et al.* (2022). In total, we ran two additional uni-moderator multilevel meta-analytic models for lnCVR of between- and within-individual variation respectively (Model 17 to 20, Table 1). Each of these models included a single moderator either the square-root of the inverse of the effective sample size or the mean-centred year of study publication (Nakagawa *et al.* 2022; Trikalinos & Ioannidis 2005). When data were unpublished, we used the year when the data were collected in the model. The variation explained by these moderators (i.e. R^2_{marginal}) was calculated using the *R* function *r2_ml* (*orchaRd R* package v.2.0; Nakagawa *et al.* 2021).

Table 1. Summary of the different models present in the meta-analysis

Model ID	Response	Variance partitioning model	Data	Moderators	Details
Main analyses					
1	lnCVR between-individual variation	AD-LMM	All traits	Intercept	Overall meta-analysis on between-individual variation. Univariate. Table S5. Figure S2.
2	lnCVR between-individual variation	AD-LMM	All traits	Trait type	Effect per trait on between-individual variation. Quadrivariate. Table S7. Figure 2A.
3	lnCVR within-individual variation	AD-LMM	All traits	Intercept	Overall meta-analysis on within-individual variation. Univariate. Table S6. Figure S3.
4	lnCVR within-individual variation	AD-LMM	All traits	Trait type	Effect per trait on within-individual variation. Quadrivariate. Table S8. Figure 2B.
5	lnCVR within-individual variation	AD-LMM	Only behaviour	Behaviour trait type	Effect per behavioural trait on within-individual variation. Trivariate. Table S9. Figure 3.
Secondary analyses					
6	lnCVR between-individual variation	AD-LMM	All traits	Provenance of data + interval between measurement corrected for lifespan + number of fixed and random effect in AD-LMM	Effect of various moderators on between-individual variation. Multivariate. Table S10.
7	lnCVR within-individual variation	AD-LMM	All traits	Provenance of data + interval between measurement corrected for lifespan + number of fixed and random effect in AD-LMM	Effect of various moderators on within-individual variation. Multivariate. Table S11.
Sensitivity analysis					
8	lnCVR between-individual variation	IO-LMM	All traits	Intercept	Overall meta-analysis on between-individual variation. Univariate. Table S12a.
9	lnCVR between-individual variation	IO-LMM	All traits	Trait type	Effect per trait on between-individual variation. Quadrivariate. Table S12b.

10	lnCVR within-individual variation	IO-LMM	All traits	Intercept	Overall meta-analysis on within-individual variation. Univariate. Table S13a.
11	lnCVR within-individual variation	IO-LMM	All traits	Trait type	Effect per trait on within-individual variation. Quadrivariate. Table S13b.
12	lnCVR within-individual variation	IO-LMM	Only behaviour	Behaviour trait type	Effect per behavioural trait on within-individual variation. Trivariate. Table S13c.
13	lnCVR between-individual variation	AD-LMM	All traits with only bird	Intercept	Overall meta-analysis on between-individual variation only with bird. Univariate. Table S14a.
14	lnCVR within-individual variation	AD-LMM	All traits with only bird	Intercept	Overall meta-analysis on within-individual variation only with bird. Univariate. Table S14b.
15	lnCVR between-individual variation	AD-LMM	All traits without bird	Intercept	Overall meta-analysis on between-individual variation without bird. Univariate. Table S14a.
16	lnCVR within-individual variation	AD-LMM	All traits without bird	Intercept	Overall meta-analysis on within-individual variation without bird. Univariate. Table S14 b.
Publication bias					
17	lnCVR between-individual variation	AD-LMM	All traits	square-root of the inverse of the effective sample size	Overall small-study effect on between-individual variation. Table S15a.
18	lnCVR within-individual variation	AD-LMM	All traits	square-root of the inverse of the effective sample size	Overall small-study effect on within-individual variation. Table S15b.
19	lnCVR between-individual variation	AD-LMM	All traits	mean-centred year of study publication	Overall decline effect on between-individual variation. Table S16a.
20	lnCVR within-individual variation	AD-LMM	All traits	mean-centred year of study publication	Overall decline effect on within-individual variation. Table S16b.

Results

After inspecting 3,167 unique studies, our meta-analysis included 89 urban–non-urban comparisons from 31 studies for four phenotypic trait types: behaviour (61 effect sizes, 20 studies), physiology (5 effect sizes, 4 studies), cognition (12 effect sizes, 7 studies) and morphology (11 effect sizes, 9 studies). This dataset included 22 species, with most studies located in the northern hemisphere (Figure 1).

Is between-individual variation lower in the city?

Univariate and quadrivariate meta-analytical model (origin of variance: AD-LMMs)

The overall coefficient of between-individual phenotypic variation in urban populations did not differ from non-urban ones (Model 1: lnCVR estimates [95% CI] = -0.046 [-0.191, 0.098]; Figure S2; Table S5). Total heterogeneity was high (I^2_{total} = 89.5%), with 20.4% explained by species-specific effects (Table S5). Calculating urban effects per trait confirmed no effect of urbanisation on between-individual variation across different phenotypic traits (Model2: lnCVR behaviour estimates [95% CI] = -0.038 [-0.211, 0.136]; cognition estimates = -0.133 [-0.494, 0.227]; morphology estimates = -0.081 [-0.403, 0.241]; physiology estimates = 0.297 [-0.182, 0.777], Figure 2A, Table S7). Total heterogeneity was high (I^2_{total} = 89.6%), with 21.0% explained by species-specific effects (Table S7).

Is within-individual variation higher in the city?

Univariate and quadrivariate meta-analytical model (origin of variance: AD-LMMs)

We found that non-urban populations tended to have on average 6.2% higher coefficients of within-individual phenotypic variation than urban populations, but this effect did not differ from zero (Model3: lnCVR estimates [95% CI] = -0.062 [-0.165, 0.041]; Figure S3; Table S6). Total heterogeneity was high (I^2_{total} = 92.6%), with 7.9% explained by species-specific effects (Table S6). Calculating urban effects per trait suggested that the observed trend was most likely due to a pattern emerging from behavioural traits (Model4: lnCVR behaviour estimates [95% CI] = -0.073 [-0.205, 0.059]; cognition estimates = 0.125 [-0.173, 0.423]; morphology estimates = 0.053 [-0.222, 0.329]; physiology estimates = -0.227 [-0.619, 0.165], Figure 2B, Table S8). Total heterogeneity was high (I^2_{total} = 92.8%), with 11.8% explained by species-specific effects (Table S8). Additional analysis on the subset of behavioural traits revealed that there is not a specific behaviour leading the increase of within-individual variation in non-urban populations compared to urban ones (Model5: lnCVR activity/exploration estimates = -0.069 [-0.251, 0.113]; aggression estimates = 0.025 [-0.302, 0.351]; boldness estimates [95% CI] = 0.010 [-0.268, 0.288], Figure 3, Table S9). Total heterogeneity was high (I^2_{total} = 93.9%), with 13.0% explained by species-specific effects (Table S9).

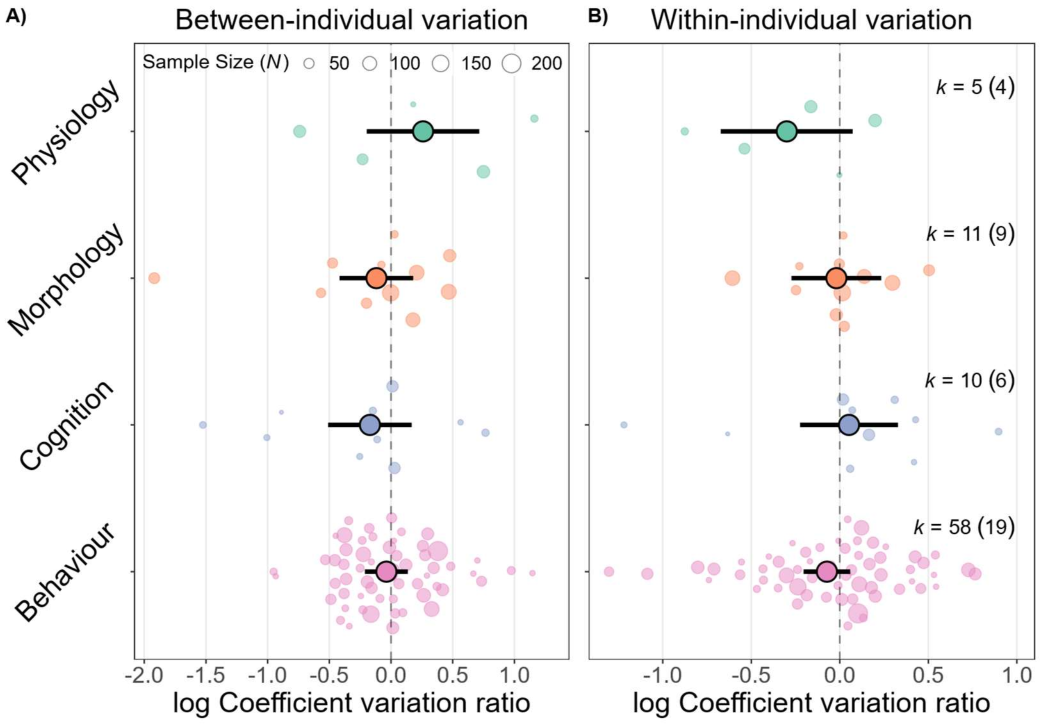

Figure 2. Model estimates per phenotypic trait for log coefficient of variation ratio (lnCVR) assessing differences between urban and non-urban populations for A) between-individual variation (model 2) and B) within-individual variation (model 4) calculated from AD-LMMs. Positive values on the x-axes represent higher between- or within-individual variation in urban populations compared to non-urban populations and *vice versa* for negative values. The large coloured points represent overall model estimates. The thick black lines show their 95% confidence intervals. Transparent small coloured dots show the raw data (their size is scaled according to their sample size from which they were estimated). k is the number of observations supplemented with the number of studies between brackets.

