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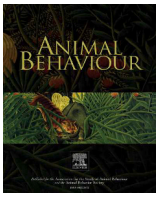

Mammals among buildings: red squirrel personality variation along an urbanization gradient

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Urbanization is a major form of land use change, entailing the creation of novel environments where unique dynamics and selective pressures can shape wildlife phenotypes, with behaviour being especially affected. These environmental changes can shape animal personality, resulting in differences between populations along an urbanization gradient. To fill the knowledge gap about the role of personality traits in population persistence in cities, we investigated whether the mean expression of activity, exploration and social tendency, as well as their among-individual variance and within-individual variance, changed between urban, suburban and rural populations. We conducted 490 repeated arena tests on 169 Eurasian red squirrels, *Sciurus vulgaris*, to estimate personality trait expression through an open field test followed by a mirror image stimulation test. We found no differences in the mean expression of activity, exploration and social tendency between populations living at different degrees of urbanization, even if exploration decreased at higher population densities. However, we observed minor changes in the variance components of all the personality traits. Rural populations tended to be more heterogeneous (higher among-individual variance) in the expression of exploration and social tendency, and individuals in suburban populations were more flexible (greater within-individual variance) in activity than rural conspecifics. Our findings provide insights into how the variance components change along an urbanization gradient, a topic still largely unexplored despite its implications for ecology, evolution and management of populations, as it could support population response to the highly dynamic urban environments.

The modern world is undergoing significant changes in natural ecosystems due to human-induced global environmental shifts, leading to increased habitat loss and fragmentation (Powers & Jetz, 2019). Urbanization, one of the major forms of recent land use change, entails the creation of a novel environment characterized by unique ecological dynamics (Alberti, 2015; Johnson & Munshi-South, 2017). Despite several studies pointing out the role of behaviour in coping with the challenges posed by urban expansion (Lapiedra et al., 2017; Merz et al., 2025; Ritzel & Gallo, 2020; Tranquillo, Bisi et al., 2024), there has been less research into how animal personality and its variance components support populations in cities. Such research is vital because behavioural changes can have cascading impacts on individual fitness, populations, community dynamics and ecosystem services (Hunter et al., 2022; Mortelliti, 2023; Sanderson et al., 2023; Uchida et al., 2024).

Personality is defined as consistent interindividual differences in behaviour across time and contexts (Carter et al., 2013; Dingemanse et al., 2010; Réale et al., 2007), and the mean expression of personality traits, as well as their variance

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components, might differ between populations occurring in natural and urban areas. Specifically, behaviours interpreted to be a measure of activity, exploration and sociability are particularly relevant in cities: the first two traits might mediate the discovery and exploitation of novel resources, patterns of movement and tolerance of human disturbance, whereas the latter might shape conspecific interactions in the restricted green spaces typical of urban environments (Sol et al., 2013). The among-individual variance is a measure of the differences in a phenotypic trait among the individuals of a population (Dellinger et al., 2025). Populations might differ in the level of heterogeneity in the behavioural profile, with higher among-individual variance when there are different personality types in the population (von Merten et al., 2022). The within-individual variance refers to the individual flexibility in a personality trait, that is the difference in a behaviour of an individual over repeated behavioural measurements (Dellinger et al., 2025; von Merten et al., 2022). Both variances enable populations to respond to environmental change. The among-individual variance allows an adaptive evolution over generations: a greater phenotypic variation increases the likelihood that some individuals will exhibit well-suited behaviours to changing environments (Dingemanse et al., 2012; Gervais et al., 2025). On the other hand, the within-individual variance supports phenotypic change within a generation, allowing a faster adjustment to novel situations, a process that can be especially important in the context of highly dynamic environments such as urban areas (Caspi et al., 2022; Kralj-Fišer et al., 2025; Sol et al., 2013).

In this study, we investigated differences in the mean expression of three personality traits, which have been interpreted as activity, exploration and social tendency, across urban, suburban and rural populations. We also investigated the behavioural variance components, specifically the among- and within-individual variances, which are rarely assessed separately, but are usually included in the repeatability estimates (Burkhard et al., 2024; Royauté & Dochtermann, 2021). We tested the hypothesis that the altered resource distribution, barriers creating fragmented and patchy habitats and temporally heterogeneous disturbance of urban green spaces will affect the mean expression as well as the variance components of these personality traits. We used the Eurasian red squirrel, *Sciurus vulgaris* (hereafter referred to as red squirrel) as a model species. This squirrel regularly occurs in urban parks and gardens, where it holds recreational and educational value, contributing to human wellbeing (Fingland et al., 2021). Additionally, red squirrels' space use and home range size make it possible to define local populations confined to a single urban green area, even very small ones (< 5 ha), thereby providing a clear distinction between urban, suburban and rural populations.

