Title: From a review to the field: Alternative coping styles under urbanisation

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Authors contribution statement:

According to the Contributor Role Taxonomy (CRediT) authors have the following contributions.

Jules Petit: Conceptualisation, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft, Writing – review & editing.

Melanie Dammhahn: Conceptualisation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Data availability statement:

The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.547d7wmpc. Peer reviewers can use this link to access the files: http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/zUA0dh3vgTl3gv6y8U4bWrwaV6l-hrZCxKva8WqRukc.

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Abstract

(288 words)

Under human-induced rapid environmental changes, behavioural and physiological responses of organisms are key to maintain homeostasis and minimise fitness loss. Both responses can be integrated, into among-individual correlations forming stress-coping styles or syndromes (SCS). Such SCS emerge from genetic correlations or adaptive trade-offs. In the context of environmental challenges, more proactive individuals are expected to show lower hypothalamic-pituitary-adrenal (HPA) axis (re)activity responses, whereas more reactive individuals show higher HPA axis responses. Urban environments are associated with new artificial stressors, which might alter or manifest trait integration into SCS. However, studies investigating urban-induced changes in SCS are scarce. Here, we aim to test the emergence of SCS in wood mice (*Apodemus sylvaticus*) under urbanisation. We tested for phenotypic variation in boldness (N = 140), spatial exploration (N = 137), defiantness (N = 131), and faecal corticosterone metabolite (FCM) levels (N = 93) along an urbanisation gradient in a middle-sized city (Münster) in Germany. Although all traits were repeatable over time, none changed along the imperviousness gradient (a proxy for urbanisation). We assessed behavioural and stress-coping syndromes between two non-urban and four urban sites. Analysing among-individual correlations in urban and non-urban sites separately, we found that bolder individuals were more defiant only in urban populations. However, against predictions of the SCS hypothesis bolder or more defiant individuals had higher FCM levels in urban populations. By performing a systematic review of the available literature on SCS under urbanisation, we found only two studies and those reported mixed SCS patterns. Our results highlight the complexity of organismal responses to human-induced environmental changes shaping new sets of correlated traits. Future research may focus on how differential individualised environmental feedback upon the phenotype might be key for new trait integration creating new fitness landscapes.

Introduction

Global human-induced rapid environmental changes (HIRECs) are the main drivers of the ongoing 6th mass extinction in the Anthropocene. Urbanisation is a peculiar process as it recreates a set of HIRECs at a local scale, such as habitat change (e.g. habitat fragmentation), pollution (e.g. light, air, sound), and climate change (e.g. urban heat island effect; Grimm *et al.* 2008). As cities are constantly expanding throughout the world at an unprecedented rate, it is crucial to understand their consequences on ecosystems and biodiversity (McKinney 2002). To cope with HIRECs, organisms may use both, behavioural and physiological components of the stress response to maintain homeostasis (Billman 2020; Liu *et al.* 2024; Sapolsky *et al.* 2000) and minimize fitness loss (Blas *et al.* 2007; Dingemanse *et al.* 2004; Dingemanse & Réale 2005; Thomson *et al.* 2001; Wilson & Franklin 2002). However, the empirical evidence for these patterns is mixed. A meta-analysis (Burkhard *et al.* 2026) reported a major increase in the average behavioural response of urban populations compared to non-urban ones in boldness (and a trend in exploration) which are often associated with the stress response (Koolhaas *et al.* 2007; Thomson *et al.* 2011). Two other meta-analyses did not support an average change in baseline and stress-induced glucocorticoid levels under urbanisation across taxa, suggesting that responses are likely to be species-specific (Iglesias-Carrasco *et al.* 2020; Injaian *et al.* 2020).

While change in average phenotype expression of a singular trait may inform eco-evolutionary processes, it is most likely that selection favours trait combinations, especially as populations often contain individuals harbouring a continuum of different trait mixtures (Wolf *et al.* 2007). Indeed, as individuals expressed consistent differences in their behavioural and physiological responses when analysed separately, researchers hypothesised the existence of “stress-coping styles” (SCS; Benus *et al.* 1991; Koolhaas *et al.* 1997; Korte *et al.* 2005). Stress-coping styles refer to a coherent set of behavioural and physiological stress responses showing consistent individual differences over time and/or across context (Koolhaas *et al.* 1999). The SCS hypothesis assumes that behaviour and physiology are integrated to structure divergent specialised stress responses known as proactive or reactive coping styles (Koolhaas *et al.* 1997). Proactive individuals willingly challenge stressors and harbour behavioural profiles similar to bold personalities (Koolhaas *et al.* 2007; Thomson *et al.* 2011). These individuals express high exploratory behaviour, weak conditioned immobility and a reduced hypothalamic-pituitary-adrenal (HPA) axis activity and reactivity. In contrast, reactive individuals are described as shy, less exploratory and expressing a strong conditioned immobility response with an increased HPA axis (re)activity (Carere *et al.* 2010; Øverli *et al.* 2007). Often pictured as dichotomous (Koolhaas *et al.* 1999), proactive and reactive coping styles are most likely part of a continuum and can be viewed as a stress-coping syndrome with behavioural and physiological stress responses integrating along an axis of among-individual variation.

The SCS framework was developed and initially tested mainly using laboratory rodents under standard captive conditions (Carere *et al.* 2010; Koolhaas *et al.* 1999; Veenema *et al.* 2003). Originally, the correlations between more proactive behaviours and the different physiological responses (HPA axis, (para)sympathetic systems) were expected to arise from potential evolutionary constraints related to pleiotropy and/or common physiological pathways underlying multiple behavioural traits (Koolhaas *et al.* 1999, 2010; Solovieff *et al.* 2013). However, research testing the presence of coping styles or syndromes in wild populations revealed mixed findings (Caizergues *et al.* 2022; Ferrari *et al.* 2013; Forte *et al.* 2023; Montiglio *et al.* 2012; Qu *et al.* 2018; Royauté *et al.* 2018). Such discrepancy highlights that the presence of phenotypic correlations as a suite of continuous fine-tuned strategies in natural and complex ecosystems is often context-dependent and can vary with ecological conditions of the study system (Dammhahn *et al.* 2018; Dingemanse *et al.* 2007; Sih *et al.* 2004). Urbanisation comes along with various new human-induced environmental changes, altering ecological dynamics such as predation (Corcos *et al.* 2019; meta-analysis: Eötvös *et al.* 2018), competition (Sedláček *et al.* 2004; Shochat *et al.* 2010), inter- and intra-specific interactions (Classen-Rodríguez *et al.* 2021) or social interactions (systematic review: Maune *et al.* 2026). Therefore, it seems crucial to identify whether stress-coping syndromes are expressed and/or altered in such contexts. However, we are currently lacking evidence whether SCS are present under urbanisation (but see Sadoul *et al.* 2021). While certain studies reported total phenotypic correlations (Dominoni *et al.* 2013a; Guindre-Parker *et al.* 2022; Rebolo-Ifrán *et al.* 2015), only a few assessed among-individual variation (repeatability) and reported mixed findings regarding among-individual correlations between behavioural and physiological traits under urbanisation (Caizergues *et al.* 2022; Oliveira *et al.* 2020).

In this study, we aimed to test SCS under urbanisation in free-ranging wood mice (*Apodemus sylvaticus*). Wood mice are a suitable study species to test SCS as they are small nocturnal rodents commonly found in cities (Rimbach *et al.* 2025; Schlitter *et al.* 2021; Wilson *et al.* 2016), with a relatively low level of direct interaction with humans, but high exposure to urbanisation-related disturbances (e.g. sound or light pollution). In addition, species of the genus *Apodemus* are well studied for behavioural and physiological traits (behaviour: Dammhahn *et al.* 2020; Savazza *et al.* 2026; Schirmer *et al.* 2020; Strijker *et al.* 2023; physiology: Devalloir *et al.* 2023; Łopucki *et al.* 2019; Navarro-Castilla *et al.* 2014, 2018). Along an urbanisation gradient, we repeatedly measured one physiological and three behavioural traits. Boldness and exploration were measured using the combined dark-light and open-field test (Gosling 2001; Herde & Eccard 2013), and defiantness (also called docility) using the handling bag test (Martin &

Réale 2008; Montiglio *et al.* 2012). We measured faecal corticosterone metabolites (FCMs), an integrated measure of HPA axis (re)activity (Palme 2019; Sheriff *et al.* 2011; Touma & Palme 2005).

Our main goals were to i) quantify the amount of among-individual variation present in the behavioural and physiological traits (i.e. index of individual phenotypic specialisation) and assess trait changes along a gradient of urbanisation. In addition, we tested for among-individual correlations ii) across behavioural traits (i.e. behavioural syndrome) and iii) between behavioural and physiological traits (i.e. stress-coping syndrome). We predicted that individuals from more urbanised areas were bolder, more explorative and more defiant than conspecifics from less urbanised areas. In both, urban and non-urban populations, we expected a) positive correlations between boldness, exploration and defiantness, and b) more proactive individuals (those scoring high in boldness, exploration, and defiantness) to express lower FCM levels (Table 1a). To systematically assess the current knowledge, we additionally performed two systematic reviews to summarise the findings from a) studies repeatedly measuring behavioural and physiological traits concurrently in the same individuals under urbanisation and b) studies explicitly framing their research within the SCS framework under urbanisation.

***Table 1. Summary of among-individual correlations (+: positive, -: negative) between behavioural and physiological traits for non-urban and urban populations in reference to predictions of the original stress-coping style (SCS) hypothesis.** The table combines the results from a) our field study on wood mice* (Apodemus sylvaticus)*, b) the review n°1 focusing on studies measuring behavioural and physiological traits repeatedly per individual concurrently under urbanisation (called SCS potential studies), and c) the review n°2 focusing on studies explicitly framing their research using the SCS framework under urbanisation (called SCS-framed studies). HPA stands for hypothalamic pituitary adrenal, and RMR for resting metabolic rate. Statistically significant results are reported (p < 0.05), as well as trends. Asterisks (*) means that a trend is reported. Relationships were classified as trends when the 95% confidence or credibility intervals included zero but extended no more than ± 0.05 beyond it, and when the estimated correlation coefficient was at least 3.5 times larger in magnitude than the interval's overlap with zero. Blank cell means that no correlations was observed.*

	SCS *predicted* [1]	Non-Urban *observed*	Urban *observed*
a) Field study			
Wood mouse, *Apodemus sylvaticus*			
Boldness ~ Exploration	+		
Boldness ~ Defiantness	+		+
Exploration ~ Defiantness	+		
HPA axis (re)activity ~ Boldness	-		+
HPA axis (re)activity ~ Exploration	-		
HPA axis (re)activity ~ Defiantness	-		+
b) Review n°1: SCS potential studies			
Caizergues et al. (2022) — Great tit, *Parus major*			
Handling aggression ~ Exploration	+		
Breath rate ~ Handling aggression	+	-*	
Breath rate ~ Exploration	+		-
Oliveira et al. (2020) — Greater white-toothed shrew, *Crocidura russula*			
Boldness ~ Exploration	+		
RMR ~ Boldness	+		
RMR ~ Exploration	+		
Studies with adequate datasets that did not report among-individual correlations between behavioural and physiological traits for non-urban and urban populations: Batabyal & Thaker (2019); Caspi et al. (2025); Dominoni et al. (2013a, b); Forte et al. (2023); Guindre-Parker et al. (2022); Thompson et al. (2025).			
c) Review n°2: SCS-framed studies			
None of the studies reported among-individual correlations between behavioural and physiological traits for non-urban and urban populations: Batabyal & Thaker (2019); Corbel et al. (2016); Guindre-Parker et al. (2022); Partecke et al. (2006); Senar et al. (2017).			

[1] Predictions based on Koolhaas *et al.* (1999).

Methods

Study species and study sites

The wood mouse (*Apodemus sylvaticus*) is a small nocturnal rodent widely distributed across Europe and is considered a habitat generalist (Figure 1B). Wood mice inhabit various landscapes such as woodland, moorland, arid Mediterranean scrubland and sand dunes (Schlitter *et al.* 2021). They also appear in many human-made habitats such as arable fields, pastures, gardens and urban parks (Schlitter *et al.* 2021). Therefore, it is a suitable study species to investigate wildlife adaptation in the context of urbanisation. Their diet is mainly composed of seeds, nuts, fruits and invertebrates (Butet & Delettre 2011) and – based on trapping data – their home range varies from 275 to 14,000 m^2 (Benhamou 1991; Korn 1986). Wood mice are primary prey for many predatory birds (e.g. owls, European kestrel) and mammals (e.g. weasels, martens), making them an important ecological link in the food chain (Flowerdew *et al.* 1985).

This study was conducted in the city of Münster, Germany (Latitude: 51.9625, Longitude: 7.6256), from the 6th of May until 20th of August 2024, during the breeding season. Across the city, we established 6 sites following an urbanisation gradient (Figure 1A, Table S3). The degree of urbanisation was calculated using the percentage of sealed surface (i.e. imperviousness) around each site using QGIS (QGIS Development Team 2024, version 3.36) combined with an open access data set with a land-use classification of Münster (Interministerieller Ausschuss für Geodateninfrastrukturen in Nordrhein-Westfalen 2022; as described in Rimbach *et al.* 2025). The percentage of imperviousness is known to correlate with many other urban characteristics and offers an adequate proxy of urbanisation impacts on wildlife (Szulkin *et al.* 2020). We calculated impervious surface cover for three different buffer sizes: 100-m, 500-m and 1000-m radius around each study site's centre. The 100-m buffer represents the daily movement distances of small mammals, the 500-m buffer includes the average dispersal distance of small mammals (Blair 1953; Wolton & Flowerdew 1985) and determines the most relevant buffer size for the study species (ranging from 5 to 82% imperviousness, Table S3). The 1000-m buffer represents a less relevant ecologically scale as a base for the null model. We also categorised the sites into urban and non-urban to simplify the statistical procedure and interpretations when assessing SCS syndromes under urbanisation (see section '*Among-individual correlations*' in Methods). Since no precise guidelines exist to determine the cut-off for imperviousness between non-urban and urban areas (Szulkin *et al.* 2020), we categorised study sites with ≤ 22 % of imperviousness within the 500-m radius as non-urban and study sites with > 40 % as urban. We consider our threshold fairly conservative since sites have been classified as non-urban from 10 to 50 % of imperviousness in the literature (Liu *et al.* 2014; Szulkin *et al.* 2020), and because our least urbanised site had two times the amount of sealed surface than our most non-urbanised site.

