Behavioral variation changes across an urbanization gradient in a population of great tits

Gervais Laura[1,2,] Thompson Megan[1,3], de Villemereuil Pierre[4,5], Burkhard Tracy[1,6], Teplitsky Céline[1], Class Barbara[17], Réale Denis[3], Charmantier Anne[1]

1. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
2. Station d'Ecologie Théorique et Expérimentale du CNRS, UAR 2029, Moulis, France
3. Département des sciences biologiques, Université du Québec à Montréal, 141 Avenue du Président-Kennedy, Montréal, Quebec, Canada H2X 1Y4
4. Institut de Systématique, Évolution, Biodiversité (ISYEB), École Pratique des Hautes Études | PSL, MNHN, CNRS, SU, UA, Paris, France
5. Institut Universitaire de France (IUF), France
6. ISEM: Institut des Sciences de l'Evolution de Montpellier ISEM, Univ Montpellier, CNRS, IRD, Montpellier, France
7. Department of Biology, Ludwig-Maximilians-Universität München, Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany

Corresponding author : Laura Gervais - lauragervais51@gmail.com

Abstract :

Urbanization is occurring globally at an unprecedented rate and, despite the eco-evolutionary importance of individual variation in adaptive traits, we still have very limited insight on how phenotypic variation is modified by anthropogenic environmental change. Urbanization can increase individual differences in some contexts, but whether this is generalizable to behavioral traits, which directly affect how organisms interact with and respond to environmental variation, is not known. Here we examine variation across three behavioral traits (breath rate, handling aggression and exploration behaviour) in great tits *Parus major* along an urbanization gradient (n > 1000 phenotyped individuals accross nine years) to determine whether among-individual variance in behavior increases with the degree of urbanization and spatial heterogeneity. Urban birds were more aggressive and faster explorers than forest birds. They also displayed higher among-individual variation for breath rate and aggression (1.5 and 1.8 times increase, respectively), but lower among-individual variation for exploration (3.3 times decrease). Only individual variation in exploration clearly changed along the continuous urbanization gradient; individual differences in exploration declined with increasing impervious surface area. Collectively our results suggest that individuals in the city may have more diverse behavioral stress responses, yet display stronger similarity in their behavioral responses to novelty. Our results suggest that generalizations about urbanization's impacts on behavioral variation are not appropriate. Instead our results suggest that urbanization can shape individual variation differently across behavioral functions and we may expect decreased individual diversity in urban birds for traits related to behavioral response to novelty.

Key words: among-individual variance, city, coefficient of variation, multiple-spatial scale, repeatability, trait variation

Introduction

Environmental change is a widespread process that occurs naturally across space and time, but humans have caused changes at an unprecedented scale and speed, that pose new challenges to many organisms (Merilä, 2012; Pelletier & Coltman, 2018; Vitousek et al., 1997). One of the main challenges is urbanization, *i.e.* the ultimate replacement of natural landscapes by man-made infrastructures (Dansereau 1957), resulting in a variety of environmental alterations, such as increased noise pollution, impervious surfaces or disturbance by human presence (Niemelä et al., 2011). While some organisms struggle in the face of new selective pressures induced by these changes, others survive or even thrive in urban environments, based on features they acquired in the past or by adjusting their phenotype via individual plasticity or genetic evolution (Hendry et al., 2008; Merilä & Hendry, 2014).

An increasing number of studies has documented urban-associated phenotypic change in a variety of taxa and traits (*e.g.* pigmentation in Lepidoptera moths, Kettlewell, 1956; beak morphology and vocal performance in house finches *Haemorhous mexicanus*, Giraudeau et al., 2014; toxin tolerance in killifish, Reid et al., 2016). To date, studies of urban-associated phenotypic shifts have mostly reported changes in mean phenotypes. Phenotypic change can occur not only through a shift in mean, but also through a shift in variation, with important implications for eco-evolutionary processes in the context of urban adaptation. Indeed, phenotypic variation is central to any evolutionary response to environmental change as it is the prerequisite for selection to act and thus influences the direction and magnitude of the response to selection. Furthermore, phenotypic variance can itself be shaped by eco-evolutionary processes (*e.g.* plasticity, dispersal, (epi)genetic variation, Des Roches et al., 2018; Draghi, 2019; Reed et al., 2011). In the framework of urban evolutionary ecology, however, surprisingly little is known about the relationship between urbanization and phenotypic variation. Recent reviews hypothesized that phenotypic variation could increase in urban environments due to multiple non-exclusive mechanisms (*e.g.*, limited dispersal, relaxed or heterogeneous selection, increased exposure to mutagens, developmental plasticity; Capilla-Lasheras et al., 2022; Thompson et al., 2022). To date, however, fewer than ten studies have investigated and supported this hypothesis (*e.g.* morphology in great tit *Parus major* and blue tits Cyanistes caeruleus; Thompson et al., 2022, life-history traits in bird species globally, n=35 species; Capilla-Lasheras et al., 2022).

Animal behaviour variation has been extensively studied within the personality framework (Réale et al., 2007; Sih et al., 2004; Wolf & Weissing, 2012), a growing field at the intersection between wild quantitative genetics (Charmantier et al., 2014) and behavioral ecology (Dingemanse & Dochtermann, 2014). Specifically, this framework aims at exploring among- versus within-individual (co)variation in behavioral traits, their origin, and their adaptive nature. Despite the abundant studies exploring the within-species diversity in behaviour, few studies have examined how urbanization affects behavioral variation (n=24, published between 2010 and 2022, see Burkhard, Dochtermann & Charmantier (2023) metanalysis on behaviour responses to urban environments for more details). Recent attempts to tackle this question have compared repeatability, *i.e.* the proportion of total phenotypic variation due to among-individual variance, between urban and rural populations (n=24 studies, *e.g.* Dammhahn et al., 2020; Fossett & Hyman, 2021, see Burkhard, Dochtermann & Charmantier, 2023 for the complete list) For example, speckled wood butterflies (*Pararge aegeria*) from urban landscapes were found to be more repeatable in boldness (*i.e.* latency to approach feeder) than rural ones (0.50[0.39-0.56] *vs.* 0.15[0.09-0.22]; Kaiser et al., 2019), which was partly explained by higher among-individual variance paired with lower within-individual variance in butterflies from urban landscapes. In contrast, boldness in song sparrows (*Melospiza melodia*) did not differ between urban and rural habitats (repeatability of 0.24; Fossett & Hyman, 2021), but among and within-individual variances were not reported. However, the absence of differences in these repeatability ratios does not imply the absence of differences in among- and within-individual variance (Dochtermann & Royauté, 2019) between urban and non-urban habitats.

Differences in among-individual variance across habitats may occur if they are underpinned by different genetic variances (*e.g.* due to different heterogeneous selection across habitats, Barrett & Schluter, 2008; Hedrick, 1986). It may also occur due to plasticity in response to the environment experienced during development leading to permanent differences between individuals (*e.g.* due to different exposure to stress during early life, Kristensen et al., 2018; Lazić et al., 2015; Lindström, 1999; see Thompson et al., 2022 for an exhaustive review of underpinned mechanisms). In the literature, urban dwellers have been shown to have higher among-individual variance (*e.g.* in woodchucks (*Marmota monax*); Lehrer et al., 2012 or shrews (*Crocidura russula* & *Sorex araneus*), von Merten et al., 2022). Such diversity might buffer urban populations from new or fluctuating selective pressures if urban individuals exploit a greater diversity of habitats and resources (Møller, 2010). Differences in repeatability may also result from differences in within-individual variation, partly as a result of individual behavioral plasticity. In the literature, most urban dwellers have greater behavioral plasticity (Dammhahn et al., 2020; Hendry et al., 2008; Sol & Lefebvre, 2000), which should help them adjust quickly to novel challenges in the city and, in some cases, could also hinder or facilitate adaptive evolution (Caspi et al., 2022). Both among and within-individual components are likely to play an important role in urban adaptation (Lowry et al., 2013). In short, 1) among-individual variance is frequently established as the upper limit for genetic variance, contributing to population persistence and facilitating adaptive evolution (Hughes et al., 2008) and 2) within-individual variance has been demonstrated to either constrain (Diamond & Martin, 2016; Huey et al., 2003) or, in certain cases, facilitate evolution (Caspi et al., 2022; Levis & Pfennig, 2016), and in some instances, even undergo evolutionary changes itself (Diamond et al., 2018). Hence, examining how urbanization impacts behavioral variation would allow a more comprehensive view on the processes that impact urban populations and their evolutionary potential.

Quantifying the degree of urbanization and its impacts is both challenging and crucial because sampling locations classified as urban and rural are not necessarily homogeneous. Within cities for example, the amount of urbanization at sampling locations can vary (*e.g.*, city center versus urban park) and cities can be highly heterogeneous depending on the spatial or temporal scale considered (Mohring et al., 2021; Moll et al., 2020; Strubbe et al., 2020). Therefore, the ability to detect landscape effects linked to urbanization may depend on which urban locations are considered (Evans et al., 2009) or the choice of appropriate spatial scale (Levin, 1992; Martin, 2018). For example, urban grasshoppers were shyer than rural grasshoppers only when urbanization was measured at a scale of 0.5 km, but not 3 and 5 km (Waterschoot et al., 2023). Despite growing availability of remote sensing data, the spatial scale at which environmental urbanization impacts organisms is rarely known (Moll et al., 2020; Perrier et al., 2018; Uchida et al., 2021) and even less is known about how it can influence conclusions of eco-evolutionary investigations.

Here we used a long-term monitoring study of great tits living in an urban mosaic, ranging from a natural forest habitat to highly urbanized areas, to explore differences in among- and within-individual variance in behaviors along an urbanization gradient assessed at multiple spatial scales. In this study system, urban great tits show slightly reduced gene flow compared to forest areas, with some genomic evidence of local adaptation (Perrier et al., 2018) which can promote differences in phenotypic variation between habitats. Previous research has shown that urban great tits are more aggressive, faster explorers and have faster breath rates than those from the forest (Caizergues et al., 2022), but less is known about differences in variance.

We tested if phenotypic variance was higher in the city in these three behaviors compared to the forest (P1). Throughout, we determined whether differences in phenotypic variance were due to differences in among-individual variance, differences in within-individual variance, or both. For most species, cities offer more spatially heterogeneous territories than wild habitats (Alberti et al., 2020; Cadenasso et al., 2007), which could be associated with urban selection for more diverse behavioral types. Consequently, we expect that due to higher environmental heterogeneity in the city for breeding great tits, we will find more among-individual variance in the city (P2a) than in the forest and this will be consistent across different sampling locations within the city (P2b). Finally, within the city, we expect to find greater among-individual variance within sampling locations that have the highest spatial heterogeneity in urbanization (P3) or that are the most urbanized (P4). We did not make directional predictions regarding differences in within-individual variation according to urbanization, since there are mixed findings in the literature (*e.g.* higher within-individual variation in city, Dammhahn et al., 2020; in forest Prange et al., 2004; no difference between city and forest, Sprau & Dingemanse, 2017).

Mat & Met

Study system

Great tits (*Parus major*) were monitored in southern France in La Rouvière (ROU), an oak forest 20 km northwest of Montpellier that has been monitored since 1992 with 230 nest boxes for blue tits (*Cyanistes caeruleus*) and great tits (Blondel et al., 2006). We also monitored tits at eight locations across an urbanization gradient in the city of Montpellier, which includes around 247 nest boxes monitored since 2011 and hosting mostly great tits (Charmantier et al., 2017; Demeyrier et al., 2016)(Figure 1). During the breeding season, nest boxes were visited at least weekly to follow reproduction. Adults were captured in nest boxes when feedingtheir 10-15 days old nestlings. All nestlings and adults were individually ringed with a unique metal ring provided by the French CRBPO (Centre de Recherche par le Baguage des Populations d'Oiseaux) and parents underwent behavioral assays (see below for more details). Behavioral assays were performed on both forest and urban parents captured between 2014 and 2022. See Table S1 for summary statistics on the traits studied.

All protocols were approved by the local ethics committee for animal experimentation of Languedoc Roussillon (CEEA-LR. 05/06/2018) and regional institutions (Prefecture decree no. 2012167-003). The captures were carried out under personal ringing permits issued by the CRBPO for the research ringing program number 369.

Behavioral assays and description

Once a bird was captured in its nest box, we assessed two reactions to the stress of being handled. First, we immediately recorded its handling aggression (HA) score as soon as we removed the bird from the nest box. The bird was handled while facing away from the observer and provoked with a finger of the free hand. The observer assigned a score ranging from 0 (unresponsive bird) to 3 (aggressive bird spreading wings and tail) in increments of 0.5 following a standardized protocol (see FigS2A in Caizergues et al., 2022 and table S1 in Dubuc-Messier et al., 2017). Immediately after the HA test, the bird was isolated in a cloth bag for 5 minutes for a standardized period of rest. Following these 5 minutes, the bird was removed from the bag and held on its back by the handler, who measured its breath rate index (BRI). From 2013 to 2016, BRI was estimated as the number of chest movements during 30 seconds, whereas since 2017, the protocol was updated to measure the time to complete 30 chest movements (Caizergues et al., 2022, Figure S2B). Measurements from 2013 to 2016 were therefore converted to approximate the time required to complete 30 chest movements to obtain the measurements on the same scale. BRI was taken consecutively twice in a row and averaged across these two measures. We consider breath rate index a behavioral trait because breath rate reflects both the physiological function of respiration (*i.e.*, O2 and CO2 exchange) and respiratory behaviour (*i.e.,* breath rate can be altered by classical and operant conditioning, Ley, 1994). BRI correlates with heart rate under restraint (Dubuc Messier et al., 2017) and is often used as a proxy for acute stress response (Carere & van Oers, 2004; Krams et al., 2013), with a lower BRI (and therefore faster breath rate) reflecting a greater stress response. Finally, the bird underwent an open field test using an open field cage with similar dimensions as in Stuber et al., (2013), to evaluate its exploration behaviour in a novel environment (Caizergues et al., 2022; Stuber et al., 2013). The bird was placed in an acclimation compartment adjacent to the main open-field cage for 2 min before being released into the exploration room. The videos were analyzed using the BORIS software (Friard & Gamba, 2016) to generate an exploration score (ES) by counting the number of flights and hops during the 4 min exploration trial. For a detailed protocol see Charmantier et al., (2017) and Caizergues et al., (2022), figure S3. Note that these three behaviors are not correlated among or within individual great tits in our populations (Caizergues et al., 2022).

Quantification of urbanization

We quantified the degree of urbanization at each nest box where at least one parent was captured (N = 301) using the proportion of impervious surface area (ISA), defined as sealed non-natural surfaces (*e.g.*, roads, railways, buildings), using the imperviousness density raster datasets from the Copernicus on-line database (resolution 10m. tiles: E38N22 & E38N23. Projection: LAEA EPSG 3035; EEA, 2020). ISA has previously been shown to correlate with other urban factors such as high temperature (Diamond & Martin, 2020), high noise and light pollution, low tree cover, and short distance from roads (Szulkin et al., 2020). The spatial scale at which environmental urbanization impacts organisms is rarely known and may vary across focal traits (Uchida et al., 2021; Waterschoot et al., 2023) and so we quantified the proportion of ISA around each nest box at three different spatial scales: 100, 250, and 1000 meters. We chose this range to explore different effects of urbanization at small, medium, and large spatial scales for great tits as they tend to have smaller home ranges during breeding (approx. 60-160m, van Overveld et al., 2015; Wilkin et al., 2006) but can have extensive natal dispersal (up to 900m on average in females, Dingemanse et al., 2003; Garant et al., 2005; Szulkin & Sheldon, 2008). Using circular radius buffers at these spatial scales in QGIS (v3.22.0; QGIS Development Team 2022), we counted the number of pixels associated with impervious surfaces and calculated an ISA proportion index (range = 0-1. Where 1 = all ISA) around each nest box by dividing by the total number of pixels within each buffer. When considering all nest boxes together, the amount of urbanization correlated moderately between the three spatial scales (rho > 0.75), with most discrepancy at nest boxes in the middle or at the edges of urban parks (Figure 1). We classified sampling locations as forest if the mean ISA measurements were below 5% (ROU) and urban if they were above 5% (CEF, BOT, MOS, MAS, FONT, GRAM, FAC, ZOO, Figure 1). The mean proportion of ISA around each forest nest box was zero at 100 and 250 meters and 0.0007 at 1000 meters, while the mean proportion of ISA around each urban nest box was 0.48, 0.51, and 0.53 at 100, 250, and 1000 meters, respectively, and ranged from 0 to 1 (see Table S2 for more details for each sampling location and Figure 1).