We predicted that (1) the mean expression of activity and exploration increases from rural to urban areas. More explorative red squirrels may gain more information about their surroundings, and more active ones may be more effective in locating and exploiting dispersed urban resources, thus enhancing their ability to persist in cities (Lapiedra et al., 2017; Rodríguez-Prieto et al., 2011; but see Devitz & Dantzer, 2024; Uchida et al., 2020). Moreover, we predicted that (2) red squirrels in urban environments would be more sociable. Red squirrel density in confined urban parks is often higher than in natural environments, favouring individuals prepared to share space with a greater number of conspecifics (Haigh et al., 2017; Santicchia et al., 2024). Unlike most previous studies on vertebrates, which did not specifically estimate variance in trait expression, we investigated personality trait variance and expected (3) an increase in the among-individual and within-individual variances with the level of urbanization, since a greater difference between individuals and a higher flexibility of an individual trait might favour colonization, establishment and persistence in rapidly changing urban environments (Caspi et al., 2022; Kralj-Fišer et al., 2025; Sih et al., 2011; Thompson et al., 2022). Investigating changes in behavioural patterns along rural–urban populations could provide useful elements for native species conservation in urban green spaces, which are increasingly recognized as sites for biodiversity conservation under the global change scenario (Ives et al., 2016; Merrick & Koprowski, 2016; Van Helden et al., 2020).

METHODS

Study Sites

We trapped red squirrels from October 2020 to December 2024 along an urbanization gradient spanning from city parks and private gardens to natural forests. We selected 12 study sites, all located in Lombardy, northern Italy (Table S1, Fig. S1). We selected study sites based on urbanization level, habitat characteristics and permission to access and monitor red squirrels in both public and private areas (Tranquillo, Wauters, Santicchia, Panzeri, et al., 2023). Ten study sites consisted of a single trapping grid. Trapping grids were woodland or park-like habitats with mature seed-bearing trees. We distributed traps homogeneously in each trapping grid, and we operated between seven (Crenna, urban park) and 19 (GS, rural) traps depending on study site size. Only two of our study sites (AloBass and Crenna) included more than one trapping grid, which we treated as a single study site. In these study sites, trapping grids were close to each other but divided by a road, and red squirrels repeatedly moved between trapping grids (C. Tranquillo, personal observation from telemetry data). We provide details and locations of the study sites and trapping periods in the Supplementary material (Table S1, Fig. S1).

To determine the degree of urbanization for each study site, we first constructed a buffer of 200 m (based on the mean home range size of male red squirrels in lowland mixed woods in northern Italy; Wauters et al., 2001) around each single trap location. We then merged these 200 m trap buffers into a single polygon (study site buffer). Next, we overlaid each study site buffer by a 100 m by 100 m (1 ha) raster grid and for each raster unit (pixel) we determined: (1) built-up volume estimate from the GHS (Global Human Settlement Layer; Maffenini et al., 2023); (2) number of patches of different landcover types as classified by the level-1 DUSAF land cover regional maps in Lombardy (DUSAF 7.0, https://www.geoportale.regione.lombardia.it); (3) size of anthropized areas; (4) size of agricultural areas; (5) size of forested or seminatural vegetation areas; (6) size of wetlands and other water bodies. We entered these six parameters into a principal components (PC) analysis, with the first component explaining 42% of the total variance. This first component was positively associated with GHS built-up volume (PC1 loading 0.52) and DUSAF anthropized areas (PC1 loading 0.61) and negatively related to DUSAF forested or seminatural areas (PC1 loading -0.55): hence, we used it as our measure of urbanization within each pixel. Next, we combined the PC1 scores for all pixels covering a given study site to obtain a mean value (± SD) per site. We did not expect a linear relationship between the degree of urbanized fraction and red squirrel personality traits. Therefore, we used the Jenks (1967) natural breaks method, which reduces the variance within classes and maximizes the variance between classes, to classify the study sites as rural, suburban and urban (see also Table S1). We created polygons in QGIS, version 3.38.3 (QGIS Development Team, 2024), while the calculation of the PC scores was conducted using R, version 4.4.1 (R Core Team, 2024). The analysis yielded six urban, three suburban and three rural study sites. Study sites within the

city of Varese (about 79 000 inhabitants) and Gallarate (about 52 000 inhabitants) represented the most urbanized sites (hereafter urban sites) characterized by a predominance of built surfaces and highly anthropized areas containing public or private gardens with productive trees such as hornbeam, *Carpinus betulus*, and hazel, *Corylus avellana*, that red squirrels rely on. Forested sites (hereafter rural sites) had a higher proportion of more extended forest habitats. Suburban sites were park-like habitats that included both naturally occurring and ornamental plant species, with mixed land cover reflecting moderate urban development.

Squirrel Captures

We trapped red squirrels using Tomahawk live traps (model 202.5, Tomahawk Live Trap Co., Hazelhurst, WI, U.S.A.) that, before each capture session, were blocked open and prebaited with hazelnuts and walnuts for 3–5 days. Once they were activated, we checked traps multiple times per day to minimize individual confinement in traps. In rural study sites, we inspected traps in late morning and early afternoon. In the more disturbed urban and suburban study sites, we checked traps at shorter intervals (< 1 h). Across all study sites, trap-check intervals never exceeded 3 h. We marked each newly captured red squirrel with a numbered metal ear tag (Monel 1005 1L1 National Band and Tag Co, Newport, KY, U.S.A.). At each capture, we weighed the red squirrel with a spring balance (5 g precision, Pesola AG, Baar, Switzerland) and determined sex and reproductive condition (as described in Wauters et al., 2007). We used capture–mark–recapture data (for details on periods see Table S1) to estimate density for each trapping session in each study site by dividing the minimum number of red squirrels known to be alive (MNA) by the size of the study site (Tranquillo et al., 2022; Wauters et al., 2008). In this species, capture success per trapping session is high (with over 80% of individuals captured in the previous session being recaptured) and MNA estimates are strongly correlated with density estimates from capture–mark–recapture models (Wauters et al., 2004, 2008).

