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Received: 3 June 2025 | Accepted: 6 March 2026

DOI: 10.1111/1365-2435.70312

BRITISH ECOLOGICAL SOCIETY Functional Ecology

RESEARCH ARTICLE

Functional trait interactions in a human-dominated world: Urbanization and reproduction in Eurasian red squirrels

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Funding information
NextGenerationEU, Grant/Award Number: 2022N9CSKJ

Handling Editor: William Hopkins

Abstract

1. Ecological traits such as behaviour, physiology and morphology mediate an organism's interaction with its environment, and understanding their joint contribution to reproductive fitness is essential for predicting biological responses to global change. We addressed how urbanization shapes trait–function relationships across natural, suburban or urban areas to advance the functional and mechanistic understanding of ecological processes in changing environments.
2. We investigated how interactions among ecological (urbanization, season) and phenotypic (body mass, personality) traits influence reproductive fitness in female Eurasian red squirrels (*Sciurus vulgaris*) across a natural–urban gradient in Italy. Using 204 records of 72 female squirrels across 12 sites, we found that body mass, mediating the effect of the spring season, was the main factor affecting the probability to reproduce in female red squirrels. Further, our results suggest a direct effect of urbanization on squirrels' reproduction: The probability of reproducing was higher in natural habitats than in the urban and suburban sites. Female red squirrels in natural sites also engaged more frequently in explorative behaviours than their conspecifics in urban sites, but this did not translate into either direct or significant indirect effects of personality on reproductive success. Finally, body mass of females tended to be slightly higher in urban and suburban than in natural habitats, but this did not result in a higher reproductive rate.
3. While body mass emerged as the dominant predictor of reproduction, its functional role was context-dependent, shaped by seasonality, environmental resource distribution and potentially by altered energetic dynamics in urban environments. In contrast, personality traits varied with habitat but did not mediate reproduction, highlighting how trait expression does not equate to ecological function unless matched with the appropriate environmental context.
4. This work underscores the importance of integrating multiple levels of biological organization, behaviour, body mass, life history and environmental context to understand how global change alters ecological and evolutionary trajectories.

As urbanization continues to transform natural habitats, studies that disentangle direct and indirect pathways from phenotype to fitness will be essential not only for predicting wildlife persistence but also for linking individual-level processes to population and community dynamics.

KEYWORDS
Bayesian structural equation modelling, body weight, breeding success, city parks, natural–urban gradient, rodents, sociability, urban ecology

1 | INTRODUCTION

Phenotypic variation in animal populations arises from complex interactions between intrinsic factors and extrinsic environmental pressures (Endler, 1986). Among these pressures, a defining feature of global change is urbanization, which, linked to the continuously growing human population, is rapidly transforming the composition and degree of fragmentation of natural and agricultural habitats. This transformation introduces novel selection regimes through altered resource availability, predator communities, pollution and human disturbance. Habitat heterogeneity and anthropogenic change can drive both plastic and evolved responses, shaping individual fitness across ecological gradients (Johnson & Munshi-South, 2017; Nicolaus & Edelaar, 2018; Tranquillo et al., 2023). These urban-driven changes not only affect individual behaviour (Sih, 2013; Wong & Candolin, 2015) and physiology (Petrullo et al., 2023; Stearns, 1989) but also shape broader life-history strategies, with cascading effects on population and community dynamics.

Ecological traits such as behaviour, physiology and morphology mediate an organism's interaction with its environment, and understanding their joint contribution to reproductive fitness is essential for predicting biological responses to global change. Behavioural strategies influence resource acquisition and conspecific interactions (Haave-Audet et al., 2022), phenotypic and physiological characteristics determine energy balance and resilience to stressors (Meillère, Brischoux, Ribout, & Angelier, 2015; Speakman, 2007), and ecological context sets the stage in which these traits operate (Alberti et al., 2017). Together, their integration defines reproductive success and survival. While individual traits like body mass or animal personality are often studied in isolation (e.g. Dammhahn, 2012; Gaillard et al., 2000; Wauters & Dhondt, 1995), much less is known about how multiple traits interact, modulated by seasonality and environmental context, to shape reproduction. Addressing this gap is crucial to advancing a functional and mechanistic understanding of ecological processes in changing environments (Luza et al., 2023; Verberk et al., 2013).

Species that persist across natural, suburban and urban environments can experience a shift in the relative importance of and interconnection between different phenotypic traits. Populations in urban areas face diverse stressors, including noise, light and chemical pollution, reduced habitat connectivity, altered predator communities and direct human disturbance, while also encountering novel opportunities such as stable food supplies and reduced predation (Alberti et al., 2017; Baker et al., 2003; Ritzel & Gallo, 2020). Evidence from mammals, birds and insects highlights that behavioural changes, altered physiology and shifts in other phenotypic traits can all mediate persistence in these environments (Alberti et al., 2017; Johnson & Munshi-South, 2017).