To assess spatial heterogeneity within the city, we also calculated the within-site variance of ISA (Table S2).

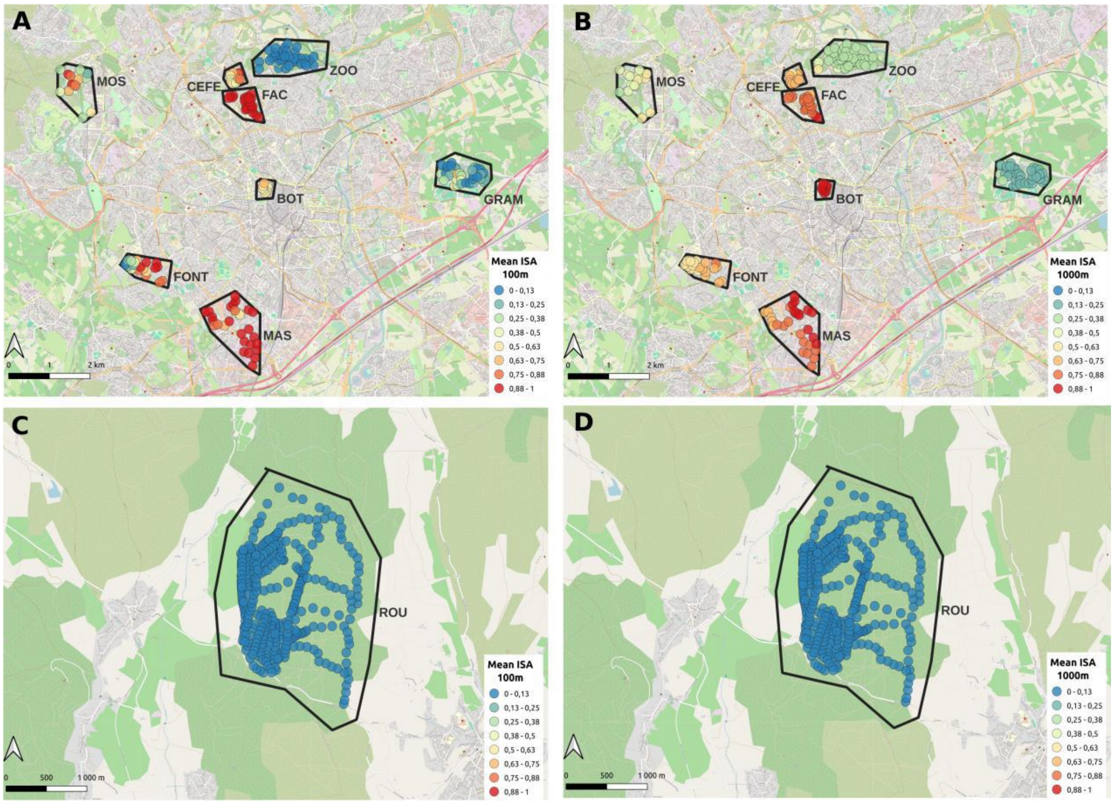


Figure 1. Spatial map of the eight urban locations (A,B) and forest location (C,D) and their associated proportion of urbanization at 100 m (A,C) and 1000 m (B,D) around each nest-box in the Montpelier area, France. Each sampling location is delineated by a black polygon. Each circle corresponds to a buffer around a nest. Each buffer is characterized by the average proportion of ISA (*i.e.,* impervious surface area) where increasing urbanization moves towards red.

Statistical analysis

We investigated differences in phenotypic means and variances between urban and forest habitats across the three behavioral traits which are known to be repeatable, not correlated, and have habitat-specific means (*i.e.,* urban *vs.* forest mean, Caizergues et al., 2022). For each trait, we used a Bayesian generalized linear mixed effects model (GLMM) that allowed the mean, among-, and within-individual variances to differ between habitats (also known as heterogeneous variance model, Gianola, 1986). We chose the error distribution to fit each trait, *i.e.* Gaussian for BRI, threshold for HA, and Poisson for ES. We ensured that effective sample sizes for each model were higher than 1000. We assessed the convergence of all parameters graphically as well as using the Heidelberger and Walch test of the 'coda' package (Plummer et al., 2006). Finally, we graphically controlled the residual assumptions with diagnostic.mcmc from the MCMC.qpcr package (Matz et al., 2013) when residuals were not fixed in the model.

a) Comparison between city and forest

To assess whether phenotypic (P1) and among-individual variance (P2a) is higher in urban than forest habitats, we first ran a heterogeneous variance model with two habitat categories (*i.e.,* two separate random intercepts for urban and forest groups of individuals). We estimated the phenotypic mean, among-individual (Vi), annual (Vy) and residual variances (Vr) for each habitat and their corresponding 95% credible intervals. We included individual identity and year as random effects with heterogeneous variance across random effect variances and error variance (model a). For all traits we included an interaction between habitat (urban/forest) and fixed effects known to influence traits: sex and age (adult *vs.* juveniles) (Caizergues et al., 2021, 2022; Charmantier et al., 2017). The interaction between habitat and decimal hour of measure was also fitted as a continuous quadratic fixed effect since behaviour and metabolism can change throughout the day (Caizergues et al., 2020,2022). To additionally account for possible habituation to multiple captures or tests, we included assay (*i.e.,* number of previous assays) as a continuous fixed effect. As the protocol for BRI changed during the study (see Caizergues et al., 2022), we included protocol type as a fixed effect for this trait. Finally, for BRI and HA, we accounted for among-observer variance by fitting observer identity as a random effect and included heterogeneous variance for each habitat like the other random effects. As among-observer variance is not biologically relevant we did not include it in the total phenotypic variance estimate. Thus, we estimated the total phenotypic variance for each habitat type as **Vp=Vi+Vy+Vf+Vr**, where Vf is the variance in biologically relevant fixed effects only (*i.e.* sex and decimal hour of the day linked to circadian rhythm, in our specific case, de Villemereuil et al., 2018).

To compare behavioral means between urban and forest birds we calculated the natural logarithm of the ratio between urban and forest means as **lnRR=log(mean_urb/mean_rur)** for each sex and age category, and its 95 % credible interval. As means and variances are related in many cases, we estimated the mean-standardized coefficient of variation of each variance component such that **CV = sd(variance)/phenotypic trait mean** and its 95 % credible interval. This approach allows a direct comparison of the magnitudes of variation across traits measured on different scales between groups. The posterior distributions of predictions were generated using the phenotypic mean across sex and age categories (table S2). To compare variance between urban and forest birds, we estimated the natural logarithm of the ratio between the coefficients of variations from urban and forest (*i.e.* coefficient of variation ratio, lnCVR, Nakagawa et al., 2014) and its 95 % credible interval such that **lnCVR= log(CV_urb/CV_rur)** for each variance component (lnCVR_P, lnCVR_I, lnCV_R,lnCVR_F, lnCVR_Y for total phenotypic, among-individual, residual, fixed-effect, year components respectively). Traits with a higher mean or variance in urban habitats will have positive lnRR and lnCVR. We also estimated adjusted repeatability **rpt=Vi/Vi+Vy+Vf+Vr** and tested differences in repeatability by calculating the log repeatability ratio **lnRPT= rpt_urb/rpt_rur** to allow comparisons to similar estimates in the literature . We interpret lnRR, lnCVR and lnRPT (*i.e.* effect sizes) as evidence for a difference between urban and forest when 95% CI does not overlap with zero.

b*) Comparison across sampling locations*

To compare whether among-individual variance at each urban sampling location was higher than the forest location (P2b), we ran a heterogeneous variance model for each trait that estimated variance components separately for each of the 9 locations (model b, *i.e.,* nine separate random intercepts grouping individuals by sampling location). The number of observations between sampling locations was fairly balanced except for the urban CEF and BOT locations, for which we have less than 30 individuals (see Supplementary Table S4). The heterogeneous variance model had the same structure as described for model a; we kept the same fixed effects but we removed the interaction term between habitat and sex, age, and the quadratic effect of decimal hour to avoid over-fitting the model. In addition, we fitted homogeneous instead of heterogeneous variance structure across the year and observer random effects as there was no evidence for differences in variance explained by year between urban and forest habitats (HA: LNCVR_Y=-0.14[-2.06;1.89]; BRI: 1[-0.66;3.83]; ES: -0.64[-3.14;2.03]) or observer (HA: LNCVR_O=-0.48 [-1.34, 0.41]; BRI: -0.53 [-1.48, 0.50]). All variance components and derived values were estimated and tested in the same way as outlined above.

c) Phenotypic variance across the urban gradient

Finally, to investigate whether among-individual variance within the city increased with the level of spatial heterogeneity (P3) and urbanization (P4), we estimated the strength and direction of the association between the mean-standardized among-individual variances (CVI, from model b mentioned above) with the variance (*i.e.,* spatial heterogeneity) and mean of ISA measures of each sampling location. As the means and variances of ISA were on very different scales, we centered and scaled them (x - mean(x)) / sd(x), where x is mean or variance ISA. We focused only on urban locations because preliminary analyses suggested that the forest location alone drove the correlation for some traits. In addition, two locations within the city had less than 30 observations and high uncertainty around the variances of model b mentioned above, so we decided to exclude these locations (CEF and BOT, table S4, note that conclusions were not sensitive to their inclusion) and used the remaining six urban locations for this analysis. To estimate the correlation between behavioral variance and ISA metrics, we ran a Bayesian regression model on the mean-standardized posterior variance estimated within each iteration of model b, thus generating the uncertainty around the phenotypic mean and variance components. We included both mean ISA and variance ISA as fixed effects, both measured on the same spatial scale. Mean and variance ISA were not colinear as the absolute values of the correlations between both variables were well below 0.8 (Young, 2018) ($\rho_{spearman}$ = -0.12, p-value = 0.793; -0.57, p-value = 0.15; and -0.26, p-value = 0.53 for 100, 250, and 1000m scales, respectively). We used each iteration from model b to run these new models (one model per iteration of model b) with the three different spatial scales of ISA independently. To determine which spatial scale was most relevant, we calculated the model fit by estimating Bayesian-R^2 (*i.e.,* the variance of the predicted values divided by the variance of the predicted values plus the expected variance of the errors, Gelman et al., 2019) and averaged the estimates across the different models generated at each spatial scale. We define here the spatial scale at which the Bayesian-R^2 is the strongest as the “scale of effect” (Martin & Fahrig, 2012).

The analyses for models a and b were conducted using the MCMCglmm package (Hadfield, 2010) with uninformative priors. For our last analysis, the model was run on the posterior distributions generated from the MCMCglmm (model b), independently utilizing the rstanarm package (Goodrich et al., 2018), which allows for linear-regression models. The analyses were performed on R version 4.3.0 (released on 2023-04-21).

Results

1. Birds from the city are faster explorers and more aggressive.

Urban birds were faster explorers (i.e., had higher exploration scores) than forest birds regardless of sex and age (lnRR_male=0.91[0.5; 1.72]; lnRR_female=0.63[0.32; 1.11]; lnRR_adult=0.77[0.44; 1.29]; lnRR_juvenile=0.76[0.41; 1.27]). By contrast, urban and forest birds did not significantly differ in either mean breath rate (lnRR=-0.04[-0.14, 0.05] across sex and age, Figure 2) or mean handling aggression (lnRR_female=-0.1[-0.36; 0.19]). However, we found that handling aggression response varied by sex, with urban males tending to be more aggressive than forest males (i.e. credible interval slightly overlapping zero) ; lnRR_male=0.22[-0.01; 0.43]).

Across urban locations, we observed consistent differences in mean behaviour between urban and forest locations (i.e., effect size of the same sign), but the magnitude and precision of the effect varied between sampling locations (Figure S1, S2). Yet we observed a significant faster breath rate and increased handling aggression at certain city locations, despite the overall trait means being similar between the city and the forest (see Figure S1 and S3).

2. City birds had higher among-individual variance in breath rate and handling aggression but less in exploration than rural ones

a) Breath rate index

We found no evidence that urban birds were phenotypically more variable in breath rate (lnCVR_P=0.04[-0.06;0.16]) than forest birds (Figure 2). This was explained by urban birds having increased among-individual variance (lnCVR_I=0.25[0.03;0.53]) but decreased within-individual variance [lnCVR_R=-0.13[-0.3;0.04]], thus balancing the effect size near zero at the overall phenotypic level. As a result of this difference in among-individual variance and within-individual variance, urban birds tended to be more repeatable in breath rate (credible interval slightly overlapping zero; lnRPT=0.31[-0.05;0.77]). All other variance components were unaffected by habitat (*i.e.* observer, fixed-effect and year variance, Table S3).
Our results showed varying among-individual variance among urban locations, with greater (positive lnCVR_I, in blue, Figure 3B) and lower (negative lnCVR_I, in red, Figure 3A) variance depending on which urban locations were compared to the forest. While the overall trend across city and forest (model a) indicated higher among-individual variance for the city, two of the eight urban locations exhibited lower among-individual variance, although the credible interval overlapped zero (lnCVR_I=-0.19 [-2.05; 0.5] and -0.38 [-2.56; 0.6], for MOS and CEF, respectively). All others urban locations had higher among-individual variance (though the credible

interval overlapped zero for ZOO, MAS and BOT, figure S1). Despite the expectation of greater among-individual variance for more urbanized locations (P4), no consistent pattern was observed in this direction for the breath rate index. For instance, MAS and MOS, which are more urbanized than FONT and GRAM, respectively (all spatial scales confounded - Table S2), displayed lower among-individual variance. Additionally, CEF and FONT, with similar levels of average urbanization (all spatial scales confounded, Table S2), exhibited different among-individual variance. Finally, we observed both greater and lower within-individual variation (positive or negative lnCVR_R) depending on which urban locations were compared to the forest, with no apparent pattern (Figure 3A, upper triangle). See figure S4A,B,C for detailed estimates related to Figure 3.

b) *Handling aggression*

Urban birds were 1.28 times more phenotypically variable in their handling aggression (lnCVR_P=0.25[0.15;0.35]) than forest birds. This was in part attributed to urban birds having 1.5 times more among-individual variance (lnCVR_I=0.41[0.1;0.71]) and 2.53 times more variance attributed to sex, age, and decimal hour (lnCVR_F=0.93[0.2;1.81]). It was not possible to assess whether differences in phenotypic variance could also be due to differences in within-individual variation as this component cannot be estimated in a threshold model. Consistent with the higher among-individual variance, there was evidence that urban birds were more repeatable in handling aggression (lnRPT=0.48[0.2;0.83]). All other variance components remained unchanged (Table S3).