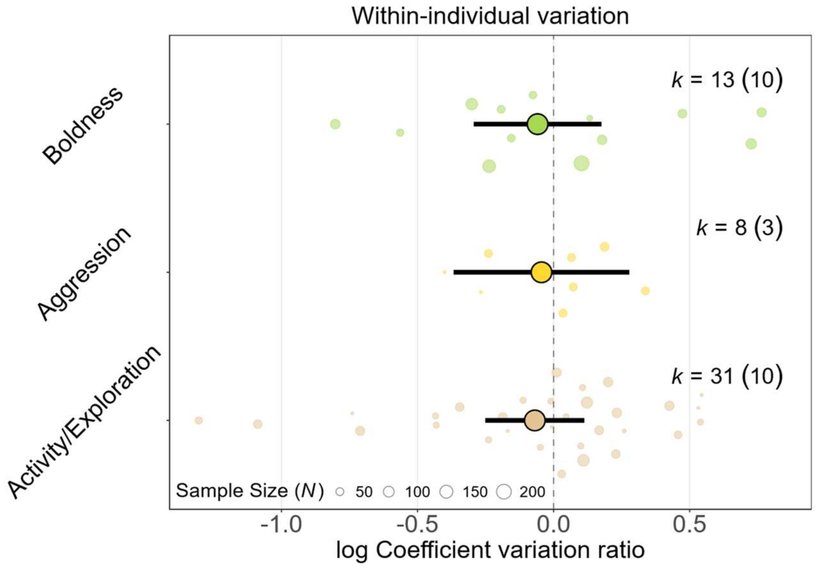

Figure 3. Model estimates per behaviour for log coefficient of variation ratio (lnCVR) assessing differences between urban and non-urban populations for within-individual variation calculated from AD-LMM. Positive values on the x-axis represent higher within-individual variation in urban populations compared to non-urban populations and *vice versa* for negative values. The large coloured points represent overall model estimates. The thick black lines show their 95% confidence intervals. Transparent small coloured dots show the raw data (their size is scaled according to their sample size from which they were estimated). k is the number of observations supplemented with the number of studies between brackets.

Are other moderators explaining heterogeneity for between- and within-individual variation in the context of urbanisation?

Meta-regression model (origin of variance: AD-LMMs)

We found a positive correlation between the number of factors added in the AD-LMMs used for variance partitioning and the lnCVR of between-individual variation (Model 6: lnCVR 'Number of factors in AD-LMM' estimates [95% CI] = 0.209 [0.044, 0.374], Table S10). Provenance of data and inter-test interval corrected for lifespan did not affect lnCVR of between-individual variation (Table S10). We ran additional analyses to understand why the number of factors affected the lnCVR of between-individual variation. We did not find any effect due to the amount of variance explained by the fixed effects in our AD-LMMs, or the average amount of variance explained by the 'trial' variable from the AD-LMMs of urban and non-urban populations as well as the lnCVR of the 'trial' variable. We did not report those additional analyses. In addition, we did not find any effect between any moderators and lnCVR of within-individual variation (Table S11).

Sensitivity analysis and assessment of publication bias

Sensitivity analysis – IO-LMMs versus AD-LMMs

We performed the same main analysis (Model 1 to Model 5) using the effect size calculated from the variance of the IO-LMMs. For between-individual variation, like in the main analysis, we found that the coefficient of between-individual phenotypic variation in urban populations did not differ from non-urban ones whether we perform the analysis on the overall dataset (Table S12a for comparisons) or per phenotypic trait (Table S12b for comparisons). For within-individual variation, like in the main analysis, we found that non-urban populations tended to have on average 5.3% higher coefficient of within-individual phenotypic variation than urban populations but again 95% confidence interval overlapped zero (Model 10: lnCVR estimates [95% CI] = -0.053 [-0.155, 0.048]; Table S13a for comparisons). We also confirmed that the observed trend was most likely due to a pattern emerging from behavioural traits (Model 11: lnCVR behaviour estimates [95% CI] = -0.057 [-0.184, 0.071]; cognition estimates = 0.062 [-0.197, 0.321]; morphology estimates = 0.001 [-0.257, 0.276]; physiology estimates = -0.162 [-0.606, 0.281], Table S13b for comparisons). Analysis on the subset of behavioural traits did not reveal a pattern of an influential behaviour driving this potential effect (Model 12: lnCVR activity/exploration estimates = 0.001 [-0.154, 0.156]; aggression estimates = 0.011 [-0.278, 0.301]; boldness estimates [95% CI] = -0.072 [-0.298, 0.154], Table S13c for comparisons).

Overall, we noted that lnCVR estimates might change between IO-LMM and AD-LMM methods but that all estimates fell within the confidence interval of each other. Only the meta-analytical model of lnCVR on within-individual variation per behavioural trait, had significant changes in the estimates probably due to the low sample sizes per trait in this analysis. Most importantly, the overall observed patterns remained.

Sensitivity analysis – Bird versus all other taxa combined

We conducted the main meta-analysis (Model 1 and Model 3) only on the bird data (Model 13 and Model 14) and excluding the bird taxa (Model 15 and Model 16). For between-individual variation, we found that non-bird taxa of non-urban population tended to have on average 7.4% higher coefficient of between-individual phenotypic variation than non-bird taxa of urban populations but the 95% confidence interval for this estimate overlapped zero (Model 15: lnCVR estimates [95% CI] = -0.074 [-0.217, 0.068]; Table S14a for comparisons). We did not find this trend in the bird taxa analysed alone (Model 14: lnCVR estimates [95% CI] = -0.030 [-0.299, 0.240]; Table S14a for comparisons).

For within-individual variation, we found the same trend as in the main analysis whether the analysis was performed only on birds (Model 14: lnCVR estimates [95% CI] = -0.069 [-0.200, 0.063], Table S14b for comparisons) or only on non-bird taxa (Model 16: lnCVR estimates [95% CI] = -0.074 [-0.244, 0.096], Table S14b for comparisons).

Sensitivity analysis – Sample size versus number of repetition

Our variance estimation to calculate the lnCVR was based on repeated measurements since we were interested in between- and within-individual variation. In the computation of the lnCVR we used the most conservative approach with the sample size of the study. In addition, we calculated two version of the number of repetitions present in the study which would be less conservative. In both versions, the uncertainties around the lnCVR estimates were slightly larger but the overall patterns did not change. Therefore, we reported only the most conservative approach and did not provide the details of these additional analyses.

Publication bias – small-study and decline effects

We did not find evidence for the existence of small-study or decline effects for lnCVR of between- and within-individual variation estimates (Model 17: *between-individual variation* slope estimate for the square-root of the inverse of the effective sample size [95% CI] = -0.437 [-1.967, 1.092], $R^2_{marginal}$ = 0.006, Table S15a; Model 18: *within-individual variation* slope estimate for the square-root of the inverse of the effective sample size [95% CI] = -0.355 [-1.501, 0.791], $R^2_{marginal}$ = 0.006, Table S15b; Model 19: *between-individual variation* slope estimate for year of publication [95% CI] = 0.024 [-0.028, 0.076], $R^2_{marginal}$ = 0.013, Table S16a); Model 20: *within-individual variation* slope estimate for year of publication [95% CI] = 0.008 [-0.050, 0.034], $R^2_{marginal}$ = 0.002, Table S16b for comparisons). According to Nakagawa *et al.* (2022), our results did not seem to suffer from publication bias.

Discussion

We used phylogenetically controlled multilevel meta-analysis to assess how urban living is related to changes in phenotypic variation for labile phenotypic traits. By decomposing phenotypic variation into within- and between-individual variation, we addressed potential changes in reversible and fixed variation between urban and non-urban populations. Contrary to our hypothesis, we found no evidence that urban individuals are more flexible than non-urban individuals. Instead, we observed a very weak tendency for urban individuals to be less flexible than non-urban ones. We also did not find evidence that urban individuals are more phenotypically similar to each other than non-urban ones. However, our sensitivity analyses revealed that other taxa than birds tended to validate this pattern, but evidence was very weak. Our findings highlight that the effects of urbanisation on the different partitions of phenotypic variation are not as straightforward and generalisable as expected and may depend on the taxa, species, and traits.