To investigate the interconnection between different phenotypic traits along an urban/natural gradient, we used the Eurasian red squirrel (*Sciurus vulgaris*) as a model species. This species occupies a wide range of habitats from continuous forests to fragmented suburban woodlands and highly urbanized parks (Davaasuren et al., 2024; de Raad et al., 2021; Fingland et al., 2022; Tranquillo et al., 2024). The broad habitat use exposes populations to contrasting ecological pressures, making squirrels well-suited for examining how environmental context modifies trait–fitness relationships. Moreover, red squirrels' limited space use and home range size permit defining populations within a single green area (even smaller than 5 ha), providing a clear distinction among urban, suburban and rural populations. We assess how interactions among ecological (urbanization, season) and phenotypic (body mass and personality) traits influence reproductive fitness in female Eurasian red squirrels across a natural–urban gradient (Figure 1). Direct influences on reproduction include body mass, season, urbanization level and personality. Heavier females will be more likely to reproduce than squirrels of lower body mass, a pattern observed across habitats and stressors (Romeo et al., 2021; Wauters et al., 2007; Wauters & Dhondt, 1989; Wauters & Lens, 1995). Season governs breeding periods in early spring and summer in response to environmental cues such as food availability and temperature (Wauters et al., 1993, 2001; Wauters & Dhondt, 1989). Urbanization level can affect both the frequency and timing of reproduction due to more stable and abundant resources and altered movement dynamics. In addition, individual personality traits, including activity, exploration and sociability, may contribute to reproductive variation by increasing access to resources or encounters with potential mates. More active and/or explorative squirrels will have a greater advantage in the more challenging urban and suburban sites than in the natural woodlands, where there is lower selective pressure for these personality types. Also, more sociable females could suffer fewer intraspecific competitions than less social ones, which could give them a reproductive advantage in urban

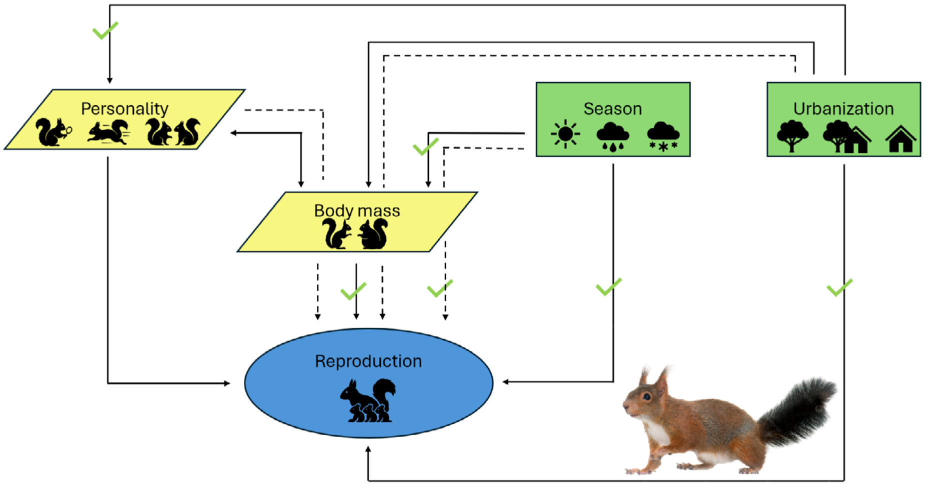

FIGURE 1 A conceptual framework illustrating the interconnected relationships between ecological (rectangles) and phenotypic factors (trapezium), and their feedback in determining reproductive success (oval). Solid arrows show direct relationships, while dashed arrows show mediated interactions through body mass. The green check marks indicate the relationships we confirmed in this study.

sites where limited space is likely to increase local density and core-area overlap (Gartland et al., 2022; but see McCowan et al., 2015). These potentially direct relationships are illustrated in Figure 1.

Moreover, these factors also affect each other in ways that can indirectly influence reproduction (Figure 1). Urbanization can promote higher body mass through more reliable food sources, while seasonal variation in resource abundance drives fluctuations in body mass (e.g. Bateman & Fleming, 2012; Castillo-Contreras et al., 2021; Meillère, Brischoux, Parenteau, & Angelier, 2015). Personality traits may influence how effectively individuals exploit their environments, with bolder or more explorative animals often achieving higher body mass (Wolf & Weissing, 2012). At the same time, body mass may also influence behavioural expression, suggesting potential bidirectional relationships between these phenotypic traits. Moreover, urban environments may favour certain personality types, such as active, explorative or more sociable individuals, either through selection or behavioural plasticity in response to increased human disturbance (Johnson & Munshi-South, 2017; Miranda et al., 2013).

By integrating multiple organismal traits with environmental variation, this study offers a mechanistic framework for understanding how global change through urbanization shapes trait-function relationships and reproductive fitness.

2 | MATERIALS AND METHODS

2.1 | Study sites

We live-trapped red squirrels from autumn 2021 to autumn 2024 along an urbanization gradient from city parks and private gardens within the cities of Varese (about 79,000 inhabitants) and Gallarate (about 52,000 inhabitants) to forests surrounded by agricultural areas corresponding to the more natural side of our gradient. In total, we monitored 12 study sites, all located in Lombardy, Northern Italy (for details see Table S1). All study sites were woodland or park-like habitats with mature seed-bearing trees.

To quantify the degree of urbanization at each study site, we first created a 200 m buffer around each trap location, based on the average home range size of male red squirrels in lowland mixed woods of Northern Italy (Wauters et al., 2001). We merged all buffers within a site into a single polygon, defining the spatial extent of the study site. We overlaid each site polygon with a 100 m × 100 m (1 ha) raster grid, and for each grid cell, we extracted the following measures: (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 (ERSAF, 2021) regional maps in Lombardy; (3) size of anthropized areas; (4) size of agricultural areas; (5) size of forested or semi-natural vegetation areas; (6) size of wetlands and other water bodies.