Accounting for between-sampling location variation (model b), all urban sites except CEF (lnCVR_I=-0.17[-0.97; 0.07]) exhibited higher among-individual variance than the forest (*i.e.*, higher lnCVR_I, blue tiles in Figure 3B). The comparison within the city did not reveal a clear pattern due to a lot of heterogeneity in the sign of lnCVR_I (red, white, and blue tiles in Figure 3B, lower triangle) and a considerable amount of uncertainty around the effect size.

c) E*xploration score*

Results for the exploration score were opposite to our predictions for phenotypic variance (P1) and to the patterns found for the first two behaviors. Phenotypic variance for exploration was 2.8 time lower in city than in forest birds (lnCVR_P=-1.03[-1.19;-0.88]). The reduced phenotypic variance variability in exploration among urban birds was explained by urban birds having 3.3 times less among-individual variance (lnCVR_I=-1.2[-1.63;-0.8]) and 1.15 times less variance due to sex, age, and decimal hour (lnCVR_f=-0.14[-0.36;0.02]). There was no evidence of a difference in within-individual variance (lnCVR_R=0.21[-0.16;0.66]) across habitats. Finally, consistent with the lower among-individual variance, there was evidence that urban birds were less repeatable in exploration (lnRPT=-0.24[-0.45;-0.06]). The variance due to the year effect remained unchanged (Table S3).

When we compared the urban locations one by one, we found that all eight urban locations exhibited less among-individual variance than the forest location. Across urban locations, the patterns of effect size for among-individual variance and within-individual variation differences were quite homogeneous (all of the same sign within each triangle, aka same colour) (Figure 3C, upper and lower triangle, respectively).

3. Among-individual variance correlates with urbanization gradient for exploration but not for stress-related behaviors.

When using different spatial scales to estimate the proportion of ISA around each nest-box, the locations classification changed depending on the spatial scale considered (see Figure 1, Table S2). For instance, the botanical garden (BOT) was one of the most urbanized locations (*i.e.*, highest level of mean ISA) at the 1000-m scale (ISA=0.93), but had intermediate levels of urbanization at the 100-m scale (ISA=0.56) because it is a small green haven in the center of town. An examination of which spatial scale of urbanization explained the most variation in among-individual variance (*i.e.*, scale of effect) showed heterogeneous results across traits leading to interesting insight into the relevant scale for each trait. The scale of effect was 250 m for breath rate index (R-squared=0.31), 100 m for handling aggression (R-squared= 0.48), and 1000 meters for exploration score (Rsq=0.63) (Figure S5). Note that although 250 m for the breathing rate index had the highest Bayesian R-squared, 100 and 1000 m were very close (R-squared=0.28 and 0.29 respectively). We will only present the following results for the corresponding scale effect (see Figure S5 for the other scales).

Contrary to our prediction (P3), we found no clear evidence for greater among-individual variance within urban environments that are more spatially heterogeneous in terms of urbanization (*i.e.*, variance in ISA). There was no evidence for greater among-individual variance in BRI and HA in environments with higher levels of urbanization (P4, mean ISA, $\beta_{meanISA}$=0.01[-0.03;0.06] and 0.02[-0.05;0.11], respectively) or greater spatial heterogeneity ($\beta_{varianceISA}$=0.01[-0.006;0.03] and 0.07[-0.02;0.20], respectively, Figure 4A,B and S4A, S4B). In contrast, we found that among-individual variance in exploration score decreased linearly with more urbanized areas within the city (with higher ISA) ($\beta_{meanISA}$=-0.12[-0.23;-0.004], Figure 4C and figure S4C), but there was no evidence of a correlation with spatial heterogeneity ($\beta_{varianceISA=}$-0.07[-0.17;0.07]). Note that the direction of the relationship between among-individual variance and spatial heterogeneity varied depending on the spatial scale analyzed. It changed from positive at small and medium scales to negative at large scales for both the breath rate index and exploration (see Figure S4)

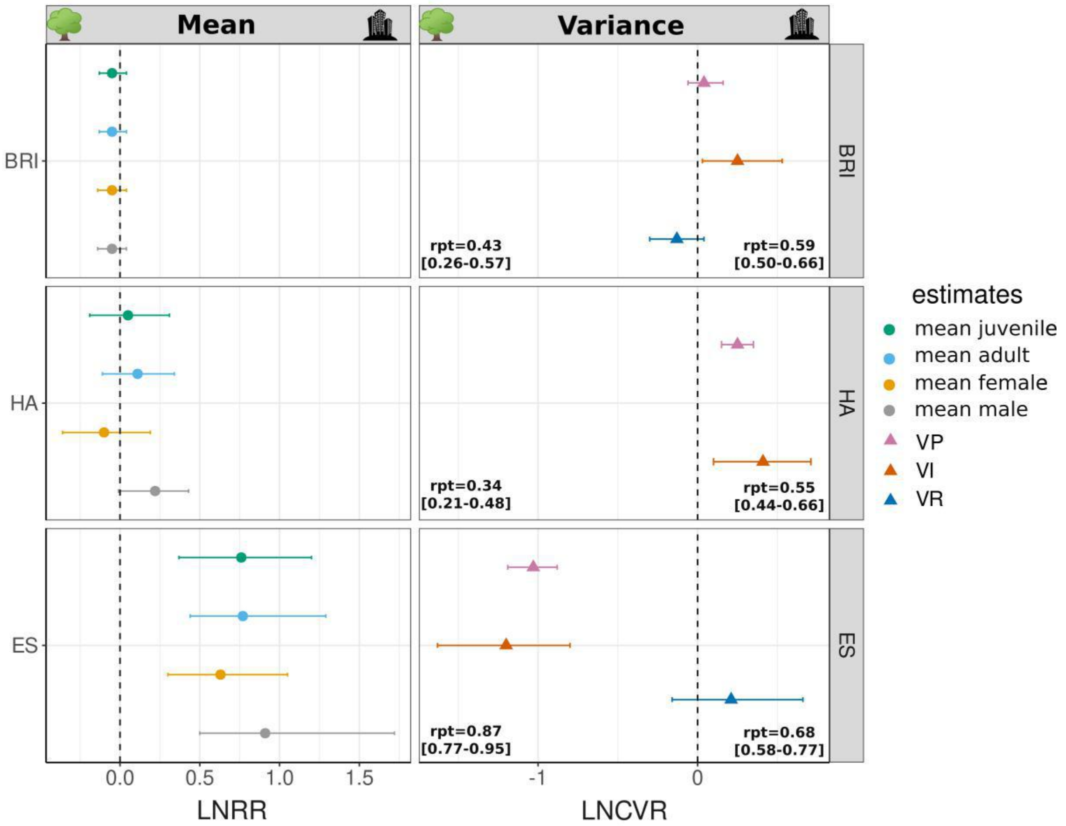


Figure 2. Log-response ratio (lnRR), log-coefficient variance ratio (lnCVR) and their 95% credible interval for behavioral traits (BRI: Breath Rate Index, HA: handling aggression, ES : Exploration score) in great tits in forest *vs.*. urban environment Montpelier area. Traits have a higher mean (lnRR) or are more variable (higher lnCVR) in urban habitats when estimates are positive (*i.e.*, right of the zero dashed line). Rpt corresponds to the repeatability and the 95% credible interval for the urban (on the right) and forest (on the left) habitat. Dots and triangles represent the mean of the posteriors distributions for lnRR and lnCVR respectively.

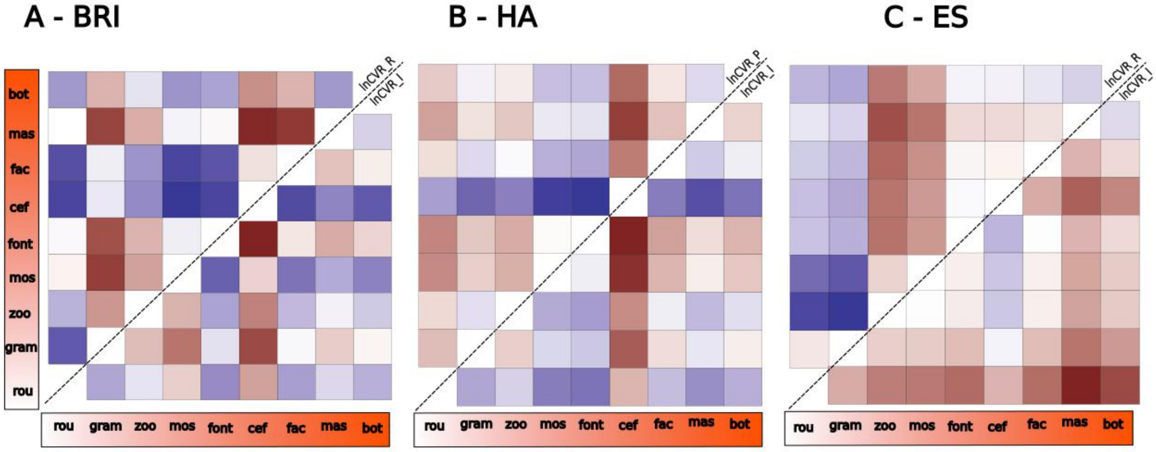


Figure 3. Pattern of pairwise log-coefficient variance ratio (lnCVR) for breath rate index BRI (A), handling aggression HA (B) and exploration score ES (C) between the 9 locations of the study system. The 9 locations are ordered by ascending mean ISA (buffer 1000m), which is also represented in an orange gradient, with dark orange

indicating higher levels of ISA. lnCVR for within individual variance (lnCVR_R) is above the diagonal while lnCVR for among-individual variance (lnCVR_I) is below the diagonal. Note that for HA, we represented lnCVR for total phenotypic variance (lnCVR_P) as the threshold model does not estimate residual variance. Positive, zero and negative lnCVR are shown in blue, white and red respectively. A positive (blue) value means that the location on the x-axis has a greater coefficient of variation (and so associated variance) than the location on the y-axis. See the supplementary materials to have access to all the values.

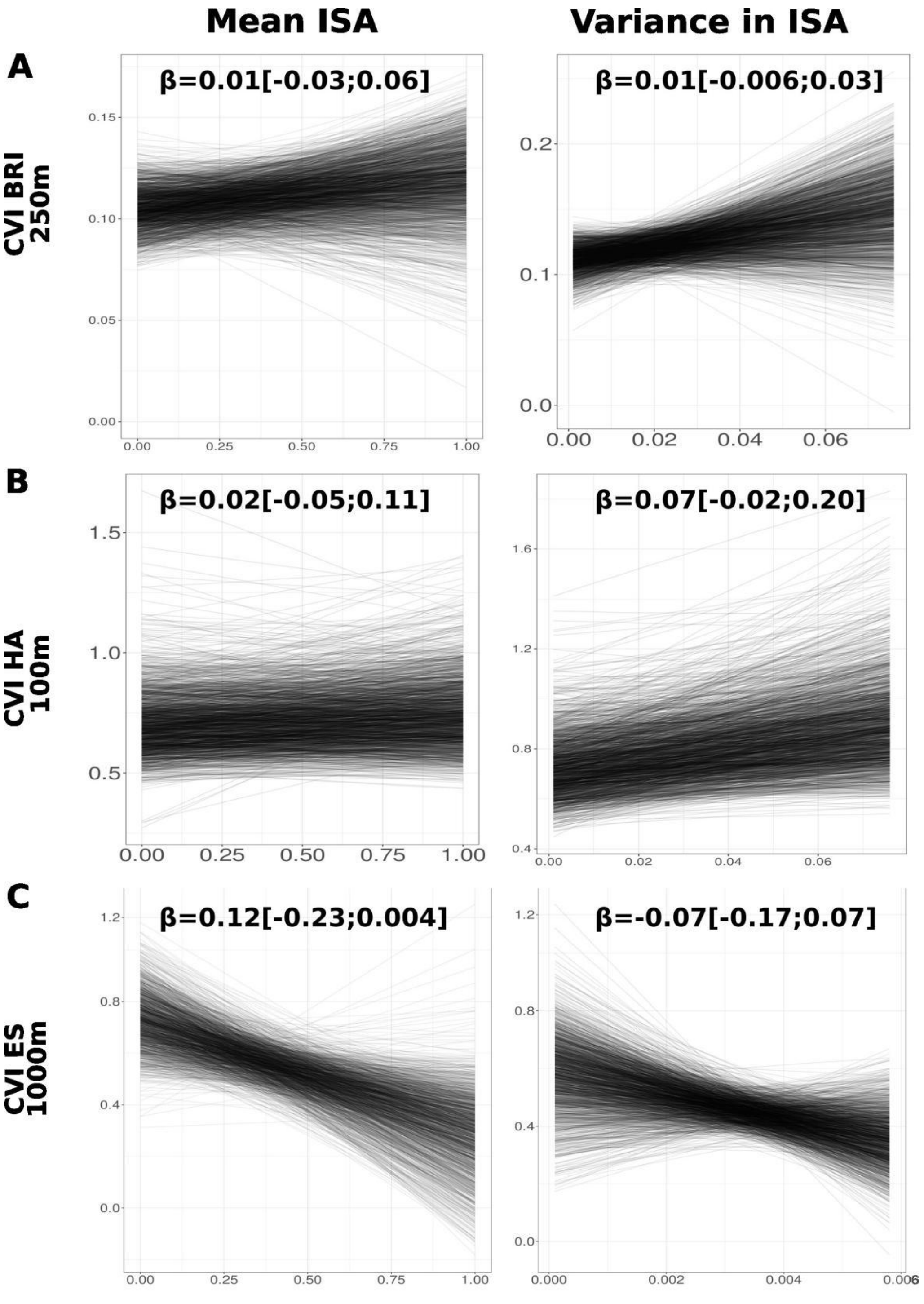


Figure 4. Relationship between predicted mean-standardized among-individual variance (CVI) and mean ISA (on the left), variance ISA (on the right) for Breath Rate Index (BRI, A), Handling aggression (HA, B) and exploration score (ES, C) and their corresponding «scale effect». CVI used here are estimated from the posteriors distributions of model b. Each line represents the predictions of one Bayesian model (one model per iteration of model b). Note that CVI are expressed on the latent-scale for HA and ES. β is the coefficient of relation between mean/variance ISA among-individual variance (CVI).

Discussion

Recent work has demonstrated that phenotypic variance across individuals, the raw material for selection, may be higher in urban populations than non-urban ones in some contexts (Thompson et al., 2022, Capilla-Lasheras et al., 2022 but see Burkhard, Dochtermann & Charmantier, 2023 Sanderson et al., 2022). We examined if urban populations contained more behavioral variation (P1) and whether this was due to higher among-individual variance (*i.e.*, between individual differences, P2a, P2b). We find that urban birds are faster explorer and more aggressive than forest birds. In addition urban birds are more variable than forest birds for breath rate and handling aggression, but less variable in their exploration of a novel environment. These results are fairly robust when examining behavioral variation at each urban sampling location compared to the forest, but also highlighted differences among urban locations in the individual diversity they contained, which is especially evident for breath rate. Finally, we find decreasing individual heterogeneity in exploration with increasing urbanization in the city, but no support for linear relationships between increasing urbanization and individual differences for the other behavioral traits. Collectively our results suggest that individuals in the city may have more diverse behavioral stress responses, yet display stronger similarity in their behavioral responses to novelty.

Behavioral differences between city and forest

In agreement with previous findings (Charmantier et al., 2017, Caizergues et al., 2022), we confirm that birds in urban areas are faster explorers than conspecifics living in the forest, and we also find a trend that males in urban areas are more aggressive. Although we find faster urban breath rates as in Caizergues et al., (2022), the uncertainty around the estimates are larger and do not allow us to conclude on a significant difference. Such disparity in the magnitude and uncertainty of effect sizes between the two studies could be explained by 1) the use of different fixed effects and 2) the use of heterogeneous variance structures (one intercept and variance per location). Interestingly, there is clear evidence of faster breath rate at three urban sites (GRAM, ZOO and FONT, Fig S1) and so our results suggest that different environmental conditions among sampling locations within a city can drive stronger differences in breath rate means. In the literature, this trait has conflicting patterns with urbanization, with some studies showing that birds breathe faster in the city (Caizergues et al., 2022, Torné-Noguera et al., 2014), while others show no difference (Abolins-Abols et al., 2016; Senar et al., 2017). Given our findings, these discrepancies could result from non-accounted for habitat heterogeneity within urban and forest habitats (e.g. human disturbance, food and predator abundance). Further studies that account for environmental heterogeneity at multiple spatial scales are needed to understand whether it might alter our interpretation of the urbanization effect on average traits.