Personality Quantification

We conducted behavioural assays using the arena test (Martinig et al., 2022). We performed two consecutive tests inside a portable arena, which consisted of a white polycarbonate box (50 × 51 cm and 51 cm high) with four blind holes on the floor, 7 cm in diameter and 4 cm deep. We conducted a hole board version of the open field test (OFT; 4 min; Martin & Réale, 2008; Mazzamuto et al., 2019; Walsh & Cummins, 1976) followed by the mirror image stimulation test (MIS; 3 min; Mazzamuto et al., 2019; Svendsen & Armitage, 1973). We repeated arena tests across trapping sessions and seasons to account for seasonal effects on personality (days between subsequent arena tests: mean ± SE = 129 ± 6). After capture, we identified the red squirrel and placed it in the arena positioned at the trap location (Mazzamuto et al., 2019). We recorded the red squirrel's behaviour with a web camera (Drift, Professional HD Action Camera, model: FD9960, Ghost S) fixed on the roof of the arena. At the end of the assay, we opened the arena door to release the red squirrel and then cleaned the arena with 90% ethyl alcohol.

We used CowLog 3.0.2 software (Hänninen & Pastell, 2009) to calculate the time that an individual spent in each behavioural state. All recorded behaviours (see Table S2) were mutually exclusive, meaning that we scored only one behaviour at a given time. Then, we grouped behaviours into personality traits, using the expert-based approach (defined and validated for *S. vulgaris* by Mazzamuto et al., 2019), specifically those that we interpreted as expressions of activity and exploration from the OFT and sociability and avoidance from the MIS (Table S2). Each trait was expressed as the time spent in the behaviours that define that trait (Mazzamuto et al., 2019; Wauters et al., 2019). However, to obtain a more accurate representation of social behaviour along its entire gradient, we decided to incorporate both amicable behaviours directed towards the mirror reflection and avoidance-like states. Avoidance included immobility during the MIS, when the red squirrel did not interact with the mirror image or showed active or explorative behaviour. Rather than focusing exclusively on sociability, this approach preserves the information of avoidance, which is the most frequent behaviour observed during the MIS (on average 69% of the total time, Table S3). Therefore, we calculated a social tendency score as the time spent in sociable behaviour minus time in avoidance behaviour. The personality traits we investigated follow the description by Réale et al. (2007), and we based the grouping of behaviours on earlier studies on the personality of rodents and, more specifically, tree squirrels (Boon et al., 2007; Haigh et al., 2017; Mazzamuto et al., 2019; Santicchia et al., 2021). We are aware that interpreting whether behaviours measured during behavioural assays are associated with personality traits is subjective, despite expert knowledge on the target species, and this remains an open discussion within animal personality research (Carter et al., 2013; Martinig et al., 2022). Table 1 reports the behaviours that we considered as expressions of the three personality traits investigated. We excluded from the data set three arena tests where the red squirrel avoided the mirror throughout the MIS (i.e. did not look in the direction of the mirror). Because of the low number of aggressive events (< 5) towards the mirror, we did not consider aggressiveness. Activity, exploration and social tendency were not correlated (Pearson correlation: $0.18 \leq r \leq 0.53$).

Overall, we analysed 490 arena tests (201 in rural, 65 in suburban and 224 in urban sites) of 169 different red squirrels (77 in rural, 20 in suburban and 72 in urban sites). We tested 106 red squirrels (females = 47, males = 59) multiple times (mean ± SE = 4.06 ± 0.22): 48 in urban (females = 26, males = 22), 14 in suburban

Table 1
Description of the behaviours representing what we interpreted as activity, exploration and social tendency

Behavioural trait	Description	Test
Activity	Locomotor actions: Included movement in the open arena space (i.e. jump, walk), the head move used to scan the environment and rising up on hindlegs	Open field test
Exploration	Interaction with the arena: Included the interaction with holes in the arena floor (i.e. putting the head into the holes) in addition to sniffing arena corners and scratching or chewing arena floor or walls	Open field test
Social tendency	Computed as the difference between sociability and avoidance. Sociability: Amicable behaviour; nonaggressive contact with the mirror and slow approach towards the mirror image. These are all the reactions to the mirror, excluding aggressive display (i.e. attacking the mirror with a fast movement). Avoidance: Immobility behaviour, characterized by a lack of direct engagement with the mirror reflection	Mirror image stimulation test

For a comprehensive description of all behaviours, see Table S2.