For each study site, we summed the values of each measure across all 1 ha cells within its site polygon to generate a single site-level value per measure. We then entered these single-level values into a principal component analysis (PCA) whose first component explained 42% of the total variance. This first principal component (PC1) was positively associated with GHS built-up volume (loading = 0.52) and DUSAF anthropized areas (loading = 0.61) and negatively related with DUSAF forested or semi-natural areas (loading = −0.55) (Appendix S1). We used PC1 as our measure of urbanization at the study site level. While these scores represent a continuous gradient, our hypotheses did not predict linear relationships between urbanization, female reproductive success and animal personality traits. Instead, we expected differences in reproductive and behavioural phenotypes across sites with varying degrees of urban development. Therefore, we discretized the continuous PC1 values into three categories, natural, suburban and urban, using the Jenks natural breaks optimization method

(Jenks, 1967), which minimizes within-class variance while maximizing between-class variance (Appendix S1). We did not intend these categories as absolute classifications but rather reflect relative differences in the degree of urbanization among our study sites. As a result, we classified six study sites as urban (squirrel density = 0.60 ind/ha ± SD 0.40), three as suburban (0.27 ± 0.18) and three as natural (0.23 ± 0.12; see also Table S1; Figure S1). We based site classification on the relative extent of forest cover, anthropogenic land use and built-up volume within each site. Specifically, we characterized urban sites by a predominance of built surfaces and highly anthropized areas and are park-like public or private sites with highly productive trees, including several species that squirrels rely on most for resources, such as hornbeam (*Carpinus betulus*) and hazel (*Corylus avellana*). Natural sites exhibited a higher proportion of forested habitats, and within each site, there is a mosaic of areas dominated by different tree species, resulting in patches of both high and low quality. Suburban sites are park-like habitats including both naturally occurring and ornamental plant species, representing an intermediate condition, with mixed land cover reflecting moderate levels of urban development. We did not quantify human provisioning or diet composition in urban and suburban sites. Because of the wide diversity of ornamental plants in these areas, simple plant availability would not provide a reliable proxy of the resources squirrels actually consumed.

2.2 | Squirrel captures

We trapped squirrels using Tomahawk live traps (model 202.5, Tomahawk Live Trap Co., WI, USA) that, before each capture session, we placed blocked open and regularly pre-baited with hazelnuts and walnuts for 3–5 days. We repeated capture sessions three times each year: one in autumn (September–November), one in winter (December–February) and one in spring (March–May). This schedule allowed us to monitor the entire reproductive cycle of females that can enter oestrus from early January to late May, and nurse young (lactation) from late February to September–October (Wauters et al., 2007; Wauters & Dhondt, 1989). Once activated, we checked traps every 1 to 3 h. We marked each newly trapped squirrel with a numbered metal ear tag (Monel 1005 1L1 National Band and Tag Co, Newport, Kentucky, USA). At each capture, we weighed females (5 g precision) with a spring balance (Pesola AG, Baar, Switzerland) and determined reproductive condition (as described in Wauters & Dhondt, 1989). In particular, we classified each female in each trapping session as (1) non-reproductive (anoestrus and not lactating with small unperforated vulva and small or unvisible nipples), or (2) reproductive, including oestrus (vulva strongly swollen and pink, perforated), post-oestrus (vulva still enlarged, longitudinal opening closing progressively, leaving a suture), pregnant (swollen abdomen, embryos can be felt at gentle palpation) and lactating (nipples pink and swollen, milk excretion can be stimulated). We measured reproduction during capture sessions as a binary variable (0 = non-reproductive; 1 = reproductive; see also Wauters et al., 2007). While our binary variable is a broad estimator of the reproduction (from females being in oestrus to lactating), we confirmed successful reproduction in 84% of cases, meaning that even early stages of reproductive events (females being in oestrus, post-oestrus or pregnant) resulted in parturition (females lactating), albeit with unknown litter size. Overall, variation in lifetime reproductive success in red squirrels is mainly associated with variation in the number of litters a female is able to produce in her lifetime, while differences in age at first breeding or litter size are less important (Wauters & Dhondt, 1995; Wauters & Lens, 1995), as also shown for other squirrel species (e.g. Hoset et al., 2017; McAdam et al., 2007; Skibiel et al., 2013). We recorded only one case of a female in post-oestrus, who was not lactating later during that reproductive season. With such a low rate of reproductive failure, our measure of reproduction (a female being reproductive or not) closely reflects the reproductive success (production of a litter) of red squirrels in these populations.

2.3 | Personality investigation

We derived red squirrel personality traits from observations of behaviour during an arena test. After capture, we identified the squirrel and released it in the arena placed within 20 m from the trap location (Mazzamuto et al., 2019). We recorded the animal's behaviour with a web camera (Drift, Professional HD Action Camera, model: FD9960, Ghost S) fixed on the roof of the arena. We tested squirrels with the open field test (OFT; 4 min), to estimate an animal's activity and exploration in a novel environment (Walsh & Cummins, 1976), followed by the mirror image stimulation test (MIS; 3 min), to determine the behavioural response toward a conspecific (Svendsen & Armitage, 1973). At the end of the experiment, we let the squirrel out and cleaned the arena with 90% ethylic alcohol. We repeated arena tests for individual squirrels in different trapping sessions.