Do individuals show higher phenotypic flexibility in the city?

Cities are characterised by high spatial variation in their landscape structure (Cadenasso *et al.* 2007; Pickett *et al.* 2001), high temporal change of anthropogenic food availability (Stofberg *et al.* 2019) and high spatial-temporal temperature fluctuations (Soltani & Sharifi 2017). In this context of rapid environmental changes, the capacity for individuals to reversibly adjust their phenotype seems to be key for adaptation (i.e. phenotypic flexibility hypothesis). However, in our study, we did not find evidence that urban individuals express higher phenotypic flexibility (i.e. within-individual variation) than non-urban ones. On the contrary, we observed a very weak tendency for urban individuals to express lower phenotypic flexibility, especially in their behaviour. Our results contribute to the mixed patterns found in literature. Indeed, Gervais et al. (2025) showed that within-individual variation of urban birds decreases for breath rate but do not change for exploration whereas Dammhahn *et al.* (2020) found that urban individuals had higher phenotypic flexibility for boldness and exploration compared to rural conspecifics. It is possible that our current assumption associating urban habitats with higher environmental heterogeneity might not be generalisable especially considering that no overall consensus of this phenomena has been reached yet (Thompson *et al.* 2022). Environmental heterogeneity measures are generally lacking in empirical studies, limiting our ability to develop broad predictive frameworks. To our knowledge, only two studies (Capilla-Lasheras *et al.* 2022; Gervais *et al.* 2025) have linked spatial heterogeneity to phenotypic changes directly with mixed findings. In our study, we were not able to extract enough spatial heterogeneity information for a meaningful comparison. Most critically, it would have been difficult, if not impossible, to decide a ‘one-size-fits-all’ species scale. Urban environments are complex systems with multiple environmental axes (Szulkin *et al.* 2020) which may have similar or different heterogeneity compared to natural environments depending on the measurement scale and the species in focus (Alberti *et al.* 2020; Pickett *et al.* 2016; Uchida *et al.* 2021). In addition, urban individuals could choose living in areas in the city that display low environmental heterogeneity to reduce environmental pressures (i.e. ‘selection of the environment’ in Edelaar *et al.* 2023, or 'niche choice' in Trappes *et al.* 2022). Therefore, such variation associated with the environmental heterogeneity effect could explain why we do not observe an overall change in phenotypic flexibility in our study.

Alternatively, no overall change in phenotypic flexibility could rise from different independent responses of the individual plasticity (Dingemanse *et al.* 2010; Snell-Rood 2013) and the individual predictability component (Hertel *et al.* 2021; Westneat *et al.* 2015) to environmental heterogeneity. Here, we postulated that both components would react similarly towards environmental heterogeneity. In the case of individual plasticity, individuals would express optimal plasticity in response to environmental heterogeneity (i.e. reaction norm). In other words, one unit of change in the environment triggers one unit of change in the phenotype (i.e. 1/1 ratio; slope of 1). However, urban populations could only adjust their phenotype every two environmental change resulting in a weaker slope response (1/2 ratio; slope of 0.5) as an adaptation to environmental heterogeneity and to new environmental stressors present in the city. Indeed, if changes in the urban environment are non-detrimental, individuals with a weaker slope response would have reduced costs of plasticity and could potentially benefit of higher fitness than individuals with a stronger slope response (DeWitt *et al.* 1998). Environmental insensitivity and environmental non-assimilation are two mechanisms that could explain a reduction in slope response. Environmental insensitivity occurs when individuals integrate environmental information but do not respond strongly to an environmental stimulus (e.g. behavioural tolerance: Čapkun-Huot *et al.* 2024; habituation: Blumstein 2016) whereas environmental non-assimilation occurs when an individual's sensory systems is not able to integrate environmental information preventing a phenotypic response (Kelley *et al.* 2018). Such a phenomenon was observed by Sprau & Dingemanse (2017) in great tits (*Parus major*) where optimal behavioural plasticity in aggressiveness and risk taking did not follow urban environmental change. However, we do not expect this phenomenon to affect our results very strongly for two reasons. First, in most cases the measurements were repeated under same conditions without any environmental change. Second, we accounted for treatment and temporal effects by including them as variables in the variance partitioning models, where possible. We note that this correction is solely an approximation of a part of the variance explained by individual plasticity and does not replace a proper estimation of individual slopes. Still, the reduced reaction norm phenomenon could explain why we observe a weak tendency of urban populations to exhibit lower phenotypic flexibility.

Lower phenotypic flexibility could also be due to changes in individual's predictability. Changes in residual within-individual variance (i.e. individual predictability) can be produced by additive effects of multidimensional reaction norms (Westneat *et al.* 2015). Transposing the example in Westneat *et al.* (2015), if territories with good food supplies are more likely to have more stable temperatures in the city due to heat island effects, then urban individuals on good territories might be less variable in foraging than non-urban individuals on good territories with less stable temperature (no heat island effect). Error in assessment (i.e. organismal error) could also explain why individual predictability differs between urban and non-urban individuals. If we assume that an individual's reaction norm slope is the optimal response to environmental change, then individuals expressing high residuality around this slope would be considered far from their optimal response (errors in plasticity). It is often shown that the urban filter strongly selects certain phenotypes, therefore allowing only certain individuals to live in the city (behaviour: Burkhard *et al.* 2024; life-history: Capilla-Lasheras *et al.* 2022; home range: O'Donnell & delBarco-Trillo 2020; morphology: Putman & Tippie 2020). This strong selection could result in a lower organismal error in urban habitats compared to non-urban habitats explaining why urban individuals tend to show lower phenotypic flexibility. Finally, changes in individual predictability could result from passive plasticity (Scheiner 2006), which creates phenotypic variation solely from physical processes. For example, food intake rate will have a component of variation associated to the time taken to find the next prey item (i.e. unpredictable variance). Small resource patches in cities may help predators to find their next prey item more rapidly, allowing lower phenotypic variance due to reduced search times. In addition, passive plasticity could be used as an environmental assessment to stabilise an individual's phenotype around their optimal reaction norm, a process analogous to canalization (Stearns & Kawecki 1994) but occurring at the within-individual level. Variance-prone foraging is one example where prey encounters may be unpredictable, but if the variance in encounter times can be assessed by foragers, then individuals could adjust their foraging decisions to experience more or less unpredictable passive plasticity and shift towards their optimal responses (Shafir 2000; Stephens 1981). Overall, our results highlight that the assumed effects of urban heterogeneity on phenotypic flexibility might not be generalisable across cities and phenotypic traits. The presence of differential feedback mechanisms between individual plasticity and individual predictability may create high heterogeneity on how urbanisation and phenotypic flexibility are linked with each other.

Do between-individual differences decrease in the city?

We know that urban environments favour certain phenotypes, leading to shifts in population averages (behaviour: Burkhard *et al.* 2024; life-history: Capilla-Lasheras *et al.* 2022; home range: O'Donnell & delBarco-Trillo 2020; morphology: Putman & Tippie 2020). However, it is unclear how this pattern affects between-individual variation at the population level. In community ecology, one major mechanism to change between-individual variation is linked to competition. High intraspecific competition can increase between-individual niche variation when it limits the use of an optimal resource leading individuals to feed on alternative items (Svanbäck & Bolnick 2005, 2006). As an individual's resource use is linked to phenotypic trait variation (Bolnick *et al.* 2011) and intraspecific competition could act similarly as interspecific competition, we assumed a similar pattern might be possible for between-individual trait variation and interspecific competition. Urban habitats are known to select mostly generalist, thermophilic or high-dispersal capacity species which tend to reduce the number of urban living species (Piano *et al.* 2017). Thus, we expected that this reduction of interspecific competition would decrease between-individual variation in the city. Surprisingly, we did not find that urban individuals were more similar to each other than non-urban ones. Although species richness often decreases in the context of urbanisation (but see Rimbach *et al.* 2025), there are several studies showing an increase of individual abundance (Batáry *et al.* 2018; Szabó *et al.* 2023). It is possible that higher densities in the city induce higher intraspecific competition which could counterbalance any interspecific competition reduction maintaining similar levels of individual phenotypic differentiation. However, it is possible that this process might be species or taxa specific. Our sensitivity analysis found a very weak evidence that urban taxa other than birds might express lower between-individual variation than non-urban ones. It is most likely that birds (and flying insects) are less affected by urban spatial fragmentation and have a higher dispersal propensity, leading to a higher gene flow (Medina *et al.* 2018; Miles *et al.* 2019; but see Delaney 2013) maintaining higher between-individual variation. On the other hand, species with low dispersal ability might endure higher selective pressures triggering adaptive evolutionary processes to canalise individual's phenotype towards the population optimum average, reducing between-individual variation (Dingemanse & Réale 2005). For example, urban habitats might display high heterogeneity in resource availability where only a few resource items are highly available and others are limited, enforcing most individuals to use the same resources. Overall, urban environmental conditions are expected to act as a filter for urban species composition with clear winners and losers. Our results regarding between-individual variation highlights a potential phenotypic homogenisation across cities due to an urban filter which is most likely taxa- or species-specific.

