

NEWS AND VIEWS

PERSPECTIVE

Urban behavioural adaptation

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A large and growing proportion of the world is impacted directly by human activities; among the most extreme of these is the spread of urban environments. Environmental change associated with urbanization represents a potentially potent source of selection. While urban environments generally have lowered biodiversity, some clades seem to thrive in urban settings. For example, many members of the bird family Turdidae, known as the 'true thrushes' and the blackbird *Turdus merula* (Fig. 1) in particular, are familiar urban species. Indeed, the colonization of urban environments by blackbirds has become a textbook case study for our understanding of the many ways a wild species can deal with urbanization. In this issue, Mueller *et al.* (*Molecular Ecology*, 00, 2013, 00) add to that story by beginning to address the genetic nature of behavioural adaptation of blackbirds colonizing urban areas. They do this by testing for divergence between paired urban and rural samples at a suite of candidate genes with hypothesized effects on behaviours thought to be important for the colonization of urban environments. They find evidence for consistent patterns of divergence at an exonic microsatellite associated with the *SERT* gene. *SERT* has a number of hypothesized behavioural effects, including harm avoidance, which may be associated with tolerating the hustle and bustle of urban environments. This is among the first evidence that behavioural differences between urban and rural environments have a genetic basis and this work suggests that urban environments can in some cases exert homogeneous selection pressures.

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A growing proportion of the of the Earth's land is impacted by human activities (Fig. 2). As of 2008, it was estimated that half of the world's population lived in urban areas (UN

2011). By the year 2030, it is expected that nearly 5 billion people will live in urbanized areas that cover greater than 1.2 million km²; very nearly a doubling in area from 2000 figures (Seto *et al.* 2012). The urbanization process is coupled with well-known habitat alterations that are predominantly destructive to biodiversity. However, a brief walk down a typical city street reveals that a subset of species persist, and sometimes seem to thrive, in urban environments. With the frenetic pace and scale of land-use change associated with urbanization and natural resource exploitation, we have unwittingly begun a multitude of natural experiments by imposing novel and severe stressors on plant and animal populations and by creating new resource bases and niche space that can be exploited. With data from these natural experiments, evolutionary ecologists are increasingly taking up the important challenge of predicting how and which organisms will respond to human-caused habitat loss and urbanization (Tuomainen & Candolin 2011).

Several lines of evidence show that populations that interact with human-altered environments may differ from their counterparts in more natural conditions in a range of characters. For example, birds (Slabbekoorn & Peet 2003) and whales (Miller *et al.* 2000) alter song structure in acoustically polluted urban landscapes and waterways, and the dawn chorus of some bird species is initiated early due to artificial light (Miller 2006), with potential consequences for mating behaviour (Kempenaers *et al.* 2010). Urbanization also alters the availability and suitability of habitats and hence the likelihood of successful dispersal and selection on dispersal strategies (Walther *et al.* 2002). It is clear that human-altered environments affect distributions, extinction and alter selection patterns, all fundamental biological processes (reviewed in Tuomainen & Candolin 2011). In many undisturbed natural populations, phenotypic plasticity enables adjustment to environmental variability or, given chance short-term severe perturbations, populations can be rescued via meta-population dynamics (i.e. the rescue effect). However, when environmental change is intense, perpetual and directional, as urbanization appears to be, the rate of change in the environment may be beyond the limits of phenotypic plasticity and populations must adapt or go extinct. The extent to which natural populations cope with human-altered environments via plasticity or selection remains an open and important question.

Human-built features on the landscape can quickly alter the genetic structure of populations by altering connectivity among natural populations (e.g. Garroway *et al.* 2011), and genetic differentiation between urban and rural populations has also been documented (Evans *et al.* 2009). Accumulating evidence also suggests that ecology and evolution can interact to exert selective pressures associated with human land use and alteration at ecological

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Fig. 1 A male (a) and female (b) blackbird (*Turdus merula*). Photo credit: Dr. Zoe Davies.