(females = 8, males = 6) and 44 in rural (females = 13, males = 31) sites. Of the red squirrels tested, 63 individuals (females = 27, males = 36) were tested only once: 24 in urban (females = 10, males = 14), six in suburban (females = 2, males = 4), 33 in rural (females = 15, males = 18) sites. Sex ratios were male-biased in rural (females = 28, males = 49), but not in suburban (females = 10, M = 10) and urban (females = 36, males = 36) sites.

Ethical Note

We captured red squirrels using live traps fixed against tree trunks in sheltered areas to protect trapped animals from sun exposure (we avoided captures on rainy days) and possible disturbance by dogs, especially in urban study sites. We had five captures of nontarget species which were immediately released. Before handling, we covered the trap with a cloth and transferred the red squirrel to a fabric handling bag. The bag has the shape of a circular truncated cone with open bases: the larger base is used to cover the trap's door, and the small base (4 cm in diameter) serves as the handling opening. The bag was used to minimize stress and reduce direct contact with the operator. We processed each red squirrel by positioning it correctly with its head in the narrow base of the handling bag and using the two front zips, which opened in opposite directions, to complete measurements. We used the back zip to examine sex, assess reproductive condition and measure hind foot length. Next, we opened the front zip to tag new individuals or check tag numbers during recaptures while the red squirrel remained in the handling bag. Ear tagging was done with special pliers that are commonly used without anaesthetic and do not cause any bleeding. We minimized time from capture to release, limiting handling to a few minutes and adding only the duration of the arena test. We released the red squirrel from the handling bag into the arena, and, at the end of the test, opened the arena door to release it at the capture location. This procedure (about 10 min in total) was the same for all squirrels, including pregnant or lactating females. We conducted trapping, marking and handling, as well as personality tests, in accordance with the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (https://doi.org/10.1016/S0003-3472(24)00376-2). We followed legal requirements according to the Italian Wildlife Protection and Hunting Law L.N. 157 from 1992 and DL 26/2014 (implementation Directive 2010/63/EU). Fieldwork was approved by authorization decrees n. 1938 of 18/02/2020 and n. 831 of 25/01/2023 from Direzione Generale Agricoltura, Alimentazione e Sistemi Verdi, Regione Lombardia, authorizations of Parco Lombardo della Valle del Ticino, Parco Pineta di Appiano Gentile e Tradate, Parco Adda Nord, Comune di Gallarate and Comune di Varese. We did not seek specific ethical committee approval as this was not required for noninvasive wildlife research and the research project that details the capture-handling-recapture methods was approved by the institutional body ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale, Prot. 3334, 24/01/2020; and Prot. 1232, 11/01/2023), as required by L.N. 157 from 1992, and L.R. 26 from 1993.

Relationship Between Personality Traits and Urbanization

We assessed personality trait expression, the among-individual and within-individual variance, and repeatability of activity, exploration and social tendency for each urbanization level (urban, suburban and rural) with three Bayesian generalized linear mixed-effects models based on a Markov chain Monte Carlo algorithm, using the package MCMCglmm in R (version 2.36; Hadfield, 2010). Specifically, we ran an MCMCglmm model for each behavioural trait with the same structure, specifying a heterogeneous variance structure with three area types (urban, suburban, rural) to obtain the among-individual variance and within-individual variance for each urbanization level from the same model (Gianola, 1986; Hadfield, 2010). We included behavioural traits in the models as dependent variables, which were centred and scaled with a Gaussian residual error distribution before the analyses across the entire data set (behavioural trait distributions before and after transformation are shown in Fig. S2). We added red squirrel identity (ID) as a random effect to account for multiple observations of the same individual, and to estimate both among-individual and within-individual variance of the dependent variables. We also added study site as a random effect to avoid pseudoreplication issues during the parameter estimation process. We included area type (urban, suburban, rural), sex, body mass (centred and scaled across the entire data set, as an indicator of an individual's body condition) and trial order as fixed effects. We used trial order (coded as 1 for the first arena test and 0 for subsequent ones) to account for individual habituation over repeated tests (Dingemanse et al., 2012; Santicchia et al., 2020). We chose a binary variable (first versus all later tests) and not a consequential trial order because of large individual variation in the number of arena tests (from 1 to 12 tests/individual; mean ± SE = 2.92 ± 0.18). Since red squirrels' personality traits could be affected by seasonal fluctuations (Tranquillo, Wauters, Santicchia, Preatoni, & Martinoli, 2023), we included season (spring–summer [April to August], autumn [September to November], winter [December to March]) in the models as a fixed effect. Furthermore, since previous studies on tree squirrels showed possible associations between population density and the expression of personality traits (Haight et al., 2017; Sanders et al., 2025; Santicchia et al., 2022) and to account for differences in red squirrel density between study sites, we included density (centred and scaled across the entire data set) as a continuous variable. We used an inverse-gamma uninformative prior for the random effect and the residual variance (Wilson et al., 2010). We ran the model for 520 000 iterations with a burn-in of 20 000 iterations and a thinning of 100, and we obtained 95% credible intervals (CrIs) with 5000 iterations. We confirmed model consistency and convergence by running multiple chains and applying Gelman and Rubin (1992) and Geweke (1992) diagnostics, as well as the Heidelberger and Walch test using R package coda (version 0.19.4.1, Plummer et al., 2006). We also assessed autocorrelation to ensure the independence of the samples.