How accounting for more factors in the LMMs could result in changes in the effect size?

When estimating within- and between-individual variation using linear mixed-effects models, it is important to integrate fixed-effects and appropriate random structures to optimize the estimation of each partition (De Villemereuil *et al.* 2018). Data-level predictors associated with individual data points (e.g. age if same individual measured at different age) will tend to reduce residual variance whereas individual-level predictors varying between individuals (e.g. sex) will reduce between-individual variance (Nakagawa & Schielzeth 2010). We tested how the number of factors in our models impacted the variance estimation. It is known that models with more factors estimate variance partition more accurately. We found that comparisons with more factors expressed higher between-individual variation in urban populations compared to non-urban ones. This phenomenon could be explicated if the integration of more fixed and random factors explained more variance in urban populations than in non-urban populations. However, in additional analyses (not reported in this paper), we did not find any effect of the amount of variance explained by those factors. It is most likely that models controlling for more variables have a stronger impact on studies made in urban environments although we could not determine it in our case. It highlights the potential of certain biological factors (e.g. sex, time) to affect phenotypic variation differently in function of the habitat in focus.

Conclusions

Our study is the first evidence synthesis partitioning and summarising reversible and fixed phenotypic variation across taxa and a broad range of labile phenotypic traits. It highlights the importance of studying both type of individual variation to advance our understanding of the biological meaning of phenotypic flexibility and its relevance for human-induced rapid environmental changes. Urbanisation – a highly impactful and spreading anthropogenic habitat development – has the potential to induce changes in phenotypic variation at different levels. Although evidence was weak, our findings showed that – against the predictions – urban individuals could have reduced phenotypic flexibility. Such changes in individual variation could lead to drastic consequences on how individuals express their ecological niche through environmental tolerance. The high heterogeneity in the available dataset and the sensitivity analyses showed that the observed patterns are most likely to be species, taxa and/or trait specific supporting recent mixed results found in the literature. Changes in phenotypic variation at the within- or between-individual level will have different eco-evolutionary consequences and affect populations persistence and species adaptation. Given that many changes observed in urban habitats foreshadow broader shifts driven by global change, it is essential to systematically examine how both partitions of phenotypic variation respond to such changes. Such studies linking environmental heterogeneity and phenotypic variation are rare especially considering change in within-individual variation. Within-individual variation (i.e. phenotypic flexibility) represents up to 60% of unexplained variation for many labile traits and contains most likely crucial biological information. For future research, we advocate for a more holistic framework that considers phenotypic flexibility alongside environmental heterogeneity to better understand organismal responses to changing environments.

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Authors contributions

Jules Petit and Melanie Dammhahn conceived the study. Jules Petit performed the literature search, extracted the effect sizes, performed all analyses and wrote the first draft of the manuscript with input from Melanie Dammhahn. Melanie Dammhahn acquired the funding for the study. All authors read and revised the manuscript.

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Conflict of interest

The authors declare no competing interests.

Supplementary information

Phenotypic flexibility in the city: A meta-analysis on variation

Authors: Jules Petit[1,2,#], Melanie Dammhahn[1,2]

Affiliations:

[1]Department of Behavioural Biology, University of Münster

[2]Joint Institute for Individualisation in a Changing Environment (JICE), University of Münster and Bielefeld University

[#] Corresponding author: jules.petit1@outlook.com (JP)

ORCID: Jules Petit (0009-0008-4061-8346); Melanie Dammhahn (0000-0003-0557-740X)

Appendix - Material and methods

Text S1. List of suitable papers from Google Scholar search

The following papers have been used for finding original keywords for the first search (Carrete & Tella 2013, 2017; Charmantier *et al.* 2017; Davies & Sewall 2016; Evans *et al.* 2010; Hardman & Dalesman 2018; Kaiser *et al.* 2018; Miranda *et al.* 2013; Møller & Tryjanowski 2014; Papp *et al.* 2015; Scales *et al.* 2011; Tabh *et al.* 2022; Uchida *et al.* 2020).

Text S2. *Web of sciences categories for **Query 1***

Environmental Sciences, Environmental studies, Ecology, Urban studies, Marine Freshwater Biology, Ornithology, Agriculture Multidisciplinary, Veterinary Sciences, Multidisciplinary Sciences, Zoology, Biodiversity Conservation, Psychology Multidisciplinary, Neurosciences, Physiology, Psychology Multidisciplinary, Behavioural Sciences, Biology, Evolutionary Biology, Parasitology, Immunology, Toxicology, Psychology Biological, Endocrinology Metabolism, Entomology, Reproductive biology.

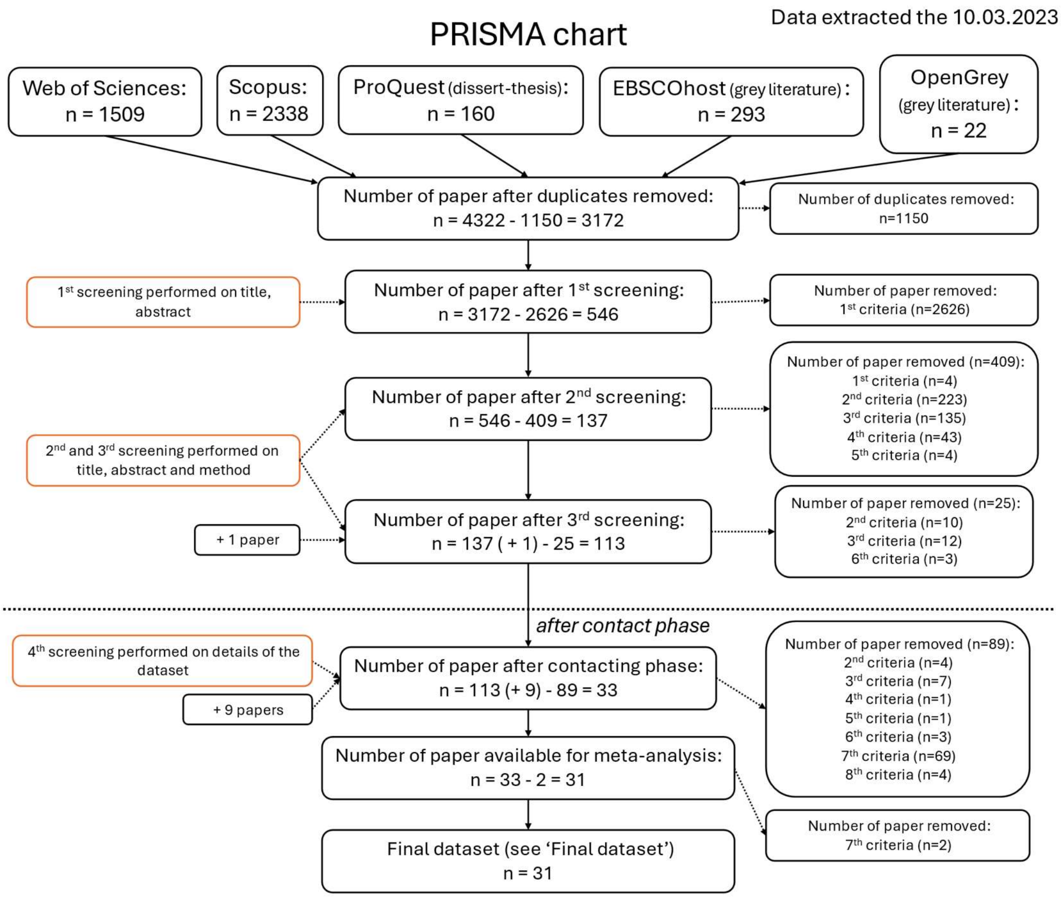
Text S3. *Web of sciences categories for **Query 2***

Environmental Sciences, Environmental studies, Ecology, Urban studies, Marine Freshwater Biology, Zoology, Psychology Multidisciplinary, Biology, Evolutionary Biology, Behavioural Sciences, Veterinary Sciences, Neurosciences, Entomology, Agriculture Multidisciplinary, Ornithology, Physiology, Toxicology, Reproductive Biology, Immunology, Parasitology, Multidisciplinary Sciences, Biodiversity Conservation.