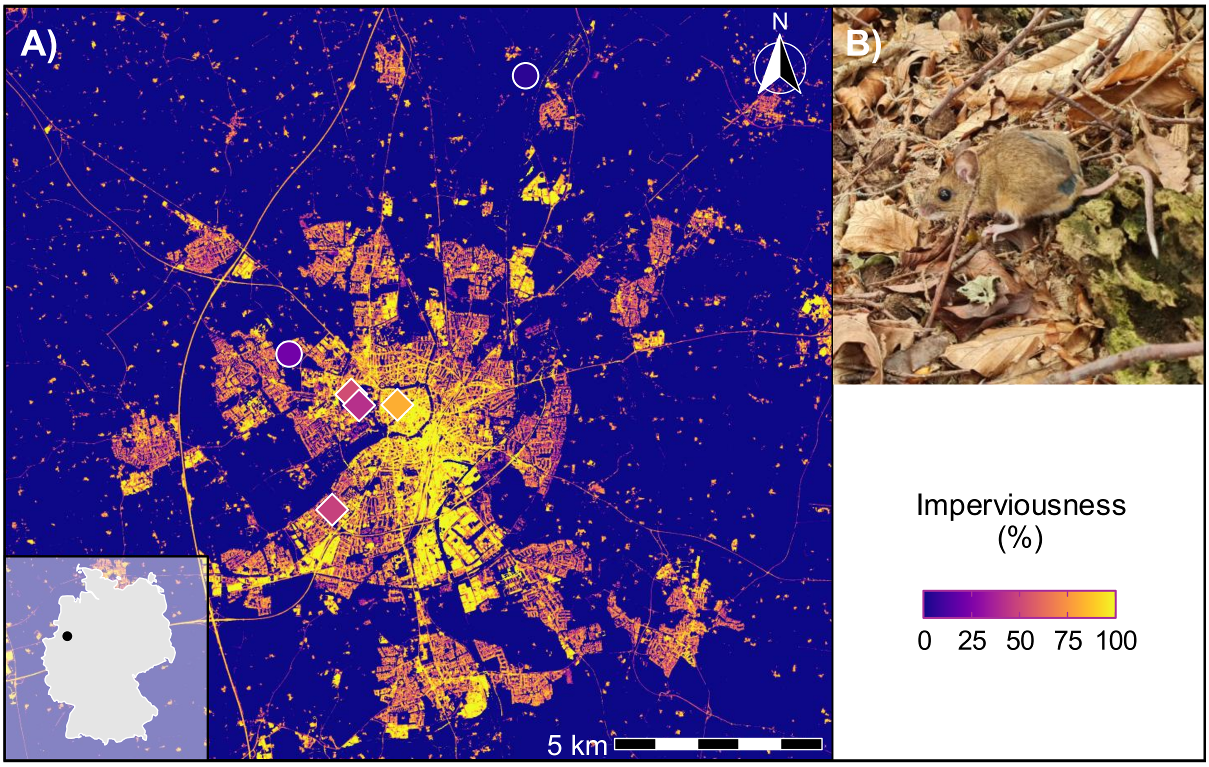

Figure 1. Graphical portrayal of the study (Münster, Germany). *A) Heat map showing the imperviousness (i.e. artificial sealed surface) density of Münster in 2021. Values range from 0 to 100% with a spatial resolution of 10 m. The 2 circles and 4 diamonds represent the 2 non-urban and 4 urban sites, respectively. The inset map (bottom left in grey) shows the location of Münster (black dot) in Germany. Imperviousness data was extracted from Copernicus Land Monitoring (2025). B) Study species of the project,* Apodemus sylvaticus *(wood mouse). The image was taken by Rebecca Rimbach. Map lines delineate study areas and do not necessarily depict accepted national boundaries.*

Capture-mark-recapture

We used a capture-mark-recapture approach using multiple-capture live-traps (Ugglan Special Traps n.1-2, Grahnab AB, Hillerstorp, Sweden, with shrew exit) baited with oat flakes, cucumber or apple. At every study site, we established a grid composed of traps spaced evenly by 10 m. The size of the grid varied between 50 m x 50 m to 90 m x 90 m according to the site's size (Table S3). We pre-baited the inactive traps with oat flakes for two days before activation. We alternated trapping between two sites, returning to each location every second week. Traps were activated at dawn (around 20:30-22:00) and checked at dusk (around 6:30) for 3 to 4 days, depending on weather conditions (no trapping under rainy conditions). Since our recapture rate was relatively low, we decided to trap again one more time in three sites (Rieselfelder, Kinderbachtal and Botanic Garden). The interval between the second and third trapping session was 12 weeks for Rieselfelder and Kinderbachtal, and one week for Botanic Garden. Overall, we captured 193 individuals (152 in urban and 41 non-urban sites). Among them, there were 41 juveniles and 152 adults, including 76 females, 94 males and 23 non-classifiable. From the individuals captured during week 1, we recaptured 60 individuals (31%) in week 2 or 3. Before the handling procedure, we performed three behavioural tests (see 'Behavioural tests'). During handling, we determined an individual's sex and age class (adult with signs of reproduction and/or body mass > 14 g, otherwise juvenile). We measured head width with a calliper (DialMax, resolution 0.1 mm), and body mass with an electric scale (Pesola PTS3000, resolution 0.1 g). We individually marked individuals with unique fur cuts and ear cuts.

Behavioural tests

We used two established behavioural tests combined in a sequence: the dark-light emergence and the open-field test that can be performed on-site without prior handling (Schirmer *et al.* 2019). Additionally, we performed a handling bag test prior to the combined dark-light open-field test. All tests were conducted between 07:00 to 15:00 Central European Time.

(i) Handling bag test

We used the handling bag test to measure individuals' behavioural response to human manipulation and presence, thereafter, referred to as defiantness (number of seconds active in the bag over 60 seconds, previously named docility when computed with number of seconds inactive, Martin & Réale 2008; Réale *et al.* 2000). Defiantness has been defined as the reaction of domesticated and wild animals towards humans (Agnani *et al.* 2020; Boivin *et al.* 1992; Montiglio *et al.* 2012). We (Jules Petit) started the handling bag test by letting the mouse entering a cotton bag (15 cm x 20 cm) on its own, directly from the trap. Then, we suspended the cotton bag in the air by its rope in a position that allowed the observer to see the outline of the individual in the bag for easier counting. For 60 s, we counted the number of seconds in which the individual was active inside the bag. We defined an individual as inactive when it was grooming itself or not moving. For any other movement the individual was considered to be active. During the test, natural background sounds (e.g. church bell, car noise) were present, reflecting the local soundscape experienced by individuals, including potential anthropogenic disturbances. At the end of the test, individuals were returned to the trap and subsequently transferred to the combined dark-light and open-field test.

(ii) Combined dark-light and open-field test

We used the combined dark-light and open-field test to measure individuals' risk-taking behaviour, thereafter referred to as boldness, and exploration (Réale *et al.* 2007). The dark-light test measures the motivation of an individual to leave a dark, enclosed and relatively safe shelter to enter an unknown, bright and potentially dangerous area. The open-field test measures individuals' aversion to brightly lit and open spaces, as well as their thigmotaxis tendency (Cavigelli *et al.* 2013).

The test set-up was made of a dark plastic tube (Ø 11 cm x 32 cm length) with swing doors at each end, connected to an open-field arena (Aquaforte Flexi-Bowl, Ø 120 cm x 60 cm height). A camera (Action Camera CU-SPC06, COOAU) was positioned above the apparatus to record the entire procedure. The set-up was placed under a tree to avoid direct sunlight and potential heat stress. The complete set-up was cleaned with 70 % ethanol between each trial. Individuals entered the tube from the trap on their own via a trap adaptor. A modified paper roll with the same diameter as the tube was inserted gently behind the animal in its full length (Ø 11 cm x 12 cm length, used to displace the animal towards the open field when maximum latency was reached). We closed both doors and let the mouse adjust for 60 s. Then, we opened the door leading to the open-field area and measured the latency for the individual to enter this arena with the full body (excluding the tail). We used the latency to emerge from the tube as a proxy of boldness (Eccard *et al.* 2023; Réale *et al.* 2007; Schirmer *et al.* 2019). If animals did not leave the dark tube within ten minutes, we attributed the maximum latency (600 s) to the individual (4 % of all performed tests) and gently guided the individual out of the tube to the open arena. Once the animal entered the arena, we closed the door using a rope and started the open-field test.

The open field was a circular foldable plastic pool (Aquaforte Flexi-Bowl, Ø 120 cm x 60 cm height) with a dark net to prevent escape. The floor of the open field was divided visually into 16 areas of equal surface with drawn lines where peripherical sections are considered safer than central ones. We video recorded the individual's behaviour for five minutes. We (Sophia Kroker) measured the following parameters from the video recordings: latency to initiate movement (s), latency to enter the middle section of the arena (s), number of crossings into the central area, number of crossings into the outer area, number of inner-inner crossings, number of outer-outer crossings, proportion of time spent active in the outer area, proportion of time spent active in the inner area, number of jumps on the wall, and number of jumps on the door (for detailed descriptions of each variable see Text S2). After several exploratory analyses, we decided to use the number of outer-outer crossings as a proxy of spatial exploration (see 'Statistical analysis', Text S3 and S4, Figure S3). The modified door mechanism of the open-field test created sound disturbances that elicited escape responses, causing individuals to immediately cross the central (riskier) area of the arena. To minimise bias from these initial disturbances, we restricted the video analyses to footage beginning 10 s after the observer had removed the rope used to operate the door and closed the arena net.

In total, we captured 193 individuals (see Table S3 for number of individuals captured per study site). After accounting for technical problems (e.g. camera issues), we successfully recorded 189 dark-light tests (from 121 adults and 19 juveniles; 57 females, 72 males and 11 undetermined; 46 individuals tested at least twice), 187 open-field tests (from 119 adults and 18 juveniles; 56 females, 70 males, 11 undetermined; 47 individuals tested at least twice) and 174 handling bag tests (from 98 adults and 33 juveniles; 53 females, 57 males, 21 undetermined; 39 individuals tested at least twice).

Faecal sample collection and measurement of corticosterone metabolites

Faecal corticosterone metabolite (FCM) levels represent an integrated measure of an animal's HPA activity over a few hours with a species-specific time delay before excretion (Palme 2019; Palme *et al.* 2005; Touma & Palme 2005). In our case, since we collected faecal samples opportunistically during the open-field test and the handling procedure, we cannot exclude that the samples may partly integrate the acute stress response to the capture. Therefore, we defined our measure of FCM level as a proxy of the HPA axis (re)activity (Palme 2019; Sheriff *et al.* 2011; Touma & Palme 2005) knowing that FCM levels have been shown to correlate with true baseline free glucocorticoids measured in blood plasma, and with an individual's plasma glucocorticoid response to a standardised stress-induced test in snowshoe hares, *Lepus americanus* (Sheriff *et al.* 2010).

Only faecal samples of adults (excluding pregnant females) were analysed. We processed faecal samples following the protocol described in detail in Touma et al. (2003). Briefly, samples were weighed, dried, homogenized, extracted in 80% methanol, and centrifuged, and the resulting extracts were stored at −20 °C until analysis. Extracts were shipped on dry ice to the University of Veterinary Medicine Vienna (Austria), where FCM levels were quantified using a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (for details see Touma et al., 2003). This assay was previously used in wood mice (Navarro-Castilla *et al.* 2014) and validated in mice and bank voles (Sipari *et al.* 2017; Touma *et al.* 2003, 2004). All extracts were analysed in duplicate (and repeated when CV% was > 10%). Inter-assay coefficients of variation were 10.7% and 8.3% for a high and low concentration pool sample, respectively. In total, after accounting for technical problems (e.g. insufficient faecal material), we successfully measured FCM levels for 127 individuals (from 52 females, 71 males and 4 undetermined; 26 individuals sampled at least twice).

Ethical note

Following each capture, mice were released where they were captured. Animals were trapped (31/08/2023; AZ: 67 20 0032) and handled (AZ: 81-02.04.2023.A246, Land Nordrhein Westfalen) with appropriate permits.

Statistical analysis

PCA analysis

We performed a principal components analysis (PCA, Abdi & Williams 2010; Hotelling 1933) to better understand the structure of wood mice behaviour during the open-field test and to select one variable summarising both the activity and exploration components. Following this analysis, we selected the behaviour 'total number of outer-outer crossings' for subsequent analyses (Text S3 and S4, Figure S1).

Modelling and interpretation procedures

All analyses were performed with the software *R* (v.4.4.0; R Core Team 2022). Visualisations were mainly created with the package *ggplot2* (v.3.5.3; Wickham 2016). All models were fitted within a Bayesian framework using the *brms* package and the default (weakly informative) priors (v.2.22.0; Bürkner 2017). For each model, we visually checked chain convergence using trace and trank plots (code inspired from Heiss & Ye 2023) as well as low serial correlation between consecutive draws using the function *mcmc_acf* from the *bayesplot* package (v.1.13.0; Gabry *et al.* 2019). We also verified model convergence and sampling efficiency by confirming that all Rhat values were < 1.05 and that the effective sample size ratios > 0.25 for the main parameters (e.g., intercept, fixed and random effects) using the functions *mcmc_rhat* and *mcmc_neff* from the *bayesplot* package (v.1.13.0; Gabry *et al.* 2019), respectively. Parameters related to model computation (e.g. iterations, thinning) are reported in the table of each specific model and were adjusted individually for optimal convergence. Normality and homoscedasticity of residuals were checked visually using the function *check_model* from the *performance* package (v.0.13.0; Lüdecke *et al.* 2021) for models using Gaussian error. We reported results using the language of evidence and interpreted estimates with 90%, 95%, 99% credible and confidence intervals (CrI and CI, respectively) non-overlapping zero as weak, moderate and strong support for an effect, respectively (Muff *et al.* 2022). The characterization of the strength of an effect was defined following cut-offs used in meta-analysis for heterogeneity, where effect size values up to 25, 50 and 75% argue for a weak, moderate and strong effect (Higgins *et al.* 2003).

Model selection – Univariate mixed effect models

Prior to our analyses, we assessed the distribution of the raw data through histogram visualisation. To facilitate further correlational analyses, we decided to log-transform latency to emerge in the dark-light test (boldness) and FCM levels to accommodate to Gaussian error. All models were run with a Gaussian distribution family, except 'proportion of time spent active in the handling bag' (defiantness), which could not be transformed adequately due to 0 and 1 inflation. Therefore, for this variable, we fitted models with an ordered beta distribution family (Kubinec 2023). For each phenotypic trait, we fitted univariate mixed effect models including important variables to control for to perform model selection and find the most parsimonious model (see Text S4 for procedure). For latency to emerge and total outer-outer crossings, the full model included trial order, age class, time of day (in hours) and date when the test was performed. Time of the day and date were centred to the median of the dataset. For the proportion of time spent active in a bag, the full model included trial order and age class. For FCM levels the full model included sex, scaled mass index, trial order and sampling date. Sampling date was centred to the median of the dataset. Scaled mass index (SMI) was calculated according to Peig & Green (2009). In short, we applied the formula $SMI_i = BM_i * (\frac{HW\overline{x}}{HW_i})^b$, where SMI_i is the scaled mass index of an individual i, BM_i is the body mass of an individual i, HW_i is the head width of an individual i, $HW\overline{x}$ is the average head width in our dataset and *b* is the coefficient of a standardised major axis (SMA) regression between log-transformed body mass and log-transformed head width (a proxy of body size). SMI, and sex were not included in the behavioural models as inclusion would significantly reduce our sample size. Date of capture was not included in the model including defiantness as sampling patterns along the season were confounded with the urbanisation gradient due to logistic problems. Indeed, the handling bag test was not performed during the first two sampling weeks of the trapping procedure, which significantly reduced the number of measurements for sites with low imperviousness (non-urban sites). Linear regressions between defiantness and date of capture, performed separately per site, confirmed that date of capture did not affect defiantness within sites. Therefore, we assume that date of capture did not affect defiantness among sites and excluded it from the full model.

Repeatability

We calculated enhanced agreement repeatability using the most parsimonious model for each trait (Stoffel *et al.* 2017). Enhanced agreement repeatability is preferred to integrate over the biologically relevant range of fixed effects, reducing the risk of upward bias repeatability compared to adjusted repeatability (De Villemereuil *et al.* 2018). Enhanced agreement repeatability was calculated as the ratio of individual variance (V_{ind}) divided by the sum of V_{ind}, residual variance (V_e) and fixed effect variance (V_f). We estimated median and 95 % credible intervals of enhanced agreement repeatability using 3,000 warm-ups, 15,000 iterations, and 4 thinning, except for bag activity, where we used 4,000 warm-ups, 10,000 iterations and 6 thinning for time and energy saving purposes.

Urbanisation effects

We tested the effect of urbanisation using the most parsimonious model of each trait by fitting univariate mixed effect models. The effect of urbanisation on all measured phenotypic traits was tested using three approaches: a) a categorical variable, distinguishing non-urban and urban habitats, b) a continuous variable representing a small-scale urban effect (impervious surface cover determined within a 100-m radius), and c) a continuous variable representing a large-scale urban effect (impervious surface cover determined within a 500 m-radius). Estimates and 95 % credible intervals were computed using 5,000 warm-ups, 15,000 iterations, 4 thinning (6 for bag activity) and adapt delta of 0.998 (0.999 for bag activity and FCMs).

