Behavioral Ecology and Sociobiology (2022) 76:95
https://doi.org/10.1007/s00265-022-03204-7

INTRODUCTION

Using behavioural ecology to explore adaptive responses to anthropogenic change — introduction

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Published online: 6 July 2022

As there are no ecosystems left in the world which are not affected by human activities, organisms have to either adapt to those changes, move on to less-affected areas or to those that have been made newly available, or risk extinction. The most obvious anthropogenic change to the environment is urbanisation, and considering the adaptations to urban environments, Szulkin et al. (2020) defined urban evolutionary biology as the study of evolutionary change in populations as a response to human-built environments and all that high densities of human population entail, with the associated allele, genotype and phenotype frequency changes in populations across generations. This is an operational view on the evolutionary consequences of anthropogenic environmental changes in general, often associated with high human population density even if the changes are not urbanisation per se.

Behavioural responses are typically faster than genetic, evolutionary adaptations, and we therefore expect changes in behaviour to be prominent in response to anthropogenic changes. For instance, song adjustment by urban birds, originally highlighted by Slabbekoorn and Peet (2003), has become a prolific area of research. What is less clear, however, is the extent to which such behavioural changes are adaptations involving genetic differences, say, between urban and rural habitats (see Partecke and Gwinner 2007), or whether they are due to behavioural plasticity. This was our starting point and motivation to put together the current collection of topical papers.

The resulting compilation of articles presents recent findings on the effects of anthropogenic changes on animal behaviour on a range of taxa, beetles, lizards, fish, toads, birds and mammals from a great geographical range including Europe, Australasia, Asia and Africa. These articles cover a range of topics but the most common were papers finding behavioural flexibility, often in connection with invasion success. In two papers, the authors found that invasive Siamese fighting fish (*Betta splenden*s) and delicate skinks (*Lampropholis delicata*) are more active than their native conspecifics, which may contribute to their survival (Brand et al. 2021; Naimo et al. 2021). In a third paper exploring similar questions, Baxter-Gilbert et al. (2021) found that invasive guttural toads (*Sclerophrys gutturalis*) were bolder in urban populations within both the native and invasive ranges, indicating that the bold phenotype evolved prior to their invasion success and then expanded. Another behavioural change found was that free ranging urban dogs (*Canis familiaris*) avoid their usual areas when festivals are being held, but mostly return to those sites when people have left (Bhattacharjee and Bhadra 2021). Using non-migratory (resident; from human-induced changes) sticklebacks, *Gasterosteus aculeatus*, and breeding them with naturally migratory sticklebacks followed by a common garden design, Ramesh et al. (2021) demonstrated that differences in the activity potential, shoaling and migratory tendency have a genetic basis in the resident population of sticklebacks. These five papers suggest that there is a selection for certain invasive phenotypes, in these cases mostly boldness, in newly adapted populations. However, more research is required to confirm this conclusion where the authors did not directly test for phenotypic plasticity or genetic basis to the behaviours.

Three other papers brought in additional contexts on the role of behaviour in responding to urbanisation. In two papers, the authors evaluated the role of artificial light at

This article is a contribution to the Topical Collection using behavioural ecology to explore adaptive responses to anthropogenic change — Guest Editors: Jan Lindström, Constantino Macias Garcia, Caitlin Gabor.

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night (ALAN) on sleeping sites in lizards (*Psammophilus dorsalis*) and glow time in sexual signalling by glow worms (*Lampyris noctiluca*). Mohanty et al. (2021) found that the sleeping sites of lizards in urban areas match the properties of those of lizards in natural sites in terms of the amount of light the lizards are exposed to and the structural and thermal traits. This creative and trail blazing study is one of the first to explore sleep behaviour, and we expect other studies to see the usefulness of exploring this question in urban areas. Unlike lizards, glow worms do not move much so they cannot easily avoid the consequences of ALAN. Elgert et al. (2021) found that especially in smaller females, ALAN causes females to stop glowing, thus decreasing their sexual signals. A third paper explored the role of urbanisation on timing of breeding and clutch size in blue tits (*Cyanistes cauruleus*) and great tits (*Parus major*) and found that blue tits laid earlier and produced smaller eggs in urban areas. This may be due to less food being available in urban areas for these birds. Together, these papers demonstrate that populations vary due to exposure to urbanisation, but as they did not study the genetic basis of these traits, this aspect remains open for further research.

