



Urban evolutionary ecology of animal behaviour in cities

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Abstract. Urbanisation represents one of the most pervasive anthropogenic forces shaping contemporary evolutionary processes. This mini-review synthesises current knowledge on how urban environments influence animal behaviour, cognition, genetic adaptation, and sexual selection. Evidence across taxa indicates that urban populations often exhibit increased boldness, exploratory behaviour, and behavioural flexibility, traits that may facilitate persistence in human-altered habitats. In parallel, urban environments impose novel cognitive and sensory challenges, driving modifications in learning, problem-solving, and communication systems, particularly in response to anthropogenic noise. At the evolutionary level, cities function as complex selective landscapes where both relaxed and intensified selection regimes can occur, often in a trait- and species-specific manner. Importantly, urbanisation alters the dynamics of sexual selection by modifying signalling environments, mate choice processes, and reproductive strategies. However, empirical evidence remains fragmented, and the adaptive significance of many observed trait shifts is still unclear. Overall, the review highlights that urban evolutionary ecology is characterised by context-dependent interactions between behavioural plasticity and genetic adaptation, with significant gaps remaining in quantifying selection pressures and fitness outcomes in urban systems.

Keywords: urbanisation, behavioural ecology, boldness, exploration, innovation, cognitive adaptation, sensory ecology, sexual selection, urban evolution, phenotypic plasticity, animal behaviour, adaptation.

Introduction. Urbanisation reshapes selection on animal behaviour and physiology, but evidence for how this translates into genetic adaptation and changed mating systems is still emerging. Behavioural shifts such as increased boldness, exploratory tendency and cognitive performance are widespread, while impacts on sexual selection range from relaxed to intensified, depending on species, traits and local conditions (Miranda 2017). The aim of this mini-review is to critically evaluate current empirical and theoretical insights into the effects of urbanisation on animal behaviour, cognition, genetic evolution, and sexual selection. Specifically, the study seeks to (i) synthesise evidence for consistent behavioural and cognitive shifts associated with urban environments, (ii) assess the extent to which these changes reflect adaptive evolution versus phenotypic plasticity, and (iii) examine how urban-induced environmental modifications reshape natural and sexual selection regimes. By integrating findings across taxa and levels of biological organisation, this review aims to clarify the mechanisms underlying urban adaptation and to identify key knowledge gaps that constrain a comprehensive understanding of evolutionary processes in cities.

Terminology. In the field of ethology, the scientific study of animal behaviour, researchers have increasingly focused on individual variation in traits that influence survival and reproductive success. **Boldness**, for instance, refers to a consistent

behavioural tendency towards risk-taking and proactive responses in novel or threatening situations, often contrasting with shyness or caution (Petrescu-Mag et al., 2026). Closely related is **exploration**, which denotes an animal’s propensity to investigate unfamiliar environments, objects, or stimuli, thereby acquiring information that may prove advantageous (Bourne & Sammons, 2008; Bourne & Watson 2009). Such behavioural dispositions frequently underpin **innovation**, defined as the capacity to devise novel solutions to ecological challenges or to exploit new resources through the modification of existing behaviours (Morton et al., 2023). These traits are often supported by **cognitive and sensory adaptations**, which encompass evolved modifications in perception, learning, memory, and problem-solving abilities, as well as refinements in sensory modalities such as vision, olfaction, or audition, enabling animals to better navigate complex social and ecological landscapes (Dăescu & Petrescu-Mag, 2024; Petrescu-Mag et al., 2025). Ultimately, many of these characteristics are shaped by **sexual selection**, the process first articulated by Darwin whereby traits that confer advantages in mate acquisition—whether through intrasexual competition or intersexual choice—become exaggerated or maintained within populations, even when they may entail survival costs (Lindholm & Breden 2002; Petrescu-Mag et al., 2019; Petrescu-Mag 2025abc).