Among-individual correlations

We quantified phenotypic among-individual correlations per habitat (non-urban and urban) using average individual's best linear unbiased predictors (BLUPs) extracted from the most parsimonious model for each trait. We estimated the correlations per habitat rather than along the urban gradient to avoid the integration of 3 continuous variables together (two phenotypic traits + imperviousness) since our dataset would not allow for such analyses. In addition, assessing phenotypic correlation per habitat provides additional insights into whether those correlations differ due to urban effects other than imperviousness or if the correlations change nonlinearly. Optimally, among-individual correlations are assessed using multivariate models (Dingemanse & Dochtermann 2013). However, due to low re-catching rate multivariate models could not estimate uncertainty appropriately (CrI spanning from -0.9 to 0.9 for correlation coefficient). Therefore, we decided to work with observed phenotypic covariance assuming a phenotypic individual gambit (Brommer 2013). We used the BLUPs approach to compute individual's average phenotypic response flattening within-individual variation in our correlations (Dingemanse *et al.* 2020). The usage of BLUPs as covariates has been criticised when uncertainty associated with BLUPs is not carried forward in statistical analysis (Hadfield *et al.* 2010; Houslay & Wilson 2017). However, Dingemanse *et al.* (2020) showed that taking forward the uncertainty in BLUP values resulted in biased estimates. Therefore, as recommended by the authors, we computed average BLUP values which produced less precise, yet unbiased, estimates. To facilitate the visualisation of the BLUPs' associations, we performed Pearson's and Kendall's correlations across all traits. We used the function *ci_cor()* from the package *confintr* (v.1.0.2; Mayer 2023) to calculate 50,000 bootstrap replications and estimate 95 % confidence intervals for each correlation coefficient. Kendall's correlation was used for correlations involving the proportion of time spent active in a bag, as the BLUPs did not follow a Gaussian distribution, but were still expected to show monotonic relationships across traits (Puth *et al.* 2015). To accommodate data to the predictions, we reversed BLUP values of latency to emerge, so that short latencies show high boldness and long latencies show low boldness.

Literature review

Scoping and search term development

Investigating SCS requires two important aspects: (i) repeated measurements to partition the total phenotypic variation into among- and within-individual (co)variation allowing to estimate among-individual correlations, and (ii) the concurrent measurements of behavioural and physiological traits to assess how the (behavioural and physiological) stress responses integrate. We performed two systematic literature reviews to contrast i) literature with the adequate data to estimate and compare SCS between urban and non-urban populations and ii) literature that frames their research using the SCS framework in the context of urbanisation.

The first review (review n°1, called SCS potential studies) aimed to summarise all empirical studies that collected repeated measurements per individual of both physiological and behavioural traits concurrently for urban and non-urban populations of non-human wild animals. The second review (review n°2, called SCS-framed studies) aimed to summarise all empirical studies clearly using the SCS concept to frame their paper in the context of urbanisation, meaning that the term ‘coping style’ or ‘stress-coping style’ appears either in the title or abstract.

To establish our preliminary query and develop our final search for review n°1, we (i) pre-identified a few studies with non-specific queries via Google Scholar, and (ii) adapted the search terms from a recent meta-analysis (Petit & Dammhahn 2025, preprint) with a similar rational as the latter focused also on repeated measurements in the context of urbanisation (Text S1, Table S1). For review n°2, since our main goal was to understand what traits are measured for studies explicitly using the SCS framework, we simply re-used the query of review n°1, deleted the part related to repeated measurements and switched the terms used to retrieve behavioural and physiological traits to the terms ‘coping style’ or ‘stress-coping style’ (Text S1). The final query can be found in Table S2.

Final search

For both reviews we performed the systematic literature review search in four databases (Web of Sciences collection, Scopus, ProQuest and EBSCOhost) on the 13th of January 2026. Details of the search can be found can be found in the supplementary materials (Text S1 and Table S1). In total, we found 1518 and 266 papers for review n°1 and n°2, respectively. After removing duplicates using the software Ryan (Ouzzani et al. 2016) and performing two screening phases, we found 9 studies for review n°1 and 5 studies for review n°2. The number of papers excluded for each screening phase is explained in Figure S1 and Figure S2 for review n°1 and n°2, respectively. All screenings and data extractions were done by J.P.

Reporting

For review n°1 and n°2, we summarised all studies that measured among-individual correlations between behavioural and physiological traits under urbanisation for non-urban and urban populations in Table 1. Additional details (total phenotypic and within-individual correlations, analyses used to estimate correlations) can be found in the supplementary materials (Table S16, Table S17).

Results

Among-individual variation

Based on enhanced agreement repeatability estimates, we found strong evidence that all phenotypic traits displayed among-individual differences (Figure 2). Latency to emerge in the dark-light test, total number of outer-outer crossings in the open-field test and FCM levels were moderately repeatable (latency: $R = 0.214$, 95% CrI = [0.002, 0.482]; outer-outer: $R = 0.314$, 95% CrI = [0.057, 0.536]; FCMs: $R = 0.331$, 95% CrI = [0.103, 0.564], Figure 2). Time spent active in the handling bag test was highly repeatable ($R = 0.767$, 95% CrI = [0.084, 0.968], Figure 2).

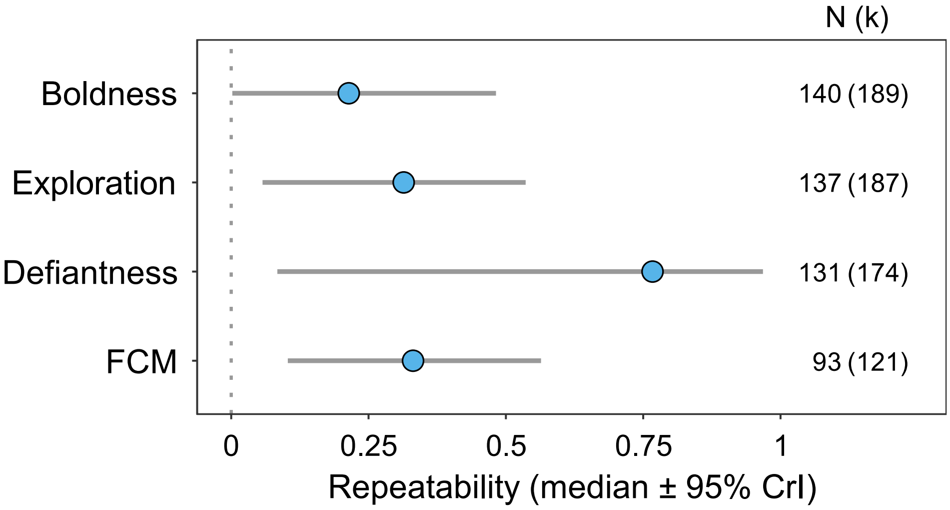

Figure 2. *Enhanced agreement repeatability of boldness (latency to emerge in the dark-light test), exploration (number of outer-outer crossings in the open-field test), defiantness (proportion of time spent active in handling bag test during 60 s), and faecal corticosterone metabolite (FCM) levels in wood mice,* Apodemus sylvaticus. *Latency to emerge and FCMs were log-transformed. Median (blue dot) and 95% credible intervals (CrI; grey line) are shown. N is the number of individuals and k is the number of observations.*

Parsimonious models from model selection: Univariate models

From all covariates included in the full model, we found moderate evidence that (log-transformed) latency to emerge in the dark-light test was weakly negatively affected by the time of the day when the test was performed (estimate ± SE = -0.14 ± 0.07, 95% CrI [-0.27, -0.00], Table S4, Table S5), but not by trial order, age class or date of capture (Table S4). We found moderate evidence that total number of outer-outer crossings in the open-field test was weakly negatively affected by trial order (Trial_2 estimate ± SE = -10.45 ± 3.94, 95% CrI [-18.01, -2.69]; Trial_3 estimate ± SE = -19.37 ± 13.97, 95% CrI [-45.47, 9.12], Table S6, Table S7), but not by age class, capture date, or time of the test (Table S6). We did not find any evidence that proportion of time spent active in the handling bag test was affected by any covariates (Table S8, Table S9). We found weak evidence that (log-transformed) FCMs were weakly positively affected by scaled mass index (estimate ± SE = 0.07 ± 0.03, 95% CrI [0.01, 0.13], Table S10, Table S11), and weakly negatively affected by date of capture (estimate ± SE = -0.01 ± 0.01, 95% CrI [-0.02, -0.00], Table S10, Table S11), but not by sex and trial order (Table S10).

Urbanisation effect: Univariate models

We did not find evidence that behavioural and physiological traits change with urbanisation, neither using two categories (non-urban versus urban, Tables S12a, S13a, S14a, S15a, Figure S1) nor using a continuous gradient of urbanisation, measured with a 100-m radius (Tables S12b, S13b, S14b, S15b) and a 500 m-radius (latency to emerge: estimate ± SE = -0.01 ± 0.01, 95% CrI [-0.02, 0.01], Table S12c, Figure 3A; outer-outer crossings: estimate ± SE = -0.01 ± 0.28, 95% CrI [-0.57, 0.56], Table S13c, Figure 3B; handling bag activity: estimate ± SE = -0.01 ± 0.02, 95% CrI [-0.04, 0.03], Table S14c, Figure 3C; FCMs: estimate ± SE = -0.01 ± 0.02, 95% CrI [-0.05, 0.03], Table S15c, Figure 3D).

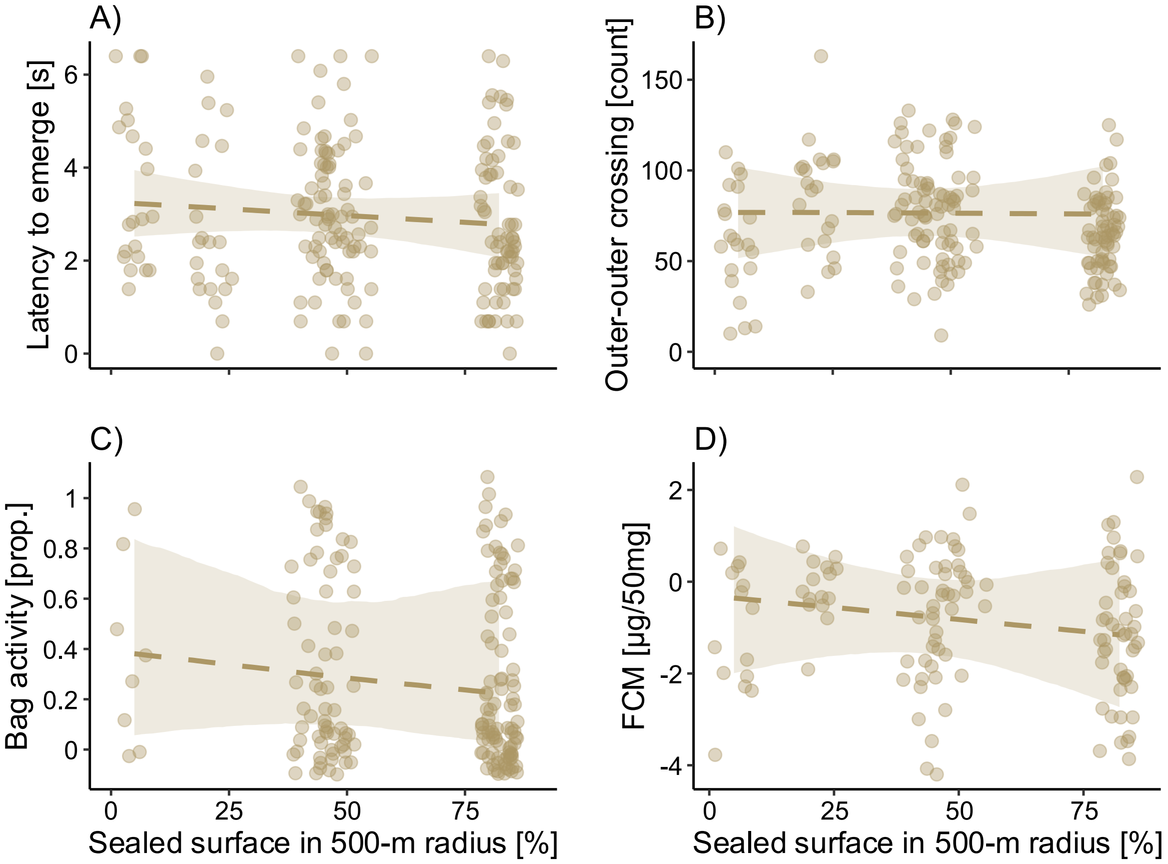

Figure 3. Effect of a gradient of urbanisation (% sealed surface in 500-m radius) *on A) log-transformed latency to emerge in dark-light test (in seconds [s]; boldness; N = 140 individuals, k = 189 observations), B) total number of outer-outer crossing in open-field test (exploration; N = 137, k = 187), C) proportion [prop.] of time spent active in handling bag test over 60 s (defiantness; N = 131, k = 174),*

and D) log-transformed faecal corticosterone metabolite (FCM) levels (µg/50 mg; HPA axis (re)activity; N = 93, k = 121) in wood mice, Apodemus sylvaticus. *Dots are raw data points plotted with a small jitter effect to facilitate visualisation. Dashed lines represent regressions from Bayesian mixed effects models with no evidence of change along the urbanisation gradient and shadings show 95% credible intervals.*

Behavioural syndrome in the city: Mean BLUPS-based among-individual correlations

We did not find evidence for a correlation between BLUPs of latency to emerge in dark-light test and total number of outer-outer crossings in open-field test in non-urban and urban habitats (Pearson's r [95% CI]; non-urban = 0.219 [-0.219, 0.606], *p* = 0.207; urban = -0.047 [-0.230, 0.162], *p* = 0.642, Figure 4A). However, we found moderate evidence for a weak positive correlation between BLUPs of latency to emerge in dark-light test and proportion of time spent active in handling bag test in urban habitats but not in non-urban habitats (Kendall's τ [95% CI]; urban = 0.159 [0.0383, 0.278], *p* = 0.024; non-urban = 0.071 [-0.772, 0.667], *p* = 0.904, Figure 4B). We did not find evidence for a correlation between BLUPs of outer-outer crossings in open-field test and proportion of time spent active in handling bag test in non-urban and urban habitats (Kendall's τ [95% CI]; non-urban = 0.429 [-0.583, 1.00], *p* = 0.179; urban = 0.082 [-0.064, 0.222], *p* = 0.246, Figure 4C).

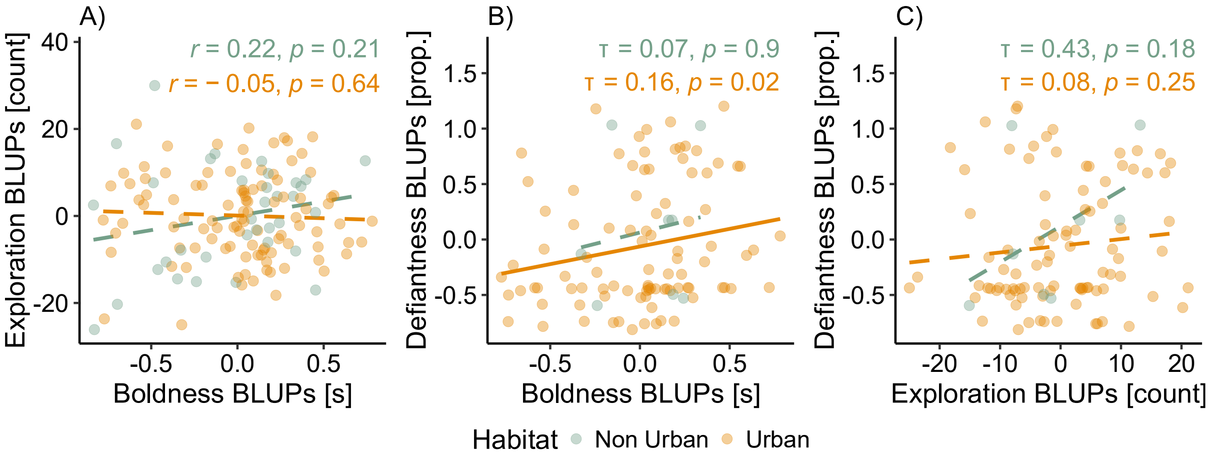

Figure 4. *Among-individual correlations based on mean BLUP estimates between three behavioural traits for non-urban (green) and urban (orange) populations of wood mice,* Apodemus sylvaticus. *Plots show correlations between A) boldness (log-transformed latency in seconds [s] to emerge in dark-light test) and exploration (total number of outer-outer crossings in open-field test; $N_{non\text{-}urban}$ = 35, N_{urban} = 102), B) boldness and defiantness (proportion [prop.] of time active in handling bag test; $N_{non\text{-}urban}$ = 8, N_{urban} = 93), and C) exploration and defiantness ($N_{non\text{-}urban}$ = 8, N_{urban} = 92). Slopes are estimated using ordinary least squares regression. r and T are Pearson's and Kendall's correlation coefficients,*

respectively. Solid and dashed lines indicate presence and absence of evidence for a relationship, respectively. N is the number of individuals.

