



Small mammals in the big city: Behavioural adjustments of non-commensal rodents to urban environments

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Abstract

A fundamental focus of current ecological and evolutionary research is to illuminate the drivers of animals' success in coping with human-induced rapid environmental change (HIREC). Behavioural adaptations are likely to play a major role in coping with HIREC because behaviour largely determines how individuals interact with their surroundings. A substantial body of research reports behavioural modifications in urban dwellers compared to rural conspecifics. However, it is often unknown whether the observed phenotypic divergence is due to phenotypic plasticity or the product of genetic adaptations. Here, we aimed at investigating (a) whether behavioural differences arise also between rural and urban populations of non-commensal rodents; and (b) whether these differences result from behavioural flexibility or from intrinsic behavioural characteristics, such as genetic or maternal effects. We captured and kept under common environment conditions 42 rural and 52 urban adult common voles (*Microtus arvalis*) from seven subpopulations along a rural–urban gradient. We investigated individual variation in behavioural responses associated with risk-taking and exploration, in situ at the time of capture in the field and ex situ after 3 months in captivity. Urban dwellers were bolder and more explorative than rural conspecifics at the time of capture in their respective sites (in situ). However, when tested under common environmental conditions ex situ, rural individuals showed little change in their behavioural responses whereas urban individuals altered their behaviour considerably and were consistently shyer and less explorative than when tested in situ. The combination of elevated risk-taking and exploration with high behavioural flexibility might allow urban populations to successfully cope with the challenges of HIREC. Investigating whether the observed differences in behavioural flexibility are adaptive and how they are shaped by additive and interactive effects of genetic make-up and past environmental conditions will help illuminate eco-evolutionary dynamics under HIREC and predict persistence of populations under urban conditions.

KEYWORDS

animal personality, behavioural adjustment, behavioural flexibility, environmental change, HIREC, rodents, urbanization

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1 | INTRODUCTION

Human activities caused unprecedented changes to environments worldwide—from climate change and habitat destruction to over-harvesting and the introduction of invasive species (e.g. Vitousek, Mooney, Lubchenco, & Melillo, 1997; Wong & Candolin, 2015). Urbanization represents one of the most extreme forms of land-use alterations and causes unparalleled environmental variation (e.g. Grimm et al., 2008; Johnson & Munshi-South, 2017), involving substantial changes of the physical environment, ecosystem processes and ecology of organisms that inhabit these areas (Alberti, 2015; Johnson & Munshi-South, 2017; McKinney, 2002; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). Because these environmental alterations are often radical and rapid, many species cannot cope with them (e.g. Sih, Ferrari, & Harris, 2011; Sol, Lapiedra, & González-Lagos, 2013). As a result, a common outcome of the urbanization process is a loss of species diversity (e.g. Grimm et al., 2008; McKinney, 2006; Shochat et al., 2010; Sol, Bartomeus, González-Lagos, & Pavoine, 2017) mainly affecting 'urban avoiders' (e.g. Fischer, Schneider, Ahlers, & Miller, 2015). Despite this, a few species called 'urban dwellers' (e.g. Fischer et al., 2015) appear to thrive in urban habitats, which has allowed them to expand their range (e.g. Sih et al., 2011; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Urbanization thus constitutes a unique setting to investigate adaptive processes to human-induced rapid environmental change (HIREC, *sensu* Sih et al., 2011) and to learn important lessons on eco-evolutionary dynamics (e.g. Alberti, Marzluff, & Hunt, 2017; Sih et al., 2011; Sprau, Mouchet, & Dingemanse, 2017).

Behavioural responses to HIREC are likely a key factor in driving the successful colonization of urban habitats because behaviour largely determines how individuals interact with their surroundings (e.g. Sih, 2013; Sih et al., 2011; Tuomainen & Candolin, 2011) which, in turn, can expose individuals to challenges that may substantially alter their behaviour (e.g. Alberti et al., 2017; Baxter-Gilbert, Riley, & Whiting, 2019; Lapiedra, Chejanovski, & Kolbe, 2017; Sol et al., 2013) or reveal previously unexpressed behaviours (e.g. Cook, Weaver, Hutten, & McGraw, 2017; Ducatez, Sol, Sayol, & Lefebvre, 2020; Roth, LaDage, & Pravosudov, 2010; Sol, Timmermans, & Lefebvre, 2002). This fundamental role of behaviour is epitomized by the intraspecific behavioural shifts of urban dwellers towards being more tolerant to disturbance, bolder and more aggressive or territorial, as well as showing increased or altered activity patterns (reviewed in e.g. Lowry, Lill, & Wong, 2013; Miranda, Schielzeth, Sonntag, & Partecke, 2013; Sol et al., 2013).

Although there is ample evidence that the successful colonization of urban habitats is related to intraspecific behavioural shifts, the underlying mechanisms remain unclear (but see Baxter-Gilbert et al., 2019; Miranda et al., 2013). Two main factors are usually considered as potential drivers of differences in behavioural responses to human disturbance in urban wildlife: (a) higher behavioural flexibility in urban individuals compared to rural ones or (b) evolutionary change via divergent selection (e.g. Baxter-Gilbert et al., 2019; Lowry et al., 2013; Miranda et al., 2013; Sih et al., 2011; Sol et al., 2013) or

