For submission in Int Comparative Biol, invited introduction to symposium Behavior and physiological adaptations to urban environments

A new framework for urban ecology:
An integration of proximate and ultimate responses to anthropogenic change

Jenny Q Ouyang[1*], Caroline Isaksson[2], Chloé Schmidt[3], Pierce Hutton[4], Frances Bonier[5], Davide Dominoni[6,7]

[1] Department of Biology, University of Nevada, Reno, Reno, NV USA
[2] Department of Biology, Lund University, Lund, Sweden
[3] Department of Biological Sciences, University of Manitoba, Manitoba, Canada
[4] School of Life Sciences, Arizona State University, Tempe, AZ USA
[5] Biology Department, Queen's University, Kingston, ON Canada
[6] Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands
[7] Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

[*] To whom correspondence should be addressed: Department of Biology, University of Nevada, Reno, 1664 N Virginia St., Reno, NV 89557. Telephone: 805-703-4135 Email: jouyang@unr.edu

Keywords: urbanization, light pollution, air pollution, noise pollution, adaptation, life-history, fitness, physiology, behavior

Abstract

As urban areas continue to grow, understanding how species respond and adapt to urban habitats is becoming increasingly important. Knowledge of the mechanisms behind observed phenotypic changes of urban-dwelling animals will enable us to better evaluate the impact of urbanization on current and future generations of wildlife and predict how animals respond to novel environments. Recently, urban ecology has emerged as a means of understanding organismal adaptation but also as a framework for exploring mechanisms mediating evolutionary phenomena. Here, we have identified four important research topics that will advance the field of urban ecology and shed light on the proximate and ultimate causes of the phenotypic differences commonly seen among species and populations that vary in their responses to urbanization. First, we address the ecological and socio-economic factors that characterize cities, how they might interact with each other, and how they affect urban species. Second, we ask which are the proximate mechanisms underlying the emergence over time of novel traits in urban organisms, focusing on developmental effects. Third, we stress the need to understand the ultimate causations that link phenotypic shifts to function. This question highlights the need to quantify the strength and direction of selection that urban individuals are exposed to, and whether the phenotypic shifts associated with life in the city are adaptive. Lastly, we stress the need to translate how individual-level responses scale up to population dynamics. Understanding the mechanistic underpinnings of variation among populations and species in their responses to urbanization will unravel species resilience to environmental perturbation, which will facilitate predictive models for sustainability and development of green cities that maintain or even increase urban biodiversity and wildlife health and wellbeing.

Introduction

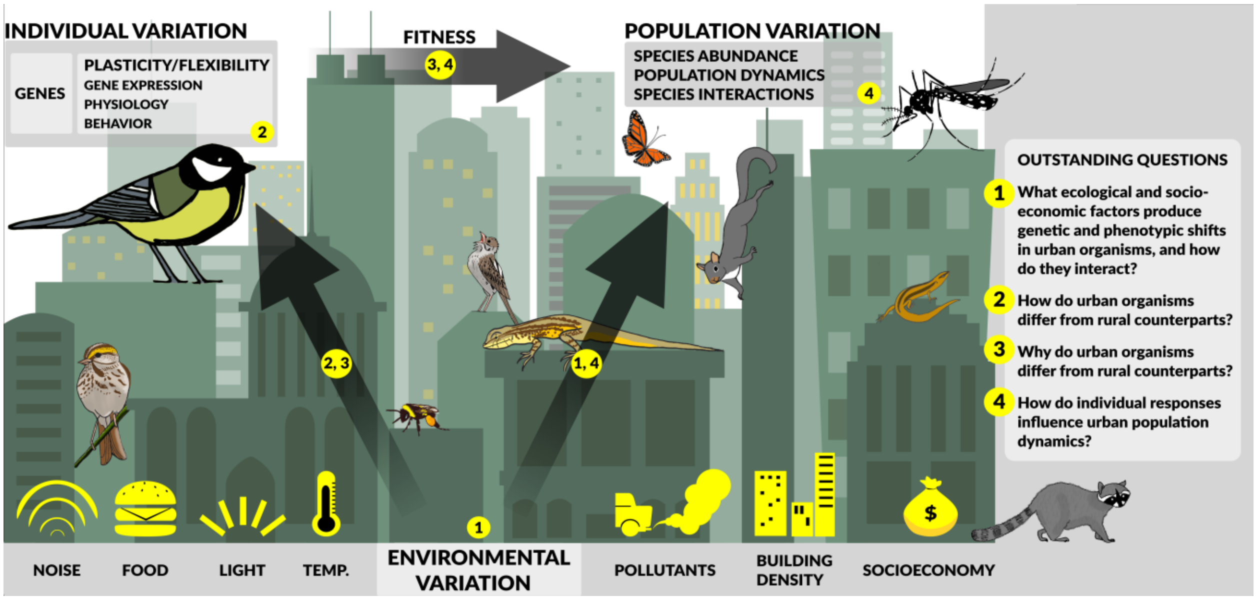
A prevailing source of environmental change in the 21st century is rapid human population growth in urban areas. Today, 54% of the world's human population lives in urban areas, and by 2050, this number is expected to increase to 66% (United Nations 2014). Urban land cover continually expands to accommodate this growth, leading to the destruction of natural habitat and reduced biodiversity as a result of local extinction processes (Kalnay and Cai 2003; While and Whitehead 2013). Responses to these changes vary considerably between and within species. Indeed, some species are unable to occupy urban habitats (urban avoiders) while others persist (urban adapters) and even thrive (urban exploiters; Blair 1996; Moller 2009; Sepp and others 2017; Sol and others 2014). Similarly, it has been suggested that within species, only individuals possessing certain traits may be able to colonize urban areas (Sol and others 2013; Sprau and Dingemanse 2017). Recently, interest in urban ecology has grown exponentially, as evidenced by a proliferation of empirical studies, meta-analyses and reviews (LaPiedra this issue; Mulholland and others this issue; Audet and others 2016; Goddard and others 2010; Liker and others 2008; Marzluff 2017; McIntyre 2000; Sepp and others 2017; Tucker and others 2018).