timescales (Smith & Bernatchez 2008), and so it is possible, and perhaps even likely, that some populations will begin to diverge as a result of selection in these novel environments. Here Mueller *et al.* (2013) contribute an important piece of the evolutionary puzzle by providing evidence for a genetic basis of behavioural adaptations to human-created urban environments. Blackbirds (Fig. 1) are an urban success story; this historically forest-dependent species is now one of the most common urban birds in Europe. There is a strong spatial component to the urban colonization history of blackbirds suggesting the possibility for a 'leapfrog' type colonizing model, whereby initial groups of urban-adapted individuals sequentially colonized multiple urban areas (Evans *et al.* 2010). However, previous analysis of neutral markers from birds sampled from the same sites analysed in Mueller *et al.*'s work in this issue (Fig. 2 inset) strongly suggests independent colonizations of urban areas were much more typical (Evans *et al.* 2009).

To address whether genetic differentiation between urban and rural populations was in some part adaptive, in addition to likely differences associated with founder events, Mueller *et al.* (2013) tested for differentiation between 12 pairs of urban and rural sites at 16 candidate loci putatively associated with circadian rhythms, harm

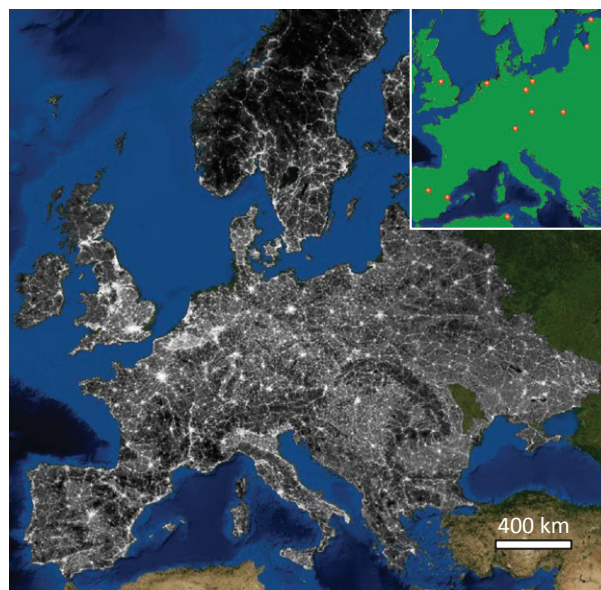


Fig. 2 A map of the 'Human Footprint Index' (HFI) for Europe (Sanderson *et al.* 2002; Global Human Footprint Dataset 2005). The HFI expresses the relative human influence for an area as a percentage (1 black – 100 white). The index incorporates multiple measures of human-population density, land use, infrastructure and human access. Inset are sample sites from Mueller *et al.* (2013).

avoidance, migration and exploratory behaviour. They found evidence for consistent divergence at a *SERT* polymorphism at 10 of the 12 pairs of sampled sites. *SERT* is thought to contribute to the reuptake of serotonin, thus playing an important role in the degree and timing of serotonergic signalling in the brain. There was also some evidence for habitat-based associations at some of the other markers selected; however, these did not reach study-wide significance levels. Mueller *et al.* (2013) controlled for sample sites within their models by treating effects associated with the region within which the population pairs were sampled as random. Given that there was a strong spatial signal associated with the urbanization process in this species (Evans *et al.* 2010) and the lack of a correlation between the level of *SERT* divergence and the date of urbanization, it would have been interesting to know more about spatial genetic patterns such as isolation by distance, if indeed they are present. Although we doubt it would alter the conclusions regarding *SERT*, a more spatially explicit approach might help to understand the relative importance of spatial processes and selection at this locus. They could also perhaps shed light on the nature of some weaker patterns of variation found at other loci which hint at adaptive importance, but could possibly be better explained by other processes.