We used CowLog 3.0.2 software (Hänninen & Pastell, 2009) to calculate the time that an individual spent in each behavioural state (unique, non-overlapping behaviours defined in the ethogram of Table S2). Next, we applied the Expert-Based approach: We grouped mutually exclusive behaviours based on their relatedness to a certain personality trait, and we summed their values (time spent per behaviour state). We are aware that the association of behaviours measured during behavioural assays with personality traits can create subjective judgement and interpretation, and this remains a current open conversation within animal personality research (Beckmann & Biro, 2013; Carter et al., 2013; Martinig et al., 2022). In this study, we selected the single behaviours and classified them within the personality traits activity and exploration (from OFT) and sociability (from MIS). Due to the low number of aggressive events toward the mirror, we did not consider aggressiveness. 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., 2008; Haigh et al., 2017; Mazzamuto et al., 2019; Santicchia et al., 2021). This expert-based method was previously defined and validated for *S. vulgaris* by Mazzamuto et al. (2019). Each trait was expressed as the percentage of time spent in the behaviours that define that trait (Mazzamuto et al., 2019; Wauters et al., 2019). We distinguished activity and exploration during the OFT thanks to the presence of four blind holes (7 cm diameter × 4 cm deep) in the floor of the arena (hole board test, Martin & Réale, 2008). We defined exploration as interacting with holes, that is, putting the head into the holes, in addition to scratching or chewing the floor/walls, and sniffing the corners of the arena. We defined activity as movement in the open arena space (detailed in Table S2).

To adhere to the ethical norms, in this study, trapping, marking and handling of squirrels, as well as personality tests, were performed under the Guidelines for the treatment of animals in behavioural research and teaching (Animal Behaviour, 2020, 159, I–XI; https://doi.org/10.1016/j.anbehav.2019.11.002). Legal requirements according to the Italian Wildlife Protection and Hunting Law L.N. 157 from 1992 and fieldwork was legally and ethically 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.

2.4 | Data analysis

To examine the relationships between reproduction, body mass and personality traits across habitats and seasons, we implemented a multivariate Bayesian structural equation model using the R package *brms* version 2.22.0 (Bürkner, 2017). This modelling framework allowed us to account for shared individual identity across multiple responses while estimating covariance among traits and testing for direct and indirect effects.

The response variables of the five sub-models within the multivariate framework included:

(1) reproduction, females being reproductive (1) or not reproductive (0); the logistic model predicted reproductive condition from body mass, season (spring, winter, autumn), area type (natural, suburban, urban) and all three personality traits.

(2) Body mass in a Gaussian model investigating the effects of season and area type.

(3–5) Three personality traits, activity (beta distribution), sociability and exploration (both with a zero-inflated beta distribution), in three models with predictors including area type, body mass and trial order. We included trial order as a binary novelty indicator (1 = first test; 0 = later tests) to control for the qualitative difference between truly naïve and previously exposed individuals. Given the highly variable number of and time between repeated tests (see Results), treating trial number as a continuous measure would not reflect habituation.

In all models, we used squirrel ID as a random factor to account for repeated measurements.

We scaled body mass values across the entire dataset (mean = 0, SD = 1). All models included a random intercept for individual ID to account for repeated measures. We used weakly informative priors and fit the model using Hamiltonian Monte Carlo (HMC) sampling: fixed effects had normal (0, 2) priors (appropriate for predictors that have been standardized), intercepts used Student-*t* (3, 0, 2.5) priors to accommodate potential outliers while still promoting regularization (Gelman et al., 2008, 2013), and random effect standard deviations were given Student-*t* (3, 0, 1) priors, a weakly informative prior that avoids overfitting individual-level variation but still permits moderate heterogeneity (Bürkner, 2017). These choices provide mild regularization while allowing flexibility for estimation across varied distributions and scales. We ran the model using 4 chains for 4000 iterations each, with 1000 warmup cycles yielding 12,000 post-warmup samples. We assessed model convergence using the potential scale reduction statistic ($\hat{R}$), which was equal to 1.00 for all parameters, indicating excellent convergence. We also inspected effective sample sizes for both bulk and tail distributions, which were consistently high (>1000), further supporting the reliability of the posterior estimates.

To assess whether the effects of area type, season and personality traits on reproduction were mediated through body mass, we conducted post hoc mediation analysis using posterior samples drawn from all multivariate models. Mediation occurs when the influence of an independent variable (e.g. area type or personality) on an outcome (reproduction) is transmitted in part through a third variable, or mediator, in this case, body mass. We calculated indirect effects for each hypothesized mediation pathway as the product of the posterior distributions of two path coefficients: (a) the effect of the predictor on the mediator (e.g. effect of urban area on body mass) and (b) the effect of the mediator on the outcome (i.e. effect of body mass on reproduction). This product-of-coefficients approach allowed us to compute the full posterior distribution of each indirect effect. We evaluated mediation pathways for area type, season and personality traits (activity, sociability, exploration). We obtained each indirect effect by the posterior mean and its 95% credible interval (CI), calculated as the 2.5th and 97.5th percentiles of the posterior.

We estimated repeatability of the three behavioural traits directly from the fitted Bayesian structural equation model using a model-based variance decomposition on the observation scale. For each response, we extracted posterior samples of the distributional parameters and computed, for every observation and posterior draw, the conditional mean of the trait given the fixed effects and individual random effect, as well as the conditional variance implied by the fitted family. We then decomposed observation-level variances into between-individual variance, calculated as the variance of conditional means averaged within each individual, and within-individual variance, calculated as the mean conditional variance

TABLE 1 Number of events of females lactating (successful breeding events) in spring and autumn, and numbers of cases with 2 litters/year per area type. ID = number of different individuals between brackets. For the full sample analysed, see Materials and Methods.