Higher among-individual variation in two urban behaviors

While earlier studies found higher phenotypic variance in life-history and morphological traits among urban versus non-urban birds (Thompson et al., 2022; Capilla-Lasheras et al., 2022), our present study reveals increased phenotypic variance (P1) exclusively in one behavioral trait—handling aggression. Inconsistent support for P1 across traits aligns with Sanderson et al.'s (2023) recent findings that human-related disturbances can both increase and decrease phenotypic variation across different trait types. Consistent with our second prediction, we find higher among-individual variance (P2a) in urban habitats for breath rate and handing aggression, which translates into higher urban repeatability. Previous studies on great tits showed contrasting patterns with both higher (Charmantier et al., 2017) and lower (Hardman & Dalesman, 2018) repeatability of handling aggression for urban compared to forest populations. However, these studies did not report variance estimates and thus did not conclude on whether changes in repeatability were due to higher or lower among-individual variance. Burkhard, Dochtermann & Charmantier (2023) only found seven studies testing explicitly for differences in behavioral variance at the among- and within-individual levels between urban and non-urban environments in other birds and mammals species for behavioral traits (Bokony et al., 2012; Kaiser et al., 2019; Lehrer et al., 2012; Thompson et al., 2018; von Merten et al., 2022; Williams et al., 2020). For aggressive behaviour, only one study had reported differences in among-individual variance in an urbanization context (Von Merten et al., 2022, in shrews), where they showed higher repeatability due to higher among-individual variance in urban shrews, consistent with our results. Our results illustrate that examining among- and within-individual variance component, that have different eco-evolutionary implications, can be critical to reveal differences that might otherwise remain cryptic. For example, higher among- and lower within-individual variation in urban breath rates (Fig 2B) contribute to similar amounts of total phenotypic variation between the city and forest. This could suggest that variance is shaped by different processes in the city, *e.g.,* less plasticity in breath rates in the city than the forest, an inference that would be missed if not evaluating among and within- individual variance separately.

While high among-individual variance in behaviour is often associated with increased population stability and resilience (Wolf & Weissing, 2012), it is important to note that for this to hold true, among-individual variance should partly include genetic variance, which is vital for adaptive evolution and long-term population persistence (Barrett & Schluter, 2008). The greater among-individual variance we find in the city can be underpinned by genetic variance in response to relaxed or fluctuating selection or by developmental plasticity in response to spatial environmental heterogeneity (Wolf & Weissing 2010). Studies comparing urban and forest great tit genomes found evidence of differences in genes (Perrier et al., 2018; Riyahi et al., 2017), in DNA methylation (Caizergues, Le Luyer, et al., 2022; Riyahi et al., 2015), or expression of genes (Watson et al., 2017) that are inextricably linked to behaviour (*e.g.,* genes linked to the nervous system and stress responses). Specifically, urbanization has been repeatedly associated with shifts in allele frequencies in the

SERT gene (Mueller et al., 2013; van Dongen et al., 2015) which affects a wide diversity of behavioral traits such as stress sensitivity and handling aggression in great tits (Craig & Halton, 2009; Savitz & Ramesar, 2004), but also in other bird and mammals species (Grunst et al., 2021, Mueller et al., 2013, 2020 ,Savitz & Ramesar, 2004). In our study system, reduced genomic diversity was found in the most urbanized locations and genetic differentiation increased with urbanization differences (maximum FST=0.009, Perrier et al., 2018) suggesting that the high among-individual variance we uncovered for aggression and breath rate in the city may not necessarily comprise high among-individual genetic variation (Yates et al., 2019). While they are difficult to implement in vertebrates, common garden and quantitative genetic (genomic) approaches may be the most useful opportunities to uncover the mechanisms underpinning trait variation and further understand how urbanization impacts the ability of species to persist and evolve (Schell, 2018).

Higher homogeneity in exploration among urban birds

Contrary to our predictions P1, P2a and P4 we find that urban birds exhibit both lower phenotypic and among-individual variance in exploration compared to forest birds (Fig 2D). Exploration is closely linked to resource acquisition and risk avoidance (Toscano et al., 2016) and faster explorers have been shown to be better at detecting environmental cues associated with resources (in blue tits, Delaitre et al., *unpublished*). It suggests that urban birds might employ less diverse strategies for resource acquisition and predator avoidance in the city. While there is evidence in the literature that urban individuals tend to be more homogeneous in predator avoidance behaviors (Geffroy et al., 2020) and that the repeatability of exploration is lower in urban great tits (Charmantier et al., 2017) and house finches (Weaver et al., 2019), it is unknown whether there are consequences for intra-specific competition, predation, or even demography (Araújo et al., 2011; Bolnick et al., 2003). A reduction in among-individual variance is hypothesized to have consequences for population viability, as it may render the population vulnerable to new or fluctuating selective pressures due to individuals exploiting a smaller diversity of habitats and resources

(Møller, 2010). However, fast exploring great tits (such as urban birds in our study system) have been shown to adjust their behaviour more rapidly in response to changes in food resources and find new food resources more quickly than their slower counterparts (Coomes et al., 2022; van Overveld & Matthysen, 2009). In the literature there are conflicting hypotheses linking plasticity to the fast-slow exploration continuum. While the behavioral flexibility hypothesis predicts that fast explorers are less behaviorally flexible (forming routine-like behaviour and taking more time to adjust; Coppens et al., 2010; Logan, 2016; Mazza et al., 2018), the information gathering hypothesis predicts the opposite where higher sampling behaviors allow more rapid responses; Arvidsson & Matthysen, 2016; Herborn et al., 2014; Rojas-Ferrer et al., 2020). Further studies would be needed to investigate whether urban individuals, in our study system, could adjust to environmental conditions as a result of individual differences in plasticity despite low among-individual variance in average behaviour.

Lower total phenotypic variation and among-individual variance in exploration of urban birds could partly be a consequence of genetic diversity loss. While we did not investigate differences in genetic variation for this trait among habitats, exploration has been shown to harbour genetic variance for some species (*e.g.* Careau et al., 2009 in deer mice, *Peromyscus maniculatus*, Dingemanse et al., 2012 in stickleback *Gasterosteus aculeatus*) including great tits (Drent et al., 2003, Dingemanse et al., 2002), so we could hypothesize that some of the differences we found arise from differences in genetic variance across habitats. However, given we do not see consistent patterns of variation along the urbanization gradient across all the behavioral traits, it is likely that other mechanisms such as matching habitat choice (Edelaar et al., 2017) or plasticity explain reduced individual diversity of exploration in more urbanized contexts. For example, urban individuals could plastically adjust to novel stimuli in the same direction through habituation (as shown in blue-tailed skinks, Williams et al., 2021) and, in our novel environment assay, urban tits may similarly reduce responses to novelty and explore more quickly while forests tits may have shown more varied exploration responses. Indeed, a recent meta-analysis suggests that decreases in phenotypic variation in human-disturbed habitats may be more common for behavioral traits (Sanderson et al., 2023), which would support this alternative explanation.

Mean urbanization, not spatial heterogeneity, influences among-individual variation in exploration

Our measure of impervious surface assessed at three different spatial scales, illustrated how locations within the same city are characterized by different levels of impervious surface (*i.e.* proxy for urbanization) (Table S2). The ordering of locations by urbanization intensity depends on the spatial scales considered (*e.g.*, FAC is the most urbanized at 100 m, but BOT is the most urbanized at 1000 m). Such heterogeneity in urbanization metrics within a single city may explain why our ability to detect urbanization effects depends on the specific urban locations considered (Evans et al., 2009). Differences in behavioral variation for the same trait among our urban sampling locations highlights a need to examine variation at finer spatial scales within cities and investigate other unmeasured environmental or ecological features (*e.g.*, native and non-native tree composition; Jensen et al., 2023) that may drive heterogeneity in phenotypic variation across the urban matrix. Note that the historical nest box set-up in our focal locations was not optimal to explore such heterogeneity since we only had one fairly homogeneous forest location versus multiple urban locations. Hence, going beyond analyzing overall variation in the city and estimating variation at finer scales was a crucial step. While differences in trait variation between city and forest can not be solely attributed to the effect of urbanization, the urban gradient approach allows for a more comprehensive exploration of the effects of urbanization proxies. For instance, our findings illustrate that the average impervious surface partially explains the reduction in among-individual variance in great tit exploration within the urban environment (Fig 4C). By combining multiple approaches (city vs. forest, location heterogeneity and urbanization gradient), we show inconsistencies among these approaches for breath rate and handling aggression but robust conclusions across the approaches for exploration. For example, there a are higher urban individual differences for breath rate and handling aggression when comparing urban and forest habitat categories, but there are no strong relationships between individual variation in these behaviors across the urbanization gradient. This highlights the value of incorporating at least two different approaches to comprehensively understand effects of urbanization on wild populations.

Recent studies suggest that higher among-individual variance in behavior should be favored in environments with greater spatial heterogeneity as it would allow the exploitation of more diverse resources or niches (Montiglio et al., 2013; Pamela Delarue et al., 2015; von Merten et al., 2022). Partly in line with these studies and our prediction P2a, we find greater among-individual variance for breath rate and handling aggression in the city than in the forest, although we could not demonstrate that this was related to spatial heterogeneity in impervious surface (P3). This is surprising given that previous research has demonstrated a positive association between trait variance and land cover spatial heterogeneity within cities, particularly for life-history traits in great tits (Capilla-Lasheras et al., 2022). One limitation of our study is that we do not account for non-linear relationships between mean and spatial heterogeneity in impervious surface. Locations with extreme proportions of impervious surface (0 or 1) inherently exhibit less variability in their impervious surface cover. In contrast, two locations with an intermediate level of imperviousness has more variation in the spatial distribution of impervious surfaces. For example in our study system, CEF and FONT have the same average percentage of impervious surface (*i.e.* 70%), but the variability in impervious surface is 50 times higher in FONT. Under these conditions, if we hypothesize that among-individual variance in behavior is influenced by spatial heterogeneity, we might expect lower among-individual variance at the extremes of the urban gradient and higher among-individual variance in the middle. While a more suitable approach would involve using an independent, more integrative, and continuous measure of spatial heterogeneity (*e.g.*, Simpson diversity of land cover), it is not feasible to assess this at smaller spatial resolutions in our study system. Another limitation of our study is that in our study system, birds occupy urban locations with high spatial variability in human disturbances, such as pedestrian frequency, car and tramway density, or air and light pollution. This high variability in urban stressors could influence the diversity of behavioral stress responses among urban tits, but these stressors may not correlate strongly to impervious surface. Exploring these other dimensions of the urban matrix would be particularly useful to identify which urban environmental features shape variation in different avian behaviors (Alberti et al., 2020; Rivkin et al., 2019; Szulkin et al., 2020).

Behaviors are influenced by the environment at different spatial scales

The spatial scale that urbanization affects organisms is an important yet still overlooked issue (Moll et al., 2020), while the increasing availability of remote sensing data provides a great opportunity to extract environmental heterogeneity at multiple scales (Kuenzer et al., 2014). The urbanization gradient approach applied at multiple scales highlights that the most relevant spatial scale for the effect of urbanization (*i.e.* scale of effect) is dependent on the trait studied (Capilla-Lasheras et al., 2022; Martin, 2018; Waterschoot et al., 2023). The «scale of effect» for exploration was a buffer radius of 1000 meters, which aligns with great tits exploring and foraging at large spatial scales around their nest (approximately 3,500-4,000 m2, 95% KDE density, according to Naef-Daenzer, 2000). In contrast, the «scale of effect» for stress-related behaviors reflected more local impacts of the environment on breath rate (250 m) and handling aggression (100 m). Similar results have been shown in blue tits, where average exploration and handling aggression were influenced by large and small scale ecological conditions respectively (Dubuc-Messier et al., 2017). The use of remote sensing data opens an exciting avenue for investigating the different temporal and spatial scale effects of urban-driven evolutionary processes, while providing standardized environmental metrics that allow comparison of effect sizes across studies (Szulkin et al., 2020).

Conclusion and perspectives

This study aimed at exploring the impacts of urbanization on both the total phenotypic and among-individual variance for three behavioral traits. Higher among-individual variance may enhance a population’s ecological success, as demonstrated by studies indicating that populations with greater diversity are less susceptible to environmental changes, more demographically stable, more successful in colonizing new environments, and less prone to extinction compared to less variable populations (Forsman & Wennersten, 2016). Our findings present a contrasting scenario wherein urban birds exhibited higher among-individual variance in stress-related behaviors but lower diversity in novelty-related exploration compared to forest birds. This suggests that urban great tit populations may possess the ability to quickly adapt to changes in stressors, such as human disturbance, albeit adaptation could be slowed down and countered by a low diversity of exploration strategies. While among-individual variance is frequently regarded as the upper limit for genetic variance, additional studies are necessary to examine whether cities contain populations with higher genetic variance or, alternatively, higher individual variation in plasticity. This will be essential to fully comprehend whether wild populations can continue to thrive in a context of increasing global urbanization.

Acknowledgements

The authors thank numerous co-workers and volunteers who contributed to fieldwork, especially those associated with the CEFE PLT platform (including Sam Perret, Annick Lucas, Pablo Giovannini, Christophe de Franceschi), the City Council of Montpellier, and the Zoo du Lunaret. They also thank Alexis Chaine, Aisha Bruendle, Amy Chaine and Amelie Fargeveille for insightful discussions regarding the interpretation of results. This study is part of the long-term Studies in Ecology and Evolution (SEE-Life) program of the CNRS. This project was funded by the OSU-OREME and the Agence Nationale de la Recherche (project SoCo, grant ANR-18-CE02-0023-04 & project URBANTIT, grant ANR-19-CE34-0008-05)

References

Abolins-Abols, M., Hope, S. F., & Ketterson, E. D. (2016). Effect of acute stressor on reproductive behavior differs between urban and rural birds. Ecology and Evolution, 6(18), 6546–6555. https://doi.org/10.1002/ece3.2347

Alberti, M., Palkovacs, E. P., Roches, S. D., Meester, L. D., Brans, K. I., Govaert, L., Grimm, N. B., Harris, N. C., Hendry, A. P., Schell, C. J., Szulkin, M., Munshi-South, J., Urban, M. C., & Verrelli, B. C. (2020). The Complexity of Urban Eco-evolutionary Dynamics. BioScience, 70(9), 772–793. https://doi.org/10.1093/biosci/biaa079

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. Ecology Letters, 14(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Arvidsson, L. K., & Matthysen, E. (2016). Individual differences in foraging decisions: Information-gathering strategies or flexibility? Behavioral Ecology, 27(5), 1353–1361. https://doi.org/10.1093/beheco/arw054

Barrett, R. D. H., & Schluter, D. (2008). Adaptation from standing genetic variation. Trends in Ecology & Evolution, 23(1), 38–44. https://doi.org/10.1016/j.tree.2007.09.008

Blondel, J., Thomas, D. W., Charmantier, A., Perret, P., Bourgault, P., & Lambrechts, M. M. (2006). A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. Bioscience, 56(8), 661–673.