SCS in the city: Mean BLUPS-based among-individual correlations

We found moderate evidence for a weak positive correlation between (reversed) BLUPs of latency to emerge (boldness) and FCM levels in urban habitats (Pearson's *r* [95% CI] = 0.231 [0.001, 0.452], *p* = 0.073, Figure 5A) but not in non-urban ones (Pearson's *r* [95% CI] = -0.025 [-0.421, 0.336], *p* = 0.901, Figure 5A). We did not find evidence for a correlation between BLUPs of total number of outer-outer crossings (exploration) and FCM levels in non-urban and urban habitats (Pearson's *r* [95% CI]; non-urban = 0.033 [-0.352, 0.418], *p* = 0.881; urban = 0.211 [-0.052, 0.442], *p* = 0.108, Figure 5B). Finally, we found strong evidence for a weak positive correlation between BLUPs of proportion of time spent active in the handling bag (defiantness) and FCM levels in urban but not in non-urban habitats (Kendall's *τ* [95% CI]; urban = 0.184 [0.018, 0.344], *p* = 0.037; non-urban = 0.000 [-1.000, 0.714], *p* > 0.999, Figure 5C).

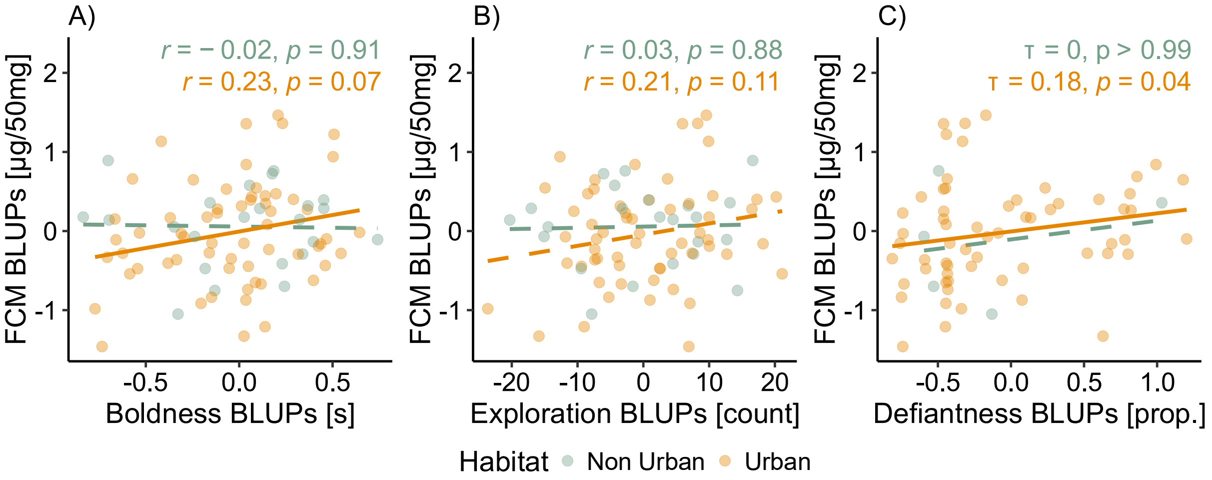

Figure 5. *Among-individuals correlations based on mean BLUP estimates between A) log-transformed latency to emerge in dark-light test and log-transformed faecal corticosterone metabolite (FCM) levels ($N_{non\text{-}urban} = 23$, $N_{urban} = 61$), B) number of outer-outer crossings in open-field test and log-transformed FCMs ($N_{non\text{-}urban} = 23$, $N_{urban} = 59$), and C) proportion of time spent active in a bag over 60 s and log-transformed FCMs ($N_{non\text{-}urban} = 5$, $N_{urban} = 82$) for non-urban (green) and urban (orange) populations of wood mice,* Apodemus sylvaticus*. Slopes are estimated using ordinary least squares regression. r and T are Pearson's and Kendall's correlation coefficients, respectively. Solid and dashed lines indicate presence and absence of evidence for a relationship, respectively. N is the number of individuals.*

Literature review

Based on the systematic review n°1, we found nine studies with the adequate dataset to investigate SCS under urbanisation (Batabyal & Thaker 2019; Caizergues *et al.* 2022; Caspi *et al.* 2025; Dominoni *et al.*

2013b, a; Forte *et al.* 2023; Guindre-Parker *et al.* 2022; Oliveira *et al.* 2020; Thompson *et al.* 2025; Table 1b, Table S16). Among those 9 studies, only Caizergues *et al.* (2022) and Oliveira *et al.* (2020) assessed among-individual correlations underlying SCS. Contrary to predictions of SCS hypothesis, Caizergues *et al.* (2022) found that breath rate was negatively correlated with exploration in urban populations of great tits (*Parus major*), while breath rate tended to be negatively correlated with handling aggression in non-urban ones. Oliveira *et al.* (2020) did not find any evidence that resting metabolic rate was correlated with either boldness or exploration in urban and non-urban populations of greater white-toothed shrews, *Crocidura russula*. Based on the systematic review n°2, we found only five studies framing their research to SCS either in their title and/or in their abstract (Batabyal & Thaker 2019; Corbel *et al.* 2016; Guindre-Parker *et al.* 2022; Partecke *et al.* 2006; Senar *et al.* 2017; Table 1c, Table S17). Out of those five studies, only two had repeated measurements for both, behavioural and physiological traits. However, none assessed among-individual correlations and instead focused on total phenotypic correlations. In both reviews, we found evidence of a significant lack of adequate testing to assess correlations between behavioural and physiological traits among-individuals in the context of urbanisation.

Discussion

In this study, we performed two systematic literature reviews summarising the literature related to SCS under urbanisation. We found that solely two studies estimated among-individual correlations between urban and non-urban populations, and only five studies framed their research within the SCS framework (although without estimating among-individual correlations). These results demonstrated a clear gap of research regarding the role of SCS under urbanisation and a strong taxonomic bias towards bird species. With our field study, we tested the emergence of SCS under urbanisation in wood mice. We did not find evidence of average phenotypic change for boldness, exploration, defiantness, and FCMs along an urbanisation gradient (nor when contrasting urban versus non-urban populations). In addition, we did not find evidence for among-individual correlations between any phenotypic traits in our non-urban populations. However, we found moderate evidence for positive among-individual correlations between boldness and defiantness, boldness and FCMs, and defiantness and FCMs in urban populations. Our empirical findings highlighted that alternative stress-coping styles can be present in human-altered ecosystems emphasising the role of ecological parameters for multiple trait integration.

The effect of urbanisation on population average behavioural and physiological trait responses

Urbanisation, as part of the HIRECs, is often described as a major driver of phenotypic change (Alberti *et al.* 2017; Sih *et al.* 2016) propelling new eco-evolutionary dynamics (Alberti 2015). For physiological traits, synthesis evidence did not reveal an average shift in basal and stress-induced glucocorticoid between urban and non-urban populations (Iglesias-Carrasco *et al.* 2020). Similarly, we did not find any evidence for phenotypic change in physiological traits along an urbanisation gradient in wood mice (and when using urban vs non-urban categories). This pattern is in line with a unique study in Lublin, Poland, that also did not found evidence for a change in FCM levels under urbanisation in striped field mice, *Apodemus agrarius* (Łopucki *et al.* 2019). However, synthesis evidence found strong evidence for major shifts in average behavioural responses of urban populations compared to non-urban ones for boldness and aggression as well as a trend for exploration (Burkhard *et al.* 2026). Our results are in contrast to this general pattern and also contradict results of other small rodent studies, which reported strong evidence for an increase in boldness and exploration with urbanisation in striped field mice, *Apodemus agarius*, (Dammhahn et al. 2020) and common voles, *Microtus arvalis* (Mazza *et al.* 2020).

i - Change in urbanisation history

Increases in average response of urban populations in exploration, boldness, defiantness and FCM levels appear consistent with the need to colonise new, fragmented patches or areas where established populations have been weakened by intense urbanisation (Atwell *et al.* 2012; Clobert *et al.* 2009).

However, when urbanisation is more gradual and less intense, established populations might express the full range of phenotypic traits containing also less defiant, explorative and risk-taking individuals as more cautious individuals should be favoured (i.e. dangerous niche hypothesis, Greenberg 2003). A specific temporality and intensity of urbanisation in the city of Münster might explain why, in general (and compared to the studies of Dammhahn *et al.* 2020 and Mazza *et al.* 2020 in Berlin), we did not find phenotypic differences between urban and non-urban populations.

ii - Spatial scale effect

Favourable habitats in cities often include the presence of urban green spaces comprising a wide continuum of habitat types from intact remnant patches of native vegetation, unmanaged or managed gardens to terraformed patches made of non-native species (Lepczyk *et al.* 2017). In our study, we sampled wood mice exclusively in green areas forming relatively large isolated green islands in the urban mosaic (due to logistic reasons and to ensure safety of trapped animals). Generally, such patches are quite rare in cities and offer exceptionally good but restructured environmental conditions for small mammals compared to the rest of the urban matrix (Kowarik 2011). Such urban green islands could overshadow the effect of urbanisation and work as source populations holding large amounts of total phenotypic variation having similar phenotypic trait average values than non-urban populations, as predicted by metacommunity and metapopulation dynamics (Hanski 1998; Holyoak *et al.* 2005). Indeed, urbanisation is typically quantified using environmental measurements at a macrohabitat scale and often quantified singularly as such macro-environmental features have been found to highly correlated with each other (e.g., imperviousness, light or sound pollution, human presence; Szulkin *et al.* 2020). The assessment of the global landscape surrounding a patch of interest has been shown to be useful to answer questions related to the large-scale response of organisms (Holland *et al.* 2004). However, macrohabitat measures may not follow microhabitat features and such discrepancy might be crucial in our understanding of individuals' response to habitat change (Jackson & Fahrig 2015). For small mammals, such as *Apodemus sylvaticus*, it has been suggested that they do not perceive the urban environment directly, but rather respond to factors modifying the growth or structure of patch vegetation (Dickman & Doncaster 1987) which may affect artificial light at night effects (but see Shuai *et al.* 2023) or perceived predation risk (Dammhahn *et al.* 2022). Urban locations included in this study had strict public access restrictions, reducing the presence of humans on site and diverging from what a large-scale urban gradient predicts for urban locations. Following along those lines, we found strong evidence that location explained a significant and important amount of phenotypic variation across our traits (95% CrI did not overlap zero) indicating local phenotypic specialisation which might be a signature of local adaption processes happening at a microhabitat scale. Therefore, we believe that micro-habitat characteristics of our urban sites could mitigate/overshadow expected effects of urbanisation which might be reinforced by sampling in urban green islands.

iii - Changes or not in predation regime or perceived predation risk

Changes in predation regime or perceived predation risk might also explained why certain populations express (or not) differences in their phenotypic traits (physiology: Boonstra *et al.* 2014; Yin *et al.* 2017, behaviour: Dingemanse *et al.* 2009; Merz & Mortelliti 2025). In cities, although predator abundance may increase, there is substantial support that predation rate may decrease compared to non-urban areas (Fischer *et al.* 2012). Such reduction of top-down trophic control may allow urban populations to have higher expression of risk taking, exploratory and defiant behaviours (observed in Burkhard *et al.* 2026) or higher FCM levels (not observed in Iglesias-Carrasco *et al.* 2020). However, a recent meta-analysis found strong evidence (mainly from bird species) that predation rate increases in the city (Eötvös *et al.* 2018), indicating that changes in predation pressure is most likely species- and city-dependent. In the city of Münster, we observed that diversity and abundance of small mammal predators did not change along our gradient of urbanisation (Rimbach *et al.* 2025). In addition, we anecdotally observed the presence of common aerial predators in non-urban and urban study sites (e.g., European kestrel, common buzzard, short-eared owl). Those findings might indicate that predation pressure could be stable along our urbanisation gradient, alleviating selective pressure and maintaining similar population phenotypic expression. Finally, microhabitat features such as vegetation cover might shape perceived predation risk for small rodent species (Dammhahn *et al.* 2022; Erixon *et al.* 2025) and mitigate expected phenotypic changes to due direct predation risk.

Trait integration: Stress-coping styles in the wild

Assessing average change of a single phenotypic trait at a population level may inform one side of broad eco-evolutionary processes in action. However, it is most likely that selective processes favour trait combinations rather that single traits, especially as populations often contain individuals expressing a continuum of different trait mixtures (also called strategies, Wolf *et al.* 2007). Behavioural and physiological trait integration have been found in various taxa including mammals, birds, fish and reptiles (Groothuis & Carere 2005; Koolhaas et al. 1999; Øverli et al. 2007), advocating that such trait associations have been maintained throughout evolution (Øverli et al. 2007). The original framework of SCS advocates that individuals cope with stress in different ways, where more proactive (i.e. bolder, more explorative/defiant) individuals use a fight or flight strategy through the activation of the parasympathetic systems (instead of HPA axis), whereas more reactive (more shy, less explorative/defiant) individuals display freezing behaviour via the activation of the HPA axis (Koolhaas *et al.* 1999; Korte *et al.* 2005). Such negative correlation between more proactive behaviours (boldness and defiantness) and the HPA axis (here FCMs) is thought to originate from potential evolutionary constraints related to pleiotropy and/or common physiological pathways underlying multiple behavioural traits maintaining organisms' developmental stability and homeostasis (Koolhaas *et al.* 1999, 2010; supported in male Sprague-Dawley rat, *Rattus norvegicus domestica*, by Roozendaall *et al.* 1996). In our study, we did not find any evidence of phenotypic correlations between behavioural and physiological traits in the non-urban populations. However, contrary to the predictions of the SCS hypothesis, we found strong evidence that more proactive (bolder and more defiant) individuals had higher expressions of the HPA axis than more reactive (shier, less defiant) individuals in urban populations. We noted that exploratory behaviour was not part of this alternative urban SCS.

i - Genetic versus Environmental effects

As revealed by our review n°1, mixed findings seem to be the norm regarding among-individual correlations between behavioural and physiological traits. Indeed, Oliveira *et al.* (2020) did not find any evidence that resting metabolic rate was correlated with either boldness or exploration in urban and non-urban populations of greater white-toothed shrews, *Crocidura russula*. Caizergues *et al.* (2022) retrieved alternative SCS among-individual correlations between breath rate and exploration only in urban populations of great tits, *Parus major*. We note that those studies investigated other physiological axes than the HPA axis. Therefore, taken together, our review and empirical study suggest that mechanistic (genetic and developmental) factors may not be the major driver of phenotypic trait integration in wild population under urbanisation. Indeed, after reviewing how often SCS was found or not in rats and mice, Koolhaas *et al.* (2010) plead that neuroendocrine features are most likely a consequence of the behavioural differentiation rather than the cause. Since then, broader synthesis evidence also concluded that expected phenotypic correlations (also called syndromes) are rarely present in populations (behavioural syndrome: Garamszegi *et al.* 2013; pace-of-life (PLOS) syndrome: Royauté *et al.* 2018), most likely because genetic correlations underlying among-individual phenotypic correlations may also vary due to long- or short- term environmental effects hiding expected correlations (Dammhahn *et al.* 2018; Santostefano *et al.* 2017).