Area type	Spring (ID)	Autumn (ID)	2 litters/year (ID)
Natural	20 (15)	11 (9)	2 (1)
Suburban	12 (7)	3 (2)	2 (2)
Urban	27 (23)	13 (12)	3 (3)
Total	59 (45)	27 (23)	7 (6)

across observations. We defined repeatability for each posterior draw as the ratio of between-individual variance to the sum of between- and within-individual variances.

3 | RESULTS

We recorded 204 captures and recaptures of 72 female red squirrels (27 individuals captured once). In 103 cases (50.49%) 54 females were reproductive (oestrus, post-oestrus, pregnant or lactating); in 101 cases (49.51%) 56 females were non-reproductive. Overall, we

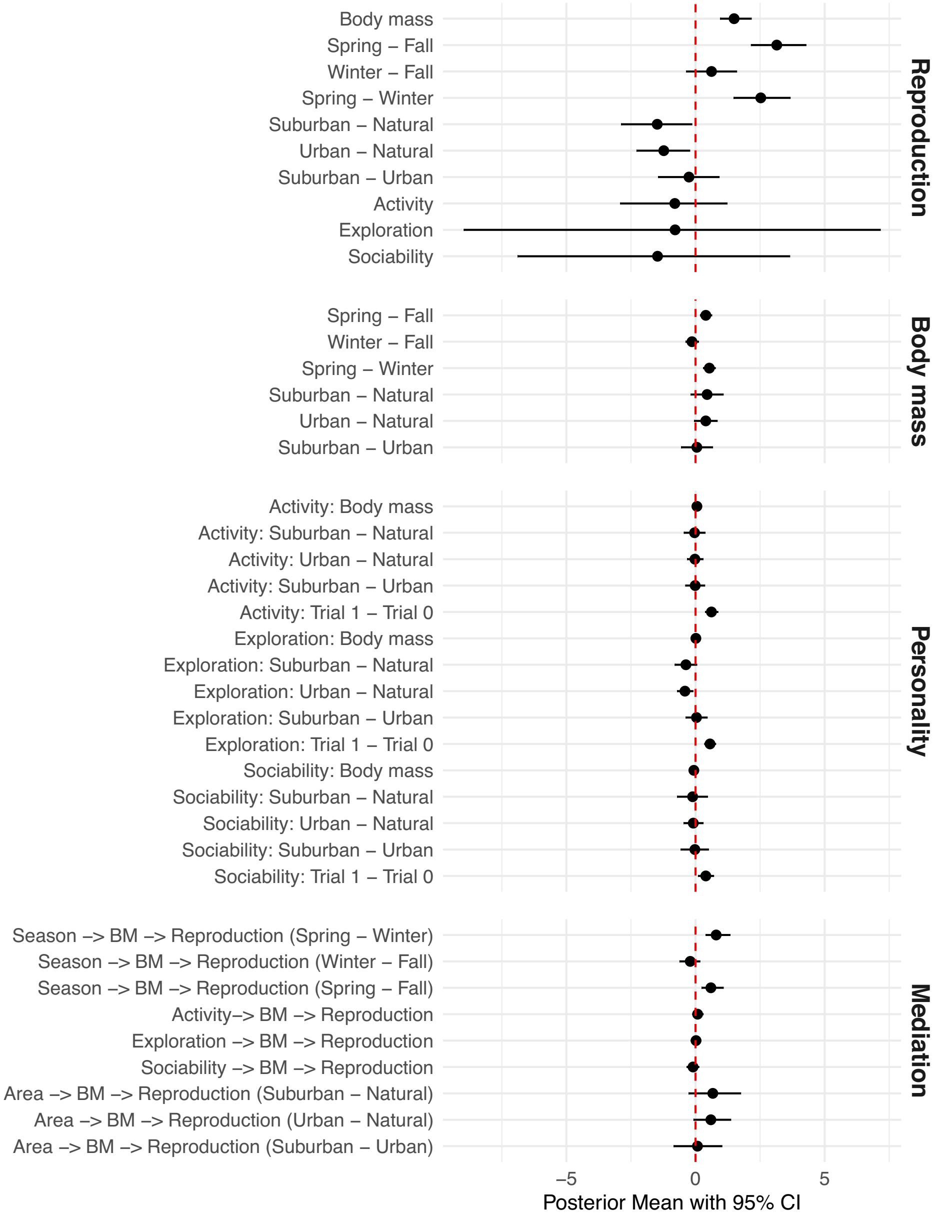

FIGURE 2 Forest plot showing posterior means and 95% credible intervals for the direct relationships between reproduction, body mass, personality, season and level of urbanization. The mediation shows the effects of season, personality, and urbanization level through the mediation of body mass on reproduction. In the mediation panel, each line represents the estimated effect of a predictor on reproduction via its influence on body mass. Trial order was coded as 1 for the first arena test and 0 for subsequent ones.

registered 86 events of females actually lactating young, 59 in spring and 27 in autumn (Table 1).

Of the 46 lactating females monitored in at least one trapping session, 26 (56.5%) had one litter, 12 (26.1%) produced two litters, 6 (13.0%) produced three litters, and two (2.2%) each with 4 and 5 litters during their entire time of presence in the study sites (range 1–630 days).