Table S1. Final search terms used per literature database

Database	Search used	Specific filter used
Web of Sciences Collection	**TOPIC** = "phenotypic plasticity" or repeata* or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*" AND **ABSTRACT** = urban* or rural* NOT **ABSTRACT** = "planning" or "management" or emission* or polic* or carbon* or child*	In Web of Science Core Collection. All dates until 10.03.2024 *Web of sciences categories:* 'Environmental Sciences', 'Environmental studies', 'Ecology, Urban studies', 'Marine Freshwater 'Biology, Zoology', 'Psychology Multidisciplinary', 'Biology', 'Evolutionary Biology', 'Behavioural Sciences', 'Veterinary Sciences', 'Neurosciences', 'Entomology', 'Agriculture Multidisciplinary', 'Ornithology', 'Physiology', 'Toxicology', 'Reproductive Biology', 'Immunology', 'Parasitology', 'Multidisciplinary Sciences', 'Biodiversity Conservation'

Scopus	**(article, abstract, keyword)** = "phenotypic plasticity" or repeata* or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*" AND **ABSTRACT** = urban* or rural* NOT **ABSTRACT** = "planning" or "management" or emission* or polic* or carbon* or child*	All dates until 10.03.2024 *Subject area*: 'Environmental Sciences', 'Agricultural and Biological Sciences', 'Psychology', 'Multidisciplinary', 'Decision Sciences', 'Immunology and Microbiology', 'Pharmacology, Toxicology and Pharmaceutics', 'Neuroscience', 'Veterinary', 'Undefined'
ProQuest	"phenotypic plasticity" or repeata* or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*" **IN abstract – ABSTRACT°** AND urban* or rural* **IN abstract – ABSTRACT°** NOT "planning" or "management" or emission* or polic* or carbon* or child* **IN abstract – ABSTRACT°**	All dates until 10.03.2024
EBSCOhost Open Dissertations	("phenotypic plasticity" or repeata* or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*") AND (urban* or rural*) NOT ("planning" or "management" or emission* or polic* or carbon* or child*)	Publication data: 1970-2020
Open Grey	("phenotypic plasticity" or repeata* or consistenc* or "inter-individual" or "intra-individual" or flexibilit* or "individual plasticity" or "animal personality" or "repeated disturbance*" or "repeated exposure*" or "repeated trial*") AND (urban* or rural*) NOT ("planning" or "management" or emission* or polic* or carbon* or child*)	All dates until 10.03.2024



Criteria number	Exclusion criteria
1.	Studies on human subjects, plants, domesticated and zoo animals
2.	Studies with no non-urban AND urban populations
3.	Studies with no repeated measurements per individual for each habitat
4.	Studies which are meta-analysis or systematics review or opinion paper or comment paper
5.	Duplicate
6.	Dataset with experimental flaws
7.	Data not accessible
8.	Not a continuous or count data labile trait

Figure S1. PRISMA chart of the three screening phases and after the contact phase with criteria table.

Text S4. Contact procedure

We used a template letter inspired from Foo *et al.* (2021). This first contacting phase added 9 potential papers resulting in 122 papers. All authors were contacted at least three times over a one year and a half period to increase the chance of responses. In total, we collected 39 dataset, and 2 researchers were willing to run our script without sharing data. After the last contacting phase and a deep check of the data we could use 33 datasets to estimate the between- and within-individual variance partitions. We would like to emphasize that, unfortunately, about half of our emails did not receive any answer whether to share the data.

Table S2. Functional definitions of the phenotypic traits incorporated in the meta-analysis.

Phenotypic traits	**Definitions**
BEHAVIOUR	
Aggression	Agonistic behaviour including all behaviours associated with the contest or struggle between individuals (King 1973).
Boldness	Behaviour expressed in any risky situation (but not new situations) where direct confrontation can be avoided (Réale *et al.* 2007).
Activity/Exploration	Behaviour directed toward acquiring information about the environment (Meyer 1998). We included activity as disentangle information gathering from pure movement is difficult and original paper did not make this difference (Crawley 1985; Paré & Glavin 1993).
Foraging	Behaviour related to food acquisition.
Neophilia	Refer to the tendency to approach novel stimuli. Differ from 'Neophobia' as it should be in a familiar/non-dangerous situation (Greenberg & Mettke-hofmann 2001; Mettke-Hofmann *et al.* 2002).
Neophobia	(1-Non neophobic) the mere preference for feeding on or visiting familiar foods, objects, or places. (2-Neophobic) the aversion or fear demonstrated to the same novel stimuli (e.g., new object, new colour, new type of food) in a foraging context. (Greenberg & Mettke-hofmann 2001; Mettke-Hofmann *et al.* 2002)
COGNITION	
Innovation (also called problem solving or innovative problem solving)	Adoption of behaviours that allow individuals to exploit newly available, previously used or familiar resources in a new way (Greenberg 2003). **One apparatus used once to avoid learning effect. Per definition can be only contextual repeatability.** We did not discard individuals that did not solve the problem because individuals who took the maximum time are still informative of the individual variation happening in the population (experimental artefact from the length of test)
Associative learning (also called learning or repetitive problem solving)	The ability of an organism to learn the correct association in a stimulus-reward contingencies (Griffin *et al.* 2015). **One apparatus re-use multiple time (minimum re-use is 2-trial for repeatability)** We did not discard individuals that did not solve the problem because individuals who took the maximum time are still informative of the individual variation happening in the population (experimental artefact from the length of test)
Reversal learning	The ability of an organism to learn a reverse previously learned association in a stimulus-reward contingencies (Williams 1942).
MORPHOLOGY	
Body mass	Weight of the individual
Testis size	Width of the testis
Fat score	Amount of subcutaneous fat scaled from 0 to 8 (Dominoni *et al.* 2015)
PHYSIOLOGY	
Corticosterone baseline	Corticosterone measure without any intentional stress induced on animals (following the expertise of the authors of the paper)
Corticosterone acute stress	Corticosterone measure after an intentional stress induced on animals after a relatively short interval (following the expertise of the authors of the paper)

Corticosterone long stress	Corticosterone measure after an intentional stress induced on animals after a relatively long interval (following the expertise of the authors of the paper)
Luteinizing hormone	Luteinizing hormone concentration in plasma
Body surface temperature	Body surface temperature is measured on the periorbital region of the eye

Text S5. Procedure of mean and variance extraction check

Mean and variance estimates calculated via the 'intercept-only' linear mixed effects models (IO-LMM) were compared to the variance estimates obtained via classical mean and variance computations (*mean()* and *var()* function used in *R* on the raw dataset) to verify that our models accurately estimated our parameters. For adjusted linear mixed effects models (AD-LMM) we could check only the variance since the inclusion of fixed factors deviated the model intercept from the 'true' mean. We calculated a coefficient of deviation (Δ_{LMM}) for each mean and variance estimates separately (see *Equation 1*).

(*Equation 1*) $\Delta_{LMM} = \frac{X_{model} - X_{classical}}{X_{classical}} \times 100$, *where* X_{model} *represents the mean or variance estimated from the model and* $X_{classical}$ *represents the mean or variance estimated from the classical computations.*

We aimed that our LMM estimates did not deviate for more than 5% from the classical estimates.

When $5\% < \Delta_{LMM} < 6\%$, we checked the presence of 'Influential Observations' using the function *check_model()* from the *performance* package (Lüdecke *et al.* 2021).

- **If influential observations had a Leverage < 0.5,** we checked the presence of outliers using the function *check_model()* and looking at the 'Posterior Predictive Check'.
  - **If a clear right or left-skew distribution was present,** we accepted the estimates as it is still very close to the 5% threshold of acceptation. we decided to not remove the outlier as we assumed that authors checked the biological validity of these outliers.
  - **If we did not observe any outliers,** the estimate was classified as unusable as we were not able to run a LMM giving an acceptable accuracy.
- **If influential observations had a Leverage ≥ 0.5,** we rerun the model without the influential observations. In this case, we accepted the deletion of the influential observations even if the observations seemed biologically relevant. We prefer to stay conservative in our estimations with reduced amount of information on variation than calculate inaccurate variance estimations. The maximum deletion applied in a dataset was five datapoints.
  - **If the new estimate reached the 5% threshold of acceptation**, the new estimate was accepted.
  - **If the new estimate did not reach the 5% threshold of acceptation**, the estimate was classified as unusable as we were not able to run a LMM giving an acceptable accuracy.

When $\Delta_{LMM} > 6\%$, we performed the same procedure although if a clear right or left skew was observed we did not accept the estimates and instead tried to improve Δ_{LMM} by removing outliers.

We used 'Homogeneity of variance' to select which value were to be prioritized for removal. Observations with high fitted values and high standard deviation residuals were removed in priority.

What we noticed is that outlier without repeated values had strong effect on the variance estimation. In addition, dataset with Poisson looking-like residual's distribution had more chance to cause problems in variance estimation as well.