ii - Environmental feedback on the phenotype

Faecal corticosterone metabolites are known to integrate adrenocortical activity over a certain time (but delayed by faecal excretion) and therefore include short- and middle-term environmental stress responses (Palme 2019; Palme *et al.* 2005; Touma & Palme 2005). Thus, our HPA axis measurements most likely contained additional environmental effects which could nullify the expected negative genetically-based SCS correlations. In rodents, we know that more risk-taking (proactive) individuals use shorter vegetation than less risk-taking individuals (*Myodes glareolus*: Dammhahn *et al.* 2022, Schirmer *et al.* 2019; *Apodemus agrarius*: Schirmer *et al.* 2020). In addition, still in rodents, individuals living in shorter (i.e. presumably more risky) vegetation have higher hair corticosterone metabolites (also an integrated measure of HPA axis; *Apodemus sylvaticus* and *Mus spretus*: Afonso *et al.* 2025). Thus, the permanent environmental feedback due to non-random microhabitat use (maintained by niche choice: Erixon *et al.* 2025) between risk-taking phenotypes and the physiological response to living in more or less risky microhabitats might result in altered correlations between boldness and FCM levels. More proactive individuals may have increased FCM levels due to greater use of lower vegetation, whereas more reactive individuals may exhibit reduced FCM levels due to greater use of higher vegetation, explaining the deviation and nullification of the expected negative genetically based SCS correlation. However, only specific ecological conditions will allow such correlation to arise when correlational or negative frequency dependent selection (Maynard Smith 1982) are present and when differential ecological pay-off along the SCS continuum exist (Dingemanse & Réale 2005).

iii - Urbanisation effect

In the context of urbanisation, individuals are expected to face new additional human-induced environmental challenges potentially being a source of stress compared to non-urban populations (Bonier 2012; Lowry *et al.* 2013). Although synthesis evidence did not find an overall shift in baseline and acute stress responses in urban populations compared to rural ones (Iglesias-Carrasco *et al.* 2020), stress responses associated with anthropogenic disturbances might be hindered by individual-specific responses. Indeed, according to the SCS framework, more proactive individuals seem to willingly challenge stressors and do better in predictable environments, whereas more reactive individuals seem to use environmental cues more efficiently and perform better in unpredictable conditions (Koolhaas *et al.* 1999). Consequently, more proactive individuals might be more exposed to inescapable stimuli (e.g. constant light or noise pollution) and may need to use additional endocrinological regulation to maintain homeostasis, whereas more reactive individuals may be able to habituate by perceiving human-induced disturbances as non-lethal (Cavalli *et al.* 2018; Vincze *et al.* 2016) and protective of predators (Arroyo *et al.* 2017; Geffroy *et al.* 2020). Individualised perception, and thus response to environmental change, have already been proposed regarding predation risk (Dammhahn *et al.* 2022) or conspecific density (Berthelsen *et al.* 2026). In addition, knowing that among-individual differences in plasticity exist (Dingemanse *et al.* 2010), it is possible that such differences are expressed according to where individuals are situated on the SCS continuum. Although SCS individual-specific responses have been found in Atlantic cod, *Gadus morhua*, where only reactive individuals reduced their home range when sea temperature increased (Villegas-Ríos *et al.* 2018), experiments tackling how specific SCS respond to human-induced disturbances are still lacking (but see Sadoul *et al.* 2021). The root of differential responses may also come from the way each individual phenotypic profile mitigates risk (control of risk hypothesis, Creel 2018). The control of risk hypothesis stipulates that more proactive individuals have food-mediated costs while reactive individuals have stress-mediated costs. In general, more proactive (bolder) individuals are expected to obtain better food rewards than more reactive ones (Réale *et al.* 2010). In rodents, we may assume that bolder individuals access better food rewards by exploiting more risky area (often described by lower vegetation cover). Urbanisation could potentially alter the relationship between risk-taking phenotypes and microhabitat use (e.g. vegetation for small rodent) due to human protection (predation paradox, Fischer *et al.* 2012), and so, ultimately change (e.g. nullify) dynamics related to access of high quality food items. In this case, the expected cost mediation process from the control of risk hypothesis could be reversed. Proactive individuals could use endocrinological responses whereas more reactive individuals may use the new food reward as mediator. However, more specific datasets and experiments are needed to test such mechanisms. Finally, in highly fragmented habitat such as cities, adaptive dispersal strategies might be key of success (Atwell *et al.* 2012; Clobert *et al.* 2009). Among-individual correlation between proactive behaviours and faecal corticosterone metabolites could result from correlational selection favouring such trait associations which align with the positive relationship between FCM levels and scaled mass index (proxy of fitness). As other syndromes, SCS might only be expressed under specific environmental conditions depending on species characteristics (Montiglio *et al.* 2018) without necessarily changing population average trait expression. Therefore, it seems crucial that further studies focus on more taxa and include key environmental components along with urbanisation gradients to understand finer scale effect of HIRECs.

Conclusion

Our integrative approach, combing a systematic literature review with an empirical assessment of coping styles under urbanisation, revealed that among-individual correlations underlying SCS were rarely studied in the context of urbanisation, even in studies that explicitly framed their work using the SCS approach. As a result, we observed mixed findings on whether behavioural and physiological stress responses integrate along a proactive-reactive continuum. More importantly, our empirical study found that although behavioural and physiological traits did not differ along a gradient of urbanisation, alternative correlations between proactive behaviour and HPA axis exist in the urban populations. Our results highlight the complexity of organisms' responses to human-induced environmental change, where urbanisation reshapes not only phenotypes but the integration of traits, generating new covariance structures. Differential environmental feedback upon the phenotype due to individualised interaction or perception of the environment might be key to understand such new trait integration. Future studies would greatly benefit to include individualised responses to HIRECs as they may modify eco-evolutionary dynamics and redirect evolutionary trajectories in human-altered landscapes.

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Supplementary information

This file contains supplementary figures, tables, and texts of the following study.

Title: From a review to the field: Alternative coping styles under urbanisation

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Keywords: stress coping style, behavioural syndrome, individual variation, among-individual correlation, personality trait, faecal corticosterone metabolite, urbanisation, *Apodemus sylvaticus*

Authors contribution statement:

According to the Contributor Role Taxonomy (CRediT) authors have the following contributions.

Jules Petit: Conceptualisation, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft, Writing – review & editing.

Melanie Dammhahn: Conceptualisation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Data availability statement:

The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.547d7wmpc. Peer reviewers can use this link to access the files: http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/zUA0dh3vgTl3gv6y8U4bWrwaV6l-hrZCxKva8WqRukc.

Supplementary information - Methods

Literature review

Text S1. Scoping, search term development and search for review n°1 and 2.

We started by developing the preliminary query of review n°1. Our Population, Exposure, Comparison, and Outcome (PECO, Morgan et al. 2018) framework had the following structure: P = among wild populations of non-human animals, E = urban living conditions, C = non-urban living conditions, O = repeated measurements per individual for both physiological and behavioural traits concurrently. Here, a physiological trait is defined as a measurable characteristics of an organism's internal functional state (e.g. metabolic rate, respiration, hormone regulation, thermoregulation, immunological response). A behavioural trait is defined as any observable external action made by the body of an organism. We first identified few studies fitting the two main requirements for the meta-analysis (e.g. urban versus non-urban populations comparisons, and measurement for behavioural and physiological traits concurrently). Using the bibliography of Sadoul *et al.* (2021) and non-specific queries in Google Scholar, we found five suitable papers (Batabyal & Thaker 2019; Caizergues *et al.* 2022; Guindre-Parker *et al.* 2022; Rebolo-Ifrán *et al.* 2015; Thompson *et al.* 2025). In addition, we also used a recent meta-analysis (Petit & Dammhahn 2025, preprint) with a similar rational regarding the requirement of repeated measurements to refine our preliminary query (also regarding exclusion words). The preliminary query was tested in Scopus and only the final query was transposed to the different search databases.

Preliminary query:

TITLE-ABS-KEY(behavi*) AND (TITLE-ABS-KEY(physio*) OR TITLE-ABS-KEY(endocr*) OR TITLE-ABS-KEY(metabol*)) AND (TITLE-ABS-KEY(urban*) OR TITLE-ABS-KEY(city) OR TITLE-ABS-KEY(cities)) OR (TITLE-ABS-KEY(non-urban*) OR TITLE-ABS-KEY(rural) OR TITLE-ABS-KEY(natural)) AND (TITLE-ABS-KEY(repeat*) OR TITLE-ABS-KEY(consistenc*) OR TITLE-ABS-KEY(inter-individual*) OR TITLE-ABS-KEY(intra-individual*) OR TITLE-ABS-KEY(among-individual*) OR TITLE-ABS-KEY(within-individual*) OR TITLE-ABS-KEY(repeated disturbance*) OR TITLE-ABS-KEY(repeated exposure*) OR TITLE-ABS-KEY(repeated trial*) OR TITLE-ABS-KEY(repeated session*)) AND NOT (TITLE-ABS-KEY(people) OR TITLE-ABS-KEY(child*) OR TITLE-ABS-KEY(patient*) OR TITLE-ABS-KEY(clinical*) OR TITLE-ABS-KEY(ethni*))

Several keywords were added in the advice of four people with expertise in the field of behavioural ecology and ecophysiology. Once we retrieved all five aforementioned papers, we deemed the query for review n°1 complete. The final query can be found in Table S1.

For review n°2, our PECO framework had the following structure: P = among wild populations of non-human animals, E = urban living conditions, C = non-urban living conditions, O = the term ‘coping style’ or ‘stress-coping style’ appears either in the title or abstract. Since our main goal was to understand what traits are measured for studies explicitly using the SCS framework, we simply re-used the query of review n°1, deleted the part of the query selecting studies with repeated measurements and switched the terms used for behavioural and physiological traits to the terms ‘coping style’ or ‘stress-coping style’. The final query can be found in Table S2.

For both reviews, the search allowed for the inclusion of published and unpublished literature (e.g. grey literature) across all continents and languages as well as personal communications. However, search terms were only used in English, which might introduce some bias to the evidence base. We removed 613 and 115 duplicates using the software Ryan (Ouzzani et al. 2016) resulting in 905 and 151 papers for review n°1 and n°2, respectively.

Table S1. Search procedure of review n°1.

Database	**Search used**	**Extraction date and specifics**
Scopus	(TITLE-ABS("behavi*") OR TITLE-ABS("animal personalit*") OR TITLE-ABS("personality trait*")) AND (TITLE-ABS("physio*") OR TITLE-ABS("endocr*") OR TITLE-ABS("metabol*") OR TITLE-ABS("hormon*") OR TITLE-ABS("stress-response*")) AND (TITLE-ABS("urban*") OR TITLE-ABS("city") OR TITLE-ABS("cities") OR TITLE-ABS("non-urban*") OR TITLE-ABS("rural") OR TITLE-ABS("suburban*")) AND (TITLE-ABS-KEY("repeat*") OR TITLE-ABS-KEY("consistenc*") OR TITLE-ABS-KEY("inter-individual*") OR TITLE-ABS-KEY("intra-individual*") OR TITLE-ABS-KEY("among-individual*") OR TITLE-ABS-KEY("between-individual*") OR TITLE-ABS-KEY("within-individual*") OR TITLE-ABS-KEY("repeated disturbance*") OR TITLE-ABS-KEY("repeated exposure*") OR TITLE-ABS-KEY("repeated trial*") OR TITLE-ABS-KEY("repeated session*") OR TITLE-ABS-KEY("time*") OR TITLE-ABS-KEY("context*") OR TITLE-ABS-KEY("capture-mark-recapture")) AND NOT (TITLE-ABS({people}) OR TITLE-ABS({child*}) OR TITLE-ABS({patient*}) OR TITLE-ABS({clinical*}) OR TITLE-ABS({ethni*}) OR TITLE-ABS({student*}) OR TITLE-ABS({woman}) OR TITLE-ABS({women}) OR TITLE-ABS({girl*}) OR TI-	All dates until 13.01.2026 Search performed at different levels in function of keywords. TITLE-ABS = Title and abstract, TITLE-ABS-KEY = Title, abstract and keywords. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Braces are used to look for exact phrase. Asterisks are added to represent any group of characters, including no character.

	TLE-ABS({boy*}) OR TITLE-ABS({firefighter*}) OR TITLE-ABS({man}) OR TITLE-ABS({men}))	
Web of Science	(AB=(“behavi*” OR “animal personalit*” OR “personality trait*”) OR TI=(“behavi*” OR “animal personalit*” OR “personality trait*”)) AND (AB=(“physio*” OR “endocr*” OR “metabol*” OR “hormon*” OR "stress-response*") OR TI=(“physio*” OR “endocr*” OR “metabol*” OR “hormon*” OR "stress-response*")) AND (AB=(“urban*” OR "city" OR "cities" OR “non-urban*” OR "rural" OR “suburban”) OR TI=(“urban*” OR "city" OR "cities" OR “non-urban*” OR "rural" or “suburban”)) AND (TS=(“repeat*” OR “consistenc*” OR “inter-individual*” OR “intra-individual*” OR “among-individual*” OR “between-individual*” OR “within-individual*” OR “repeated disturbance*” OR “repeated exposure*” OR “repeated trial*” OR “repeated session*” OR "time*" OR "context*" OR “capture-mark-recapture”)) NOT (AB=("people" OR "child*" OR "patient*" OR "clinical*" OR "ethni*" OR "student*" OR "woman" OR "women" OR "girl*" OR "boy*" OR "firefighter*" OR "man" OR "men")) NOT (TI=("people" OR "child*" OR "patient*" OR "clinical*" OR "ethni*" OR "student*" OR "woman" OR "women" OR "girl*" OR "boy*" OR "firefighter*" OR "man" OR "men"))	All dates until 13.01.2026 Search performed in all databases. Collections used are *Web of Science Core collection*, *KCI-Korean Journal Database*, *MEDLINE*, *ProQuest Dissertations & Theses Citation Index*, *SciELO Citation Index*. Search performed at different levels in function of keywords. AB = Abstract, TI = Title, TS = Topic (title, abstract and indexing). No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Asterisks are added to represent any group of characters, including no character.
EBSCO OpenDisserations	(TI(“behavi*” OR “animal personalit*” OR “personality trait*”) OR AB(“behavi*” OR “animal personalit*” OR “personality trait*”)) AND (TI("physio*" OR "endocr*" OR "metabol*" OR "hormon*" OR "stress-response*") OR AB("physio*" OR "endocr*" OR "metabol*" OR "hormon*" OR "stress-response*")) AND (TI("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*") OR AB("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*")) AND (TI("repeat*" OR "consistenc*" OR "inter-individual*" OR "intra-individual*" OR "among-individual*" OR "between-individual*" OR "within-individual*" OR "repeated disturbance*" OR "repeated exposure*" OR "repeated trial*" OR “repeated session*" OR “time*" OR "context*" OR "capture-mark-recapture") OR AB("repeat*" OR "consistenc*" OR "inter-individual*" OR "intra-individual*" OR "among-individual*" OR "between-individual*" OR "within-individual*" OR "repeated	All dates until 13.01.2026 Database is OpenDissertations. Search performed at different levels in function of keywords. TI = Title, AB = Abstract. Search mode used is proximity. Searches for terms in proximity to one another by five words or less. Expanders: Apply equivalent subjects. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together

	disturbance*" OR "repeated exposure*" OR "repeated trial*" OR “repeated session*" OR “time*" OR "context*" OR "capture-mark-recapture")) NOT (TI(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”) OR AB(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”))	and not separately. Asterisks are added to represent any group of characters, including no character.
ProQuest (including ProQuest Dissertations and Thesis)	(TIAB("behavi*" OR "animal personalit*" OR "personality trait*")) AND (TIAB("physio*" OR "endocr*" OR "metabol*" OR "hormon*" OR "stress-response*")) AND (TIAB("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*")) AND (TIAB("repeat*" OR "consistenc*" OR "inter-individual*" OR "intra-individual*" OR "among-individual*" OR "between-individual*" OR "within-individual*" OR "repeated disturbance*" OR "repeated exposure*" OR "repeated trial*" OR “repeated session*" OR “time*" OR "context*" OR "capture-mark-recapture")) AND NOT (TIAB(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”))	All dates until 13.01.2026 Search performed at different levels in function of keywords. TIAB = Title and abstract. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Asterisks are added to represent any group of characters, including no character.