Urban Behavioural Adaptations: Boldness, Exploration and Innovation. Across taxa, urban dwellers tend to be bolder and more explorative than rural conspecifics. Striped field mice along an urban gradient showed higher boldness, spatial exploration and behavioural flexibility in more urbanised sites (Caizergues et al., 2022). Common voles captured in cities were bolder and more explorative in situ, combining elevated risk-taking with high behavioural flexibility, which may facilitate coping with human-induced rapid environmental change (Slabbekoorn, 2013). Urban coyotes likewise scored higher on boldness and exploratory behaviour than rural coyotes (Perry & Göttert, 2024). Reviews emphasise that disturbance tolerance, behavioural flexibility and problem-solving are key for urban success (Küçüктаş & Guenther, 2022; To et al., 2021). Experimental work shows enhanced innovative problem-solving in urban striped field mice (Breck et al., 2019) and other rodents, supporting a link between urban life and greater innovation propensity (Breck et al., 2019; Slabbekoorn, 2013; Cronin et al., 2022) (Table 1, Figure 1).

Table 1

Examples of boldness and exploration changes in urban mammals:
urban mammals show elevated boldness and flexibility

| <i>Taxon / system</i> | <i>Urban vs. non-urban behavioural shift</i> | <i>References</i> |
|--|--|-------------------------|
| Striped field mouse | More bold, explorative, flexible with increasing urbanisation | Caizergues et al., 2022 |
| Common vole | Urban: bolder/explorative in field; strong behavioural flexibility under common garden | Slabbekoorn, 2013 |
| Coyote | Urban population consistently bolder and more exploratory than rural | Perry & Göttert, 2024 |
| Noncommensal rodents (problem solving) | Urban striped field mice better problem solvers; boldness predicts success | Breck et al., 2019. |

Not all behavioural shifts are clearly adaptive. In great tits, urban individuals were more exploratory, aggressive and had higher breath rates than forest birds, yet these traits were not favoured by selection and could be maladaptive (Iglesias-Carrasco et al., 2019).

Cognitive and Sensory Adaptations to Urban Environments. Reviews of “animal cognition in an urbanised world” highlight that novel problems, unpredictable resources and complex information landscapes select for enhanced learning, attention and problem solving (Küçüктаş & Guenther, 2022). Cognitive phenotypes may thus be both selected and developmentally shaped in cities (Küçüктаş & Guenther, 2022; To et al., 2021).

Acoustic behaviour in birds provides a well-developed model of urban sensory adaptation. Many urban bird populations sing at higher minimum or dominant frequencies than rural populations, a plastic or possibly evolved response to low-frequency anthropogenic noise (Lowry et al., 2013; Zhan et al., 2021; Branston et al., 2021; Marques et al., 2022). A continental-scale study in China showed higher dominant frequencies in urban than peri-urban/rural birds, driven by noise and structural features such as open understory; vegetation density and tree height moderated this upward shift (Zhan et al., 2021). Similar noise-linked spectral adjustments have been documented for individual species (e.g. Oriental Magpie-robin; (Branston et al., 2021)) and for multiple Hong Kong passerines influenced by both anthropogenic and insect noise (Marques et al., 2022). Reviews argue that this “acoustic phenotype” illustrates environmentally induced signal change with potential cultural and genetic consequences, though direct fitness benefits are still rarely quantified (Lowry et al., 2013).

Genetic Evolution and Selection Regimes in Cities. At the evolutionary scale, cities can act as “evolutionary hothouses”, concentrating strong and novel selection, while also changing mutation, drift and gene flow patterns (Mazza & Guenther, 2021; Johnson & Munshi-South, 2017). A broad review of natural and genomic selection estimates found surprisingly few studies that quantify selection coefficients in urban vs non-urban populations, and insufficient standardisation to compare effect sizes across taxa or traits (Dammhahn et al., 2020). Nonetheless, scattered studies reveal genomic footprints of urban adaptation in some songbirds and other taxa (Dammhahn et al., 2020; Mazza et al., 2020; Johnson & Munshi-South, 2017).

Whether selection is globally stronger or weaker in cities remains unresolved. A multi-year comparison of urban vs forest blue tits and great tits found weakened selection on timing of breeding and clutch size in urban blue tits, but not in great tits (Mazza et al., 2020). Likewise, selection analyses on great tit exploratory behaviour, aggressiveness and stress-related breath rate showed that urban trait shifts were not aligned with ongoing selection; stabilising selection on aggression and breath rate was in some cases stronger in cities, whereas selection on exploration was relaxed for urban males (Iglesias-Carrasco et al., 2019). These results suggest complex, trait- and species-specific mosaics of relaxed and intensified selection in urban habitats (Dammhahn et al., 2020; Mazza et al., 2020; Iglesias-Carrasco et al., 2019).