Table S3. Summary of mean and variance check for intercept-only linear mixed effects models (IO-LMMs) and adjusted linear mixed effects models (AD-LMMs)

Paper	**Trait**	**Data point removed**	**Conclusion**
For IO-LMM			
Dominoni *et al.* 2015	Luteinizing, Urban	NA	Accepted, could not fix but because high right skew and close to 5%
Dominoni *et al.* 2015	Body mass, Urban	1	Corrected
Garitano-Zavala *et al.* 2022	Latency to solve, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of flight, Urban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of flight, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of hop, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Active scanning, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Prop. Perch visited, Urban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Prop. Ground visited, NonUrban	NA	Accepted, could not fix but close to 5%
Kozlovsky *et al.* 2017	Latency to solve “repeat” problem solving	NA	Discarded, could not fix variance
Mazza & Guenther 2021	Boldness, urban	NA	Accepted, could not fix but close to 5%
Petit unpubl.	Prop. Activity, WM, NonUrban	2	Corrected
Petit unpubl.	Body mass, WM, NonUrban	3	Corrected
Petit unpubl.	Boldness, YM, NonUrban	NA	Discarded, could not fix mean
Petit unpubl.	Boldness, YM, Urban	NA	Discarded, could not fix the variance and mean
Petit unpubl.	Docility, YM, Urban	NA	Discarded, could not fix mean
Rimbach unpubl.	CORT, YM, Urban	NA	Discarded, could not fix the variance
Rimbach unpubl.	CORT, WM, NonUrban	NA	Discarded, could not fix the variance and mean
Rimbach unpubl.	CORT, BV, NonUrban	2	Corrected
Solaro & Sarasola 2019	Innovation, latency, NonUrban	NA	Discarded, could not fix the variance

Stansell *et al.* 2022	Boldness, NonUrban	6	Corrected
Thompson & Morand-Ferron 2019	Latency to solve, Nonurban, Juv	NA	Accepted, could not fix but because high right skew and close to 5%
Thompson & Morand-Ferron 2019	Incorrect cache, Nonurban, Juv	NA	Accepted, could not fix but because high right skew and close to 5%
Thompson *et al.* 2018	Hop duration, NonUrban, Adult	3	Corrected
For AD-LMM			
Bar-Ziv *et al.* 2023	Boldness:FID:jackdal, Urban	NA	Discarded, could not fix the variance
Dominoni *et al.* 2015	Luteinizing, Urban	NA	Accepted, could not fix but because high right skew and close to 5%
Dominoni *et al.* 2015	Body mass, Urban	1	Corrected
Huang *et al.* 2020	Number of flight, Urban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of flight, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of hop, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Active scanning, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Prop. Perch visited, Urban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Prop. Ground visited, NonUrban	NA	Accepted, could not fix but close to 5%
Huang *et al.* 2020	Number of hop, urban	2	Corrected
Kozlovsky *et al.* 2017	Latency to solve "repeat" problem solving	NA	Discarded, could not fix variance
Petit & Dammhahn unpubl.	Prop. Activity, WM, NonUrban	2	Corrected
Petit & Dammhahn unpubl.	Body mass, WM, NonUrban	3	Corrected
Petit & Dammhahn unpubl.	Boldness, YM, NonUrban	NA	Discarded, could not fix mean
Petit & Dammhahn unpubl.	Boldness, YM, Urban	NA	Discarded, could not fix the variance and mean
Petit & Dammhahn unpubl.	Docility, YM, Urban	NA	Discarded, could not fix mean

Petit & Dammhahn unpubl.	Active_total_proportion, nonurban, WM	1	Corrected
Petit & Dammhahn unpubl.	Active_total_proportion, nonurban, YM	NA	Accepted, could not fix but a little skew but close to 5%
Petit & Dammhahn unpubl.	Mass, urban, YM	NA	Accepted, could not fix but a little skew but close to 5%
Prasher *et al.* 2019	Latency, nonurban, juvenile	NA	Accepted, could not fix but because binomial like skew and close to 5%
Rimbach & Dammhahn unpubl.	CORT, YM, Urban	NA	Discarded, could not fix the variance
Rimbach & Dammhahn unpubl.	CORT, WM, NonUrban	NA	Discarded, could not fix the variance and mean
Rimbach & Dammhahn unpubl.	CORT, BV, NonUrban	2	Corrected
Rimbach & Dammhahn unpubl.	Mass, urban	2	Corrected
Solaro & Sarasola 2019	Innovation, latency, NonUrban	NA	Discarded, could not fix the variance
Stansell *et al.* 2022	Boldness, NonUrban	NA	Discarded nonurban because off with 20%
Thompson & Morand-Ferron 2019	Latency to solve, Nonurban, Juv	NA	Accepted, could not fix but because high right skew and close to 5%
Thompson & Morand-Ferron 2019	Incorrect cache, Nonurban, Juv	NA	Accepted, could not fix but because high right skew and close to 5%
Thompson & Morand-Ferron 2019	Latency learning, urban, adult	1	Corrected
Thompson *et al.* 2018	Hop duration, NonUrban, Adult	3	Corrected
Thompson *et al.* 2018	Number of tree visited, nonurban, adult	NA	Accepted, could not fix but close to 5%
Thompson *et al.* 2018	Flight duration, nonurban, adult	NA	Accepted, could not fix but a little skew but close to 5%
Thompson *et al.* 2018	Hop duration, urban, adult	1	Corrected
Tüzün *et al.* 2017	Mass, urban	2	Corrected

Table S4. Summary of estimates discarded due to impossibility of variance estimation

Paper	**Traits**	**Habitat**	**Model type**
Bar-Ziv *et al.* 2023	Boldness:FID:jackdal	urban urban & non-urban	IO-LMM AD-LMM
Dominoni *et al.* 2015	Testis size	urban & non-urban urban & non-urban	IO-LMM AD-LMM
Garitano-Zavala *et al.* 2022	Innovation: Latency to solve	non-urban	IO-LMM
Grunst *et al.* 2014	CORT_contextA	urban & non-urban non-urban	IO-LMM AD-LMM
Harten *et al.* 2021	Boldness: prop. Landing (female)	non-urban non-urban	IO-LMM AD-LMM
Heppner *et al.* 2023	Body mass (Juvenile)	urban & non-urban	IO-LMM
Huang *et al.* 2020	Neophobia: latency score differences	urban urban	IO-LMM AD-LMM
Huang *et al.* 2020	CORT_contextB	urban urban	IO-LMM AD-LMM
Kozlovsky *et al.* 2017	Neophobia: Latency to approach	urban & non-urban	IO-LMM
Kozlovsky *et al.* 2017	Associative learning: Latency to solve	urban	IO-LMM
Mazza & Guenther 2021	Activity/exploration: prop. Of activity	urban	AD-LMM
Mazza & Guenther 2021	Innovation: Latency to solve	urban	AD-LMM
Ouyang *et al.* 2019	CORT_temporal (Juvenile)	urban & non-urban	IO-LMM
Ouyang *et al.* 2019	Body mass (Juvenile)	urban & non-urban	IO-LMM
Papp *et al.* 2015	Innovation: Latency to solve	non-urban non-urban	IO-LMM AD-LMM
Petit unpubl.	Boldness: Latency to emerge (*Apodemus sylvaticus*)	urban urban	IO-LMM AD-LMM
Petit unpubl.	Activity/exploration: prop. Of activity (*Apodemus sylvaticus*)	non-urban	IO-LMM
Prasher *et al.* 2019	Innovation: Latency to solve (Juvenile)	urban & non-urban urban & non-urban	IO-LMM AD-LMM
Prasher *et al.* 2019	Innovation: Latency to solve (Adult)	urban	AD-LMM
Rimbach unpubl.	CORT_temporal	urban urban	IO-LMM AD-LMM
Tabh *et al.* 2022	Body surface temperature	non-urban	IO-LMM
Thompson & Morand-Ferron 2019	Associative learning: Latency to solve (Juvenile)	urban & non-urban urban & non-urban	IO-LMM AD-LMM
Thompson & Morand-Ferron 2019	Associative learning: Latency to solve (Adult)	urban & non-urban non-urban	IO-LMM AD-LMM
Thompson & Morand-Ferron 2019	Associative learning: Incorrect cache (Juvenile)	urban & non-urban non-urban	IO-LMM AD-LMM
Thompson & Morand-Ferron 2019	Associative learning: Incorrect cache (Adult)	urban & non-urban urban	IO-LMM AD-LMM
Thompson *et al.* 2018	Activity/exploration: Flight duration (Juvenile)	non-urban non-urban	IO-LMM AD-LMM

Thompson *et al.* 2018	Activity/exploration: Flight duration (Adult)	urban	IO-LMM
Thompson *et al.* 2018	Activity/exploration: Hop duration (Juvenile)	non-urban	IO-LMM
Thompson *et al.* 2018	Activity/exploration: Number of tree (Juvenile)	non-urban	IO-LMM

Text S6. Copyright usage

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Appendix - Results

Overall meta-analysis of lnCVR (variance from AD-LMMs)