We measured the behaviour of 26 female red squirrels in natural sites, 10 in suburban and 36 in urban sites, using a total of 69, 36 and 99 arena tests, respectively. We tested each squirrel on average 2.83 ± 1.98 times (range 1–9), with an average time between tests of 158 ± 102 days (range 47–630). Activity ($R=0.17$, CI = 0.07–0.30), exploration ($R=0.33$, CI = 0.18–0.49) and sociability ($R=0.13$, CI = 0.02–0.26) showed some consistency within individuals.

The multivariate model captured individual-level variation in all responses with the strongest variation observed in body mass (SD = 0.74, 95% CI = 0.58–0.92) and minimal variation in activity (SD = 0.26, 95% CI = 0.03–0.47).

Reproduction was positively associated with body mass ($\beta=1.49$, 95% CI = 0.95–2.16) and significantly higher during spring compared to autumn ($\beta=3.15$, 95% CI = 2.14–4.27) and winter ($\beta=2.53$, 95% CI = 1.48–3.66). Reproductive probability was lower in both suburban ($\beta=-1.48$, 95% CI = −2.88 to 0.14) and urban ($\beta=-1.23$, 95% CI = −2.29 to −0.25) areas compared to natural habitats, but it was similar between suburban and urban areas ($\beta=-0.25$, 95% CI = −1.45 to 0.91). Personality traits did not have significant direct effects on reproduction (activity: $\beta=-0.80$, 95% CI = −2.92 to 1.22; exploration: $\beta=-0.79$, 95% CI = −8.97 to 7.15; sociability: $\beta=-1.47$, 95% CI = −6.89 to 3.65) (Figure 2).

Body mass was positively associated with spring compared to autumn ($\beta=0.40$, 95% CI = 0.17–0.63) and winter ($\beta=0.53$, 95% CI = 0.30–0.77). Body mass was marginally higher in suburban (345 ± 34 g; $\beta=0.44$, CI = −0.19 to 1.07) and urban (337 ± 30.6 g; $\beta=0.39$, CI = −0.05 to 0.84) areas compared to natural (322 ± 31.3 g), though credible intervals for habitat overlapped zero (Figure 2).

Activity ($\beta=0.62$, 95% CI = 0.37–0.87), exploration ($\beta=0.56$, 95% CI = 0.34–0.78) and sociability ($\beta=0.40$, 95% CI = 0.09–0.70) were positively associated with trial order, suggesting a potential habituation or learning effect across testing sessions. Exploration was significantly lower in urban compared to natural areas ($\beta=-0.41$, 95% CI = −0.70 to −0.10). No clear effects of body mass or area type were observed on activity and sociability (Figure 2).

We found evidence that body mass mediated the effects of season on reproductive condition (Figure 2). The indirect effect of spring on reproduction through increased body mass was positive (spring–autumn: $\beta=0.59$, 95% CI = 0.23–1.07; spring–winter: $\beta=0.80$, 95% CI = 0.39–1.33), suggesting that part of the seasonal increase in reproductive probability during spring was explained by heavier body mass in that season compared to the others. Similarly, the indirect effect of suburban habitat on reproduction via body mass was positive ($\beta=0.67$), but the 95% CI spanned zero (−0.27 to 1.75), as did the urban effect ($\beta=0.59$, 95% CI = −0.08 to 1.36) (Figure 2), suggesting that while body mass tended to be higher in these areas, this did not translate into a statistically robust increase in reproduction.

For the personality traits, all indirect effects through body mass were small in magnitude and had credible intervals that overlapped zero (activity: $\beta=0.08$, 95% CI = −0.11 to 0.29; exploration: $\beta=0.02$, 95% CI = −0.17 to 0.21; sociability: $\beta=-0.10$, 95% CI = −0.35 to 0.13) (Figure 2). These results suggest that while body mass was a strong predictor of reproduction, its role as a mediator between personality traits and reproduction was limited in the studied populations.

4 | DISCUSSION

Body mass was the main factor directly affecting the probability of reproducing in female red squirrels, and most females reproduced in spring. This seasonal pattern, common also to other populations (Wauters et al., 1993; Wauters & Dhondt, 1989, 1995), was at least partly explained by indirect effects of season on body mass, with higher mass in spring than in other seasons supporting the increased spring breeding. Further, our results suggest a direct effect of urbanization on squirrels' reproduction: The probability of reproducing was higher in natural habitats than in the urban and suburban sites, despite average body mass being slightly lower in natural habitats. Female red squirrels in natural sites also engaged more frequently in what we interpreted as explorative behaviours than their conspecifics in urban sites, but this did not translate into either direct or significant indirect effects of personality on reproduction. Finally, body mass of females tended to be slightly higher in urban and suburban than in natural habitats (see also Tranquillo et al., 2023), but this did not result in higher reproductive rate, which, as mentioned above, was highest in the populations living in natural sites.

4.1 | The role of body mass in reproduction along a natural–urban gradient

Our results demonstrate that body mass was the strongest determinant of reproduction. This supports the idea that reproduction is condition-dependent and that body reserves play a functional role in determining whether females initiate and sustain gestation and lactation under varying ecological constraints, in line with previous studies (Wauters et al., 2007; Wauters & Dhondt, 1989, 1995; Wauters & Lens, 1995). Higher body mass is generally indicative of better access to resources, improved body condition and greater capacity for reproductive investment. This pattern was reinforced by seasonal differences, with squirrels being heavier and reproducing more frequently in spring, a season generally associated with increased activity and consumption of cached high-energy food resources (Wauters et al., 1995) and the species' main breeding period. In our data, body mass significantly mediated the effect of spring on reproduction, suggesting that the seasonal increase in reproductive output is at least partly driven by spring-related gains in body mass.