Bokony, V., Kulcsar, A., Toth, Z., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (Passer domesticus). PloS One, 7(5), e36639.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist, 161(1), 1–28. https://doi.org/10.1086/343878

Burkhard, T., Dochtermann, N., & Charmantier, A. (2023). Global meta-analysis of behavioral response to urban environments. *Under review* https://doi.org/10.17605/OSF.IO/GSXBM

Cadenasso, M. L., Pickett, S. T. A., & Schwarz, K. (2007). Spatial heterogeneity in urban ecosystems: Reconceptualizing land cover and a framework for classification. Frontiers in Ecology and the Environment, 5(2), 80–88. https://doi.org/10.1890/1540-9295(2007)5[80:SHIUER]2.0.CO;2

Caizergues, A. E., Charmantier, A., Lambrechts, M. M., Perret, S., Demeyrier, V., Lucas, A., & Grégoire, A. (2021). An avian urban morphotype: How the city environment shapes great tit morphology at different life stages. Urban Ecosystems, 24(5), 929–941. https://doi.org/10.1007/s11252-020-01077-0

Caizergues, A. E., Grégoire, A., Choquet, R., Perret, S., & Charmantier, A. (2022). Are behaviour and stress-related phenotypes in urban birds adaptive? Journal of Animal Ecology, 91(8), 1627–1641. https://doi.org/10.1111/1365-2656.13740

Caizergues, A. E., Le Luyer, J., Grégoire, A., Szulkin, M., Senar, J.-C., Charmantier, A., & Perrier, C. (2022). Epigenetics and the city: Non-parallel DNA methylation modifications across pairs of urban-forest Great tit populations. Evolutionary Applications, 15(1), 149–165. https://doi.org/10.1111/eva.13334

Capilla-Lasheras, P., Thompson, M. J., Sánchez-Tójar, A., Haddou, Y., Branston, C. J., Réale, D., Charmantier, A., & Dominoni, D. M. (2022). A global meta-analysis reveals higher variation in breeding phenology in urban birds than in their non-urban neighbours. Ecology Letters, 25(11), 2552–2570. https://doi.org/10.1111/ele.14099

Careau, V., Bininda-Emonds, O. R. P., Thomas, D. W., Réale, D., & Humphries, M. M. (2009). Exploration strategies map along fast-slow metabolic and life-history continua in muroid rodents. Functional Ecology, 150–156.

Carere, C., & van Oers, K. (2004). Shy and bold great tits (Parus major): Body temperature and breath rate in response to handling stress. Physiology & Behavior, 82(5), 905–912. https://doi.org/10.1016/j.physbeh.2004.07.009

Caspi, T., Johnson, J. R., Lambert, M. R., Schell, C. J., & Sih, A. (2022). Behavioral plasticity can facilitate evolution in urban environments. Trends in Ecology & Evolution, 37(12), 1092–1103. https://doi.org/10.1016/j.tree.2022.08.002

Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., & Grégoire, A. (2017). Urbanization Is Associated with Divergence in Pace-of-Life in Great Tits. Frontiers in Ecology and Evolution, 5. https://doi.org/10.3389/fevo.2017.00053

Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). Quantitative Genetics in the Wild. OUP Oxford.

Coomes, J. R., Davidson, G. L., Reichert, M. S., Kulahci, I. G., Troisi, C. A., & Quinn, J. L. (2022). Inhibitory control, exploration behaviour and manipulated ecological context are associated with foraging flexibility in the great tit. Journal of Animal Ecology, 91(2), 320–333. https://doi.org/10.1111/1365-2656.13600

Coppens, C. M., Boer, S. F. de, & Koolhaas, J. M. (2010). Coping styles and behavioral flexibility: Towards underlying mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1560), 4021–4028. https://doi.org/10.1098/rstb.2010.0217

Craig, I. W., & Halton, K. E. (2009). Genetics of human aggressive behaviour. Human Genetics, 126, 101–113.

Dammhahn, M., Mazza, V., Schirmer, A., Göttsche, C., & Eccard, J. A. (2020). Of city and village mice: behavioral adjustments of striped field mice to urban environments. Scientific Reports, 10(1), Article 1. https://doi.org/10.1038/s41598-020-69998-6

Dansereau, P. (1957). Biogeography. An ecological perspective. Biogeography. An Ecological Perspective. The Ronald Press Company, New York.

Delaitre, S., Graham, J., Buatois, B., De Franceschi, C., Giovannini,P., Lucas, A., Bonadonna, F., Caro, SP. (*under review*). Olfactory communication from trees to birds: Effects of herbivore-induced plant defences on a songbird behaviours and reproductive decisions.

de Villemereuil, P., Morrissey, M. B., Nakagawa, S., & Schielzeth, H. (2018). Fixed-effect variance and the estimation of repeatabilities and heritabilities: Issues and solutions. Journal of Evolutionary Biology, 31(4), 621–632. https://doi.org/10.1111/jeb.13232

Demeyrier, V., Lambrechts, M. M., Perret, P., & Grégoire, A. (2016). Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. Animal Behaviour, 118, 181–190. https://doi.org/10.1016/j.anbehav.2016.06.007

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. Nature Ecology & Evolution, 2(1), Article 1. https://doi.org/10.1038/s41559-017-0402-5

Diamond, S. E., Chick, L. D., Perez, A., Strickler, S. A., & Martin, R. A. (2018). Evolution of thermal tolerance and its fitness consequences: Parallel and non-parallel responses to urban heat islands across three cities. Proceedings of the Royal Society B: Biological Sciences, 285(1882), 20180036. https://doi.org/10.1098/rspb.2018.0036

Diamond, S. E., & Martin, R. A. (2016). The interplay between plasticity and evolution in response to human-induced environmental change (5:2835). F1000Research. https://doi.org/10.12688/f1000research.9731.1

Diamond, S. E., & Martin, R. A. (2020). Evolutionary Consequences of the Urban Heat Island. In M. Szulkin, J. Munshi-South, & A. Charmantier (Eds.), Urban Evolutionary Biology (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780198836841.003.0006

Dingemanse, N. J., Barber, I., Wright, J., & Brommer, J. E. (2012). Quantitative genetics of behavioral reaction norms: Genetic correlations between personality and behavioral plasticity vary across stickleback populations: behavioral reaction norm quantitative genetics. Journal of Evolutionary Biology, 25(3), 485–496. https://doi.org/10.1111/j.1420-9101.2011.02439.x

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. Animal Behaviour, 64(6), 929–938. https://doi.org/10.1006/anbe.2002.2006

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (Parus major). Proceedings of the Royal Society B: Biological Sciences, 270(1516), 741–747. https://doi.org/10.1098/rspb.2002.2300

Dingemanse, N. J., & Dochtermann, N. A. (2014). Individual behaviour: behavioral ecology meets quantitative genetics. Quantitative Genetics in the Wild, 54–67.

Dochtermann, N. A., & Royauté, R. (2019). The mean matters: Going beyond repeatability to interpret behavioral variation. Animal Behaviour, 153, 147–150. https://doi.org/10.1016/j.anbehav.2019.05.012

Draghi, J. (2019). Phenotypic variability can promote the evolution of adaptive plasticity by reducing the stringency of natural selection. Journal of Evolutionary Biology, 32(11), 1274–1289. https://doi.org/10.1111/jeb.13527

Drent, P. J., Oers, K. V., & Noordwijk, A. J. V. (2003). Realized heritability of personalities in the great tit (Parus major). Proceedings of the Royal Society of London. Series B: Biological Sciences, 270(1510), 45–51. https://doi.org/10.1098/rspb.2002.2168

Dubuc-Messier, G., Réale, D., Perret, P., & Charmantier, A. (2017). Environmental heterogeneity and population differences in blue tits personality traits. Behavioral Ecology, 28(2), 448–459. https://doi.org/10.1093/beheco/arw148

Edelaar, P., Jovani, R., & Gomez-Mestre, I. (2017). Should I Change or Should I Go? Phenotypic Plasticity and Matching Habitat Choice in the Adaptation to Environmental Heterogeneity. The American Naturalist, 190(4), 506–520. https://doi.org/10.1086/693345

Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., & Moretti, M. (2019). Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. Journal of Animal Ecology, 88(10), 1522–1533. https://doi.org/10.1111/1365-2656.13051

European Environment Agency & European Environment Agency. (2020). Imperviousness Density 2018 (raster 10 m), Europe, 3-yearly, Aug. 2020 (01.00) [GeoTIFF]. European Environment Agency. https://doi.org/10.2909/3BF542BD-EEBD-4D73-B53C-A0243F2ED862

Evans, K. L., Gaston, K. J., Sharp, S. P., McGowan, A., & Hatchwell, B. J. (2009). The effect of urbanization on avian morphology and latitudinal gradients in body size. Oikos, 118(2), 251–259. https://doi.org/10.1111/j.1600-0706.2008.17092.x

Falvey, C. H., Aviles-Rodriguez, K. J., Hagey, T. J., & Winchell, K. M. (2020). The finer points of urban adaptation: Intraspecific variation in lizard claw morphology. Biological Journal of the Linnean Society, 131(2), 304–318. https://doi.org/10.1093/biolinnean/blaa123

Forsman, A., & Wennersten, L. (2016). Inter-individual variation promotes ecological success of populations and species: Evidence from experimental and comparative studies. Ecography, 39(7), 630–648. https://doi.org/10.1111/ecog.01357

Fossett, T. E., & Hyman, J. (2021). The effects of habituation on boldness of urban and rural song sparrows (Melospiza melodia). Behaviour, 159(3–4), 243–257.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution, 7(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Garant, D., Kruuk, L. E. B., Wilkin, T. A., McCleery, R. H., & Sheldon, B. C. (2005). Evolution driven by differential dispersal within a wild bird population. Nature, 433(7021), Article 7021. https://doi.org/10.1038/nature03051

Geffroy, B., Sadoul, B., Putman, B. J., Berger-Tal, O., Garamszegi, L. Z., Møller, A. P., & Blumstein, D. T. (2020). Evolutionary dynamics in the Anthropocene: Life history and intensity of human contact shape antipredator responses. PLOS Biology, 18(9), e3000818. https://doi.org/10.1371/journal.pbio.3000818

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian Regression Models. The American Statistician, 73(3), 307–309. https://doi.org/10.1080/00031305.2018.1549100

Gianola, D. (1986). On selection criteria and estimation of parameters when the variance is heterogeneous. TAG. Theoretical and Applied Genetics. Theoretische Und Angewandte Genetik, 72(5), 671–677. https://doi.org/10.1007/BF00289007

Giraudeau, M., Nolan, P. M., Black, C. E., Earl, S. R., Hasegawa, M., & McGraw, K. J. (2014). Song characteristics track bill morphology along a gradient of urbanization in house finches (Haemorhous mexicanus). Frontiers in Zoology, 11(1), 83. https://doi.org/10.1186/s12983-014-0083-8

Goodrich, B., Gabry, J., Ali, I., & Brilleman, S. (2018). rstanarm: Bayesian applied regression modeling via Stan. R package version 2.17. 4. Online< Http://Mc-Stan. Org.

Grunst, A. S., Grunst, M. L., Staes, N., Thys, B., Pinxten, R., & Eens, M. (2021). Serotonin transporter (SERT) polymorphisms, personality and problem-solving in urban great tits. Scientific Reports, 11, 24270. https://doi.org/10.1038/s41598-021-03466-7

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. Journal of Statistical Software, 33(2), 1–22.

Hardman, S. I., & Dalesman, S. (2018). Repeatability and degree of territorial aggression differs among urban and rural great tits (Parus major). Scientific Reports, 8(1), Article 1. https://doi.org/10.1038/s41598-018-23463-7

Hedrick, P. W. (1986). Genetic polymorphism in heterogeneous environments: A decade later. Annual Review of Ecology and Systematics, 17(1), 535–566.

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. Molecular Ecology, 17(1), 20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. Behavioral Ecology, 25(6), 1374–1379. https://doi.org/10.1093/beheco/aru131

Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: A null model approach. The American Naturalist, 161(3), 357–366. https://doi.org/10.1086/346135

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. Ecology Letters, 11(6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

Jensen, J. K., Ekroos, J., Watson, H., Salmón, P., Olsson, P., & Isaksson, C. (2023). Urban tree composition is associated with breeding success of a passerine bird, but effects vary within and between years. Oecologia, 201(3), 585–597. https://doi.org/10.1007/s00442-023-05319-8

Kaiser, A., Merckx, T., & Van Dyck, H. (2019). behavioral repeatability is affected by early developmental conditions in a butterfly. Animal Behaviour, 157, 219–226.

Krams, I., Vrublevska, J., Cirule, D., Kivleniece, I., Krama, T., Rantala, M. J., Kaasik, A., Hõrak, P., & Sepp, T. (2013). Stress, Behaviour and Immunity in Wild-Caught Wintering Great Tits (Parus major). Ethology, 119(5), 397–406. https://doi.org/10.1111/eth.12075

Kristensen, N. P., Johansson, J., Chisholm, R. A., Smith, H. G., & Kokko, H. (2018). Carryover effects from natal habitat type upon competitive ability lead to trait divergence or source-sink dynamics. Ecology Letters, 21(9), 1341–1352. https://doi.org/10.1111/ele.13100

Kuenzer, C., Ottinger, M., Wegmann, M., Guo, H., Wang, C., Zhang, J., Dech, S., & Wikelski, M. (2014). Earth observation satellite sensors for biodiversity monitoring: Potentials and bottlenecks. International Journal of Remote Sensing, 35(18), 6599–6647. https://doi.org/10.1080/01431161.2014.964349

Lazić, M. M., Carretero, M. A., Crnobrnja-Isailović, J., & Kaliontzopoulou, A. (2015). Effects of Environmental Disturbance on Phenotypic Variation: An Integrated Assessment of Canalization, Developmental Stability, Modularity, and Allometry in Lizard Head Shape. The American Naturalist, 185(1), 44–58. https://doi.org/10.1086/679011

Lehrer, E. W., Schooley, R. L., & Whittington, J. K. (2012). Survival and antipredator behavior of woodchucks (Marmota monax) along an urban–agricultural gradient. Canadian Journal of Zoology, 90(1), 12–21. https://doi.org/10.1139/z11-107

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology, 73(6), 1943–1967. https://doi.org/10.2307/1941447

Levis, N. A., & Pfennig, D. W. (2016). Evaluating 'Plasticity-First' Evolution in Nature: Key Criteria and Empirical Approaches. Trends in Ecology & Evolution, 31(7), 563–574. https://doi.org/10.1016/j.tree.2016.03.012

Ley, R. (1994). An introduction to the psychophysiology of breathing. Biofeedback and Self-Regulation, 19(2), 95–96. https://doi.org/10.1007/BF01776482

Lindström, J. (1999). Early development and fitness in birds and mammals. Trends in Ecology & Evolution, 14(9), 343–348.