Taking a different track than all of the other articles, the thought-provoking review by Beckman et al. (2022) invites us to understand the several ways, plastic and selective alike, in which both intentional and accidental domestication has modified vertebrate behaviour, as a guide to inform our studies on the behavioural responses of wild animals to urbanisation. As the authors point out, traits linked to successful domestication, such as behavioural plasticity, may also predict adaptation of wild animals to environments transformed by humans.

When we proposed our topical collection, it was already clear that behavioural traits vary in urban populations from rural ones in many species. We hoped to attract papers that extended this knowledge by exploring new contexts and extending the knowledge gap about the processes generating behavioural differences. The work on ALAN has extended the contexts of behavioural changes in urban areas, and the elegant study of sticklebacks provides evidence of a genetic basis to behavioural differences. But none of the papers explored the physiological basis to these traits or evaluated other alternative measures to assess whether traits at other levels vary similarly with the effects of urbanisation. Ouyang et al. (2018) in their review of the proximate and ultimate responses to anthropogenic change indicated the importance of exploring such questions. There is, therefore, still much work to be done in this area.

Studies of behaviour, physiology and genetics may be harder to generate due to limitations of appropriate/viable organisms. Much work and reviews have covered topics about evolution in cities (Diamond and Martin 2021; Lambert et al. 2021), but these reviews do not include behaviour. Although some examples do exist on the relationship between genetics and behaviour (reviewed by Lambert et al. 2021), this research still lags. As we first noted, behaviour frequently changes sooner than genetics, but now that it is easier to study gene expression, these relationships will be easier to explore. There is some evidence for transcriptional response to environmental change across populations exposed to different levels of urbanisation, but the link to behaviour has not been as clear (Connon et al. 2018; but see Mueller et al. 2013). It is also possible to link or explore both physiology and behaviour if organisms can be sampled non-invasively and repeatedly, so both can be measured from the same individual. Kolonin et al. (2022) found that mosquitofish (*Gambusia affinis)* showed flexible glucocorticoid profiles that aid in coping with urban streams, but behavioural traits did not vary systematically with urbanisation. Indeed, Lapiedra (2018) indicated that by understanding the mechanistic basis of behavioural variation associated with urbanisation, we could gain a better understanding of how to manage population declines. In this respect, comparing the physiology —and indeed the transcriptomes — of domestic and wild organisms should provide testable predictions regarding the effects of anthropogenic factors on urban organisms.

The review by Beckman et al. (2022) made use of a powerful analogy first exploited by Darwin (1859, 1868) to inform our understanding of adaptation — in this case to anthropogenic environments — by looking at the processes and consequences of artificial selection. There is much scope still, however, to investigate how general processes such as sexual selection (Cronin et al. 2022) differ, if indeed they do, in natural and anthropogenic environments.

Conclusions

Direct measurements of natural selection in action in urban environments so far are rare (Johnson and Munshi-South 2017; Macías Garcia et al. 2017). Remarkably, a recent review (Lambert et al. 2021) found only six compelling examples of adaptive changes due to urbanisation after reviewing hundreds of studies, so it is hardly surprising that examples of adaptive behavioural changes are rare as well. Schell (2018) makes suggestions on how behavioural studies could be linked with genetics i.e. animal personalities have heritable components. Therefore, behavioural ecology is well placed in advancing our understanding of adaptation to anthropogenic changes from the short-term adjustments of behaviour to long-term evolutionary changes.

Declarations

Competing interests The authors declare no competing interests.

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