Present and past research in urban ecology has primarily focused on two questions: 1) do urban and rural populations differ in certain traits? and 2) do urban and rural areas differ in biodiversity and/or species abundance? The evidence accumulated so far points to globally widespread influences of urbanization on phenotypes (Alberti et al 2017). Likewise, urbanization has been linked to profound and complex effects on biodiversity, which is often greatly reduced at intense levels of urban development, but can also flourish in sub-urban and peri-urban areas (Aronson Myla and others 2017). As these two questions have already been widely investigated, we now need a deeper understanding of how and why patterns of phenotypic shift and biodiversity emerge in cities. To do so, we draw on Niko Tinbergen's four questions of 'survival value', 'ontogeny', 'evolution' and 'causation' (Tinbergen 1963). In the context of an integrative framework for urban ecology, we first need mechanistic studies that examine how novel phenotypic traits emerge in urban areas, focusing on ontogeny, developmental plasticity and co-variation between different behavioral and physiological traits. We then need to identify whether phenotypic responses of urban populations are adaptive, what their function is, and to which urban-specific selective pressures they are subjected. The question of whether populations truly adapt to urban life (via genetic change and local adaptation) or only acclimate (via plasticity) is difficult to resolve (Isaksson 2015; Tucker and others 2018). It is thus important to investigate proximate mechanisms, including genetic and epigenetic effects underlying the emergence of novel traits at the individual level (Sol and others 2013), the modification of existing traits (Badyaev and others 2008), or the filtering of individuals and species possessing specific traits from an original, non-urban population (Banaszak-Cibicka and Żmihorski 2012; Moller 2009; Sol and others 2014). Individual responses can then be tied to population dynamics by quantifying how fitness of urban individuals scale up to influence the demography of populations. To date, few studies have successfully integrated all of these components (but see Badyaev and others 2008).

Moreover, the field of urban ecology is hindered by the lack of a clear, standardized approach to quantifying urbanization. Cities are extremely complex environments that differ in ecological, structural, and socio-economic characteristics; such variation also exists within cities. This limits our ability to design comparative studies and interpret their results (Aronson and others 2014; Moller 2009; Ramalho and Hobbs 2012; Sepp and others 2017; Sol and others 2014). Further, the majority of urban ecology studies to date have focused on only one or a few urban and rural areas (e.g., Fokidis and others 2009; Foltz and others 2015; Partecke and others 2005). Given the potentially important effects of variation among cities, our ability to generalize from these focused studies is uncertain.

Outstanding questions

We have identified four pressing topics that will advance our knowledge of individual and population-level responses to urban environments. In the following sections, we give background to each question, outline gaps in knowledge, and suggest how these gaps can be addressed (Figure 1).



OUTSTANDING QUESTIONS

1 What ecological and socio-economic factors produce genetic and phenotypic shifts in urban organisms, and how do they interact?

2 How do urban organisms differ from rural counterparts?

3 Why do urban organisms differ from rural counterparts?

4 How do individual responses influence urban population dynamics?

Figure 1. Outstanding questions for urban ecology (1-4) in the context of environmental, individual, and population variation. Pictured are some representative common animals found in cities around the globe. Environmental variation can affect individual and population-level variation. Individual variation affects individual fitness which then can lead to changes at the population-level.