Logan, C. J. (2016). Behavioral flexibility in an invasive bird is independent of other behaviors. PeerJ, 4, e2215. https://doi.org/10.7717/peerj.2215

Lowry, H., Lill, A., & Wong, B. B. M. (2013). behavioral responses of wildlife to urban environments. Biological Reviews, 88(3), 537–549. https://doi.org/10.1111/brv.12012

Martin, A. E. (2018). The Spatial Scale of a Species' Response to the Landscape Context Depends on which Biological Response You Measure. Current Landscape Ecology Reports, 3(1), 23–33. https://doi.org/10.1007/s40823-018-0030-z

Martin, A. E., & Fahrig, L. (2012). Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecological Applications, 22(8), 2277–2292. https://doi.org/10.1890/11-2224.1

Matz, M. V., Wright, R. M., & Scott, J. G. (2013). No Control Genes Required: Bayesian Analysis of qRT-PCR Data. PLOS ONE, 8(8), e71448. https://doi.org/10.1371/journal.pone.0071448

Mazza, V., Eccard, J. A., Zaccaroni, M., Jacob, J., & Dammhahn, M. (2018). The fast and the flexible: Cognitive style drives individual variation in cognition in a small mammal. Animal Behaviour, 137, 119–132. https://doi.org/10.1016/j.anbehav.2018.01.011

Merilä, J. (2012). Evolution in response to climate change: In pursuit of the missing evidence. BioEssays: News and Reviews in Molecular, Cellular and Developmental Biology, 34(9), 811–818. https://doi.org/10.1002/bies.201200054

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. Evolutionary Applications, 7(1), 1–14. https://doi.org/10.1111/eva.12137

Mohring, B., Henry, P.-Y., Jiguet, F., Malher, F., & Angelier, F. (2021). Investigating temporal and spatial correlates of the sharp decline of an urban exploiter bird in a large European city. Urban Ecosystems, 24(3), 501–513. https://doi.org/10.1007/s11252-020-01052-9

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Robison, T., & Montgomery, R. A. (2020). At what spatial scale(s) do mammals respond to urbanization? Ecography, 43(2), 171–183. https://doi.org/10.1111/ecog.04762

Møller, A. P. (2010). Interspecific variation in fear responses predicts urbanization in birds. Behavioral Ecology, 21(2), 365–371. https://doi.org/10.1093/beheco/arp199

Montiglio, P.-O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1618), 20120343. https://doi.org/10.1098/rstb.2012.0343

Mueller, J. C., Partecke, J., Hatchwell, B. J., Gaston, K. J., & Evans, K. L. (2013). Candidate gene polymorphisms for behavioral adaptations during urbanization in blackbirds. Molecular Ecology, 22(13), 3629–3637. https://doi.org/10.1111/mec.12288

Mueller, J. C., Carrete, M., Boerno, S., Kuhl, H., Tella, J. L., & Kempenaers, B. (2020). Genes acting in synapses and neuron projections are early targets of selection during urban colonization. Molecular Ecology, 29(18), 3403–3412. https://doi.org/10.1111/mec.15451

Naef-Daenzer, B. (2000). Patch time allocation and patch sampling by foraging Great and Blue Tits. Animal Behaviour, 59, 989–999. https://doi.org/10.1006/anbe.1999.1380

Nakagawa, S., Poulin, R., Mengersen, K., Reinhold, K., Engqvist, L., Lagisz, M., & Senior, A. M. (2015). Meta-analysis of variation: Ecological and evolutionary applications and beyond. Methods in Ecology and Evolution, 6(2), 143–152. https://doi.org/10.1111/2041-210X.12309

Niemelä, J., Breuste, J.H., Guntenspergen, G., McIntyre, N.E., Elmqvist, T., and James, P. (eds) (2011). Urban Ecology: Patterns, Processes, and Applications. OxfordUniversity Press, Oxford.

Delarue E.M.P., E. M., Kerr, S. E., & Lee Rymer, T. (2015). Habitat complexity, environmental change and personality: A tropical perspective. behavioral Processes, 120, 101–110. https://doi.org/10.1016/j.beproc.2015.09.006

Pelletier, F., & Coltman, D. W. (2018). Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? BMC Biology, 16(1), 7. https://doi.org/10.1186/s12915-017-0476-1

Perrier, C., Lozano del Campo, A., Szulkin, M., Demeyrier, V., Gregoire, A., & Charmantier, A. (2018). Great tits and the city: Distribution of genomic diversity and gene–environment associations along an urbanization gradient. Evolutionary Applications, 11(5), 593–613. https://doi.org/10.1111/eva.12580

Pickett, S. T. A., Cadenasso, M. L., Rosi-Marshall, E. J., Belt, K. T., Groffman, P. M., Grove, J. M., Irwin, E. G., Kaushal, S. S., LaDeau, S. L., Nilon, C. H., Swan, C. M., & Warren, P. S. (2017). Dynamic heterogeneity: A framework to promote ecological integration and hypothesis generation in urban systems. Urban Ecosystems, 20(1), 1–14. https://doi.org/10.1007/s11252-016-0574-9

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. R News, 6(1), Article 1.

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2004). Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. Journal of Mammalogy, 85(3), 483–490.

QGIS.org, 2022. QGIS 3.28. Geographic Information System Developers Manual. QGIS Association. Electronic document: https://docs.qgis.org/3.28/en/docs/developers_guide/index.html

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. Biological Reviews, 82(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Reed, T. E., Schindler, D. E., Hague, M. J., Patterson, D. A., Meir, E., Waples, R. S., & Hinch, S. G. (2011). Time to Evolve? Potential Evolutionary Responses of Fraser River Sockeye Salmon to Climate Change and Effects on Persistence. PLOS ONE, 6(6), e20380. https://doi.org/10.1371/journal.pone.0020380

Reid, N. M., Proestou, D. A., Clark, B. W., Warren, W. C., Colbourne, J. K., Shaw, J. R., Karchner, S. I., Hahn, M. E., Nacci, D., Oleksiak, M. F., Crawford, D. L., & Whitehead, A. (2016). The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. Science, 354(6317), 1305–1308. https://doi.org/10.1126/science.aah4993

Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F. J., de Keyzer, C. W., Diamond, S. E., Fortin, M.-J., Frazee, L. J., Gorton, A. J., Hendry, A. P., Liu, Y., Losos, J. B., MacIvor, J. S., Martin, R. A., McDonnell, M. J., Miles, L. S., Munshi-South, J., Ness, R. W., Newman, A. E. M., … Johnson, M. T. J. (2019). A roadmap for urban evolutionary ecology. Evolutionary Applications, 12(3), 384–398. https://doi.org/10.1111/eva.12734

Riyahi, S., Björklund, M., Mateos-Gonzalez, F., & Senar, J. C. (2017). Personality and urbanization: behavioral traits and DRD4 SNP830 polymorphisms in great tits in Barcelona city. Journal of Ethology, 35(1), 101–108. https://doi.org/10.1007/s10164-016-0496-2

Riyahi, S., Sánchez-Delgado, M., Calafell, F., Monk, D., & Senar, J. C. (2015). Combined epigenetic and intraspecific variation of the DRD4 and SERT genes influence novelty seeking behavior in great tit Parus major. Epigenetics, 10(6), 516–525. https://doi.org/10.1080/15592294.2015.1046027

Rojas-Ferrer, I., Thompson, M. J., & Morand-Ferron, J. (2020). Is exploration a metric for information gathering? Attraction to novelty and plasticity in black-capped chickadees. Ethology, 126(4), 383–392. https://doi.org/10.1111/eth.12982

Sanderson, S., Beausoleil, M.-O., O'Dea, R. E., Wood, Z. T., Correa, C., Frankel, V., Gorné, L. D., Haines, G. E., Kinnison, M. T., Oke, K. B., Pelletier, F., Pérez-Jvostov, F., Reyes-Corral, W. D., Ritchot, Y., Sorbara, F., Gotanda, K. M., & Hendry, A. P. (2022). The pace of modern life, revisited. Molecular Ecology, 31(4), 1028–1043. https://doi.org/10.1111/mec.16299

Savitz, J. B., & Ramesar, R. S. (2004). Genetic variants implicated in personality: A review of the more promising candidates. American Journal of Medical Genetics Part B: Neuropsychiatric Genetics, 131B(1), 20–32. https://doi.org/10.1002/ajmg.b.20155

Schell, C. J. (2018). Urban Evolutionary Ecology and the Potential Benefits of Implementing Genomics. Journal of Heredity, 109(2), 138–151. https://doi.org/10.1093/jhered/esy001

Senar, J. C., Garamszegi, L. Z., Tilgar, V., Biard, C., Moreno-Rueda, G., Salmón, P., Rivas, J. M., Sprau, P., Dingemanse, N. J., Charmantier, A., Demeyrier, V., Navalpotro, H., & Isaksson, C. (2017). Urban Great Tits (Parus major) Show Higher Distress Calling and Pecking Rates than Rural Birds across Europe. Frontiers in Ecology and Evolution, 5. https://www.frontiersin.org/articles/10.3389/fevo.2017.00163

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral Syndromes: An Integrative Overview. The Quarterly Review of Biology, 79(3), 241–277. https://doi.org/10.1086/422893

Sol, D., & Lefebvre, L. (2000). behavioral flexibility predicts invasion success in birds introduced to New Zealand. Oikos, 90(3), 599–605. https://doi.org/10.1034/j.1600-0706.2000.900317.x

Sprau, P., & Dingemanse, N. J. (2017). An Approach to Distinguish between Plasticity and Non-random Distributions of Behavioral Types Along Urban Gradients in a Wild Passerine Bird. Frontiers in Ecology and Evolution, 5. https://doi.org/10.3389/fevo.2017.00092

Strubbe, D., Salleh Hudin, N., Teyssier, A., Vantieghem, P., Aerts, J., & Lens, L. (2020). Phenotypic signatures of urbanization are scale-dependent: A multi-trait study on a classic urban exploiter. Landscape and Urban Planning, 197, 103767. https://doi.org/10.1016/j.landurbplan.2020.103767

Stuber, E. F., Araya-Ajoy, Y. G., Mathot, K. J., Mutzel, A., Nicolaus, M., Wijmenga, J. J., Mueller, J. C., & Dingemanse, N. J. (2013). Slow explorers take less risk: A problem of sampling bias in ecological studies. Behavioral Ecology, 24(5), 1092–1098. https://doi.org/10.1093/beheco/art035

Szulkin, M., Garroway, C. J., Corsini, M., Kotarba, A. Z., & Dominoni, D. (2020). How to Quantify Urbanization When Testing for Urban Evolution? In M. Szulkin, J. Munshi-South, & A. Charmantier (Eds.), Urban Evolutionary Biology (p. 0). Oxford University Press. https://doi.org/10.1093/oso/9780198836841.003.0002

Szulkin, M., & Sheldon, B. C. (2008). Dispersal as a means of inbreeding avoidance in a wild bird population. Proceedings of the Royal Society B: Biological Sciences, 275(1635), 703–711. https://doi.org/10.1098/rspb.2007.0989

Taylor, R. W., Boon, A. K., Dantzer, B., Réale, D., Humphries, M. M., Boutin, S., Gorrell, J. C., Coltman, D. W., & McAdam, A. G. (2012). Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. Journal of Evolutionary Biology, 25(4), 614–624. https://doi.org/10.1111/j.1420-9101.2012.02456.x

Theodorou, P., Baltz, L. M., Paxton, R. J., & Soro, A. (2021). Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. Evolutionary Applications, 14(1), 53–68. https://doi.org/10.1111/eva.13087

Thompson, M. J., Capilla-Lasheras, P., Dominoni, D. M., Réale, D., & Charmantier, A. (2022). Phenotypic variation in urban environments: Mechanisms and implications.

Trends in Ecology & Evolution, 37(2), 171–182. https://doi.org/10.1016/j.tree.2021.09.009

Thompson, M. J., Evans, J. C., Parsons, S., & Morand-Ferron, J. (2018). Urbanization and individual differences in exploration and plasticity. Behavioral Ecology, 29(6), 1415–1425. https://doi.org/10.1093/beheco/ary103

Torné-Noguera, A., Pagani-Núñez, E., & Senar, J. C. (2014). Great Tit (Parus major) breath rate in response to handling stress: Urban and forest birds differ. Journal of Ornithology, 155(1), 315–318. https://doi.org/10.1007/s10336-013-1025-5

Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. Oecologia, 182(1), 55–69. https://doi.org/10.1007/s00442-016-3648-8

Uchida, K., Blakey, R. V., Burger, J. R., Cooper, D. S., Niesner, C. A., & Blumstein, D. T. (2021). Urban Biodiversity and the Importance of Scale. Trends in Ecology & Evolution, 36(2), 123–131. https://doi.org/10.1016/j.tree.2020.10.011

van Dongen, W. F. D., Robinson, R. W., Weston, M. A., Mulder, R. A., & Guay, P.-J. (2015). Variation at the DRD4 locus is associated with wariness and local site selection in urban black swans. BMC Evolutionary Biology, 15(1), 253. https://doi.org/10.1186/s12862-015-0533-8

van Overveld, T., Adriaensen, F., & Matthysen, E. (2015). No evidence for correlational selection on exploratory behaviour and natal dispersal in the great tit. Evolutionary Ecology, 29(1), 137–156. https://doi.org/10.1007/s10682-014-9737-4

van Overveld, T., & Matthysen, E. (2009). Personality predicts spatial responses to food manipulations in free-ranging great tits (Parus major). Biology Letters, 6(2), 187–190. https://doi.org/10.1098/rsbl.2009.0764

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human Domination of Earth’s Ecosystems. Science, 277(5325), 494–499. https://doi.org/10.1126/science.277.5325.494

von Merten, S., Oliveira, F. G., Tapisso, J. T., Pustelnik, A., Mathias, M. da L., & Rychlik, L. (2022). Urban populations of shrews show larger behavioral differences among individuals than rural populations. Animal Behaviour, 187, 35–46. https://doi.org/10.1016/j.anbehav.2022.02.012

Waterschoot, B. O. G., Bataille, G., & Van Dyck, H. (2023). Spatial scale-dependent effects of urbanization on phenotypic traits in a thermophilous grasshopper. Behavioral Ecology and Sociobiology, 77(5), 54. https://doi.org/10.1007/s00265-023-03325-7

Watson, H., Videvall, E., Andersson, M. N., & Isaksson, C. (2017). Transcriptome analysis of a wild bird reveals physiological responses to the urban environment. Scientific Reports, 7(1), Article 1. https://doi.org/10.1038/srep44180

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2006). Density effects on life-history traits in a wild population of the great tit Parus major: Analyses of long-term data with GIS techniques. Journal of Animal Ecology, 75(2), 604–615. https://doi.org/10.1111/j.1365-2656.2006.01078.x

Williams, D. M., Nguyen, P.-T., Chan, K., Krohn, M., & Blumstein, D. T. (2020). High human disturbance decreases individual variability in skink escape behavior. Current Zoology, 66(1), 63–70.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1560), 3959–3968.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. Trends in Ecology & Evolution, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Yates, M. C., Bowles, E., & Fraser, D. J. (2019). Small population size and low genomic diversity have no effect on fitness in experimental translocations of a wild fish. Proceedings of the Royal Society B: Biological Sciences, 286(1916), 20191989. https://doi.org/10.1098/rspb.2019.1989

Supplementary files

Table S1. Summary statistics on the raw data for three behavioral traits analysed in this study

Traits	**Metrics**	**Urban**	**Forest**
Breath rate index	Number of individuals	760	299
	Number of observations	1089	386
	Mean number of obs/individual	1.53	1.31
	Raw Phenotypic mean (sd)	13.44 (2.23)	14.14 (2.23)
Handling aggression	Number of individuals	855	434
	Number of observations	1327	776
	Mean number of obs/individual	1.61	1.77
	Raw phenotypic mean (sd)	1.75 (1.09)	1.73(0.97)
Exploration	Number of individuals	529	193

score	Number of observations	679	227
	Mean number of obs/individual	1.35	1.25
	Raw Phenotypic mean (sd)	60.32 (62.52)	31.51 (51.56)

Table S2 - Predicted phenotypic mean per location and their associated 95% credible interval. Model accounted for sex, age, number of captures, decimal hour of measure and methodological fixed-effects (see methods for more details). Locations are ordered by ascending proportion of urbanization within a 1000-metre buffer around the nest.