spatial sorting (e.g. Shine, Brown, & Phillips, 2011; Sol et al., 2013). Behavioural flexibility (or reversible phenotypic plasticity), defined as the environmentally sensitive production of alternative phenotypes by given genotypes (DeWitt & Scheiner, 2004), might allow some individuals to habituate faster than others, become less sensitive to novel threats and find new alternative solutions to the challenges of urban life (e.g. Lowry et al., 2013; Sih et al., 2011; Sol et al., 2013), thus enabling urban dwellers to increase their exploitation of urban resources and to decrease the costs associated with urban habitats (e.g. Baxter-Gilbert et al., 2019; Kralj-Fišer, Hebets, & Kuntner, 2017; Sol, Bacher, Reader, & Lefebvre, 2008; Sol et al., 2005). Alternatively, if the observed phenotypic divergence is due to intrinsic behavioural characteristics, that is, based on genetic or maternal effects, some individuals with specific behavioural profiles might just be better suited to reach and successfully colonize urban habitats than others (e.g. Lowry et al., 2013; Miranda et al., 2013; Sih et al., 2011; Sol et al., 2013; Wolf & Weissing, 2012). Moreover, if such behavioural profiles are consistent and heritable, and provide an advantage in urban environments, then selection may favour them in urban populations (e.g. Baxter-Gilbert et al., 2019; Miranda et al., 2013). Also, if only specific behavioural types are able to pass through the filters of successful dispersal and colonization, these colonizing individuals at the expansion front will mate assortatively and select for higher expression of the traits favouring the dispersal and colonization (i.e. spatial sorting, Shine et al., 2011). Under natural conditions, phenotype and environment (e.g. urban/rural) are correlated and, thus, the role of intrinsic and extrinsic environmental factors in shaping phenotypic variation cannot be disentangled. Here, we translocated individuals into a common environment to investigate whether phenotypic divergence in behaviour observed in nature between rural and urban individuals is due to phenotypic plasticity or to intrinsic factors (genetic or maternal effects; e.g. Garcia, Suárez-Rodríguez, & López-Rull, 2017; Purcell, Piroga, Avril, Bouyarden, & Chapuisat, 2016).

A genetic heritable base is required for any focal trait that undergoes selective pressures. Numerous studies have shown that between-individual behavioural differences that are stable over time and across contexts, that is, animal personality (e.g. Réale, Reader, Sol, McDougall, & Dingemanse, 2007), do have a heritable component (e.g. Dochtermann, Schwab, Anderson Berdal, Dalos, & Royauté, 2019) and can have a direct influence on the individuals' response to novel, high-risk or challenging situations (e.g. Koolhaas et al., 1999; Réale et al., 2007), thereby affecting their ability to reproduce and survive (e.g. Smith & Blumstein, 2008). Individual animals can exhibit, for example, consistent levels of exploration, boldness, activity, sociability and aggression (e.g. Réale et al., 2007). Different expression and combination of these personality traits might provide advantages when navigating and exploiting urban environments (e.g. Baxter-Gilbert et al., 2019; Kralj-Fišer et al., 2017; Miranda et al., 2013). Particularly, boldness, defined as an individual's propensity to take risks, is often found to provide advantages to urban-living animals when coping with potentially threatening novel situations and disturbances (e.g.

Baxter-Gilbert et al., 2019; Bokony, Kulcsar, Toth, & Liker, 2012; Lapiedra et al., 2017). Similarly, an individual's willingness to explore and engage with novel stimuli is bound to promote dispersal across novel landscapes (e.g. Canestrelli, Bisconti, & Carere, 2016; Duckworth & Badyaev, 2007), access to important environmental information and exploitation of novel resources (e.g. food sources or shelter; Baxter-Gilbert et al., 2019; Ducatez, Audet, Rodriguez, Kayello, & Lefebvre, 2017; Lapiedra et al., 2017; Miranda et al., 2013), all of which could substantially influence their success in urban environments.

While current research strongly focuses on species with high dispersal abilities, namely birds and larger mammals (e.g. Bateman & Fleming, 2012; Breck, Poessel, Mahoney, & Young, 2019; Carrete & Tella, 2017; Charmantier, Demeysier, Lambrechts, Perret, & Grégoire, 2017), we know very little about the determinants and constraints of successful adaptation to urban environments of species more limited in dispersal, physically restricted to specific locations within urban environments, on which selection could potentially be stronger (Baxter-Gilbert et al., 2019). Here, we focus on small ground-dwelling rodents, which are often found in urban areas. Common voles (*Microtus arvalis*) are fossorial seasonal breeding microtine rodents distributed throughout most regions of Europe (e.g. Jacob, Manson, Barfknecht, & Fredricks, 2014). They are non-commensal but known to successfully colonize urban environments (e.g. Kečkéšová & Noga, 2008; Riegert & Fuchs, 2011) and to present between-individual variation in behavioural traits such as boldness, activity and exploration under both laboratory and natural conditions (e.g. Eccard & Herde, 2013; Gracceva et al., 2014; Herde & Eccard, 2013; Lantová, Šichová, Sedláček, & Lanta, 2011).

In order to better understand the drivers of behavioural shifts in urban areas, our aim was to answer the following questions: (a) Do urban common voles present behavioural differences to their rural conspecifics? (b) Do behavioural traits display gradual phenotypic variation across an urbanization gradient? (c) Are such behavioural differences in urban animals due to flexible behavioural adjustments to extrinsic environmental conditions (phenotypic plasticity) or to stable intrinsic personality traits? To address these questions, we first quantified in situ behavioural traits associated with exploration and risk-taking propensity in replicated free-living rural and urban populations of common voles. In a second step, we transferred these individuals to a common captive environment, where we tested *ex situ* the effects of a new, common environment on adult individuals' behavioural traits. We also examined if behavioural traits were consistent throughout the experiment, and compared their repeatability among origin populations (rural/urban). We predicted higher levels of boldness and exploration in individuals from urban populations compared with their rural counterparts. If such differences were present and driven by behavioural flexibility, we expected to see the behaviour of all animals to adjust to the common environment and show similar behavioural responses, independent of their origin population. If the differences observed between rural and urban individuals were driven by stable personality traits, we expected them to be maintained also in the common environment.