1. What ecological and socio-economic factors produce the observed genotypic and phenotypic shifts in urban animals, and how do they interact with each other?

1.1 Background

Cities are complex environments. There are large differences both within and between cities in age, climate, habitat structure, human population density, and socio-economic development. All these factors could contribute to the observed phenotypic and genotypic shifts observed in urban populations of wild species, and variation in those patterns. For example, wealthier cities in developed nations may have more urban parks and green spaces whereas poorer cities may have fewer “managed” green spaces. The management of green space, as well as of urban waste, can have important consequences on the availability of food and nest sites for urban fauna. However, it is often unclear which factors are playing major roles. The reason has partly to do with sampling protocols, as few studies are explicitly designed to disentangle the effect of single factors. Nevertheless, global analyses of biodiversity datasets in urban areas have identified key ecological drivers of biodiversity loss due to urbanization, especially land cover (for instance the proportion of impervious surface) and the age of a city (Aronson and others 2014; Goddard and others 2010). In addition, socio-economic factors have also been shown to influence biodiversity (Aronson Myla and others 2017; Hope and others 2003; Kinzig and others 2005). Conversely, studies that have thoroughly disentangled the effects of urban-specific factors on individual rather than on how different species respond are lacking, and this knowledge gap limits our understanding of whether specific city traits may influence adaptation to urban areas.

1.2 Gaps in knowledge

a. How do we define and quantify what urban is (and is not)?

Defining what is urban and what is not is anything but trivial and perhaps only useful from a semantic point of view. Likewise, the term rural can also refer to villages, agricultural fields, wind farms, or energy extraction sites in forests. The important distinction for this field is to quantify the factors that are associated with urban or rural environments, and move away from categorical designations of these areas. A vast proportion of urban ecology studies defines urbanization only qualitatively, and refer to study sites as urban, sub-urban, peri-urban, or rural simply based on the researchers’ own knowledge of the study area. Other studies rely on satellite-based images to quantify land-cover types and categorize them as urban, for instance by using the proportion of impervious surface in a given area around a study site. Recent work has incorporated several landscape attributes in multi-variate analyses (for instance Principal Component Analyses) to compute an integrated “urban score” to be used in subsequent models aimed at testing the effect of urbanization on biodiversity or individual-based variables (Giraudeau and others 2014; Sprau and others 2017). While such compound variables can have the benefit of defining the “citiness” of a particular sampling location, specific environmental variables may play a disproportionately stronger role than others in particular conditions. Depending on the research question of interest either method can have its own merit. Moreover, most definitions of urbanization have so far focused on cross-sectional samplings of environmental variables along urban gradients. Such a methodology fails to take into consideration the complex spatio-temporal dynamics of urban sprawl (Ramalho and Hobbs 2012). In a recent study by Salmón and others (2018), they showed that by performing a spatio-temporal modelling on nitrogen oxide (NO_x) pollution, the long- and medium-term pollution models (one-month and one-week) were highly associated with urbanization scores of the habitat. However, short-term variation in NO_x (24-hours) was not associated with the scoring of urbanization, or with various oxidative stress parameters measured in four species of songbirds. This finding may not be surprising given the importance of local weather conditions for daily pollution estimates which do not affect other parameters of urbanization; however, approaches like this might provide a better understanding of whether a behavioral and physiological trait is an acute response to a specific and current stressor or a more long-term response to the urban environment. Although the urbanization score and NO_x modelling revealed similar large-scale patterns on physiology, it also revealed that the fine-grained resolution in the NO_x models gave better power to detect smaller effects on physiology compared to the more general urbanization scores (Salmón and others 2018). Further, urbanization often proceeds non-linearly and at different speeds in different spatial directions. The result of this process is a mosaic of urban patches embedded into a matrix of remnant natural habitats.

Each of these urban patches has its own history of urbanization. To recognize such complexity might explain large portions of variation in species abundance and diversity, and individual responses to the urban environment.