For each behavioural trait, we obtained the among-individual and within-individual variances and their corresponding 95% CrIs from the posterior distributions of each model. We estimated the differences in variances between area types (ΔV) by subtracting the variance components of the different urbanization levels (e.g. ΔV activity between urban and rural was $V_{\text{activity urban}} - V_{\text{activity rural}}$; see also Royauté & Dochtermann, 2021; Santicchia et al., 2022). We considered the difference in variance between area types significant when 95% CrIs excluded 0. Next, from each of these models, we derived the repeatability (R) of the three behavioural traits in each area type. We estimated R as the among-individual variance divided by the total phenotypic variance, which was considered as the sum of among-individual variance, within-individual variance, study sites variance (random effect) and variance in biologically relevant fixed effects (i.e. body mass, sex, season and density; de Villemereuil et al., 2018; Gervais et al., 2025). We conducted all the statistical analyses using R version 4.4.1 (R Core Team, 2024).

Table 2
Values of the among- and within-individual variances and repeatability for what we interpreted as measures of activity, exploration and social tendency of Eurasian red squirrels (490 arena tests on 169 individuals) for each area type

	Among-individual variance mean ± SD (95% CrI)	Within-individual variance mean ± SD (95% CrI)	Repeatability *R* (95% CrI)
Urban *N*=224 (72, F = 36, M = 36)			
Activity	0.08 ± 0.057 (0.00–0.22)	0.67 ± 0.077 (0.53–0.84)	0.01 (0.001–0.22)
Exploration	0.15 ± 0.074 (0.04–0.33)	0.54 ± 0.063 (0.43–0.67)	0.18 (0.03–0.33)
Social tendency	0.19 ± 0.097 (0.02–0.40)	0.66 ± 0.084 (0.52–0.84)	0.17 (0.004–0.36)
Suburban *N*=65 (20, F = 10, M = 10)			
Activity	0.21 ± 0.206 (0.00–0.73)	0.92 ± 0.198 (0.60–1.37)	0.01 (0.001–0.42)
Exploration	0.21 ± 0.193 (0.00–0.70)	0.51 ± 0.120 (0.32–0.79)	0.01 (0.001–0.52)
Social tendency	0.39 ± 0.248 (0.04–0.99)	0.54 ± 0.129 (0.35–0.84)	0.38 (0.05–0.66)
Rural *N*=201 (77, F = 28, M = 49)			
Activity	0.28 ± 0.095 (0.12–0.49)	0.53 ± 0.072 (0.43–0.71)	0.31 (0.15–0.47)
Exploration	0.50 ± 0.140 (0.27–0.82)	0.62 ± 0.080 (0.49–0.80)	0.41 (0.24–0.55)
Social tendency	0.61 ± 0.194 (0.28–1.02)	0.64 ± 0.088 (0.49–0.83)	0.46 (0.27–0.64)

We report the among- and within-individual variance estimates along with standard deviation (SD) and 95% credible intervals (CrI), and repeatability values along with credible intervals (CrI). Sample sizes (number of arena tests, *N*) and number of different red squirrels (ID in parentheses, F: females; M: males) are related to observations with arena tests.

Table 3
Pairwise differences between the posterior mean of the comparisons between the three area types for each behavioural trait

Dependent variable	Differences (95% CrI)		
	Urban − suburban	Urban − rural	Suburban − rural
Activity	-0.07 (-0.52 to 0.38)	0.02 (-0.37 to 0.39)	0.09 (-0.38 to 0.57)
Exploration	0.25 (-0.27 to 0.83)	0.12 (-0.38 to 0.70)	-0.13 (-0.76 to 0.48)
Social tendency	0.16 (-0.30 to 0.62)	0.002 (-0.38 to 0.43)	-0.16 (-0.67 to 0.36)

We report the pairwise differences, computed from the posterior distribution of the full MCMCglmm model, along with 95% credible intervals (CrI).

RESULTS

On average, during the OFT the most common behaviours were associated with activity and immobility, while exploration was observed less frequently (Table S3). During the MIS, red squirrels mainly avoided the mirror image (Table S3). Activity, exploration and social tendency were all repeatable in rural environments. Activity was not repeatable in urban environments. In suburban sites social tendency was repeatable, while activity and exploration were not (Table 2). The lack of repeatability in certain traits, in suburban and urban sites, indicates that consistent among-individual differences account for only a small portion of the total variance and suggests greater modulation of behavioural expression rather than stable personality in more disturbed environments.