2 | MATERIALS AND METHODS

2.1 | Study sites and trapping

Animals were trapped in four different urban sites in Berlin (52°31'N, 13°24'E, area 891 km²), with varying degrees of anthropogenic influences, and three rural sites in a region of NE-Germany called Uckermark (53°35'N, 13°71'E, area 3,058 km²) in NW-Brandenburg (for further details, see Schirmer, Herde, Eccard, & Dammhahn, 2019). Rural and urban trapping sites were on average 102.6 ± 3.7 km apart. Rural sites were on average 9.2 ± 6.7 km apart from each other, while urban sites were on average 13.3 ± 5.9 km apart (Figure S1). Common voles have an average home range size of 30–180 m² (e.g. Briner, Nentwig, & Airoldi, 2005; Jacob & Hempel, 2003), an average core area of 4–25 m² (e.g. Briner et al., 2005), a daily range length of 9–49 m (e.g. Briner et al., 2005) and are estimated to disperse between 76 and 110 m per generation depending on sex (e.g. Gauffre, Estoup, Bretagnolle, & Cosson, 2008; Gauffre, Petit, Brodier, Bretagnolle, & Cosson, 2009; Roos et al., 2019). We therefore consider the sampled populations to be independent replicates. All sites were part of a network of experimental platforms of the Berlin-Brandenburg Institute of Advanced Biodiversity Research, the *CityScapeLabs* and *AgroScapeLabs* (von der Lippe, Buchholz, Hiller, Seitz, & Kowarik, 2020; <https://www.bbib.org>). We estimated the coverage of natural soil with artificial impervious surface (e.g. buildings and paved roads), as a proxy of the degree of urbanization in each site and expressed it as a sealing index. The index was calculated in a 5 km radius around each trapping grid's centre. The trapping grids cover ca. 0.80 ± 0.22 ha. The proportion of artificial impervious surface was calculated within the *CityScapeLabs* project (Buchholz, Hannig, Möller, & Schirmel, 2018), based on the 'UrbanisationScore' developed by Seress, Lipovits, Bókony, and Czúni (2014) on the basis of the biotope mapping of Berlin. We used the same method for the rural sites. In brief, this method scores the abundance of vegetation, buildings and paved roads within each 100 × 100 m cell in a defined buffer area around the focal study sites using a GIS (v. 10/ESRI; <http://www.esri.com/>; Buchholz et al., 2018). Sealed surface closely corresponds to other urbanization indices, such as human population density, disturbance by humans and pets, noise and light pollution (Buchholz et al., 2018; Seress et al., 2014).

We captured animals using multiple-capture livetraps (Ugglan Special Traps n. 1-2, Grahnb AB) between July and September 2018. At each site, 48 traps were set in a regular grid of ca. 10 m distance between traps. Traps were pre-baited with oat flakes and apples for two nights, after which the traps were activated and the initial trapping session started. Traps were activated every night between 18:00 and 19:00 hr and checked and deactivated every morning between 06:00 and 07:00 hr. Trapping was performed on each site for 7–12 days and was interrupted once the capture success was <2 individuals/grid night. With this high capture effort, we ensured low bias towards trap-shy individuals. Captured animals were transferred from the trap into the testing arena, and after the behavioural observations were concluded, their sex was determined, they were weighed and checked

for reproductive status. Lactating females were immediately released at the site of capture, whereas all other animals were given additional oat flakes and apples and transported to the animal holding facility of the University of Potsdam.

2.2 | Experimental procedure

Animals were tested for the first time in situ on the field, on the day of capture, following the protocol described below (see Section 2.3). They were then transported to the animal holding facility, where they were housed individually and given 9–12 weeks to acclimatize to the new, common environment (see Section 2.4). Animals were then tested again, ex situ in the laboratory, following the same protocol (see Section 2.5). We ensured high inter-observer reliability with test trials prior to data collection. We used the same arena on the field and in the laboratory. We conducted all tests by direct observation, between 07.00 and 18.00 hr. For logistical reasons, animals were tested only once on the field, on the day and site of capture. Animals were tested twice in the laboratory, after an acclimatization period of 9–12 weeks, with an inter-trial period of 14 days.

2.3 | Personality test in the field

For behavioural testing, we modified and combined standard laboratory tests that are commonly used in personality studies of small mammals—the dark light test and the open field test (Archer, 1973; Schirmer et al., 2019; Figure S2). The dark–light test measures willingness of individuals to leave a dark and enclosed shelter to enter an unknown, bright and potentially risky area. The open field test quantifies an individual's exploratory activity and risk-taking propensity by assuming different levels of perceived risk in different arena parts (e.g. Mazza, Eccard, Zaccaroni, Jacob, & Dammhahn, 2018; Schirmer et al., 2019). The set-up was structured to be executable directly on site, without handling individuals before testing, thus precluding possible influences of handling stress on behavioural expression during the test (Schirmer et al., 2019). The test set-up consists of a dark plastic tube (10.5 × 32 cm Ø) with swing doors at both ends connected to a round PVC open field arena (130 cm Ø, 30 cm high; Figure S1). At the start of each test, animals were transferred without direct handling from the trap into the tube. The external swing door was closed and the animal was left in the tube for 60 s, after which the internal swing door was opened and we measured the subject's latency to enter into the open field arena with the full body without tail ('latency to emerge'). If the animals did not leave the dark tube within 5 min, they were gently guided out of the tube into the arena and the latency was set to 300 s (7% of all tests performed on the field). When the animal entered the circular arena, we closed the tube door and recorded for 5 min the proportion of time spent active, that is, moving around the arena ('exploration activity'), with instantaneous 1–0 sampling every 10 s (e.g. Martin & Bateson, 1993). At the end of each test, the apparatus was cleaned with 70% alcohol.

2.4 | Laboratory housing conditions (common environment)

Animals were housed individually in standard polycarbonate cages (Typ III; Ehret GmbH; dimensions: 42 cm × 27 cm × 16 cm) equipped with hay, bedding and cardboard rolls as shelters. Food (Ssniff V1594 R/M-H Ered II) and water were provided ad libitum. Light, temperature and humidity mirrored the natural conditions occurring outside the laboratory. Bedding was changed every 2 weeks. All animals from both rural and urban sites were kept in the same room and individual cages were placed into the shelves in randomized order. Animals were kept under these conditions for 9–12 weeks before being tested again.