Locations	**Breath rate index**	**Handling aggression**	**Exploration Score**
ROU	14.10 [13.61, 14.65]	3.06 [1.60, 4.73]	1.56 [1.17, 1.98]
GRAM	13.30 [12.67, 13.85]	3.72 [2.14, 5.53]	2.32 [1.92, 2.75]
ZOO	13.60 [13.07, 14.16]	3.13 [1.55, 4.82]	3.22 [2.93, 3.52]
MOS	13.82 [13.09, 14.44]	3.33 [1.82, 5.32]	3.31 [2.81, 3.74]
FONT	12.86 [12.24, 13.61]	3.84 [2.18, 5.81]	3.08 [2.64, 3.44]
CEF	13.79 [12.90, 14.63]	4.42 [2.21, 7.37]	2.94 [0.40, 4.81]
FAC	13.75 [12.92, 14.52]	4.15 [2.33, 6.18]	3.37 [2.81, 3.99]
MAS	13.74 [13.15, 14.38]	3.55 [2.15, 5.55]	3.54 [3.21, 3.87]
BOT	13.79 [12.54, 14.92]	3.74 [1.77, 6.19]	3.41 [2.48, 4.36]

Table S3. Mean and variance of proportion of impervious surface area(ISA) at 100, 250 and 1000 meters per sampling location (1 rural location ROU and 8 urban locations). Locations are ordered by ascending proportion of urbanization within a 1000-metre buffer around the nest.

	100 meters		250 meters		1000 meters	
Locations	**Mean**	**Variance**	**Mean**	**Variance**	**Mean**	**Variance**
ROU	0.000	0.000	0.000	0.000	0.001	0.000
GRAM	0.177	0.028	0.171	0.017	0.185	0.002
ZOO	0.049	0.002	0.092	0.005	0.303	0.003
MOS	0.565	0.07	0.547	0.026	0.499	0.003
FONT	0.61	0.09	0.682	0.05	0.633	0.005
CEF	0.669	0.025	0.709	0.001	0.671	0.001
FAC	0.975	0.001	0.931	0.002	0.826	0.001
MAS	0.903	0.022	0.9	0.005	0.83	0.005
BOT	0.557	0.008	0.818	0.000	0.933	0.000

Table S4. Repeatability (rpt), variance components, predicted trait mean and their 95% credible interval for breath rate index, handling aggression and exploration score. For handling aggression, the residual variance is fixed to one due to the family distribution of the model.

metric	**habitat**	**Breath rate index**	**Handling aggression**	**Exploration Score**
rpt	urban	0.59[0.50-0.66]	0.55[0.441-0.655]	0.68[0.58-0.77]
rpt	forest	0.43[0.26-0.57]	0.34[0.21-0.483]	0.87[0.766-0.951]
Vp	urban	4.892[4.301-5.657]	2.611[1.906-3.445]	3.019[2.57-3.546]
Vp	forest	4.500[3.784-5.222]	1.646[1.283-2.088]	6.498[4.783-8.29]
Vy	urban	0.346[0.04-0.852]	2.782[1.984-3.631]	0.125[0-0.394]
Vy	forest	0.109[0-0.440]	1.670[1.293-2.108]	0.170[0-0.680]
Vf	urban	0.021[0-0.052]	0.059[0-0.178]	0.010[0-0.032]
Vf	forest	0.046[0-0.125]	0.065[0-0.201]	0.098[0-0.287]
Vi	urban	2.864[2.39-3.369]	0.171[0.078-0.276]	2.061[1.636-2.492]
Vi	forest	1.927[1.066-2.665]	0.025[0.001-0.054]	5.652[4.018-7.44]
Vr	urban	1.661[1.399-1.915]	Fixed to 1	0.822[0.609-1.086]
Vr	forest	2.418[1.797-3.112]	Fixed to 1	0.578[0.221-1.075]
Predicted mean	urban	13.47[12.79, 14.08]	1.97[1.56, 2.44]	3.12 [2.83, 3.43]
Predicted mean	forest	14.20[13.26, 15.17]	1.80[1.37, 2.25]	1.55 [1.06, 2.02]

Table S5. Number of observations per location (9 locations) and sex for each traits BRI (Breath rate index),HA (Handling aggression) and ES (Exploration score). The 9 locations are ordered by ascending mean ISA (buffer 1000m).

	rou	**gram**	**zoo**	**mos**	**font**	**cef**	**fac**	**mas**	**bot**

BRI female	238	115	178	45	79	14	49	81	11
BRI male	148	103	163	41	69	11	39	81	10
HA female	409	137	188	69	101	14	60	100	15
HA male	367	132	209	61	95	10	50	101	13
ES female	128	77	95	35	48	6	25	60	7
ES male	99	69	94	31	42	4	20	60	6

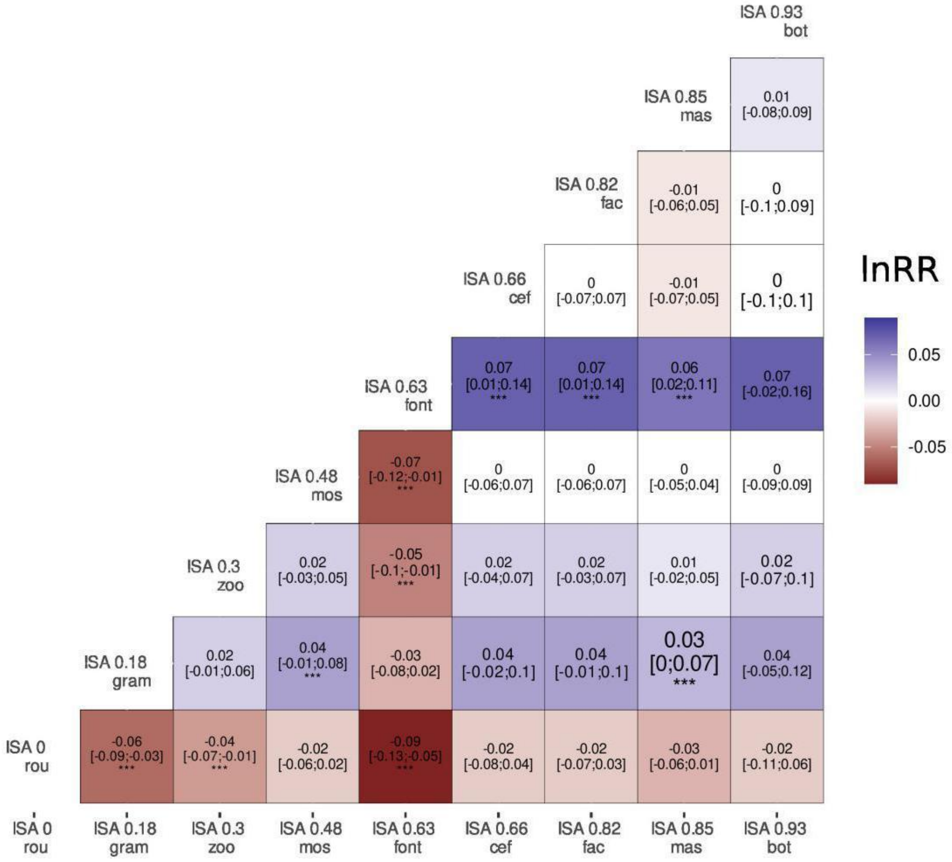


Figure S1. Pairwise log response ratio (lnRR) and their 95% credible interval for Breath Rate Index between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m). A positive lnRR (in blue) value means that location on the x-axis as a higher mean than the location on the y-axis.

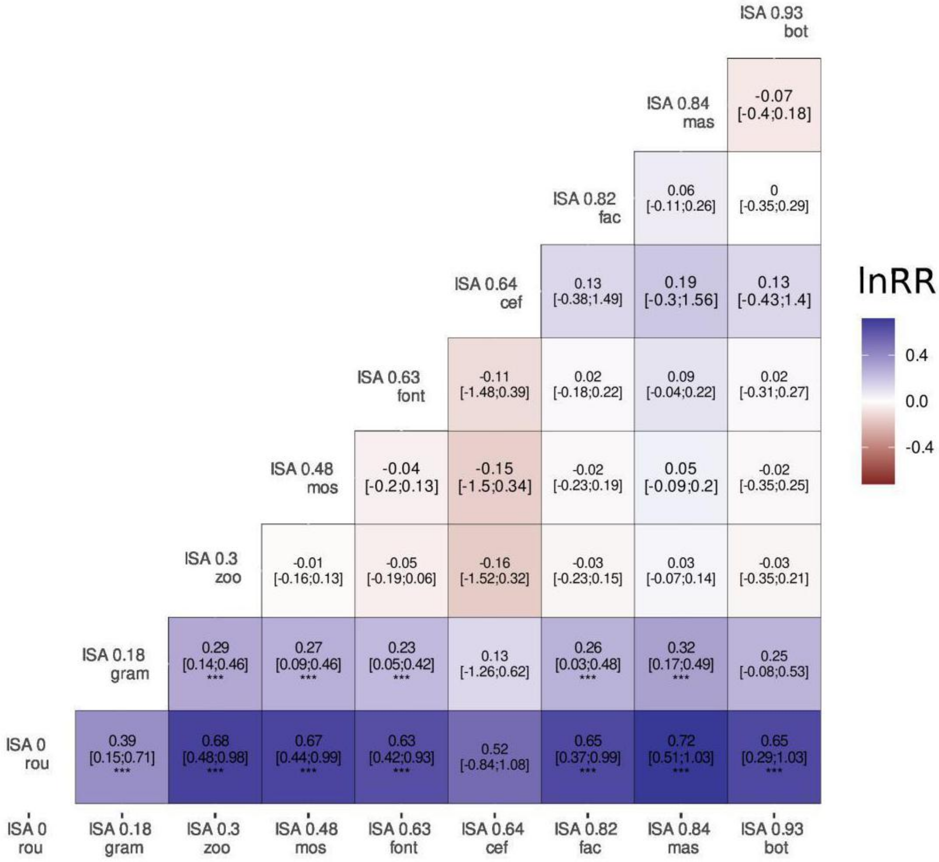


Figure S2. Pairwise log response ratio (lnRR) and their 95% credible interval for ES between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m). A positive lnRR (in blue) value means that location on the x-axis as a higher mean than the location on the y-axis.

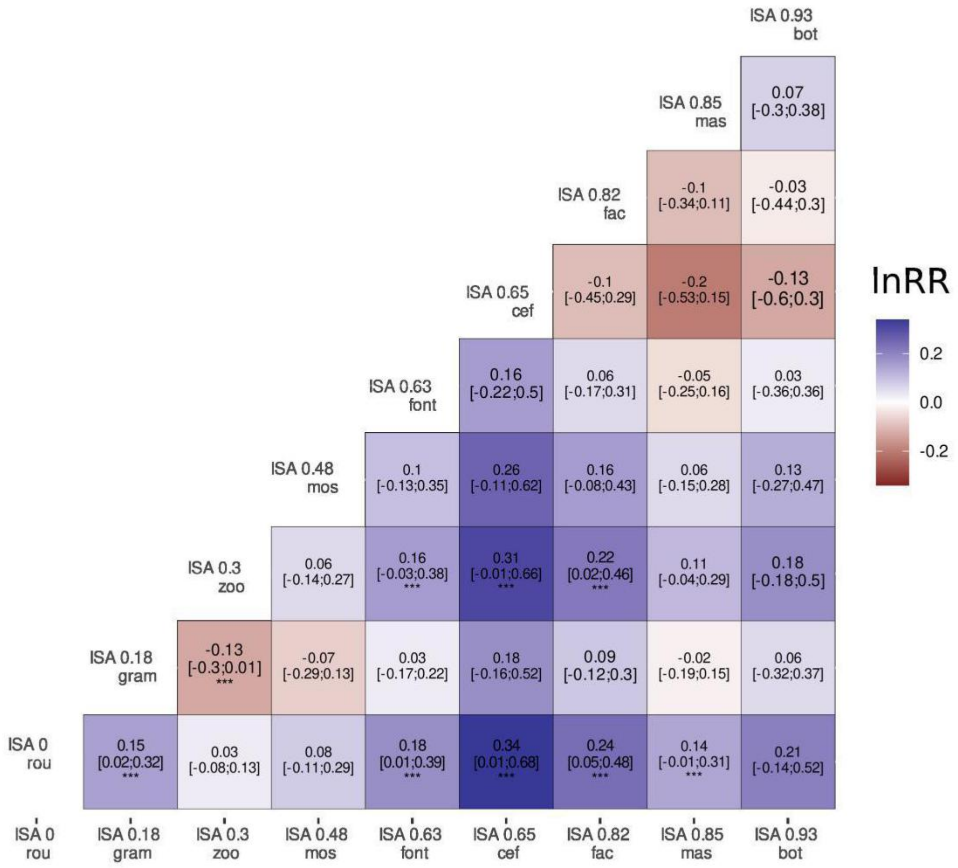
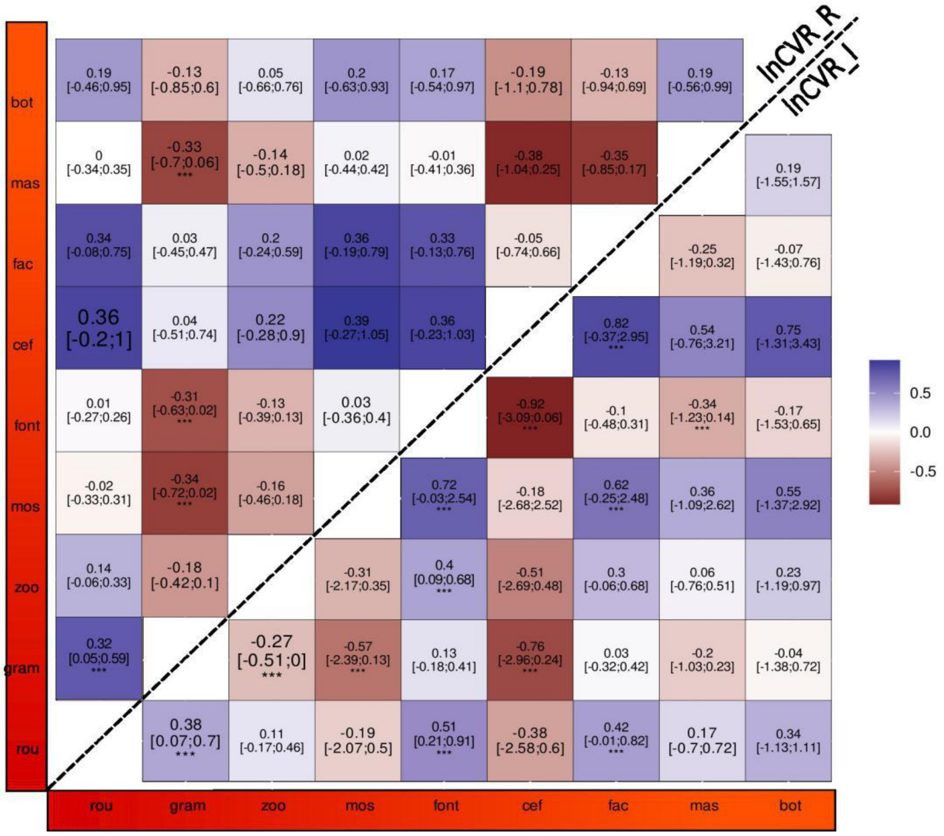


Figure S3. Pairwise log response ratio (lnRR) and their 95% credible interval for HA between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m). A positive lnRR (in blue) value means that location on the x-axis as a higher mean than the location on the y-axis.