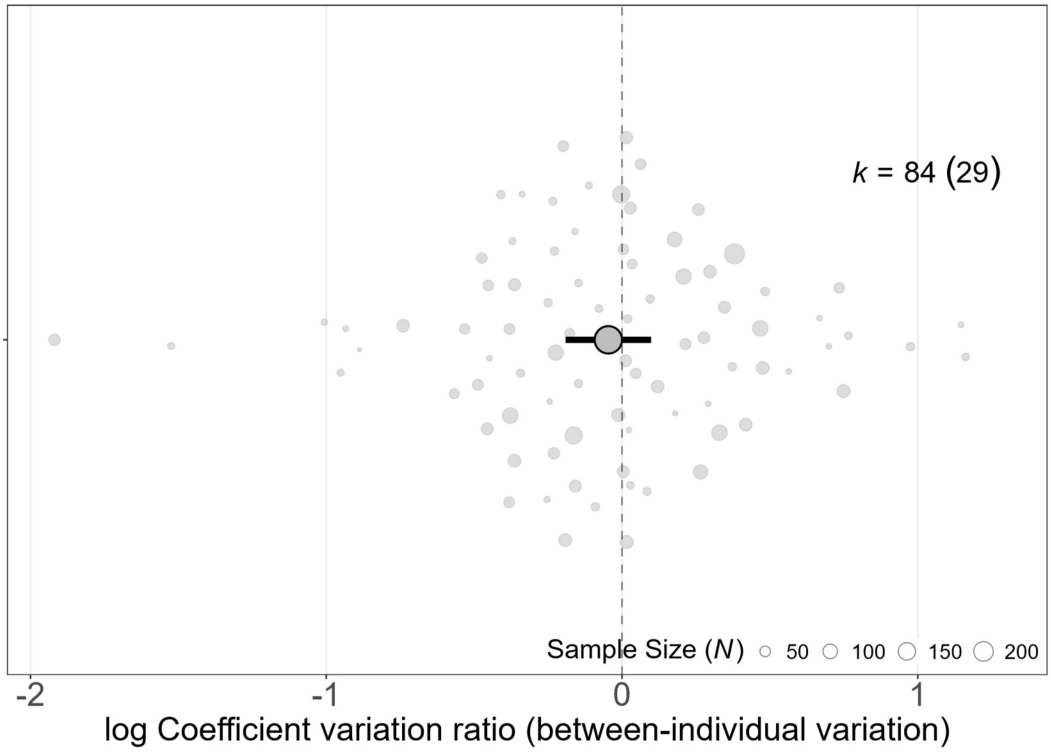

Figure S2. Overall model estimates for lnCVR assessing differences between urban and non-urban populations for between-individual variation calculated from AD-LMMs (Model 1). Positive values on the x axis represent higher between-individual variation in urban populations compared to non-urban populations whereas negative values represent the opposite phenomena. The large grey point represents the overall model estimate. The thick black line shows the 95% confidence intervals. Transparent small grey dots show the raw data (their size is scaled according to their sample size from which they were estimated). k is the number of observations supplemented with the number of studies between brackets.

Table S5. Meta-analytic model estimates explaining overall variation in lnCVR of between-individual variation (Model 1, i.e. differences in between-individual variance between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Intercept	-0.046	-0.191	0.098

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	29
Phylogeny	0.000	0.00	21
Species ID	0.049	20.43	21
Observation ID	0.167	69.07	84
	I^2_{total}:	89.50	

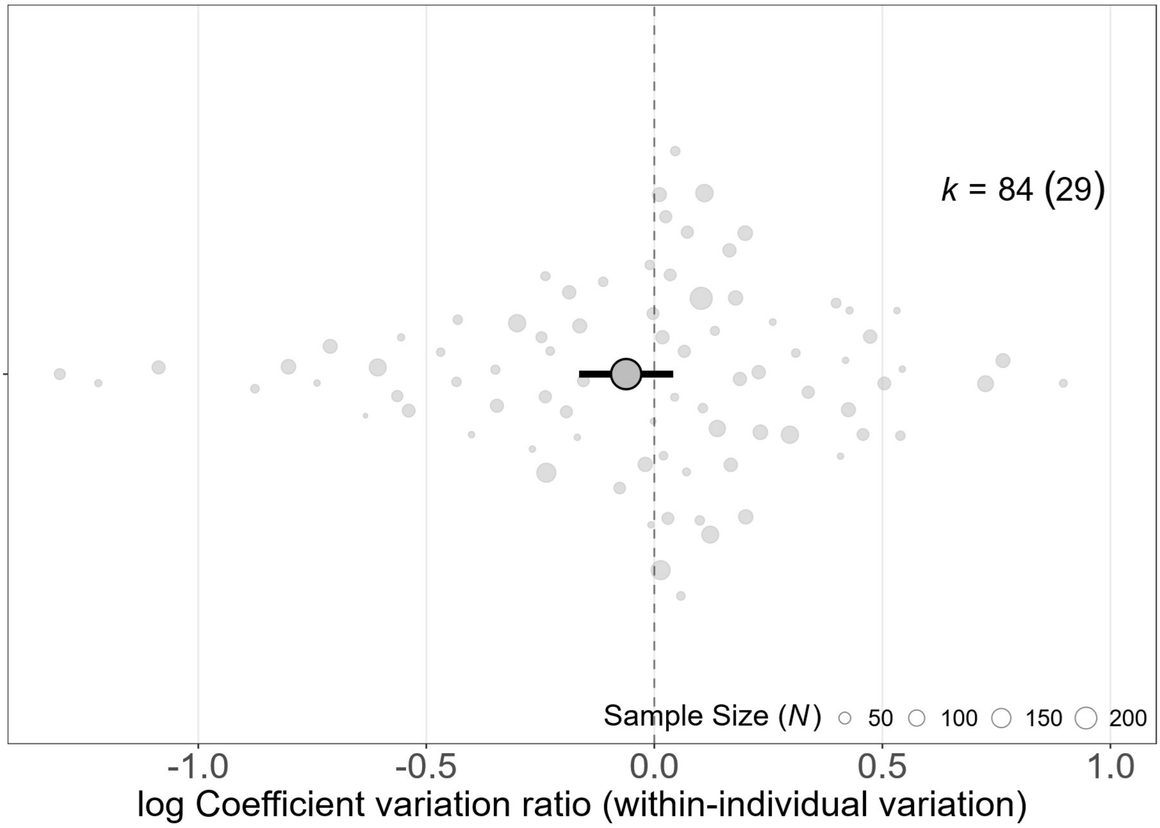

Figure S3. Overall model estimates for lnCVR assessing differences between urban and non-urban populations for within-individual variation calculated from AD-LMMs (Model 3). Positive values on the x axis represent higher within-individual variation in urban populations compared to non-urban populations whereas negative values represent the opposite phenomena. The large grey point represents the overall model estimate. The thick black line shows the 95% confidence intervals. Transparent small grey dots show the raw data (their size is scaled according to their sample size from which they were estimated). k is the number of observations supplemented with the number of studies between brackets.

Table S6. Meta-analytic model estimates explaining overall variation in lnCVR of within-individual variation (Model 3, i.e. differences in within-individual variance between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Intercept	-0.062	-0.165	0.041

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	29
Phylogeny	0.000	0.00	21
Species ID	0.012	7.86	21
Observation ID	0.134	84.75	84
	I^2_{total}:	92.61	

Meta-analysis of lnCVR per trait (variance from AD-LMMs)

Table S7. Meta-analytic model estimates explaining variation in lnCVR of between-individual variation per phenotypic trait (Model 2, i.e. differences in between-individual variance per phenotypic trait between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Behaviour	-0.038	-0.211	0.136
Cognition	-0.133	-0.494	0.227
Morphology	-0.081	-0.403	0.241
Physiology	0.297	-0.182	0.777

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	29
Phylogeny	0.000	0.00	21
Species ID	0.051	20.99	21
Observation ID	0.168	68.66	84
	I^2_{total}:	89.65	

Table S8. Meta-analytic model estimates explaining variation in lnCVR of within-individual variation per phenotypic trait (Model 4, i.e. differences in within-individual variance per phenotypic trait between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Behaviour	-0.073	-0.205	0.059
Cognition	0.125	-0.173	0.423
Morphology	0.053	-0.222	0.329
Physiology	-0.227	-0.619	0.165

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	29
Phylogeny	0.000	0.00	21
Species ID	0.019	11.80	21
Observation ID	0.131	80.98	84
	I^2_{total}:	92.78	

Meta-analysis of lnCVR per behaviour (variance from AD-LMM)

Table S9. Meta-analytic model estimates explaining variation in lnCVR of within-individual variation per behavioural trait (Model 5, i.e. differences in within-individual variance per behavioural trait between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Activity/Exploration	-0.069	-0.251	0.113
Aggression	0.025	-0.302	0.351
Boldness	0.010	-0.268	0.288

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	16
Phylogeny	0.000	0.00	13
Species ID	0.022	13.03	13
Observation ID	0.136	80.88	52
	I^2_{total}:	93.91	

Meta-analysis of lnCVR with all moderators (variance from AD-LMMs)