2.5 | Personality test in the laboratory

On the day of the test, animals were taken from their cage and transported into a separate testing room, without direct handling. Animals were placed into the dark–light tube and the external swing door was closed. After 60 s, the internal swing door was opened and we measured the subject's latency to enter into the open field arena with the full body without tail ('latency to emerge'). Based on previous experience with wild animals tested in captivity, the time in the tube was extended to 10 min for all animals, and a corroborative analysis was carried out to ensure that results would be qualitatively unchanged. If the animals did not leave the dark tube within this time, they were gently guided out of the tube into the arena and the latency was set to 600 s (16% of all performed tests performed in the lab). When the animal entered the circular arena, we closed the tube door and recorded for 5 min the proportion of time spent active, that is, moving around the arena ('exploration activity'), with instantaneous 1–0 sampling every 10 s (e.g. Martin & Bateson, 1993). At the end of the test, animals were transported back to their home cage and the apparatus was cleaned with 70% alcohol. The test in the laboratory was executed twice, with an inter-trial period of 14 days.

2.6 | Statistical analyses

We tested whether individual behavioural responses were repeatable, that is, consistent across contexts, using the *rtpR* package and adjusting for testing environment (field vs. laboratory; Nakagawa & Schielzeth, 2010; Stoffel, Nakagawa, Schielzeth, & Goslee, 2017). We estimated 95% confidence interval of repeatabilities for each variable by parametric bootstrapping ($N = 1,000$ simulation iterations) and p values by 1,000 permutations. Latency to leave the dark shelter was log-transformed, and the proportion of time intervals animal spent active was arcsine-square-root transformed. Before analyses, we also ensured there was no strong collinearity between model predictor variables (i.e. an $R^2 > .70$).

We assessed the experiment pre-conditions by comparing behavioural responses of rural and urban individuals on the field.

We used linear mixed effects models (LMMs) fitted by restricted maximum-likelihood. We included trapping site as a random factor, specified as random intercept, in each model. In a first step of the analyses, we compared each behavioural variable across rural and urban populations, since the proportion of sealed surface was very similar for all rural sites. In a second step, we used the same statistical approach to evaluate the relationship between behavioural variables and sealed surface as a proxy for urbanization. This allowed us to investigate possible gradual changes along the rural–urban gradient. In all models, sex of the tested individual was added as fixed factor.

We used restricted maximum-likelihood LMMs with a Gaussian error distribution to evaluate the effect of the change of environment on behavioural responses. We included origin of the animals (rural/urban), test environment (field/lab) and their interaction as fixed effects. Sex was initially included as fixed factor and excluded from all models based on its lack of explanatory importance using stepwise backward model selection based on log-likelihood ratio tests comparing nested models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To account for repeated measures, we added the individual identity as a random intercept nested in trapping site. Analyses were first performed on the whole data sets; since the interaction between the explanatory variables origin of the animals and testing environment was found in each case, we ran post hoc analyses on subsets of data including only rural individuals or only urban individuals respectively. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We used the R packages *lme4* (Bates, Mächler, Bolker, & Walker, 2014) and *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2017).

Lastly, we quantified the magnitude of the within-individual change in behaviour occurred between the field and the first test in the lab, and subsequently from the first to the second test in the lab, to evaluate whether the observed changes in behaviour were stable over time in the common environment. Since Bayesian mixed effects models allow less biased estimates of individual random effects (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010), we applied this approach for this step of the analysis, using the R package *MCMCglmm*, Markov-chain Monte Carlo generalized linear mixed models (Hadfield, 2010). We fitted each behaviour as the response and built a random intercept–slope model with test environment (field/lab) or the test round (lab1/lab2) fitted as a covariance term to estimate within-individual flexibility of behaviour over time and context. All models had a slightly informative prior calculated by dividing the total phenotypic variance of the behavioural trait by the number of random effects ($N = 2$) in the model and we set a low degree of belief ($\nu = 0.002$; Hadfield, 2010). Models were run for 1,010,000 iterations and sampled every 100 iterations with a burn-in of 5,000. These parameter settings resulted in low temporal autocorrelation between estimates of subsequent models, which were assessed by graphical diagnostics. We estimated 95% credible intervals from the posterior distribution and any interval not including 0 was considered significant. Subsequently, we extracted individual random intercepts (i.e. best linear unbiased predictors) and individual random slopes (i.e. within-individual behavioural flexibility over time/context) and compared these traits between urban and rural

animals with a Mann–Whitney U test. The accepted significance level was $\alpha \leq 0.05$. All data analyses were conducted with R version 3.2.3 (R Core Team, 2015).

2.7 | Ethical note

Animal capture and behavioural tests were conducted under the permission of the 'Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg' (reference number: LUGV_7RO-4610/34+5#86908/2011; V3-2347-7-2019 and RO7/SOB-0998A-C) and the 'Landesamt für Gesundheit und Soziales Berlin' (reference number: G 0072/16). Experiments were performed in accordance with all applicable international, national and/or institutional guidelines for the use of animals, including the ASAB/ABS guidelines for the Use of Animals in Research. Captured animals were released at the capture site after the conclusion of the experiment. We provided each animal with a waterproof shelter with hay and food to allow them to slowly re-acclimatize to their former habitat.