A - BRI



	rou	gram	zoo	mos	font	cef	fac	mas	bot
bot	0.19 [-0.46;0.95]	-0.13 [-0.85;0.6]	0.05 [-0.66;0.76]	0.2 [-0.63;0.93]	0.17 [-0.54;0.97]	-0.19 [-1.1;0.78]	-0.13 [-0.94;0.69]	0.19 [-0.56;0.99]	
mas	0 [-0.34;0.35]	-0.33 [-0.7;0.06] ***	-0.14 [-0.5;0.18]	0.02 [-0.44;0.42]	-0.01 [-0.41;0.36]	-0.38 [-1.04;0.25]	-0.35 [-0.85;0.17]		0.19 [-1.55;1.57]
fac	0.34 [-0.08;0.75]	0.03 [-0.45;0.47]	0.2 [-0.24;0.59]	0.36 [-0.19;0.79]	0.33 [-0.13;0.76]	-0.05 [-0.74;0.66]		-0.25 [-1.19;0.32]	-0.07 [-1.43;0.76]
cef	0.36 [-0.2;1]	0.04 [-0.51;0.74]	0.22 [-0.28;0.9]	0.39 [-0.27;1.05]	0.36 [-0.23;1.03]		0.82 [-0.37;2.95] ***	0.54 [-0.76;3.21]	0.75 [-1.31;3.43]
font	0.01 [-0.27;0.26]	-0.31 [-0.63;0.02] ***	-0.13 [-0.39;0.13]	0.03 [-0.36;0.4]		-0.92 [-3.09;0.06] ***	-0.1 [-0.48;0.31]	-0.34 [-1.23;0.14] ***	-0.17 [-1.53;0.65]
mos	-0.02 [-0.33;0.31]	-0.34 [-0.72;0.02] ***	-0.16 [-0.46;0.18]		0.72 [-0.03;2.54] ***	-0.18 [-2.68;2.52]	0.62 [-0.25;2.48] ***	0.36 [-1.09;2.62]	0.55 [-1.37;2.92]
zoo	0.14 [-0.06;0.33]	-0.18 [-0.42;0.1]		-0.31 [-2.17;0.35]	0.4 [0.09;0.68] ***	-0.51 [-2.69;0.48]	0.3 [-0.06;0.68]	0.06 [-0.76;0.51]	0.23 [-1.19;0.97]
gram	0.32 [0.05;0.59] ***		-0.27 [-0.51;0] ***	-0.57 [-2.39;0.13] ***	0.13 [-0.18;0.41]	-0.76 [-2.96;0.24] ***	0.03 [-0.32;0.42]	-0.2 [-1.03;0.23]	-0.04 [-1.38;0.72]
rou		0.38 [0.07;0.7] ***	0.11 [-0.17;0.46]	-0.19 [-2.07;0.5]	0.51 [0.21;0.91] ***	-0.38 [-2.58;0.6]	0.42 [-0.01;0.82] ***	0.17 [-0.7;0.72]	0.34 [-1.13;1.11]

Figure S4A. Pairwise log-coefficient variance ratio (lnCVR) and their 95% credible interval for BRI between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m), which is also represented in an orange gradient, with dark orange indicating higher levels of ISA. lnCVR for within individual variance (lnCVR_R) is above the diagonal while lnCVR for among-individual variance (lnCVR_I) is below the diagonal. Note that for HA we represented lnCVR for total phenotypic variance (lnCVR_P) as the threshold model does not estimate residual variance. Positive, zero and negative lnCVR are shown in blue, white and red respectively. A positive (in blue) value means that the location on the x-axis has a greater coefficient of variation (and so associated variance) than the location on the y-axis. See the supplementary materials to have access to all the values.

B - HA

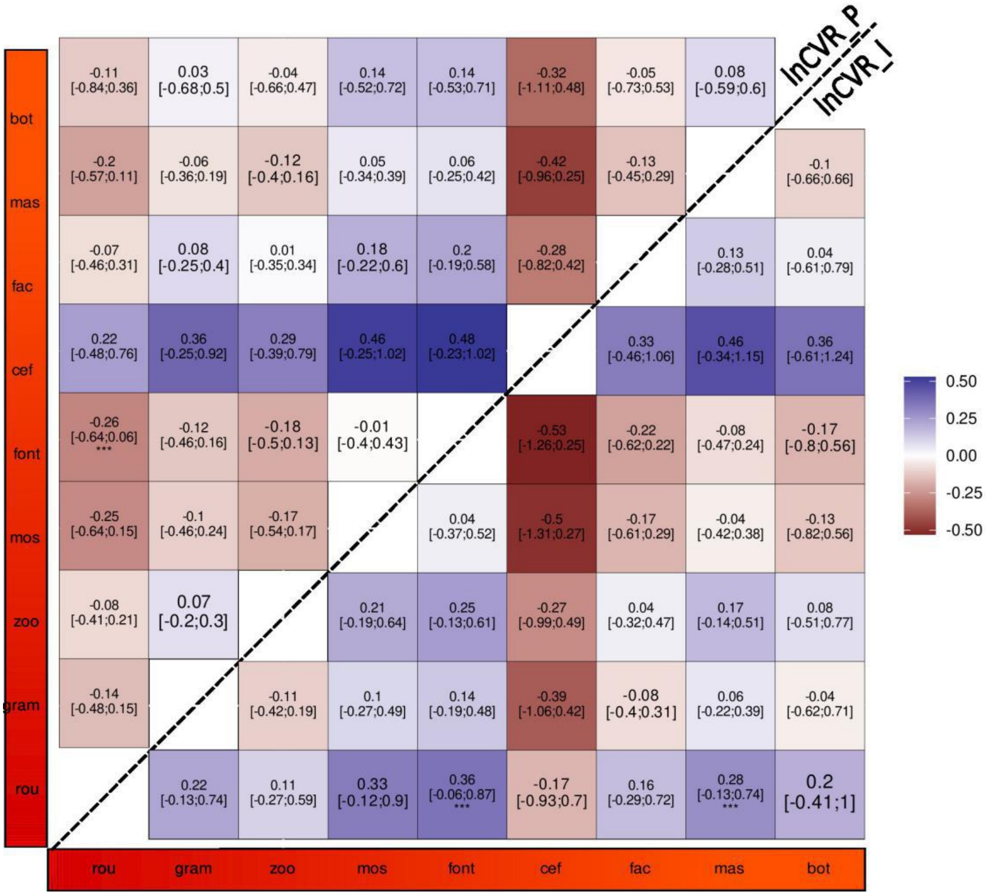
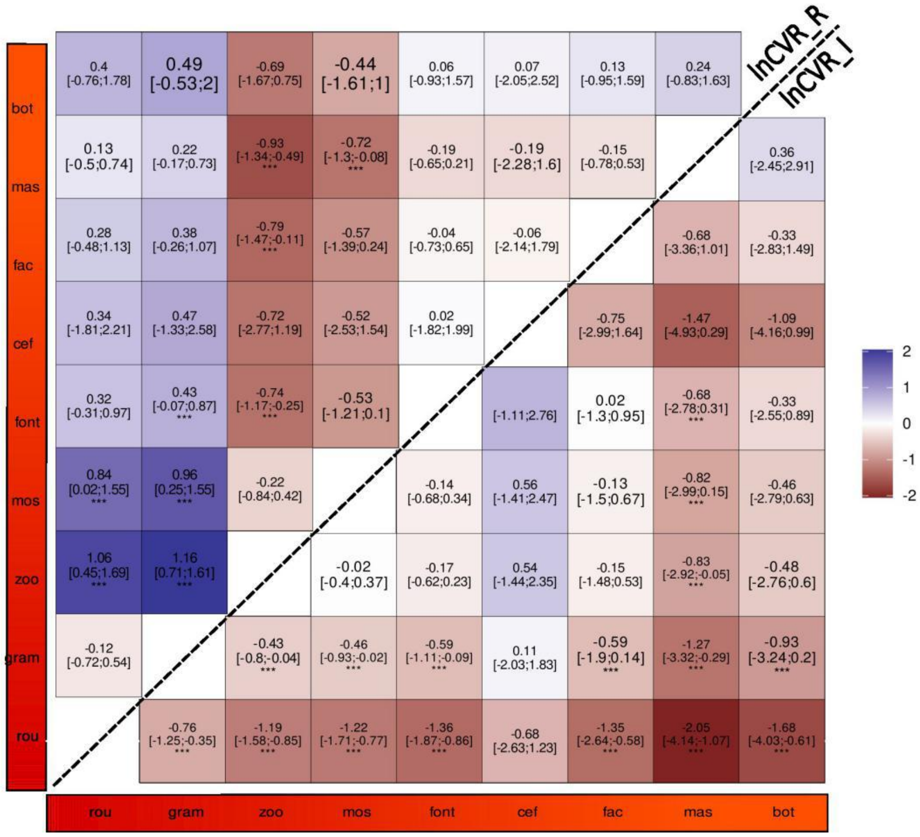


Figure S4B. Pairwise log-coefficient variance ratio (lnCVR) and their 95% credible interval for HA between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m), which is also represented in an orange gradient, with dark orange indicating higher levels of ISA. lnCVR for within individual variance (lnCVR_R) is above the diagonal while lnCVR for among-individual variance (lnCVR_I) is below the diagonal. Note that for HA we represented lnCVR for total phenotypic variance (lnCVR_P) as the threshold model does not estimate residual variance. Positive, zero and negative lnCVR are shown in blue, white and red respectively. A positive (in blue) value means that the location on the x-axis has a greater coefficient of variation (and so associated variance) than the location on the y-axis. See the supplementary materials to have access to all the values.

C - ES



	rou	gram	zoo	mos	font	cef	fac	mas	bot
bot	0.4 [-0.76;1.78]	0.49 [-0.53;2]	-0.69 [-1.67;0.75]	-0.44 [-1.61;1]	0.06 [-0.93;1.57]	0.07 [-2.05;2.52]	0.13 [-0.95;1.59]	0.24 [-0.83;1.63]	
mas	0.13 [-0.5;0.74]	0.22 [-0.17;0.73]	-0.93 [-1.34;-0.49] ***	-0.72 [-1.3;-0.08] ***	-0.19 [-0.65;0.21]	-0.19 [-2.28;1.6]	-0.15 [-0.78;0.53]		0.36 [-2.45;2.91]
fac	0.28 [-0.48;1.13]	0.38 [-0.26;1.07]	-0.79 [-1.47;-0.11] ***	-0.57 [-1.39;0.24]	-0.04 [-0.73;0.65]	-0.06 [-2.14;1.79]		-0.68 [-3.36;1.01]	-0.33 [-2.83;1.49]
cef	0.34 [-1.81;2.21]	0.47 [-1.33;2.58]	-0.72 [-2.77;1.19]	-0.52 [-2.53;1.54]	0.02 [-1.82;1.99]		-0.75 [-2.99;1.64]	-1.47 [-4.93;0.29]	-1.09 [-4.16;0.99]
font	0.32 [-0.31;0.97]	0.43 [-0.07;0.87] ***	-0.74 [-1.17;-0.25] ***	-0.53 [-1.21;0.1]		[-1.11;2.76]	0.02 [-1.3;0.95]	-0.68 [-2.78;0.31] ***	-0.33 [-2.55;0.89]
mos	0.84 [0.02;1.55] ***	0.96 [0.25;1.55] ***	-0.22 [-0.84;0.42]		-0.14 [-0.68;0.34]	0.56 [-1.41;2.47]	-0.13 [-1.5;0.67]	-0.82 [-2.99;0.15] ***	-0.46 [-2.79;0.63]
zoo	1.06 [0.45;1.69] ***	1.16 [0.71;1.61] ***		-0.02 [-0.4;0.37]	-0.17 [-0.62;0.23]	0.54 [-1.44;2.35]	-0.15 [-1.48;0.53]	-0.83 [-2.92;-0.05] ***	-0.48 [-2.76;0.6]
gram	-0.12 [-0.72;0.54]		-0.43 [-0.8;-0.04] ***	-0.46 [-0.93;-0.02] ***	-0.59 [-1.11;-0.09] ***	0.11 [-2.03;1.83]	-0.59 [-1.9;0.14] ***	-1.27 [-3.32;-0.29] ***	-0.93 [-3.24;0.2] ***
rou		-0.76 [-1.25;-0.35] ***	-1.19 [-1.58;-0.85] ***	-1.22 [-1.71;-0.77] ***	-1.36 [-1.87;-0.86] ***	-0.68 [-2.63;1.23]	-1.35 [-2.64;-0.58] ***	-2.05 [-4.14;-1.07] ***	-1.68 [-4.03;-0.61] ***

Figure S4C. Pairwise log-coefficient variance ratio (lnCVR) and their 95% credible interval for ES between the 9 locations of the study system (and their corresponding 1000 metres ISA). The 9 locations are ordered by ascending mean ISA (buffer 1000m), which is also represented in an orange gradient, with dark orange indicating higher levels of ISA. lnCVR for within individual variance (lnCVR_R) is above the diagonal while lnCVR for among-individual variance (lnCVR_I) is below the diagonal. Note that for HA we represented lnCVR for total phenotypic variance (lnCVR_P) as the threshold model does not estimate residual variance. Positive, zero and negative lnCVR are shown in blue, white and red respectively. A positive (in blue) value means that the location on the x-axis has a greater coefficient of variation (and so associated variance) than the location on the y-axis. See the supplementary materials to have access to all the values.

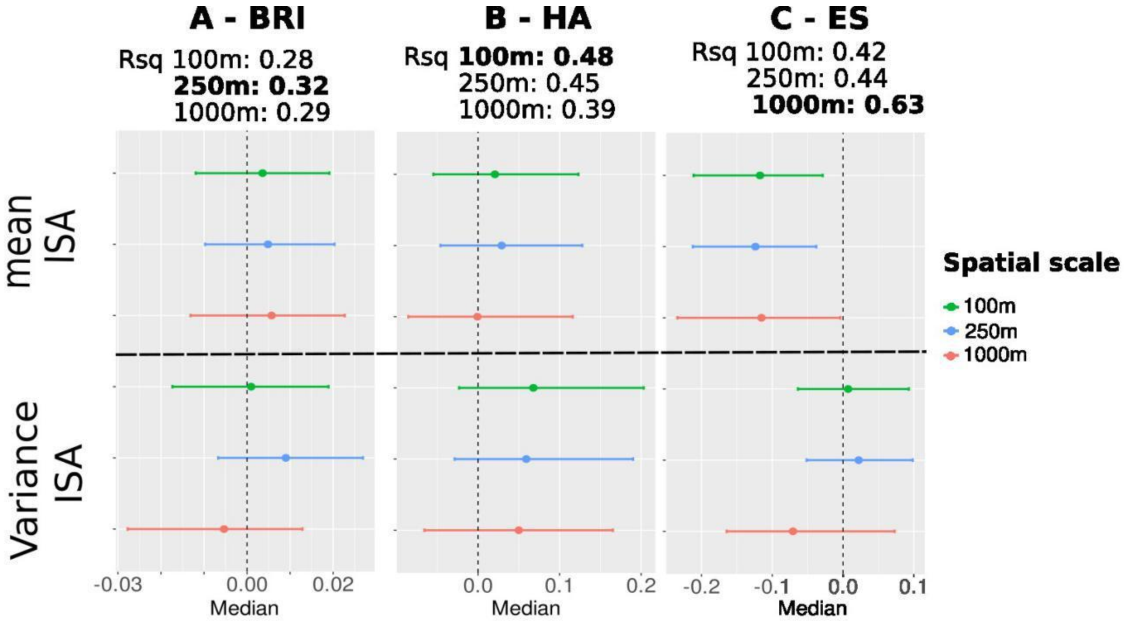


Figure S5. Magnitude of relationship between mean ISA and variance in ISA with the mean-standardized among-individual variance (CVI) and their associated 95 % credible intervals, for breath rate index (BRI) handling aggression (HA) and exploration score (ES). ISA was measured at different scales (100, 250 and 1000 metres, in green, blue and red respectively). Rsq refers to the mean of bayesian-R2 over the iterations of the models and the highest rsq is reported in bold.