Mean Expression of Activity, Exploration and Sociability

Red squirrel populations at different urbanization levels did not differ in the mean expression of activity, exploration and social tendency (Tables 3, S4, Fig. 1). Although urban sites tended

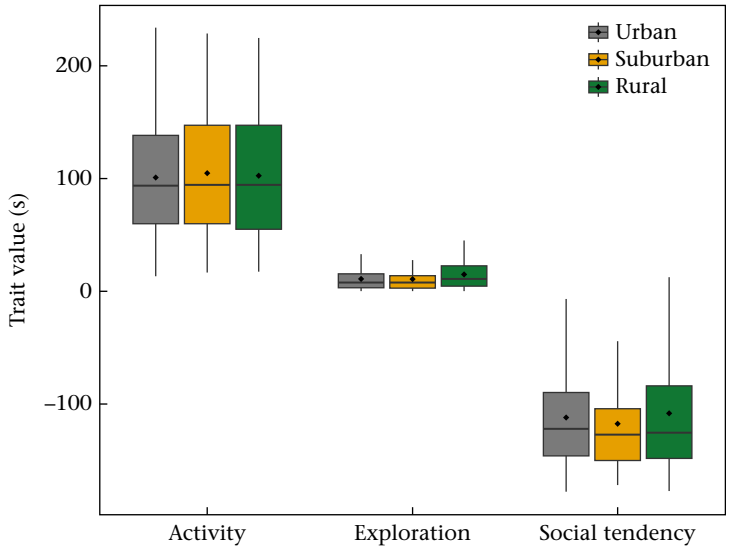

Figure 1. Expression (trait value) of activity, exploration and calculated (see Methods) social tendency of Eurasian red squirrel populations in urban, suburban and rural sites measured using arena tests (490 arena tests on 169 individuals; urban: 224 arena tests on 72 individuals; suburban: 65 arena tests on 20 individuals; rural: 201 arena tests on 77 individuals). Box plots show median (solid horizontal line), mean (black diamond), first (25%) and third (75%) quartiles, whiskers indicate variability outside the upper and lower quartiles.

to have higher red squirrel densities than suburban and rural ones (Table S1), we did not find a significant association of activity, or social tendency, with red squirrel density (see Table S4 for model outputs). However, red squirrels were less explorative at higher densities (β = -0.17, 95% CrI = -0.30 to -0.03, pMCMC = 0.013). The expression of activity differed between seasons: during spring–summer (β = 0.35, 95% CrI = 0.16 to 0.53, pMCMC < 0.001) and winter (β = 0.25, 95% CrI = 0.04 to 0.44, pMCMC = 0.015) red squirrels showed greater activity than during autumn. There were no differences in the expression of any of the traits between spring–summer and winter, and the traits were not affected by a red squirrel's sex or body mass (Table S4). Finally, all traits had higher values during the first trial in the arena than in subsequent ones (activity: β = 0.85, 95% CrI = 0.68 to 1.01, pMCMC < 0.001; exploration: β = 0.64, 95% CrI = 0.47 to 0.79, pMCMC < 0.001; social tendency: β = 0.53, 95% CrI = 0.37 to 0.70, pMCMC < 0.001).

Among-Individual and Within-Individual Variances

Considering the variances of the behavioural traits (raw values are in Table 2), we found that activity had significantly higher within-individual variance in suburban than in rural environments (Fig. 2, Table S5). Red squirrels in rural sites showed higher among-individual variance in exploration and social tendency than individuals in urban sites (Fig. 2, S3, Table S5). We did not find any difference in either the among- or the within-individual variances in behavioural trait expression between urban and suburban red squirrels. Our sample sizes (number of red squirrels) differed between area types, with fewer individuals in the suburban sites compared to urban and rural ones. While our modelling approach can accommodate unbalanced data, the reduced number of suburban individuals limited the precision of parameter estimates for this area type. This is reflected in the wider posterior credible intervals for both fixed and random effects associated with suburban red squirrels. Consequently, inferences regarding suburban populations should be interpreted with caution, as our ability to detect subtle differences relative to urban or rural habitats was reduced. Nonetheless, including suburban sites was critical for characterizing the full gradient of urbanization and ensuring that comparisons were not restricted to urban and rural extremes.

DISCUSSION

We measured the expression of activity, exploration and social tendency, as well as their among- and within-individual variances, in red squirrels distributed over an urbanization gradient. Overall, these three behavioural traits varied markedly among individuals, but their mean expression did not differ with the degree of urbanization. Where repeatability was absent, our results indicate limited consistent among-individual variance, with larger variation in behavioural expression attributed to other sources of variance (within-individual variance, study sites variance and variance in biologically relevant fixed effects). This outcome is in contrast with our first and second predictions, since the mean expression of activity, exploration and social tendency did not increase with urbanization. Considering our third prediction, we observed only limited alterations in the variance components. We found minor differences in the within-individual variance (i.e. flexibility of an individual trait) of activity between suburban and rural environments; individuals showed less flexibility in activity in rural sites. This result reflects the lack of repeatability of activity in suburban sites compared to the moderate repeatability found in the rural environments. Indeed, the loss of repeatability for activity and exploration in disturbed habitats suggests highly variable behavioural responses in the suburban and urban populations. Among-individual variance (i.e. differences between individuals) differed between urban and rural populations only for exploration and social tendency, with rural populations being more heterogeneous. Additionally, we found that red squirrels exhibited higher exploration levels at lower population densities, although this was not directly related to urbanization, in line with findings from forested habitats (Santicchia et al., 2022). Mean activity levels varied seasonally, reflecting changes in foraging resource availability and mating periods, with higher activity in spring–summer and during the winter mating season than in the autumn nonbreeding period.