3 | RESULTS

We captured 98 common voles, 44 of which in the rural sites and 54 in the urban sites; a total of 94 individuals were transported to the laboratory and 80 were tested multiple times (average $\pm$ SD number of tests per individual: 2.7 ± 0.7). At data set level, both behavioural responses were repeatable over time when adjusted for testing environment (field/lab; Figure 1; Table S2). While habitat-specific repeatabilities were based on smaller sample sizes, they suggested that behavioural traits might be more repeatable in rural than urban habitats (Figure 1; Table S2). Behavioural responses were moderately correlated at the phenotypic level to each other both in the field ($r_s = -.29$; $p = .003$) and in the laboratory ($r_s = -.48$; $p < .001$).

Under field/natural conditions, urban voles had a shorter latency to emerge from the dark shelter ($\beta = -0.94 \pm 0.28$, $t = -3.41$, $p = .019$ —Figure 2; Table 1) and spent more time exploring the arena ($\beta = 0.27 \pm 0.06$, $t = 4.24$, $p = .008$ —Figure 2; Table 1) than rural conspecifics. The test environment had no effect on the latency to leave the shelter ($\beta = -0.21 \pm 0.20$, $t = -0.96$, $p = .34$; Table 2) nor exploration activity in the arena ($\beta = -0.05 \pm 0.06$, $t = -0.81$, $p = .42$) in the rural animals. However, urban animals showed an increase in latency to emerge from the dark shelter ($\beta = 1.98 \pm 0.25$, $t = 8.03$, $p < .001$; Table 2) and a decrease of exploration activity ($\beta = -0.50 \pm 0.05$, $t = -9.96$, $p < .001$; Table 2) with the change of testing environment from field to laboratory (Figures 3 and 4).

Individual slopes describing the magnitude of the change from natural environment to common laboratory environment differed between rural and urban animals for both behaviours (latency to leave the shelter: $W = 409$, $p < .001$; exploration activity: $W = 523$, $p = .019$; Figure 4), with urban individuals having steeper slopes compared to rural conspecifics (Figure 4; Table S3). Individual slopes

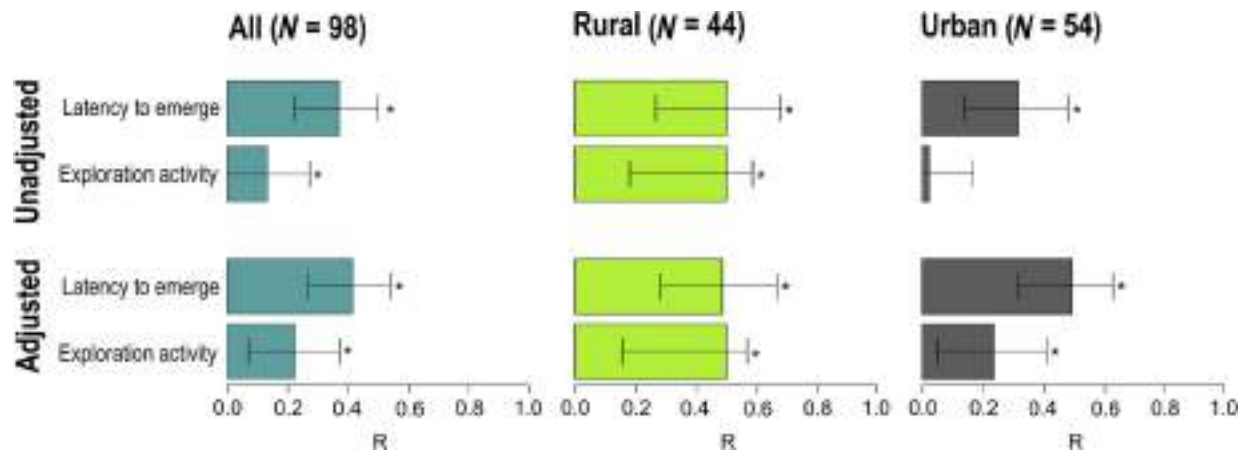


FIGURE 1 Repeatability estimates (R) and their 95% confidence intervals of behavioural variables for common voles (*Microtus arvalis*) quantified in repeated short behavioural tests. Shown are (upper panel) unadjusted repeatability and (lower panel) repeatability adjusted for testing environment (field/lab). Asterisks indicate significant differences from zero with $p < .05$

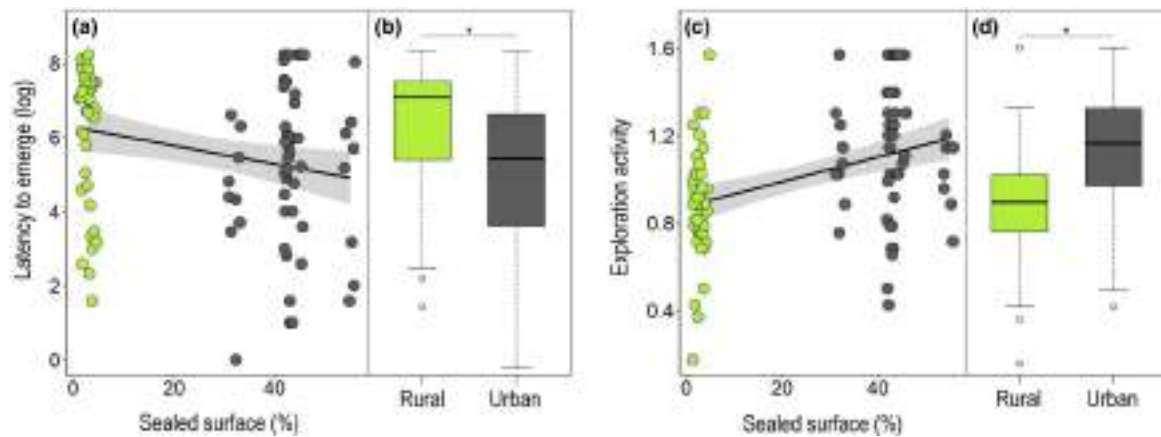


FIGURE 2 For individuals of common voles (*Microtus arvalis*, $N = 98$), two aspects of repeatable behaviours tested in situ vary with the degree of urbanization: (a, b) latency to emerge from the shelter and (c, d) exploration activity (arcsine-square root transformed). (a, c) With increasing percentage of sealed surface in a 5 km buffer (i.e. degree of urbanization), latency to emerge decreases and exploration activity increases; shown are jittered raw data points and prediction lines with their 95% confidence bands (grey shading) from linear mixed effects models. (b, d) Grouping individuals by origin, urban individuals have lower latencies to emerge and higher exploration activity than rural conspecifics; shown are median (line), inter-quartile range (box), min-max range (whiskers) and outliers (dots) for urban ($N = 54$, grey) and rural ($N = 44$, green) voles. Asterisks indicate significance with $p < .05$