Despite the slightly higher body mass observed in urban and suburban squirrels, females had 16.2% fewer reproductive events compared to natural populations. In populations occurring in montane and subalpine conifer forests in the Alps, there was evidence for small-scale habitat-related differential selection for size and body mass, and the probability of female reproduction increased with body mass but varied greatly between habitats and years, in relation to seed-crop size (Wauters et al., 2007). The urbanization-related pattern of higher body mass but lower reproduction in this study may stem from density-dependent mechanisms, and/or space use differences (McCleery, 2010). Moreover, the sex ratio was consistent across urbanization levels, indicating a similar potential for reproduction (Table S1). Previous studies have shown that in red squirrels failure to wean offspring and delayed or absent breeding are more frequent in poor food years or high-density populations (Wauters et al., 2004; Wauters & Lens, 1995). Although food abundance in urban areas might promote body mass accumulation, higher population densities, which are common in urban red squirrels (Babińska-Werka & Żółw, 2008; Jokimäki et al., 2017; this study: natural: 0.23 ind/ha ± SD 0.12, urban: 0.62 ind/ha ± SD 0.40), could increase intraspecific competition or stress, leading to suppressed reproductive performance (but see Crespi et al., 2013). For example, Eastern grey squirrel (*S. carolinensis*) densities in native urban areas often exceed 10–20 individuals/ha, while natural densities rarely surpass 3/ha (Koprowski, 1994). High densities are often sustained by enhanced survival and reduced dispersal but do not necessarily lead to higher reproduction, potentially due to space constraints, social stress or reduced breeding opportunities (Descamps et al., 2008; Luna et al., 2021; Prange et al., 2003; Wauters et al., 2004).

An additional explanation is that predictable anthropogenic food in urban areas may promote body mass increases without necessarily improving reproductive condition if food quality is lower, contaminated or if hormonal cues are disrupted by chronic human disturbance (Birnie-Gauvin et al., 2016; Thompson et al., 2022). Higher body mass in urban and suburban squirrels might not reflect better body condition or greater energy reserves, but could result from altered metabolism (Turner et al., 2017) or lower energy expenditure in these habitats. Both the quantity and quality of food items in urban environments, which could also be affected by pollutants, have direct and indirect effects on fitness that might be altered in comparison to natural habitats (Birnie-Gauvin et al., 2016). Urban squirrels may have access to predictable anthropogenic food sources, and this could also affect their space use as it would lead to smaller home ranges and less exploratory behaviour or movement effort (Birnie-Gauvin et al., 2016). This is supported by our finding of lower levels of what we interpreted to be a measure of exploration in urban sites compared to natural ones. The higher exploration observed in natural areas likely reflects the patchy distribution of high-energy food resources, such as tree seeds from chestnut (*Castanea sativa*), hornbeam and hazel. These preferred species occurred in scattered patches amid black locust (*Robinia pseudoacacia*), aging Scots pine (*Pinus sylvestris*), black cherry (*Prunus serotina*) and *Salix* spp., which are less or not used for foraging (Wauters et al., 1992, 2001). Future work combining focal observations across seasons or genetic analyses of faecal samples will be necessary to clarify how provisioning and diet composition differ among habitat types, and how these factors contribute to observed variation in body mass and behaviour.

This pattern suggests that in urban squirrels, predictable anthropogenic resources may inflate body mass through higher intake and lower expenditure, but without the physiological readiness or hormonal cues to sustain reproduction (Thompson et al., 2022); when combined with the effects of high densities and chronic disturbance, these pressures weaken the link between condition and reproductive output, consistent with the emergence of new coping styles under human-driven environments (Sadoul et al., 2021).

These findings emphasize the context-dependent nature of trait–function relationships. In other taxa, reproduction in urban populations varies widely. Urban black bears (*Ursus americanus*) and raccoons (*Procyon lotor*) have larger litter sizes than counterparts living in natural habitats (Beckmann & Berger, 2003; Prange et al., 2003), and urban fox squirrels (*Sciurus niger*) have a higher frequency of multiple litters per year (Mccleery, 2009). However, such trends are not universal. For instance, reproductive investment in starlings (*Sturnus vulgaris*) does not differ between urban and natural habitats (Guindre-Parker et al., 2025), and in house sparrows (*Passer domesticus*), reproductive failure in urban settings has been linked to food quality deterioration due to air pollution and reduced invertebrate prey (Peach et al., 2008). This variability across taxa highlights the species-specific and multifaceted nature of reproductive strategies under urban pressure.