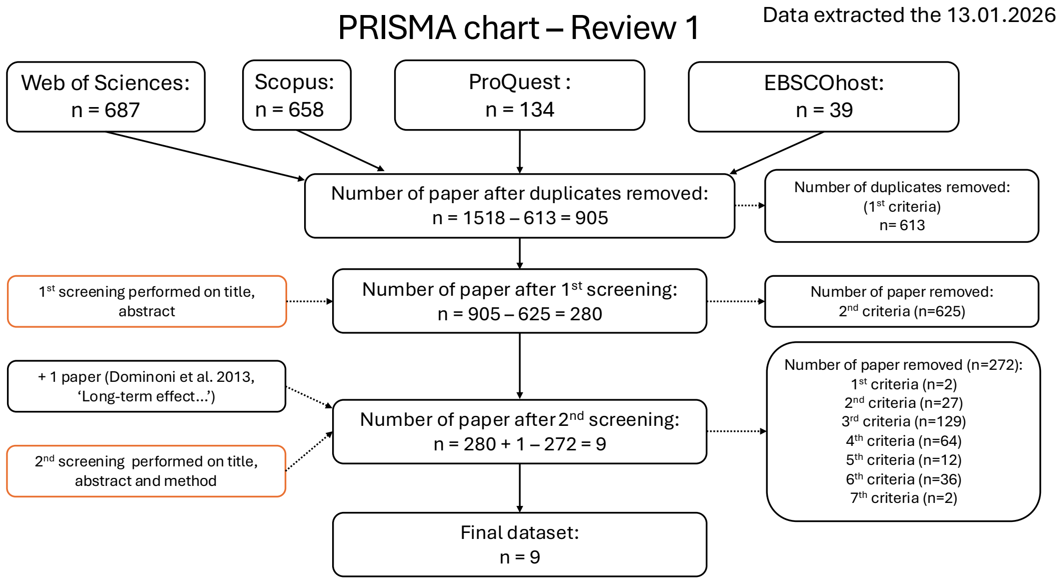
Table S2. Search procedure of review n°2.

Database	Search used	Extraction date and specifics
Scopus	(TITLE-ABS(“coping style*”) OR TITLE-ABS(“stress-coping style*”)) AND (TITLE-ABS(“urban*”) OR TITLE-ABS(“city”) OR TITLE-ABS(“cities”) OR TITLE-ABS(“non-urban*”) OR TITLE-ABS(“rural”) OR TITLE-ABS("suburban*”)) AND NOT (TITLE-ABS({people}) OR TITLE-ABS({child*}) OR TITLE-ABS({patient*}) OR TITLE-ABS({clinical*}) OR TITLE-ABS({ethni*}) OR TITLE-ABS({student*}) OR TITLE-ABS({woman}) OR TITLE-ABS({women}) OR TITLE-ABS({girl*}) OR TITLE-ABS({boy*}) OR TITLE-ABS({firefighter*}) OR TITLE-ABS({man}) OR TITLE-ABS({men}))	All dates until 13.01.2026 Search performed at different levels in function of keywords. TITLE-ABS = Title and abstract, TITLE-ABS-KEY = Title, abstract and keywords. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Braces are used to look for exact phrase. Asterisks

		are added to represent any group of characters, including no character.
Web of Science	(AB=("coping style*" OR "stress-coping style*") OR TI=("coping style*" OR "stress-coping style*")) AND (AB=("urban*" OR "city" OR "cities" OR "non-urban*" OR "rural" OR "suburban") OR TI=("urban*" OR "city" OR "cities" OR "non-urban*" OR "rural" OR "suburban")) NOT (AB=("people" OR "child*" OR "patient*" OR "clinical*" OR "ethni*" OR "student*" OR "woman" OR "women" OR "girl*" OR "boy*" OR "firefighter*" OR "man" OR "men") OR TI=("people" OR "child*" OR "patient*" OR "clinical*" OR "ethni*" OR "student*" OR "woman" OR "women" OR "girl*" OR "boy*" OR "firefighter*" OR "man" OR "men"))	All dates until 13.01.2026 Search performed in all databases. Collections used are *Web of Science Core collection*, *KCI-Korean Journal Database*, *MEDLINE*, *ProQuest Dissertations & Theses Citation Index*, *SciELO Citation Index* Search performed on at different levels in function of keywords. AB = Abstract, TI = Title, TS = Topic (title, abstract and indexing). Quotation marks are used to search the keyword with exact match, but asterisks are added to represent any group of characters, including no character
EBSCO OpenDisserations	(TI("coping style*" OR "stress-coping style*") OR AB("coping style*" OR "stress-coping style*")) AND (TI("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*") OR AB("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*")) NOT (TI(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”) OR AB(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”))	All dates until 13.01.2026 Database is OpenDissertations. Search performed at different levels in function of keywords. TI = Title, AB = Abstract. Search mode used is proximity. Searches for terms in proximity to one another by five words or less. Expanders: Apply equivalent subjects. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Asterisks are added to represent any group of characters, including no character.

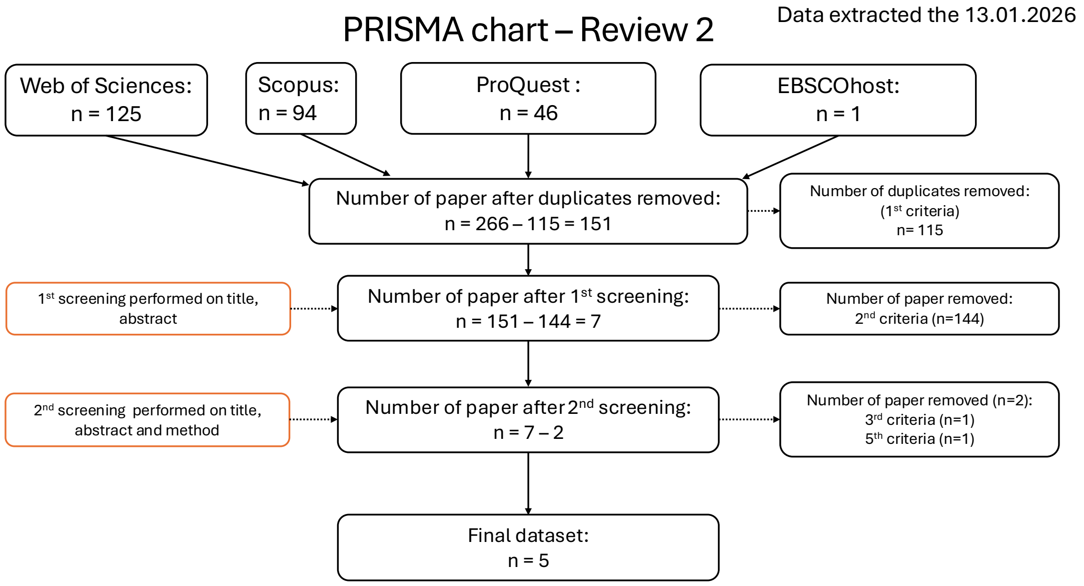
ProQuest (including ProQuest Dissertations and Thesis)	(TIAB("coping style*" OR "stress-coping style*")) AND (TIAB("urban*" OR "city" OR "cities" OR "non-urban*" OR “rural" OR "suburban*")) AND NOT (TIAB(“people” OR “child*” OR “patient*” OR “clinical*” OR “ethni*” OR “student*” OR “woman” OR “women” OR “girl*” OR “boy*” OR “firefighter*” OR “man” OR “men”))	All dates until 13.01.2026 Search performed at different levels in function of keywords. TIAB = Title and abstract. No specific filter aside of the exclusion keywords specified in the search. Quotation marks are used to search the keywords together and not separately. Asterisks are added to represent any group of characters, including no character.

Figure S1. PRISMA chart of review n°1 and exclusion criteria table.



Criteria number	Exclusion criteria
1.	Duplicate
2.	Studies on human subjects, plants, domesticated and zoo animals
3.	Studies without non-urban AND urban populations
4.	Studies without behavioural and physiological measurements for the same individual
5.	Studies without repeated measurements per individual for each habitat for both behavioural and physiological traits
6.	Studies which are meta-analysis or systematic reviews or opinion papers or comment papers
7.	Paper not accessible

Figure S2. PRISMA chart of review n°2 and exclusion criteria table.



Criteria number	Exclusion criteria
1.	Duplicate
2.	Studies on human subjects, plants, domesticated and zoo animals
3.	Studies without non-urban AND urban populations
4.	Studies without coping style of stress-coping style in their title or abstract
5.	Studies which are meta-analysis or systematic reviews or opinion papers or comment papers
6.	Paper not accessible

Study sites

Table S3. Environmental and trapping characteristics of the six study sites. *Study sites are ordered from the least to the most urbanised according to imperviousness in a 500-m radius around the site (values in bold). Human presence is determined from our personal experience of the site which is highly linked to the accessibility of the area.*

	Study sites					
Environmental features	*Rieselfelder*	*Kinderbachtal*	*Botanic Garden*	*Fraternity Canisianer*	*Apotheker Garden*	*Bishop Garden*
Imperviousness 100-m radius (%)	5.89	1.96	7.42	36.12	19.27	48.67
Imperviousness 500-m radius (%)	**4.94**	**21.75**	**41.83**	**47.66**	**51.91**	**82.22**
Imperviousness 1000-m radius (%)	8.59	33.21	59.81	48.13	61.98	69.43
Human density (habitant/ha)	2.166	7.595	14.057	67.022	3.437	31.828
Distance from hyper city centre (Domplatz, km)	8.34	3.06	1.14	3.06	1.34	0.24
Habitat	Non-Urban	Non-Urban	Urban	Urban	Urban	Urban
Accessibility	Private, un-enclosed	Public, unen-closed	Public, enclosed	Private, en-closed	Private, en-closed	Private, enclosed
Human presence	Very rare	Common	Common	Common	Rare	Rare
Trapping features						
Grid size (m^2)	5400	5540	2455	3400	8100	3507
Number of traps	64	65	35	54	78	45
Total day of trapping						
- Week 1	4	4	3	4	4	3
- Week 2	3	3	3	4	3	4
- Week 3	4	4	4	/	/	/
Number of individual captured	19	22	18	30	17	87

PCA analysis

Text S2. Description of the different measurements recording during the open field test.
The name in italic are the names used in the R script (see associated Dryad repository).

- Latency to start moving:
  - *Latency_first_movement_s*: latency time until the individual moves at least one paw for the first time after exiting the tube. This measurement starts 10 sec. after the rope to close to the door is removed
- Latency to enter the central area with the full body (excluding tail):
  - *Latency_central_area_s*: latency time until the individual enters the central circle of the arena for the first time with the full body without the tail
  - *Latency_central_area_2_s*: latency time until the individual enters the central circle of the arena for the first time with the full body without the tail. This measurement starts 10 sec after the rope to close the door is removed
- Proportion of time spent active: Use instantaneous sampling every 10 seconds (Active = 1, Inactive =0)

    - *Active_inner_proportion*: Proportion of time an individual is active within the central area
    - *Active_outer_proportion*: Proportion of time an individual is active within the outer area
    - *Active_total_porportion*: Proportion of time an individual is active in the test
        - Active = all behaviours that are not defined as resting and grooming
        - Inactive = Resting or grooming behaviour
- Number of jumps: individual leaves the ground with all four paws at the same time
    - *Wall*: Jump on the wall. Individual leaves the ground with all four paws at the same time and touches the wall of the arena with any part of the body.
    - *Door*: Jump or climb on the door. Individual leaves the ground with all four paws at the same time or climbs up the door and lands on the door with all four paws
    - *Jump_undefined*: Jump on the net. Individual leaves the ground with all four paws at the same time and touches the upper net with at least one paw
    - *undefined*: individual jumps or climbs from the door to the ground
    - *Jumps_sum*: Total jump on wall and door
- Number of all line-crossings with the whole body (excluding the tail):
    - *Outer_outer*: line crossings from an outer to an outer section
    - *Inner_inner*: line crossings from an inner to an inner section
    - *Inner_outer*: line crossings from the inner to an outer section and from an outer to an inner section
    - *LineCrossing_sum*: the sum of all line crossings

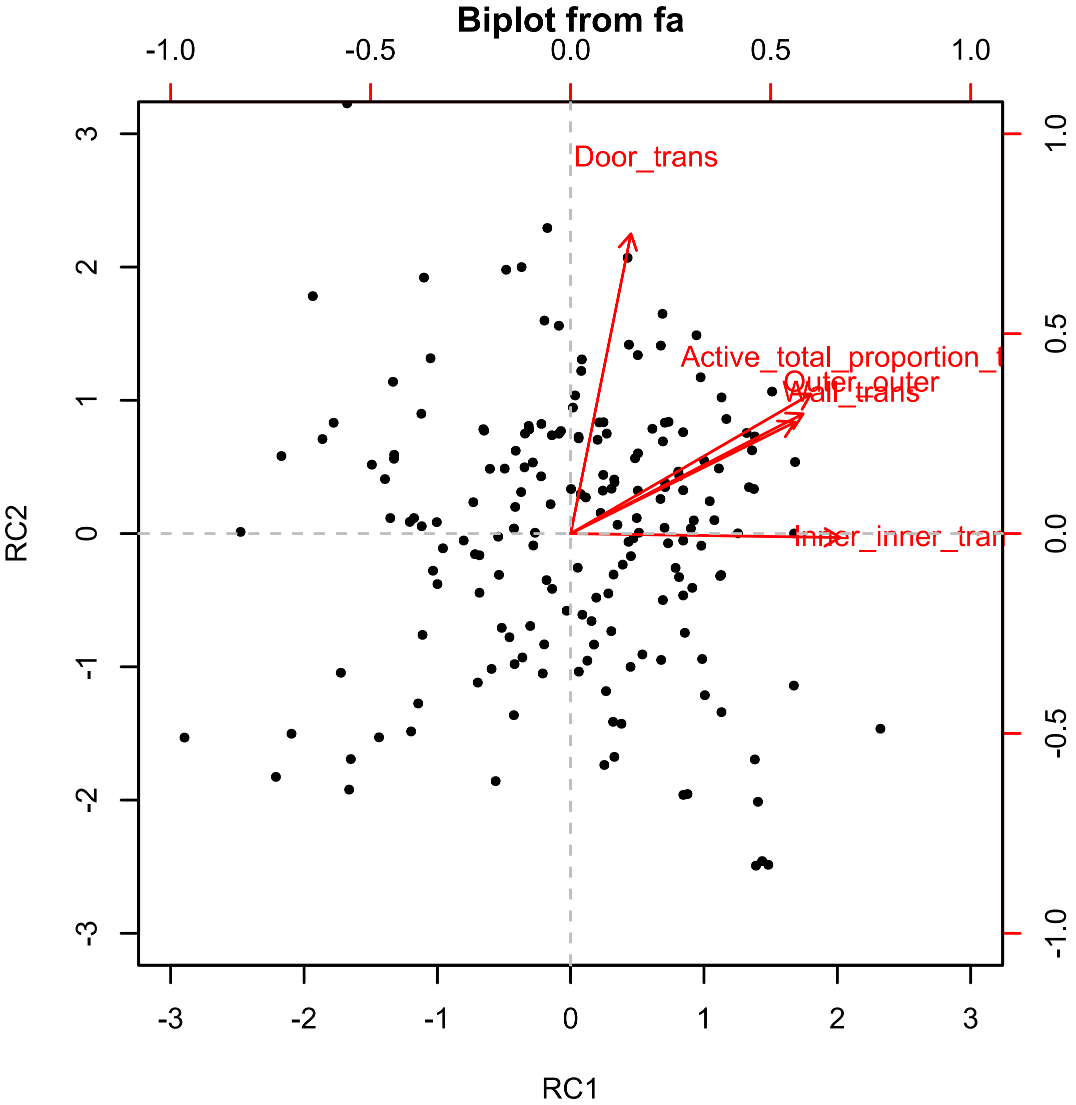
Text S3. Rationale of the principal component analysis (PCA)

First, we checked the distribution of each variable and apply a transformation when needed to obtain a Gaussian distribution. '*active_inner_proportion*' and '*latency_first_movement_s*' were discarded because we could not correct their distribution with transformation to satisfy the requirement of the PCA. Second, we assessed the repeatability of each variable using the package *RptR* (Stoffel *et al.* 2017) in the software *R* (R Core Team 2022) since we were interested to summarise the measurements with the ability to express among-individual differences. We excluded 'latency central area_2' because it was not repeatable. Before running the PCA, we checked for the presence of high correlation (correlation above 0.80) between every variable to avoid overfitting the PCA, and discarded jumps_sum, exterior_area, central_area, active_outer_prop, sum_line_crossing. Therefore, we ran the PCA with the variables 'outer_outer', 'door', 'wall', 'inner_inner', 'active_total_proportion' using the function *principal* from the package *psych* in *R* (R Core Team 2022). We used the variables with their transformation (if it was necessary) and scaled them to optimize the computation of the PCA. We forced the PCA to compute only two components and used the 'varimax' rotation to maximize the variance of the loadings.