Mean Expression of Behaviour along the Urbanization Gradient

Activity and exploration have sometimes been found to be key traits in the colonization of cities by wildlife. Some urban small mammals (*Microtus arvalis*, Dammhahn et al., 2020; *Apodemus agrarius*, Mazza et al., 2020; *Crocidura russula*, Oliveira et al., 2021)

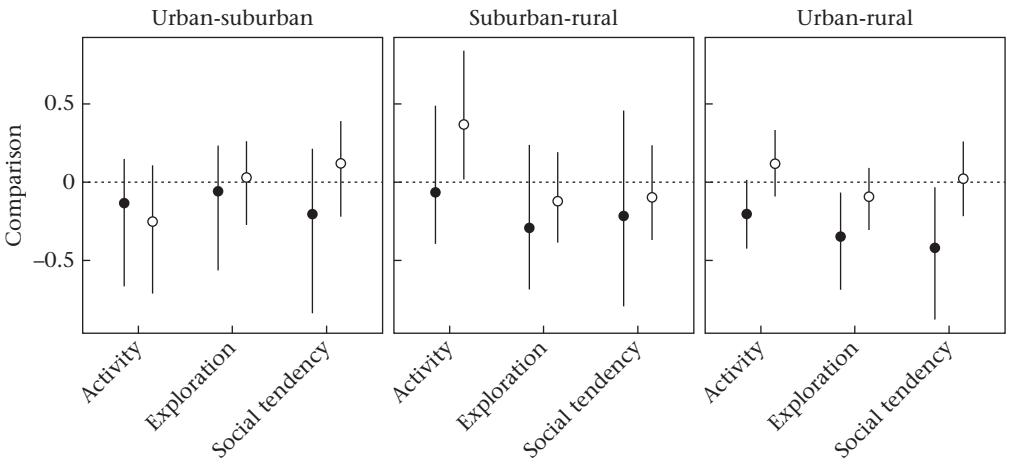

Figure 2. Comparisons (estimate ± 95% credible intervals) of the among-individual variances (black dots) and within-individual variances (white dots) between area types. Calculated as the difference of each area type variances obtained from the three models. A positive comparison value of the among- or within-individual variance means that the first area type has a higher value than the second area type. If the 95% credible intervals do not cross the comparison value of zero, there is a meaningful difference in the comparison.

behave more actively and exploratively than their rural conspecifics. These findings are consistent with studies on other vertebrate orders (e.g. Carnivora, Greenberg & Holekamp, 2017; Squamata, Lapiedra et al., 2017; Passeriformes, Thompson et al., 2018). In a parallel study, invasive alien grey squirrels, *Sciurus carolinensis*, in northern Italy also showed higher activity and sociability, measured with the same method, in urban than suburban and rural sites (Tranquillo, Santicchia et al., 2024). In contrast, our results showed that the expression of activity, exploration and social tendency did not change along the rural–urban gradient. This result agrees with previous research on other native arboreal squirrels examined through the arena test. *Sciurus vulgaris* in Japan (Uchida et al., 2020) and *Sciurus niger* in Michigan, U.S.A. (Devitz & Dantzer, 2024) also showed no differences in activity, exploration and sociability between urban and rural sites. These studies suggest that an arboreal lifestyle may alter behavioural responses to urban environments. Arboreal squirrels use trees because they provide food resources, nest sites and shelter from many terrestrial predators (Lurz et al., 2005). Therefore, they occupy a three-dimensional space, exploiting habitat both vertically and horizontally, a characteristic that could change the selective pressures of urbanization.

The lack of differences in activity, exploration and social tendency along the urbanization gradient in our study may reflect a complex interplay of factors. Urban individuals are generally expected to be more active and exploratory to navigate fragmented habitats (Lapiedra et al., 2017; Rodríguez-Prieto et al., 2011), but this advantage may be offset by predation risk. Although rural sites host natural predators such as foxes, *Vulpes vulpes*, stone martens, *Martes foina*, and Eurasian goshawks, *Accipiter gentilis*, some urban environments also support these predators with the added threat of domestic cats (C. Tranquillo, personal observation), potentially increasing the risks for more active and/or explorative red squirrels. Additionally, stable food availability in urban habitats, due to diverse tree species and occasional supplemental feeding (Takahata et al., 2023; Tranquillo, Wauters, Santicchia, Panzeri, et al., 2023), may reduce the selective pressure for activity and exploration present in food-limited rural environments (Tranquillo, Wauters, Santicchia, Preatoni, & Martinoli, 2023).

Because individual behavioural differences can have a heritable component (Dochtermann et al., 2015), another explanation for the lack of divergence may be gene flow between rural and urban sites via juvenile dispersal, as found in Finnish red squirrel populations (Selonen et al., 2018). However, limited gene flow was reported in Japanese red squirrels along an urbanization gradient (Takahata et al., 2024) and in red squirrels in fragmented habitats (Wauters et al., 1994), suggesting that urban isolation and landscape structure may influence whether behavioural divergence occurs.