TABLE 1 Model results for field data in relation to habitat type (rural vs. urban), sealed surface in a 5 km buffer and sex for 98 individual common voles (*Microtus arvalis*). R_m reports the marginal R^2 value based on the fixed factors, R_c the conditional R^2 value including the study site as a random factor. Reference levels are given in (). For statistically significant effects, p values are highlighted in bold

Variable	Fixed factors	Estimate	SE	t	p	R_m	R_c
Latency to emerge	Intercept	4.18	0.26	16.17	<.001	.13	.13
	Area (Urban)	−0.94	0.28	−3.41	.019		
	Sex (Male)	0.46	0.28	1.68	.097		
Exploration activity	Intercept	0.92	0.06	16.52	<.001	.22	.24
	Area (Urban)	0.27	0.06	4.25	.008		
	Sex (Male)	−0.11	0.05	−1.94	.055		
Latency to emerge	Intercept	4.20	0.27	15.54	<.001	.12	.12
	Sealing	−0.02	0.01	−3.19	.024		
	Sex (Male)	0.46	0.28	1.66	.101		
Exploration activity	Intercept	0.91	0.06	14.14	<.001	.20	.24
	Sealing	0.01	0.002	3.51	.017		
	Sex (Male)	−0.10	0.05	−1.90	.061		

TABLE 2 Results of linear mixed effects models (LMMs) including the full models of all individuals and of the post hoc analyses for latency to emerge from the dark shelter and exploration activity in relation to origin of the animals (rural vs. urban) and test environment (field vs. laboratory) for 94 individual common voles (*Microtus arvalis*). Reference levels are given in (). For statistically significant effects, *p* values are highlighted in bold.

Variable	Fixed factors	Full model					Rural					Urban				
		Estimate	SE	t/z	<i>p</i>	<i>R_m</i>	<i>R_c</i>	Estimate	SE	t/z	<i>p</i>	<i>R_m</i>	<i>R_c</i>	Estimate	SE	t/z
Latency to emerge	Intercept	6.30	0.44	14.27	<.001	.14	.54	4.37	0.31	14.03	<.001	.01	.50	5.19	0.40	13.03
	Origin (Urban)	-1.12	0.60	-1.88	.50				/						/	
	Test environment (Lab)	-0.27	0.30	-0.92	.32			-0.21	0.20	-0.96	.34			1.98	0.25	8.03
	Origin × Test environment	2.25	0.39	5.84	<.001				/							
Exploration activity	Intercept	0.85	0.06	13.6	<.001	.23	.47	0.85	0.07	12.50	<.001	.004	.41	1.12	0.05	21.82
	Origin (Urban)	0.27	0.08	3.1	.002				/						/	
	Test environment (Lab)	-0.05	0.06	-0.9	.37			-0.05	0.06	-0.81	.42			-0.50	0.05	-9.96
	Origin × Test environment	-0.45	0.08	-5.8	<.001				/							

quantifying the magnitude of the change between first and second test in the laboratory did not differ between urban and rural animals for both behaviours (latency to leave the shelter: $W = 746$, $p = .89$; exploration activity: $W = 858$, $p = .33$; Figure 4).

4 | DISCUSSION

Our study revealed that in situ common voles living in urban habitats were bolder and more explorative than those from rural populations. Also, urban common voles showed high levels of behavioural flexibility when translocated from their familiar habitat to the novel laboratory environment, while rural individuals maintained stable and repeatable behavioural responses independent of the living and testing environment, suggesting phenotypic divergence not only in behavioural traits but also in the degree of behavioural flexibility.

According to our predictions, behavioural responses connected to exploration activity and boldness scaled positively with the degree of urbanization. These findings are in line with previous studies carried out with multiple taxa (e.g. Atwell et al., 2012; Carrete & Tella, 2017; Evans, Boudreau, & Hyman, 2010; Vines & Lill, 2015), showing how urbanization can act as an ecological filter favouring more urban-tolerant individuals, thus leading to phenotypic divergence in population compositions across urbanization gradients (e.g. Canestrelli et al., 2016; Charmantier et al., 2017). Among behavioural traits, boldness and exploration represent key determinants of success in all the stages of colonization of novel, challenging habitats (arrival, establishment and increase, sensu Sol et al., 2013). Higher levels of exploration tendencies and risk-taking might promote the abandonment of the native habitat and dispersal to distant areas (e.g. Canestrelli et al., 2016; Lindström, Brown, Sisson, Phillips, & Shine, 2013; Wolf & Weissing, 2012) improve responses to predators and competitors, while better coping with disturbance and pollution (e.g. Sih, Stamps, Yang, McElreath, & Ramenofsky, 2010; Sol et al., 2013). In fact, these traits are often found coupled in newly invading populations (e.g. Carrete & Tella, 2017). In the present study, boldness and exploration activity were phenotypically correlated, supporting the idea that the expression of integrated sets of behaviours (i.e. behavioural syndromes, Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) can enhance invasion success by coupling traits that are favoured in a novel environment with the propensity to disperse into it (e.g. Canestrelli et al., 2016; Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003; Duckworth & Badyaev, 2007; Lindström et al., 2013; Sih, 2013; Wolf & Weissing, 2012). Novelty seeking behavioural traits (including boldness, exploration, risk-taking and reactivity to novel stressors) were implicated in a recent island colonization and in the range expansion of two amphibian species (Brodin, Lind, Wiberg, & Johansson, 2013; Canestrelli et al., 2016; Lindström et al., 2013). However, the role of different behavioural types in spatial sorting and population dynamics might be more complex than covered by directional selection of higher trait levels (Canestrelli et al., 2016). For example, enhanced exploration activity and aggressiveness