Text S4. Results of the PCA.

The principal components n°1 (RC1) and n°2 (RC2) had a sum of squared loadings of 2.33 and 1.33, respectively. RC1 and RC2 explained 47 % and 27 % of variance for a cumulated total of 74 % of variance. The variables were forming three distinctive groups with 'door' alone, 'wall', 'outer_outer' and 'active_total_proportion' together, and 'inner_inner' alone (Graph S1). We interpreted the second group as the most representative for spatial exploration in the open field test as it encompassed activity ('active_total_proportion') and movement in the test area with the lowest perceived risk level ('outer_outer') at the contrary of the 'inner_inner' variable for example. Finally, we decided to use 'outer_outer' as a proxy of spatial exploration instead of 'active_total_proportion' because it (i) explained simultaneously a high amount of variation in RC1 and RC2 (similar to 'active_total_proportion'), but (ii) had a better Gaussian distribution without transformation. '*wall*' and '*door*' were not considered due to their ambiguity involving escape response and their need of data transformation.

Figure S3. Final PCA plot. *RC1 and RC2 explained 47 % and 27 % of variance, respectively, for a grand total of 74 % of variance explained. Variables that were transformed have '_trans' in their name. For explanations of names see Text S2.*



Text S4. Model selection procedure

To select which covariate to test first from the full model, we determined which covariate had the smallest effect overlapping largely zero using the function *describe_posterior()* from the *bayestestR* package (Makowski *et al.* 2019). In addition, we checked whether the covariate was reducing the sample size due to incomplete measurements. Then, we computed leave-one-out cross-validation information criterion (LOOIC, Vehtari *et al.* 2017), expected log predictive density (ELPD, Vehtari *et al.* 2017) and p_loo. In general, higher elpd_loo or lower LOOIC indicates better predictive performance (Vehtari *et al.* 2017). p_loo quantifies flexibility where a larger value indicates more parameters used more effectively. Stability of the LOOIC computation was checked (Pareto $\hat{k} < 0.7$). If LOOIC between models was at least 4 (ΔLOOIC = 4), we kept the model with the smallest LOOIC and repeated the procedure until we obtained the most parsimonious model. In cases where ΔLOOIC < 4 but the covariate had a strict positive or negative estimate according to their 95% credibility intervals, we kept the covariate in the parsimonious model (for an example see Table S5).

Supplementary information - Results

Univariate model: Model selection

Table S4. Summary of the backward model selection performed for latency to emerge (Latency, boldness). *Latency was log-transformed to achieve Gaussian distribution. Date of capture (Date) and time of the test (Time) were centred. Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals and study sites. Model parameters were thin = 4 and adapt_delta = 0.99. We used 3,000 warm-ups, 9,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. N is the number of individuals and k is the number of observations. 95 % credible intervals (CrI) are shown between square brackets. Parsimonious model is highlighted in bold. LOOIC, p_loo and elpd_loo are criteria used to assess model performance (see Text S1).*

Models	LOOIC	p_loo	elpd_loo	R^2c and R^2m	N (k)
Latency ~ Trial + Age_class + Time + Date	703.5	43.3	-351.7	0.266 [0.052, 0.497] 0.070 [0.011, 0.134]	140 (189)
Latency ~ Age_class + Time + Date	702.1	42.6	-351.0	0.258 [0.038, 0.476] 0.048 [0.003, 0.112]	140 (189)
Latency ~ Date + Time	701.1	42.3	-350.5	0.256 [0.021, 0.470] 0.037 [<0.001, 0.093]	140 (189)
Latency ~ Time	699.3	42.4	-349.6	0.257 [0.029, 0.480] 0.022 [<0.001, 0.069]	140 (189)
Latency ~ 1	700.9	43.2	-350.5	0.251 [0.004, 0.466] /	140 (189)

Table S5. Model summary of the most parsimonious model performed on latency to emerge (Latency, boldness). *Latency was log-transformed to achieve Gaussian distribution. Time of the test (Time) was centred. Model uses univariate regression following Gaussian distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters were thin = 4 and adapt_delta = 0.99. We used 3,000 warm-ups, 15,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
Latency ~ Intercept	3.04	0.18	[2.69, 3.38]	189	
Time	-0.14	0.07	[-0.27, -0.00]		
Sd(1|ID)	0.70	0.28	[0.08, 1.16]	140	0.255 [0.017, 0.467] 0.023 [<0.001, 0.070]
Sd(1|Location)	0.22	0.21	[0.01, 0.76]	6	
Residuals	1.36	0.14	[1.10, 1.62]		

Table S6. Summary of the backward model selection procedure performed for outer-outer crossings (Outer-outer, exploration). *Date of capture (Date) and time of the test (Time) were centred. Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals and study sites. Model parameters were thin = 4 and adapt_delta = 0.99. We used 3,000 warm-ups, 9,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. N is the number of individuals and k is the number of observations. 95 % credible intervals (CrI) are shown between square brackets. Parsimonious model is highlighted in bold. LOOIC, p_loo and elpd_loo are criteria used to assess model performance (see Text S1).*

Models	LOOIC	p_loo	elpd_loo	R^2c and R^2m	N (k)
Outer-outer ~ Trial + Age_class + Time + Date	1738.9	66.2	-869.4	0.471 [0.222, 0.656] 0.064 [0.015, 0.121]	137 (187)
Outer-outer ~ Trial + Age_class + Time	1736.0	65.7	-868.0	0.471 [0.237, 0.657] 0.058 [0.013, 0.114]	137 (187)
Outer-outer ~ Trial + Time	1736.5	64.3	-868.3	0.463 [0.223, 0.647] 0.049 [0.007, 0.101]	137 (187)
Outer-outer ~ Trial	1736.7	62.7	-868.4	0.451 [0.188, 0.635] 0.037 [0.002, 0.080]	137 (187)
Outer-outer ~ 1	1747.3	42.5	-873.7	0.297 [0.075, 0.505] /	137 (187)

Table S7. Model summary of the most parsimonious model performed on outer-outer crossings (Outer-outer, exploration). *Model uses univariate regression following Gaussian distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters were thin = 4 and adapt_delta = 0.99. We used 3,000 warm-ups, 15,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
Outer-outer ~ Intercept	76.49	5.54	[65.28, 87.73]	187	
Trial_2	-10.45	3.94	[-18.01, -2.69]		
Trial_3	-19.37	13.97	[-45.47, 9.12]		0.454 [0.201, 0.636] 0.037 [<0.001, 0.081]
Sd(1|ID)	15.75	2.24	[6.99, 21.79]	137	
Sd(1|Location)	11.37	3.66	[3.11, 25.80]	6	
Residuals	20.27	5.84	[16.39, 25.13]		

Table S8. Summary of the backward model selection procedure performed for proportion of time spent active in a bag over 60 seconds (Time active, defiantness). *Date of capture (Date) was centred. Models are univariate ordered beta regressions following ordinal and beta distribution. Random structure included ID of individuals and study sites. Model parameters were thin = 6 and adapt_delta = 0.999. We used 4,000 warm-ups, 10,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. N is the number of individuals and k is the number of observations. 95 % credible intervals (CrI) are shown between square brackets. Parsimonious model is highlighted in bold. LOOIC, p_loo and elpd_loo are criteria used to assess model performance (see Text S1).*

Models	LOOIC	p_loo	elpd_loo	R^2c and R^2m	N (k)
Time active ~ Trial + Age_class	268.9	63.5	-134.5	0.399 [0.101, 0.628] 0.013 [<0.001, 0.051]	131 (174)
Time active ~ Trial	270.0	59.7	-135.0	0.368 [0.057, 0.598] 0.006 [<0.001, 0.025]	
Time active ~ 1	263.6	56.5	-131.8	0.360 [0.059, 0.606] /	

Table S9. Model summary of the most parsimonious model performed on proportion of time spent active in a bag over 60 seconds (Time active, defiantness). *Model uses univariate ordered beta regression following ordinal and beta distributions. Random structure included ID of individuals (ID) and study sites (Location). Model parameters are thin = 6 and adapt_delta = 0.999. We used 4,000 warm-ups, 10,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
Time active ~ Intercept	0.37	0.36	[-0.36, 1.07]	174	
Sd(1|ID)	0.89	0.31	[0.20, 1.47]	131	0.360 [0.059, 0.606] /
Sd(1|Location)	0.49	0.46	[0.02, 1.74]	4	
phi	4.01	1.28	[2.17, 6.98]		
cutzero	-3.34	0.45	[-4.30, -2.52]		
cutone	1.46	0.12	[1.23, 1.69]		

Table S10. Summary of the backward model selection procedure for faecal corticosterone metabolite (FCM) concentration. *FCMs were log-transformed to achieve Gaussian distribution. Date of capture (Date) was centred. Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals and study sites. Model parameters were thin=4 and adapt_delta = 0.99. We used 3,000 warm-ups, 9,000 iterations and default weakly informative priors. SMI is individuals scaled mass index.* R^2*c and* R^2*m are conditional and marginal effect sizes, respectively. N is the number of individuals and k is the number of observations. 95 % credible intervals (CrI) are shown between square brackets. Parsimonious model is highlighted in bold. LOOIC, p_loo and elpd_loo are criteria used to assess model performance (see Text S1).*

Models	LOOIC	p_loo	elpd_loo	R^2c and R^2m	N (k)
FCMs ~ Sex + Trial + Date + SMI	369.7	51.9	-184.8	0.621 [0.412, 0.781] 0.121 [0.032, 0.211]	111 (88)
FCMs ~ Trial + Date + SMI	368.1	51.7	-184.0	0.624 [0.419, 0.764] 0.113 [0.027, 0.211]	
FCMs ~ Date + SMI	370.0	48.8	-185.0	0.596 [0.394, 0.758] 0.086 [0.011, 0.177]	
FCMs ~ SMI	370.1	49.2	-185.0	0.597 [0.377, 0.759] 0.044 [<0.001, 0.124]	
FCMs ~ Date	373.9	49.4	-186.9	0.584 [0.359, 0.751] 0.044 [<0.001, 0.130]	
FCMs ~ 1	375.8	50.1	-187.9	0.580 [0.339, 0.752] /	

Table S11. Model summary of the most parsimonious model for faecal corticosterone metabolite (FCM) concentration. FCMs *were log-transformed to achieve Gaussian distribution. Date of capture (Date) was centred. Models are univariate regressions following Gaussian distribution. SMI is scaled body mass index. Random structure included ID of individuals (ID) and study sites (Location). Model parameters were thin = 4 and adapt_delta = 0.99. We used 3,000 warm-ups, 15,000 iterations and default weakly informative priors.* R^2*c and* R^2*m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
FCMs ~ Intercept	-2.23	0.72	[-3.71, -0.86]	121	0.600 [0.401, 0.757] 0.086 [0.011, 0.173]
SMI	0.07	0.03	[0.01, 0.13]		
Date	-0.01	0.01	[-0.02, -0.00]		
Sd(1|ID)	0.86	0.15	[0.55, 1.13]	93	
Sd(1|Location)	0.77	0.43	[0.20, 1.84]	6	
Residuals	0.87	0.11	[0.69, 1.11]		

Univariate model: Urbanisation effect

Table S12. Model summary of urbanisation effect on latency to emerge (Latency, boldness), a) based on environmental dichotomy (non-urban versus urban), b) based on a 100-m radius imperviousness gradient and, c) based on a 500-m radius imperviousness gradient. *Latency was log-transformed to achieve Gaussian distribution. Time of the test (Time) was centred. Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters were thin = 4 and adapt_delta = 0.998. We used 5,000 warm-ups, 15,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

Models	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
a) Habitat					
Latency ~ Intercept	3.19	0.37	[2.45, 3.89]	189	0.269 [0.027, 0.484] 0.035 [<0.001, 0.096]
Habitat_Urban	-0.22	0.44	[-1.08, 0.65]		
Time	-0.14	0.07	[-0.27, -0.00]		
Sd(1|ID)	0.71	0.29	[0.08, 1.17]	140	
Sd(1|Location)	0.27	0.27	[0.01, 0.97]	6	
Residuals	1.35	0.14	[1.09, 1.62]		
b) Imperviousness 100-m					
Latency ~ Intercept	3.21	0.32	[2.57, 3.83	189	0.272 [0.035, 0.489] 0.040 [<0.001, 0.120]
Imperv_100	-0.01	0.01	[-0.03, 0.01		
Time	-0.13	0.07	[-0.27, 0.01		
Sd(1|ID)	0.71	0.28	[0.08,1.16]	140	
Sd(1|Location)	0.28	0.29	[0.01,1.02]	6	
Residuals	1.35	0.14	[1.09, 1.61]		
c) Imperviousness 500-m					
Latency ~ Intercept	3.31	0.40	[2.54, 4.09]	189	0.272 [0.031, 0.486] 0.042 [<0.001, 0.123]
Imperv_500	-0.01	0.01	[-0.02, 0.01]		
Time	-0.13	0.07	[-0.26, 0.01]		
Sd(1|ID)	0.71	0.28	[0.08, 1.17]	140	
Sd(1|Location)	0.26	0.27	[0.01, 0.95]	6	
Residuals	1.35	0.14	[1.09, 1.61]		

Table S13. Summary of urbanisation effect on outer-outer crossings (Outer-outer, exploration), a) based on environmental dichotomy (non-urban versus urban), b) based on a 100-m radius imperviousness gradient and, c) based on a 500-m radius imperviousness gradient. *Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters were thin = 4 and adapt_delta = 0.998. We used 5,000 warm-ups, 15,000 iterations and default weakly informative priors. R^2c and R^2m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