Behavioural Variances along the Urbanization Gradient

The role of phenotypic variation in response to selective pressures has been recognized (Caspi et al., 2022; Sih, 2013; Thompson et al., 2022), but, among terrestrial vertebrates, few studies have empirically investigated differences in behavioural trait variances between populations living in urban versus rural sites. In our study, we found within-individual variance of activity, exploration and social tendency did not differ between urban and rural environments. Our results are in contrast with previous studies that documented higher variation in some behaviours in urban sites (Dammhahn et al., 2020; Mazza et al., 2020; Thompson et al., 2022).

For among-individual variance, we found that exploration and social tendency were lower in urban than in rural environments, suggesting a narrowing of behavioural expression across urban individuals. This result does not support our third prediction but agrees with a long-term study on great tits, *Parus major*, which found more similarity in exploratory behaviour in urban individuals (Gervais et al., 2025). In contrast, other studies found that behavioural heterogeneity was higher in populations from more urbanized sites (von Merten et al., 2022: boldness and aggression in the greater white-toothed shrew, *Crocidura russola*; Thompson et al., 2018: exploration in the black-capped chickadee, *Poecile atricapillus*). Because exploration and social tendency showed low or no repeatability in urban and suburban habitats compared with rural ones, these patterns suggest both convergence at the population level and flexibility at the individual level, outcomes consistent with either urban filtering (where only certain behavioural types persist) or behavioural convergence (where individuals come to behave more similarly). In contrast, rural sites showed high among-individual variance in exploration and social tendency, likely reflecting different responses to the mosaic of patch types and habitat quality found in these larger forests. Our larger rural study sites were characterized by a patchy forest structure, unlike the more spatially homogeneous urban and suburban sites, which are limited in size. In the rural sites, different-sized patches had high habitat quality when dominated by chestnuts, *Castanea sativa*, hornbeam and hazel, and poor habitat quality when dominated by black locust, *Robinia pseudoacacia*, willow, *Salix* sp., birch, *Betula* sp. and old, unproductive Scots pines, *Pinus sylvestris* (see also Wauters et al., 2001). This mosaic of patches of different habitat quality may influence the heterogeneity of exploration in the population, resulting in a relatively high among-individual variation in this trait in rural populations. At the same time, the greater heterogeneity in social tendency may also reflect the diverse patterns of space use among individuals in rural sites. In high-quality patches, encounters between conspecifics could be higher because of the locally higher densities than in low-quality patches, providing suitable areas for individuals with both higher and lower social tendencies. Furthermore, these rural environments are likely to be more homogeneous over time, with fewer unpredictable disturbances than in suburban environments. Thus, the lower within-individual variance in activity in rural red squirrels may reflect different selective pressures, with suburban sites experiencing more unpredictable human disturbance and more variable predator occurrence. Hence, the greater flexibility in activity could increase red squirrels' capacity to adapt to short-term environmental changes.

However, inferences regarding suburban populations should be interpreted with caution, as our ability to detect subtle differences relative to urban or rural habitats was diminished by our reduced sample size. Additional data from suburban populations are needed to confirm whether these differences reflect true biological variation or are a consequence of sampling limitations.

Conclusions

We found no evidence of differences in mean activity, exploration and social tendency among urban, suburban and rural red squirrel populations, but we detected subtle shifts in among- and within-individual variance components. Activity in urban sites, and both activity and exploration in suburban sites, was not repeatable indicating greater behavioural variation rather than consistent personality in these habitats. These patterns suggest that while urbanization may not exert strong directional selection on behavioural traits in this species, local ecological factors, such as habitat heterogeneity in space or time, predation pressure and population density, can influence both the stability of personality

and the degree of behavioural flexibility within individuals. Suburban sites may combine features of both rural and urban environments, and experience varying degrees of human disturbance, making them a potentially valuable, yet underexplored, habitat for urban ecology studies.

This work adds to the limited evidence on how variance components of behavioural traits change along urbanization gradients and advances our understanding of how native mammals respond to complex anthropogenic environments. Urban environments impose multiple stressors that shape animal phenotypes not only in behaviour but also in morphology (Tranquillo, Wauters, Santicchia, Panzeri, et al., 2023), physiology (Santicchia et al., 2024) and possibly other traits, such as the functional diversity of the microbiome (Romeo et al., 2025). Investigating these responses across levels of urbanization is crucial for informing conservation strategies that enhance the suitability of cities for native species, especially in the presence of invasive competitors that often thrive in urban landscapes (Tranquillo, Santicchia et al., 2024).

Author Contributions

Claudia Tranquillo: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maria Vittoria Mazzamuto:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Francesca Santicchia:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Francesco Bisi:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Damiano Preatoni:** Writing – review & editing, Software, Methodology, Conceptualization. **Adriano Martinoli:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Martina Spada:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Rosa Maria Di Biase:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sara Franceschi:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marzia Marcheselli:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Caterina Pisani:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sandro Bertolino:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Lucas A. Wauters:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Formal analysis, Conceptualization.

Data Availability

Data and codes to reproduce the analyses are available on the Zenodo repository: http://doi.org/10.5281/zenodo.13987609.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

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