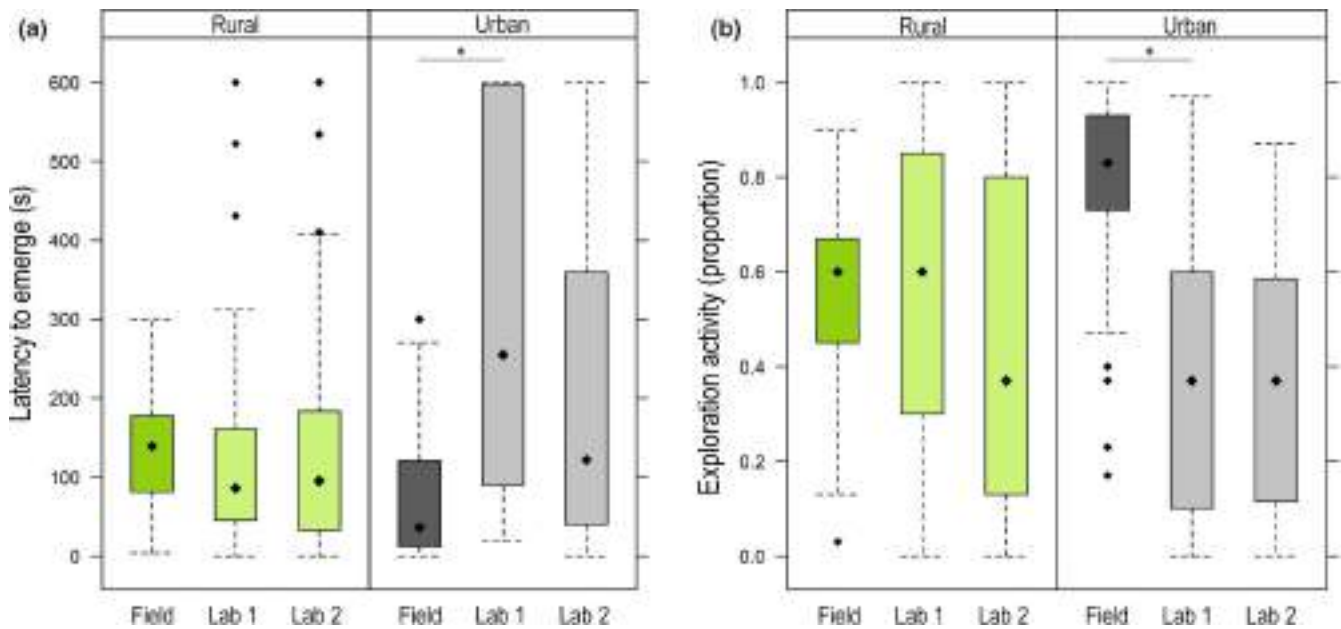


FIGURE 3 Population-level behavioural differences between common voles (*Microtus arvalis*) of different origins, rural (green, $N = 42$) and urban (grey, $N = 52$) across test environments (field and laboratory) and test sequence for (a) latency to emerge from a shelter and (b) exploration activity. Shown are median (dot), inter-quartile range (box), min–max range (whiskers) and outliers (dots). Asterisks indicate significance with $p < .05$

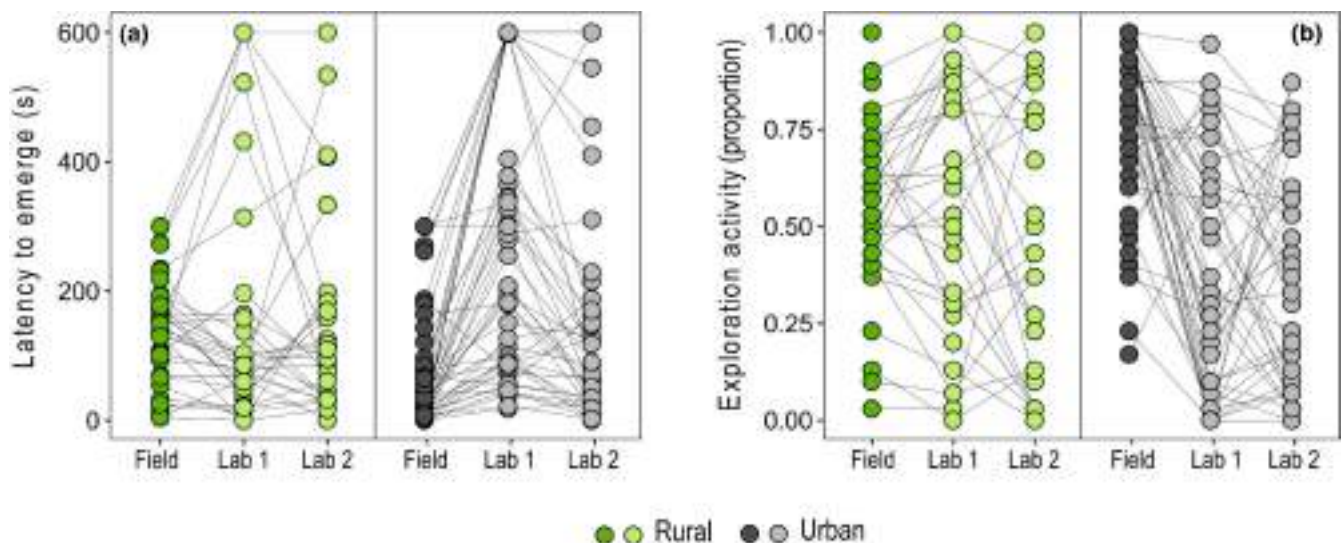


FIGURE 4 Individual reaction norms across the three tests (field and laboratory) for (a) latency to emerge from a shelter and (b) exploration activity for 42 rural (green) and 52 urban (grey) common voles (*Microtus arvalis*)

allowed western bluebirds (*Sialia mexicana*) to displace less aggressive competitors and expand their range into new areas (Duckworth & Badyaev, 2007). Interestingly, within a few generations, the level of aggressiveness rapidly decreased in concordance with local selection, suggesting that high expression of certain behavioural traits might not prove advantageous across all stages of colonization.