Models	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
a) Habitat					
Outer_outer ~ Intercept	74.65	12.24	[49.76, 98.66]	187	
Habitat_Urban	3.98	14.85	[-26.08, 33.17]		
Trial_2	-10.45	3.94	[-18.07, - 2.59]		
Trial_3	-19.41	14.03	[-46.03, 8.91]		0.461 [0.204, 0.648]
					0.059 [<0.001, 0.176]
Sd(1|ID)	15.74	3.77	[6.01, 21.80]	137	
Sd(1|Location)	13.75	7.35	[4.23, 32.17]	6	
Residuals	20.23	2.27	[16.38, 25.29]		
b) Imperviousness 100-m					
Outer_outer ~ Intercept	81.58	9.33	[62.62, 100.68]	187	
Imperv_100	-0.23	0.34	[-0.92, 0.46]		
Trial_2	-10.35	3.91	[-17.89, -2.59]		
Trial_3	-19.75	14.02	[-46.39, 8.97]		0.460 [0.219, 0.644]
					0.081 [0.003, 0.250]
Sd(1|ID)	15.84	3.55	[7.35, 21.66]	137	
Sd(1|Location)	12.03	7.12	[2.05, 29.38]	6	
Residuals	20.20	2.23	[16.35, 25.16]		
c) Imperviousness 500-m					
Outer_outer ~ Intercept	77.00	13.66	[48.32, 104.40]	187	
Imperv_500	-0.01	0.28	[-0.57, 0.56]		
Trial_2	-10.41	3.88	[-17.92, -2.63]		
Trial_3	-19.50	14.26	[-46.38, 9.61]		0.459 [0.203, 0.646]
					0.065 [0.003, 0.218]
Sd(1|ID	15.73	3.80	[6.03, 21.73]	137	
Sd(1|Location)	13.76	7.25	[4.11, 32.19]	6	
Residuals	20.25	2.29	[16.38, 25.32]		

Table S14. Summary of urbanisation effect on proportion of time spent active in a bag over 60 seconds (Time active, defiantness), a) based on environmental dichotomy (non-urban versus urban), b) based on a 100-m radius imperviousness gradient and, c) based on a 500-m radius imperviousness gradient. *Models are univariate ordered beta regressions following ordinal and beta distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters are thin = 6 and adapt_delta = 0.999. We used 5,000 warm-ups, 15,000 iterations and default weakly informative priors.* R^2*c and* R^2*m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

Models	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
a) Habitat					
Time active ~ Intercept	-0.12	1.03	[-2.19, 1.90]	174	
Habitat_Urban	-0.30	1.12	[-2.52, 2.09]		
Sd(1|ID)	0.95	0.30	[0.29, 1.53]	131	0.393 [0.103, 0.635]
Sd(1|Location)	0.71	0.71	[0.03, 2.71]	4	0.008 [<0.001, 0.089]
phi (residuals)	4.23	1.32	[2.26, 7.26]		
cutzero	-1.05	0.26	[-1.57, -0.55]		
cutone	1.47	0.12	[1.23, 1.70]		
b) Imperviousness 100-m					
Time active ~ Intercept	0.09	0.74	[-1.28, 1.53]	174	
Imperv_100	-0.02	0.02	[-0.06, 0.03]		
Sd(1|ID)	0.96	0.30	[0.30, 1.52]	131	0.404 [0.096, 0.628]
Sd(1|Location)	0.50	0.64	[0.01, 2.19]	4	0.042 [<0.001, 0.210]
Phi (residuals)	4.25	1.32	[2.26, 7.31]		
cutzero	-1.06	0.27	[-1.58, -0.55]		
cutone	1.48	0.12	[1.25, 1.70]		
c) Imperviousness 500-m					
Time active ~ Intercept	0.03	0.96	[-1.82, 1.97]	174	
Imperv_500	-0.01	0.02	[-0.04, 0.03]		
Sd(1|ID)	0.95	0.31	[0.28, 1.54]	131	0.393 [0.091, 0.631]
Sd(1|Location)	0.67	0.72	[0.02, 2.67]	4	0.024 [<0.001, 0.178]
Phi (residuals)	4.22	1.32	[2.25, 7.29]		
cutzero	-1.05	0.26	[-1.57, -0.54]		
cutone	1.48	0.12	[1.24, 1.70]		

Table S15. Summary of urbanisation effect on faecal corticosterone metabolite (FCM) concentrations, a) based on environmental dichotomy (non-urban versus urban), b) based on a 100-m radius imperviousness gradient and, c) based on a 500-m radius imperviousness gradient. *FCMs were log transformed to achieve Gaussian distribution. Date of capture (Date) was centred. Models are univariate regressions following Gaussian distribution. Random structure included ID of individuals (ID) and study sites (Location). Model parameters are thin=4, adapt_delta = 0.999 and max_treedepth = 15. We used 5,000 warm-ups, 15,000 iterations and default weakly informative priors.* R^2*c and* R^2*m are conditional and marginal effect sizes, respectively. 95 % credible intervals (CrI) are shown between square brackets.*

	Estimate	Estimated error	95% CrI	Observations	R^2c and R^2m
a) Habitat					
FCMs ~ Intercept	-1.93	0.91	[-3.77, -0.22]	121	
Habitat_Urban	-0.62	0.88	[-2.40, 1.19]		
SMI	0.08	0.03	[0.02, 0.13]		
Date	-0.01	0.01	[-0.02, -0.00]		0.604 [0.412, 0.755]
					0.129 [0.020, 0.285]
Sd(1|ID)	0.87	0.14	[0.57, 1.14]	93	
Sd(1|Location)	0.80	0.53	[0.12, 2.11]	6	
Residuals	0.87	0.11	[0.69, 1.11]		
b) Imperviousness 100-m					
FCMs ~ Intercept	-2.06	0.88	[-3.90, -0.39]	121	
Imperv_100	-0.01	0.02	[-0.06, 0.04]		
SMI	0.07	0.03	[0.02, 0.13]		
Date	-0.01	0.01	[-0.02, -0.00]		0.600 [0.393, 0.747]
					0.137 [0.018, 0.329]
Sd(1|ID)	0.86	0.15	[0.54, 1.13]	93	
Sd(1|Location)	0.87	0.56	[0.13, 2.28]	6	
Residuals	0.88	0.11	[0.69, 1.13]		
c) Imperviousness 500-m					
FCMs ~ Intercept	-1.86	1.02	[-3.99, 0.05]	121	
Imperv_500	-0.01	0.02	[-0.05, 0.03]		
SMI	0.07	0.03	[0.02, 0.13]		
Date	-0.01	0.01	[-0.02, -0.00]		0.601 [0.400, 0.750]
					0.140 [0.018, 0.334]
Sd(1|ID)	0.86	0.15	[0.56, 1.14]	93	
Sd(1|Location)	0.80	0.57	[0.07, 2.27]	6	
Residuals	0.87	0.11	[0.69, 1.12]		

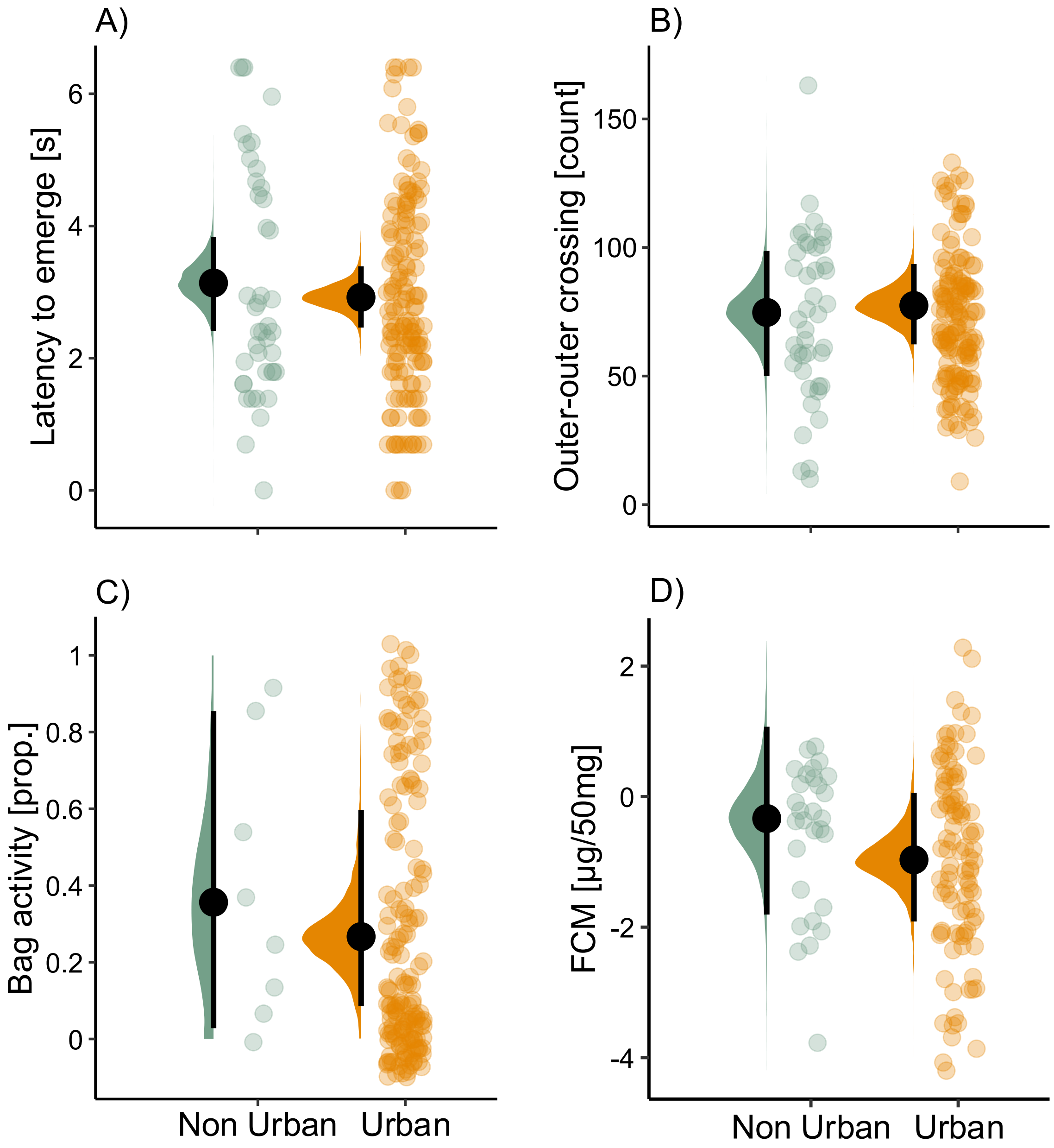


Figure S4. *Urbanisation effect on A) log-transformed latency to emerge in dark-light test (boldness, N = 140, k = 189), B) total number of outer-outer crossings in open-field test (exploration, N = 137, k = 187), C) time spent active in handling bag test (defiantness, N = 132, k = 174), and D) log-transformed faecal corticosterone metabolite (FCM) levels (N = 93, k = 121) in wood mice,* Apodemus sylvaticus. *Dots are raw data points plotted with a small jitter effect to facilitate visualisation. Black dot and black line represent mean and its 95 % credible intervals, respectively. Density plots represent the posterior distribution of the estimated mean. N is the number of unique individual and k is the number of observations.*

Literature review n°1: SCS potential studies

Table S16. Summary of the systematic review n°1. *The table shows studies that collected repeated measurements per individual, for both physiological and behavioural traits at the same time, and for urban and non-urban populations of non-human wild animals. The reported relationship between behavioural and physiological traits can be linear or non-linear. Statistical analysis did not necessarily involve all repeated measurements. Statistically significant results are reported (p-value < 0.05), as well as trends. Relationships were classified as trends when the 95% confidence or credibility intervals included zero but extended no more than ± 0.05 beyond it, and when the estimated correlation coefficient was at least 3.5 times larger in magnitude than the interval's overlap with zero. Blank cell means that no correlations was observed. GCs stands for concentrations of glucocorticoids and FCMs for concentrations of faecal corticosterone metabolites.*

Reference and species	**Traits**		**Statistical analysis**	**Stress coping style conclusion**
	Physiology	**Behaviour**		
Thompson *et al.* 2025 Great tit *Parus major*	Breath rate	Handling aggression Exploration	/	Not assessed (NA)
Guindre-Parker *et al.* 2022 European starling *Sturnus vulgaris*	Breath rate Baseline GCs Stress-induced GCs	Handling struggle Bag struggle	Pairwise correlation	*Total phenotypic correlation* Urban: Breath rate ~ Handling struggle = Positive Non-urban: No evidence of total phenotypic correlations *Among- and within-individual correlation:* NA
Caizergues *et al.* 2022 Great tit *Parus major*	Breath rate	Handling aggression Exploration	Bivariate linear mixed models	*Total phenotypic correlation* Urban: Breath rate ~ Handling aggression = Negative Breath rate ~ Exploration = Trend negative Non-urban: Breath rate ~ Handling aggression = Negative Breath rate ~ Exploration = Negative *Among-individual correlation* Urban: Breath rate ~ Exploration = Negative Non-urban: Breath rate ~ Handling aggression = Trend negative *Within-individual correlation* Urban: Breath rate ~ Handling aggression = Negative Non-urban: Breath rate ~ Handling aggression = Trend negative
Oliveira *et al.* 2020 Greater white-toothed shrew	Resting metabolic rate	Boldness Exploration	Multivariate mixed models	*Total phenotypic correlation* Urban: RMR ~ Boldness = Negative Non-urban: RMR ~ Exploration = Negative

Crocidura russula				*Among-individual correlation* No evidence of correlations in urban and non-urban habitats *Within-individual correlation* No evidence of correlations in urban and non-urban habitats
Batabyal & Thaker 2019 Indian rock agama *Psammophilus dorsalis*	Undefined GCs	Simple push-ups and head bobs Crouch walk Bite Mount	/	NA
Dominoni *et al.* 2013a European blackbird *Turdus merula*	Morning drop in melatonin	Activity	Linear model	*Total phenotypic correlation* In the winter, for the light-at-night group: Urban: Change in melatonin ~ Activity = Negative Non-urban: Change in melatonin ~ Activity = Negative
Dominoni *et al.* 2013b European blackbird *Turdus merula*	TEST Size testes	Activity	/	NA
Forte *et al.* 2023 Greater white-toothed shrew *Crocidura russula*	Undefined GCs	Exploration	/	NA
Caspi *et al.* 2025 Coyote *Canis latrans*	FCMs	Diet (DNA metabarcoding in faeces)	/	NA

Literature review n°2: SCS-framed studies

Table S17. Summary of the systematic review n°2. *The table shows studies that framed their paper using the SCS framework and comparing urban and non-urban populations of non-human wild animals. The reported relationship between behavioural and physiological traits can be linear or non-linear. Statistical analysis did not involve necessarily all repeated measurements. Statistical analysis did not necessarily involve all repeated measurements. Statistically significant results are reported (p-value < 0.05), as well as trends. Relationships were classified as trends when the 95% confidence or credibility intervals included zero but extended no more than ± 0.05 beyond it, and when the estimated correlation coefficient was at least 3.5 times larger in magnitude than the interval's overlap with zero. Blank cell means that no correlations was observed. GCs stands for concentrations of glucocorticoids.*

Reference and species	**Traits**		**Statistical analysis**	**Stress coping style findings**
	Physiology	**Behaviour**		
Guindre-Parker *et al.* 2022 European starling *Sturnus vulgaris*	Breath rate Baseline GCs Stress-induced GCs	Handling struggle Bag struggle	Pairwise correlation Repeated measurement	*Total phenotypic correlation* No evidence of total phenotypic correlations in urban and non-urban habitats *Among- and within-individual correlation:* Not assessed (NA)
Batabyal & Thaker 2019 Indian rock agama *Psammophilus dorsalis*	Undefined GCs	Simple push-ups and head bobs Crouch walk Bite Mount	/ Repeated measurement	NA
Senar *et al.* 2017 *Great tit* *Parus major*	Breath rate	Distress call Handling aggression	Bivariate linear mixed model No repeated measurement	*Total phenotypic correlation* No evidence of total phenotypic correlations in urban and non-urban habitats *Among- and within-individual correlation:* NA
Corbel *et al.* 2016 Feral pigeon *Columbia livia*	Baseline GCs Stress-induced GCs	/	/ No repeated measurement	NA
Partecke *et al.* 2006 European blackbird *Turdus merula*	Baseline GCs Stress-induced GCs	/	/ No repeated measurement	NA

Supplementary information - Literature

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