Sexual selection, mating systems and “sex in the city”. Urbanisation modifies both abiotic (noise, light, pollutants) and biotic (predators, parasites, competitors, densities) contexts for mating, with consequences for sexual traits and sexual selection. A comprehensive review of 108 papers concludes that urban conditions can alter signal production and transmission, mate choice, rival interactions and fertilisation success, with effects on behaviour, morphology, physiology and life histories (Hao et al., 2024). Many studies document trait divergence (e.g. signal frequency, brightness, complexity) between urban and non-urban populations, but often lack direct tests of whether trait changes are adaptive or reflect relaxed vs intensified sexual selection (Dammhahn et al., 2020; Mazza & Guenther, 2021; Hao et al., 2024; Iglesias-Carrasco et al., 2019).

Comparative evidence from passerines shows that strong pre-mating sexual dimorphism can hinder urban colonisation: species with higher plumage dichromatism are less likely to tolerate cities, whereas sexual size dimorphism and relative testes size do not predict urban occurrence (Halfwerk et al., 2018). This pattern is consistent with costs of expressing bright coloration in cities (dietary constraints, reduced male parental care, increased predation), implying that some forms of sexual selection may be constrained or indirectly relaxed by urban conditions (Hao et al., 2024; Halfwerk et al., 2018).

Trait- and system-specific case studies, however, show both relaxation and intensification of sexual selection. For a tropical frog, male túngara frogs in cities produce more conspicuous, complex calls than forest males, which increases female attraction while escaping natural enemies that are rarer in urban areas; translocation experiments demonstrate this altered call as an adaptive urban phenotype shaped by simultaneously

relaxed natural selection (lower predation/parasitism) and increased sexual selection due to lower female encounter rates (Hao et al., 2024; Charmantier et al., 2024). Urban males also display greater signalling flexibility when moved between habitats, suggesting evolved or plastic reaction norms aligned with urban conditions (Charmantier et al., 2024).

In urban guppies, pre-mating (coloration) and post-mating (sperm load) traits both changed in complex, size-dependent ways. Urbanisation did not alter mean body size, but reduced orange coloration in small males and iridescent coloration as well as sperm load in large males, with altered correlations between colour traits and sperm load relative to non-urban populations (Lee & Thornton, 2021). These shifts are interpreted as weaker sexual selection on both pre- and post-mating traits in urban systems, likely mediated by polluted and visually degraded urban streams (Lee & Thornton, 2021).

In birds, urban noise prompts spectral shifts in song that could affect mate choice and territory establishment (Lowry et al., 2013; Zhan et al., 2021; Branston et al., 2021; Marques et al., 2022). While song adjustments often enhance signal transmission under masking noise, clear demonstrations of associated reproductive advantages or altered mate preferences in the wild are rare, so the direction and magnitude of sexual selection on modified songs remain uncertain (Lowry et al., 2013; Hao et al., 2024; Zhan et al., 2021; Marques et al., 2022).

Across systems, reviews emphasise major knowledge gaps: the drivers of urban sexual selection, the extent to which changes in sexual traits yield adaptive benefits, and whether they reflect plasticity or evolved responses (Dammhahn et al., 2020; Mazza & Guenther, 2021; Hao et al., 2024; Iglesias-Carrasco et al., 2019). Current evidence shows that sexual selection in cities is neither uniformly relaxed nor uniformly intensified. Instead, it depends on how urban-induced changes in predation, parasitism, density, pollution and sensory environments reshape the balance between natural and sexual selection on specific traits (Lee & Thornton, 2021; Hao et al., 2024; Charmantier et al., 2024; Halfwerk et al., 2018).

Conclusions. Urban environments act as heterogeneous and dynamic selective systems that reshape animal behaviour, cognition, and evolutionary trajectories. The evidence reviewed indicates that urban populations frequently display increased boldness, exploration, and behavioural flexibility, alongside modified cognitive and sensory capacities that enhance performance in complex and unpredictable environments. However, these trait shifts are not universally adaptive, and in some cases may reflect mismatches between phenotype and current selection pressures.

At the evolutionary scale, cities generate mosaics of selection regimes in which both relaxed and intensified natural and sexual selection can occur simultaneously, depending on ecological context and trait specificity. Urbanisation also alters sexual signalling systems and mating dynamics, yet clear demonstrations of fitness consequences remain limited. A major unresolved issue is the relative contribution of phenotypic plasticity versus genetic adaptation in shaping urban phenotypes.