Table S10. Meta-analytic model estimates explaining variation in lnCVR of between-individual variation including all moderators of interest (Model 6, i.e. differences in between-individual variance between urban and non-urban populations calculated using AD-LMMs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Intercept (Behaviour_Both_short_1)	-0.634	-1.499	0.231
Cognition	-0.061	-0.437	0.315
Morphology	0.000	-0.361	0.360
Physiology	0.382	-0.108	0.872
Field	0.001	-0.805	0.807
Lab	-0.055	-0.851	0.742
Interval_veryshort	0.138	-0.198	0.474
Number of factor in AD-LMM	0.209	0.044	0.374

Random effect & residual variance

	estimate	I^2	k
Study ID	0.040	17.19	29
Phylogeny	0.004	1.86	21
Species ID	0.000	0.00	21
Observation ID	0.162	70.03	84
	I^2_{total}:	89.08	

Table S11. Meta-analytic model estimates explaining variation in lnCVR of within-individual variation including all moderators of interest (Model 7, i.e. differences in within-individual variance between urban and non-urban populations calculated using AD-LMMsqs). CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

Fixed Effect

	estimate	95% CI	
Intercept (Behaviour_Both_short_1)	-0.447	-1.175	0.281
Cognition	0.118	-0.204	0.441
Morphology	0.137	-0.184	0.458
Physiology	-0.218	-0.632	0.196
Field	0.080	-0.595	0.755
Lab	0.163	-0.507	0.832
Interval_veryshort	0.129	-0.164	0.422
Number of variable in AD-LMM	0.055	-0.085	0.195

Random effect & residual variance

	estimate	I^2	k
Study ID	0.000	0.00	29
Phylogeny	0.000	0.00	21
Species ID	0.023	13.81	21
Observation ID	0.133	79.24	84
	I^2_{total}:	93.05	

Sensitivity analysis

IOM-LMM versus AD-LMM

Table S12. Meta-analytic model estimates explaining variation in lnCVR of between-individual variation comparing variance partitioning done via IOM-LMMs with variance partitioning done via AD-LMMs. a) Comparison between model 8 and model 1. b) Comparison between model 9 and model 2. CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

	IOM-LMM			**AD-LMM**		
a) Intercept	*model 8*			*model 1*		
	estimate	95% CI		estimate	95% CI	
Intercept	**0.0073**	-0.137	0.151	**-0.046**	-0.191	0.098
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.000**	0.00	27	**0.00**	0.00	29
Phylogeny	**0.000**	0.00	20	**0.00**	0.00	21
Species ID	**0.030**	10.94	20	**0.049**	20.43	21
Observation ID	**0.234**	85.97	78	**0.167**	69.07	84
b) Type of trait	*model 9*			*model 2*		
	estimate	95% CI		estimate	95% CI	
Behaviour	**0.002**	-0.146	0.149	**-0.038**	-0.211	0.136
Cognition	**-0.294**	-0.650	0.062	**-0.133**	-0.494	0.227
Morphology	**0.076**	-0.292	0.444	**-0.081**	-0.403	0.241
Physiology	**0.501**	-0.098	1.101	**0.297**	-0.182	0.777

Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.00**	0.00	27	**0.000**	0.00	29
Phylogeny	**0.00**	0.00	20	**0.000**	0.00	21
Species ID	**0.009**	3.60	20	**0.051**	20.99	21
Observation ID	**0.239**	93.12	78	**0.168**	68.66	84

Table S13. Meta-analytic model estimates explaining variation in lnCVR of within-individual variation comparing variance partitioning done via IOM-LMMs with variance partitioning done via AD-LMMs. a) Comparison between model 10 and model 3. b) Comparison between model 11 and model 4. c) Comparison between model 12 and model 5. CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

	IOM-LMM			**AD-LMM**		
a) Intercept	*model 10*			*model 3*		
	estimate	95% CI		estimate	95% CI	
Intercept	**-0.053**	-0.155	0.048	**-0.062**	-0.165	0.041
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.000**	0.00	27	**0.00**	0.00	29
Phylogeny	**0.000**	0.00	20	**0.00**	0.00	21
Species ID	**0.017**	14.10	20	**0.012**	7.86	21
Observation ID	**0.095**	77.13	78	**0.134**	84.75	84
b) Type of trait	*model 11*			*model 4*		
	estimate	95% CI		estimate	95% CI	
Behaviour	**-0.057**	-0.184	0.071	**-0.073**	-0.205	0.059
Cognition	**0.062**	-0.197	0.321	**0.125**	-0.173	0.423
Morphology	**0.001**	-0.257	0.276	**0.053**	-0.222	0.329
Physiology	**-0.162**	-0.606	0.281	**-0.227**	-0.619	0.165
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.000**	0.00	27	**0.000**	0.00	29
Phylogeny	**0.000**	0.00	20	**0.000**	0.00	21
Species ID	**0.024**	18.52	20	**0.019**	11.80	21
Observation ID	**0.095**	73.20	78	**0.131**	80.98	84
c) Type of behaviour	*model 12*			*model 5*		
	estimate	95% CI		estimate	95% CI	
Activity/exploration	**0.001**	-0.154	0.156	**-0.069**	-0.251	0.113
Aggression	**0.011**	-0.278	0.301	**0.025**	-0.302	0.351
Boldness	**-0.072**	-0.298	0.154	**0.010**	-0.268	0.288
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.003**	2.58	17	**0.000**	0.00	16
Phylogeny	**0.000**	0.00	13	**0.000**	0.00	13
Species ID	**0.009**	7.55	13	**0.022**	13.03	13
Observation ID	**0.094**	81.32	51	**0.136**	80.88	52

Bird versus all other taxa combined

Table S1. Meta-analytic model estimates explaining variation in lnCVR of a) between-individual and b) within-individual variation comparing effect size coming only from bird taxa with effect size coming only from other taxa than bird. Variance estimates from AD-LMMs. CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations.

	Only bird			**All other taxa combined**		
a) Between-individual	*model 13*			*model 15*		
	estimate	95% CI		estimate	95% CI	
Intercept	**-0.030**	-0.299	0.240	**-0.074**	-0.217	0.068
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.000**	0.00	17	**0.00**	0.00	12
Phylogeny	**0.000**	0.00	11	**0.002**	1.35	10
Species ID	**0.138**	39.74	11	**0.000**	0.00	10
Observation ID	**0.179**	51.39	52	**0.122**	84.90	32
b) Within-individual	*model 14*			*model 16*		
	estimate	95% CI		estimate	95% CI	
Intercept	**-0.069**	-0.200	0.063	**-0.074**	-0.244	0.096
Random effect	estimate	I^2	k	estimate	I^2	k
Study ID	**0.00**	0.00	17	**0.000**	0.00	12
Phylogeny	**0.00**	0.00	11	**0.000**	0.00	10
Species ID	**0.007**	4.00	11	**0.028**	19.76	10
Observation ID	**0.154**	88.06	52	**0.105**	73.57	32

Publication bias

Table S2. Meta-analytic model estimates explaining variation in lnCVR due to small-study effect of a) between-individual and b) within-individual variation. Variance estimated from AD-LMMs. CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations, R^2 is the marginal coefficient of determination.

Small-study effect				
a) Between-individual				
	estimate	95% CI		R^2
Intercept	0.088	-0.404	0.581	
sqrt_inv_eff_ss	-0.437	-1.967	1.092	**0.006**
Random effect	estimate	I^2		k
Study ID	0.000	0.00		29
Phylogeny	0.000	0.00		21
Species ID	0.050	20.72		21
Observation ID	0.168	68.89		84
b) Within-individual				
	estimate	95% CI		R^2
Intercept	-0.049	-0.317	0.416	
sqrt_inv_eff_ss	-0.355	-1.501	0.791	**0.006**

Random effect	estimate	I^2	k
Study ID	0.00	0.00	29
Phylogeny	0.00	0.00	21
Species ID	0.010	6.44	21
Observation ID	0.137	86.19	84

Table 16. Meta-analytic model estimates explaining variation in lnCVR due to decline effect of a) between-individual and b) within-individual variation. Variance estimated from AD-LMMs. CI stands for confidence interval, I^2 for heterogeneity and k for the number of observations, R^2 is the marginal coefficient of determination.

Decline effect				
a) Between-individual				
	estimate	95% CI		R^2
Intercept	-0.054	-0.202	0.093	
pub_year_c	0.024	-0.028	0.076	**0.013**
Random effect	estimate	I^2		k
Study ID	0.000	0.00		29
Phylogeny	0.000	0.00		21
Species ID	0.052	21.49		21
Observation ID	0.166	68.11		84
b) Within-individual				
	estimate	95% CI		R^2
Intercept	-0.061	-0.166	0.044	
pub_year_c	-0.008	-0.050	0.034	**0.002**
Random effect	estimate	I^2		k
Study ID	0.00	0.00		29
Phylogeny	0.00	0.00		21
Species ID	0.014	8.49		21
Observation ID	0.135	84.23		84

Appendix - Literature

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