The function of *SERT* has not been well studied in birds. In mammals, it has been associated with anxiety, harm avoidance, novelty seeking, stress sensitivity, aggression and vigilance among other behavioural traits. Thus, how

the identified divergence at this site might be adaptive in birds remains to be tested; Mueller *et al.* (2013) speculate - quite reasonably - that it may be behaviours associated with harm avoidance at play here. Studies of flight distance (distance at which a human provoked a bird to take flight) suggest one possible hypothesis by which variation in harm-avoidance behaviour might be selected. Møller (2008) examined flight distances of 44 bird species with various levels of tolerances of urban environments and found that urban birds tended to have shorter flight distances than their rural counterparts. A selective advantage of reduced flight distance in urban environments might be related to a release from predation pressure as predators generally show higher levels of fear of humans than their prey (Møller 2012). Supporting this possibility is the observation that the number of generations since urbanization was associated with flight distance suggesting that this could possibly be an adaptive process (Møller 2008). It is also not difficult to conceive of a scenario, whereby individuals that tolerate humans gain access to resources (e.g. feeders, refuse, nesting sites) unavailable to more skittish individuals. These and other hypotheses about the nature of the relationship between variation at this locus and the environment are not mutually exclusive and could be tested by experimental transplants and by collecting longitudinal data involving the monitoring of marked individuals.

This work highlights the scope for interesting questions about the colonization of, and adaptation to novel environments, to be addressed by examining familiar species with which many people interact daily. Looking forward, there are many open questions about how, and in what way, natural populations are affected by the presence of humans and the nature of their coexistence. Understanding how the spatial heterogeneity induced by urban environments, both within urban populations and among the larger metapopulation, contributes to neutral and adaptive components of population genetic structure is both fundamentally interesting and important for conservation. Mueller *et al.* (2013) provide important evidence that homogeneous selection pressure across urban environments can occur at time-scales associated with the process of urbanization; putting putatively important candidate genes into an ecological context is a crucial next step for understanding selection in urban environments. We can hope, optimistically, that selection will continue to be as effective in rescuing populations as it has been in the face of past natural environmental change and facilitate population persistence. Pessimistically, it is clear that some environments are changing at unprecedented rates; too fast for adaptive evolution. Regardless, studies such as this one will be important for understanding and predicting the effects of urbanization.

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References

- Evans KL, Gaston KJ, Frantz AC *et al.* (2009) Independent colonization of multiple urban centres by a formerly forest specialist bird species. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2403–2410.
- Evans KL, Hatchwell BJ, Parnell M, Gaston KJ (2010) A conceptual framework for the colonisation of urban areas: the blackbird *Turdus merula* as a case study. *Biological Reviews*, **85**, 643–667.
- Garroway CJ, Bowman J, Wilson PJ (2011) Using a genetic network to parameterize a landscape resistance surface for fishers, *Martes pennanti*. *Molecular Ecology*, **20**, 3978–3988.
- GHFD Global Human Footprint Dataset (2005) Wildlife Conservation (WCS) and Center for International Earth Science Information Network (CIESIN). www.ciesin.columbia.edu. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Available at: <http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic> (accessed 1 March 2013).
- Kempenaers B, Borgström P, Loës P, Schlicht E, Valcu M (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, **20**, 1–5.
- Miller MW (2006) Apparent effects of light pollution on singing behavior of American robins. *The Condor*, **108**, 130–139.
- Miller PJO, Biassoni N, Samuels A, Tyack PL (2000) Humpback whales sing longer songs when exposed to LFA sonar. *Nature*, **405**, 903.
- Møller AP (2008) Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, **63**, 63–75.
- Møller AP (2012) Urban areas as refuges from predators and flight distance of prey. *Behavioral Ecology*, **23**, 1030–1035.
- Mueller JC, Partecke J, Hatchwell BJ, Gaston KJ, Evans KL (2013) Candidate gene polymorphisms for behavioural adaptations during urbanization in blackbirds. *Molecular Ecology*, **22**, 3629–3637.
- Sanderson E, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.
- Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, **109**, 16083–16088.
- Slabbekoorn H, Peet M (2003) Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.
- Smith TB, Bernatchez L (2008) Preface to the special issue. Evolutionary change in human-altered environments. *Molecular Ecology*, **17**, 1–8.
- Tuomainen U, Candolin U (2011) Behavioural responses to human-induced environmental change. *Biological Reviews*, **86**, 640–657.
- United Nations World Urbanization Prospects (2011) *The 2011 Revision*. United Nations Department of Economic and Social Affairs/Population Division, New York, NY. Available at: <http://esa.un.org/unpd/wup/index.htm> (Accessed February 6, 2013)
- Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

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