Overall, the field of urban evolutionary ecology remains constrained by a lack of standardised methodologies and direct estimates of selection. Future research should prioritise longitudinal and experimental approaches that link trait variation to fitness outcomes, thereby enabling a more rigorous understanding of how organisms evolve in response to rapid urban change.

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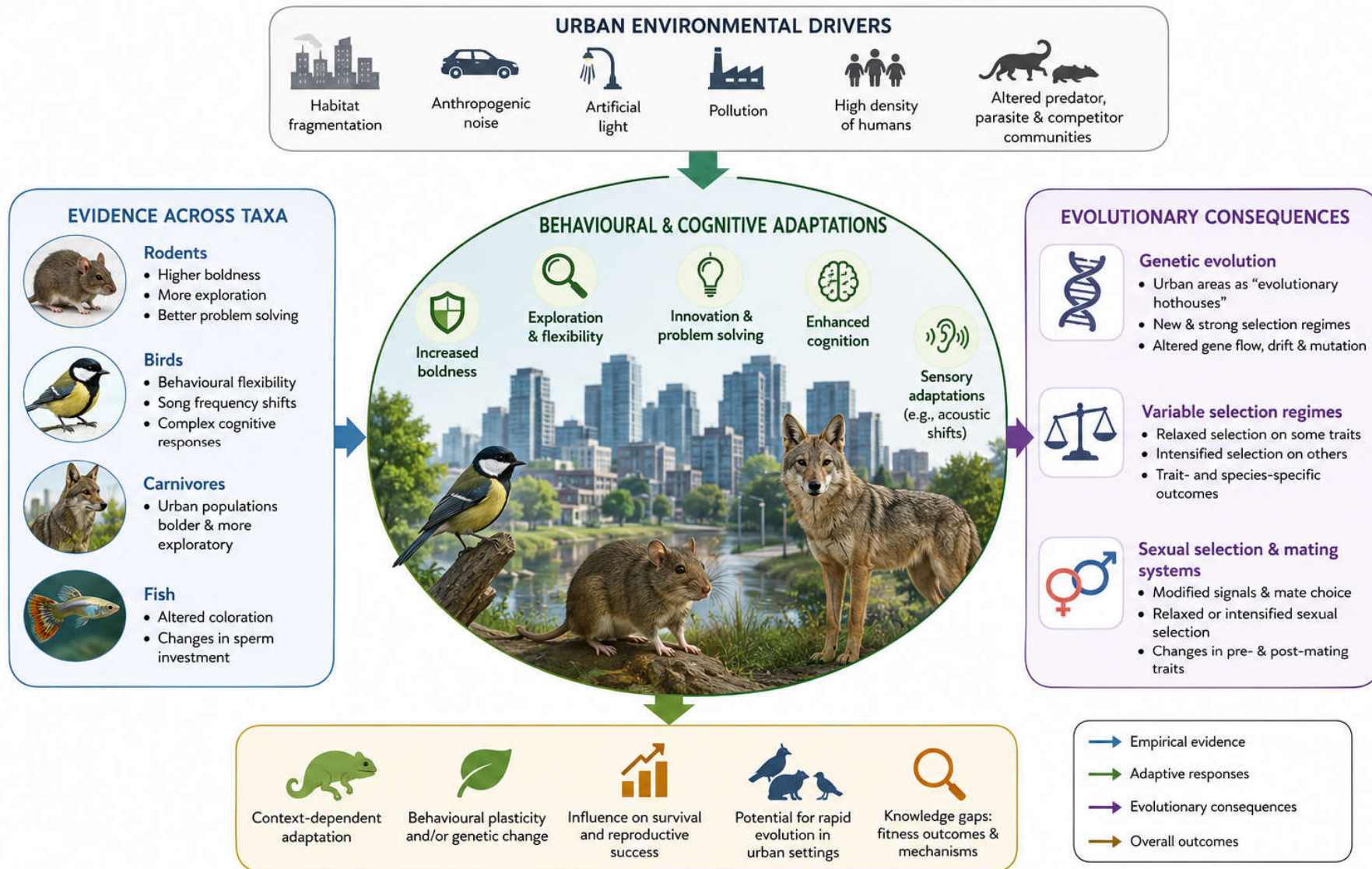


Figure 1. Urban evolutionary ecology of animal behaviour in cities.

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