4.2 | The role of personality in reproduction along a natural–urban gradient

Although personality traits such as activity, exploration and sociability are often hypothesized to influence reproduction, either through enhanced foraging efficiency, social interactions or mate access (Mutzel et al., 2013; Roth et al., 2021; Schuett et al., 2012), the personality traits we measured in this study did not mechanistically influence reproduction. In contrast to expectations that more active or sociable individuals would be favoured in complex urban environments (Miranda et al., 2013), our results indicate that individual variation in these traits did not mediate reproductive differences across the urbanization gradient. In natural habitats, females exhibited more behaviours we associated with exploration; however, this did not lead to greater reproduction compared to less exploratory individuals living in urban environments. Instead, body mass was the primary factor linking phenotype to fitness. One possible explanation is that urban environments reduce the selective advantage of active, exploratory or sociable phenotypes because resources are more predictable and human–wildlife interactions impose different pressures, resulting in a weakened association between behavioural expression and reproductive success (Sadoul et al., 2021). This separation of behaviour from fitness underscores the complexity of the relationship between personality traits and their functions, highlighting the need for caution in assuming straightforward adaptive benefits of behavioural variation in human-altered habitats, as seen in other urban-adapted species (Lowry et al., 2013; Schuett et al., 2010). An alternative, not mutually exclusive, explanation for the lack of a direct personality—reproduction relationships, is that the traits measured with the arena test assays were not significantly associated with natural behaviours occurring in the field (Carter et al., 2013; Martinig et al., 2022; McCormick & Holekamp, 2022; Tkaczynski et al., 2019). To enhance our understanding of the effects of personality traits on reproductive success in natural populations, future studies should combine standardized assay measures of traits with direct observations of exploration and social/aggressive behaviours under natural conditions in the same individuals.

Additional bidirectional feedbacks, such as effects of reproductive state on body mass (Humphries & Boutin, 1996) or potential changes in behavioural expression during pregnancy (Dantzer et al., 2011), are biologically plausible but could not be addressed within the scope of this study. Although this study focuses on individual-level reproductive success, variation in reproductive output across urban gradients can scale up to affect population dynamics and genetic structure (Hurtado & Mabry, 2019; Markowski et al., 2021). If urban squirrels maintain lower reproductive rates despite high densities, future work should explore whether these patterns affect age structure, recruitment and long-term persistence under continued urban expansion.

5 | CONCLUSION

Our findings offer a mechanistic understanding of how reproduction in a widespread small mammal arises from the interaction of ecological and phenotypic traits across an urbanization gradient. While body mass emerged as the dominant predictor of reproduction, its functional role was context-dependent, shaped by seasonality, environmental resource distribution and potentially by altered energetic dynamics in urban environments. In contrast, behavioural traits varied with habitat but did not mediate reproduction, highlighting a decoupling of trait expression and function in human-modified landscapes and showing how trait expression does not equate to ecological function unless matched with the appropriate environmental context.

Our work underscores the importance of integrating multiple levels of biological organization, behaviour, body mass, life history and environmental context to understand how global change alters ecological and evolutionary trajectories. As urbanization continues to transform natural habitats, studies that disentangle direct and indirect pathways from phenotype to fitness will be essential not only for predicting wildlife persistence but also for linking individual-level processes to population and community dynamics.

AUTHOR CONTRIBUTIONS

Lucas Armand Wauters, Maria Vittoria Mazzamuto, Claudia Tranquillo and Sandro Bertolino conceived the ideas and designed the methodology; Claudia Tranquillo, Francesca Santicchia, Lucas Armand Wauters, Francesco Bisi and Damiano Preatoni collected and curated the data; Maria Vittoria Mazzamuto and Claudia Tranquillo analysed the data; Sandro Bertolino, Adriano Martinoli, Damiano Preatoni and Lucas Armand Wauters acquired funding; Claudia Tranquillo, Lucas Armand Wauters and Francesca Santicchia carried out the investigation and developed the methodology; Francesco Bisi, Adriano Martinoli, Damiano Preatoni, Lucas Armand Wauters and Sandro Bertolino provided project administration and resources; Maria Vittoria Mazzamuto, Lucas Armand Wauters and Claudia Tranquillo led the writing of the original draft. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Research carried out within the project PRIN (Progetti di Rilevante Interesse Nazionale) 2022 'Wildlife in the Anthropocene: behavioral, genetic and physiological responses to urbanization in two mammal species' 2022N9CSKJ; funded by the European Union—Next Generation EU, Mission 4 Component 1 CUP D53D23008250006. We are grateful to Regione Lombardia, Parco Lombardo della Valle del Ticino and Parco della Pineta di Appiano Gentile e Tradate for permits and access to the study sites. We also thank the cities of Varese and Gallarate, Ville Ponti Congress Centre, Villa Panza and Fondo Ambiente Italiano (FAI), Palace Grand Hotel Varese, Scuola Europea of Varese, Aloisianum Gallarate, and the other owners of private estates for allowing fieldwork in their properties. Also, thanks to Mattia Panzeri, Alessandro Sclip and the students for their assistance in the field and arena test coding. Thanks to Rosa Maria Di Biase, Sara Franceschi, Marzia Marcheselli and Caterina Pisani from the University of Siena for their input in quantifying the degree of urbanization at each study site. We appreciate Dr. April Robin Martinig for her valuable comments on the early version of this manuscript. Artificial Intelligence was used for language editing. Open access publishing facilitated by Universita degli Studi dell'Insubria, as part of the Wiley - CRUI-CARE agreement.

CONFLICT OF INTEREST STATEMENT

Authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Zenodo: https://doi.org/10.5281/zenodo.16760822 (Mazzamuto et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Density of squirrel populations per site.

Table S1. Characteristics of the study sites and sample size.

Table S2. Ethogram for personality assessment.

Appendix S1. Principal Component Analysis to determine urbanization level.

How to cite this article: Mazzamuto, M. V., Tranquillo, C., Bertolino, S., Bisi, F., Santicchia, F., Preatoni, D., Martinoli, A., & Wauters, L. A. (2026). Functional trait interactions in a human-dominated world: Urbanization and reproduction in Eurasian red squirrels. *Functional Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2435.70312