The ability to flexibly adjust the expression of behaviours such as exploration activity and boldness should also be favoured in urban environments (e.g. Bokony et al., 2012; Lehrer, Schooley, & Whittington, 2012; Thompson, Evans, Parsons, & Morand-Ferron, 2018). Our results suggest that in rural common voles

among-individual differences in exploration activity and boldness are stable over time and across environmental conditions. Thus, this set of individuals expresses intrinsically stable behavioural traits, matching our second prediction. However, once translocated into the novel laboratory environment, urban animals substantially altered their behavioural responses, decreased the expression of both boldness and exploration activity and subsequently maintained the new levels over time. Repeatability of behavioural responses across all tests was low in the urban population but high in the rural one. When considering the tests conducted in the laboratory only, or the repeatabilities adjusted for test location

(field/lab), values were again comparable between rural and urban populations, indicating a single behavioural adjustment occurred in the urban common voles after the translocation. This flexible adjustment of behaviour to environmental conditions suggests a more pronounced role of behavioural flexibility in coping with urbanization than expected according to our second prediction. Exploration activity, in particular, had much lower repeatabilities than boldness for urban animals, which could indicate that urban common voles either require less information on novel environments than rural ones or that they are faster in collecting sufficient information (e.g. Thompson et al., 2018). Previous studies also reported more variation in the expression of measured behavioural responses in urban individuals compared to rural ones (e.g. Bokony et al., 2012; Lehrer et al., 2012; Thompson et al., 2018). Similarly, in many bird species, urban animals typically show higher habituation, for example, in flight initiation distance, and in learning rates (e.g. Papp, Vincze, Preiszner, Liker, & Bókony, 2015; Rodríguez-Prieto, Martín, & Fernández-Juricic, 2011; Sol et al., 2005; Sprau & Dingemanse, 2017). Habituation and learning are considered forms of behavioural and cognitive flexibility (e.g. Carere & Locurto, 2011; Martin & Réale, 2008). Being able to habituate faster would favour the colonization of and the establishment in new human-altered environments. In the same way, making rapid assessments of what constitutes a threat in the novel environment and what can instead be safely ignored would prove advantageous, effectively lowering stress levels and allowing optimal resource allocation (e.g. of attention or vigilance). Since urbanization increases spatial and temporal heterogeneity, it creates an unstable, unpredictable environment that ought to favour individuals with higher levels of behavioural flexibility (e.g. Dingemanse & Wolf, 2013; Mathot, Wright, Kempenaers, & Dingemanse, 2012; Niemela, Vainikka, Forsman, Loukola, & Kortet, 2013; Sol et al., 2013).

It has been suggested that environmentally initiated phenotypic change (i.e. phenotypic plasticity) may facilitate or even promote evolutionary adaptation in novel environmental conditions (e.g. Levis & Pfennig, 2016; Perry, Schield, & Castoe, 2018), and that over time natural selection will fine-tune the population to the environment by modifying the range or average phenotype of the plastic response (e.g. Baldwin, 1896; Crispo, 2007; Perry et al., 2018; Radersma, Noble, & Uller, 2020). A more recently proposed 'plasticity first' hypothesis suggests that variation in plasticity itself may be exposed to selection upon colonization of a new environment, thus allowing for adaptive evolution of the plastic response (e.g. Levis & Pfennig, 2016; Perry et al., 2018). Both hypotheses are considered highly controversial, because of the lack of robust empirical evidence from natural systems, and the inherent difficulties in obtaining it, one of the biggest limitations being that once a trait has evolved, its evolution can no longer be studied *in situ* (e.g. Levis & Pfennig, 2016; Perry et al., 2018). Human-altered environments in which naturally occurring populations experience rapid environmental change might provide an ideal setting to observe these processes in real time and to test whether flexibility might be an intrinsic individual feature and

whether it plays a role in facilitating adaptation to new environments (e.g. Levis & Pfennig, 2016; Perry et al., 2018). Including behavioural and cognitive flexibility in these studies will help shed light on the interaction between phenotypic plasticity and adaptation that could allow the establishment and persistence of wildlife in a human-altered world (e.g. Ducatez et al., 2020; Sol et al., 2002, 2005, 2008, 2013).

5 | CONCLUSIONS

Overall, our findings indicate that urban and rural populations of common voles differ in exploration activity, boldness and behavioural flexibility. Urban animals were bolder and more explorative *in situ* as well as more flexible in their response to a change of environment. These behavioural traits thus appear to represent adaptive adjustments for coping with urbanization, one of the most pervasive form of HIREC. At present, we are unable to determine whether the enhanced flexibility we observed in urban common voles is a consequence of living in a more unstable environment or if it is in itself a trait that is selected for in urban habitats. Future studies considering behavioural traits and their plastic development and expression are needed to further illuminate the complex relationship between behavioural consistency and flexibility and their role in coping with anthropogenic environments.

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AUTHOR CONTRIBUTION

V.M., M.D. and J.A.E. conceived and designed the study; V.M. and E.L. performed the data collection; V.M. and M.D. analysed the data; V.M. wrote the manuscript. All authors contributed to the final draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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