b. *Can we model "city traits" in comparative global analyses?*

The need to generalize the effects of urbanization has promoted studies at the global level. We advocate the need for such global studies, but we also think that we need to take into consideration within- and between-city differences in urbanization. Cities differ dramatically in the way they have been built in regard to the speed and pattern of urban sprawl, and this is especially evident when cities from different continents are compared (Ramalho and Hobbs, 2012). Moreover, cities differ also in the matrix habitat they are built in, mostly depending on the geographic area they are located. For instance Phoenix, a global hotspot of urban ecology research, is a relatively isolated urban area surrounded by desert habitat. Conversely, New York City is located in a heavily urbanized metropolitan area surrounded by temperate habitat with mixed deciduous and evergreen vegetation. The variation in the matrix habitat could also generate important variation in findings and thus may at least partially explain why the same species can show different responses in different cities, or in different areas within the same city (Evans and others 2009). If not accounted for, this variation may limit our ability to generalize from studies that focus on only one or a few cities. To take into account such variability and assign traits to different urban areas based on their ecological characteristics is likely to enhance the quality of global comparative analyses. Moreover, including in such analyses not only ecological but also socio-economic variables will likely improve the quality of the outcomes, as it is increasingly recognized that the type and history of urban development is crucial in determining its impact on biodiversity (Aronson Myla and others 2017; Hope and others 2003; Kinzig and others 2005).

c. How do different urban-specific ecological factors interact to affect individual and species response?

Most studies aimed at testing the effects of urbanization on individual and species response have so far mostly focused on urbanization as a whole (see section 3). In the last couple of decades urban-specific environmental factors such as anthropogenic light (Ouyang and others 2018; Swaddle and others 2015), noise (Halfwerk and Slabbekoorn 2013; Slabbekoorn and Ripmeester 2008), air pollution (Greaver and others 2012; Salmon and others 2018), toxicants (Snell Rood and others this issue; Järup 2003), temperature (Arnfield 2003; Brans and others 2017) or human presence (Chace and Walsh 2006; Corsini and others 2017) have also been the focus of field studies and captive experiments. Recent studies have also tried to disentangle the relative contribution of some of these factors (Da Silva and others 2014; Dominoni and others 2014; Sprau and others 2017). However, experiments are usually designed to separate the effects of these urban factors rather than explicitly testing their interactive effects (but see McMahon and others 2017). Future studies should focus on the outcomes of such interactions and whether they produce synergistic (additive, multiplicative, etc.) or antagonistic effects. Recent studies have proposed integrated frameworks to address interactions between different stressors/stimuli that might be useful in the context of urban ecology as well (for instance, see Hale and others 2013).

1.3 Significance and future prospects

To comprehensively understand how environmental variation influences individual, population and species responses is a challenge that every ecologist is likely to face. To further add the complexity of the urban environment on this challenge can be daunting. However, it is a challenge that needs to be met to advance urban ecology research. To do so, we need to recognize and understand the complexity of the urban habitat, and specifically: i) measure as many ecologically relevant variables as possible, including characteristics of the matrix around cities ii) measure socio-economic factors, iii) consider the spatial and temporal variation of such variables between and within cities, iv) consider the age and the history of development of a particular urban area, and, finally, v) design studies aimed at testing the interaction between different urban-specific factors. We believe that integrated, precise measurements of urbanization will ensure that each individual analysis will be robust, and will also improve the quality of large-scale comparative analyses.

2. How do urban organisms differ from their rural counterparts? A multi-trait, integrative approach.

2.1 Background

A growing body of evidence describes behavioral and physiological differences between urban and rural populations, and phenotypic shifts associated with urbanization have been globally demonstrated in plants and animals (see Alberti and others 2017 for a review). However, both behavioral and physiological shifts due to urbanization are not always consistent within the same species measured in different cities (Evans and others 2011; Ibáñez-Álamo and others 2017), and even less between closely related species (LeFebvre and others this issue; Alberti 2015; Moller 2009; Sol and others 2013). For instance, endocrine traits of birds show no general pattern of response to urbanization (Bonier 2012). Similarly, while levels of oxidative stress levels correlate overall positively with the degree of pollution, species-specific differences exist (Isaksson 2010; Salmon and others 2018). We stress that while the lack of general patterns often reported might come partly from environmental differences among urban areas, it is also important to recognize the need to shift from the paradigm of investigating one phenotypic trait in one urban area to a more holistic understanding of how populations respond to urbanization by integrated measures of different traits at different levels of biological organization (e.g., gene, physiology, behavior), their co-variation, and the underlying mechanistic links between them. Moreover, although evidence points to phenotypic differences between urban and rural populations, we still do not understand how these differences arise. Specifically, these may come about via plastic (non-genetic) or evolutionary (genetic) responses. Thus far, evidence documenting either of these two processes is still relatively rare (Johnson and Munshi-South 2017). Furthermore, trait differences can arise as a result of founder effects, and insights from invasion ecology point to phenotype-dependent dispersal (Chapple and others 2012). An additional level of complexity is given by potential non-random distributions of phenotypes in urban settings (Sprau and Dingemanse 2017). In this section, we want to highlight how these different processes can be unraveled through exploring underlying mechanisms for the observed patterns and through robust, integrative experimental designs.

2.2 Gaps in knowledge

a. Are multiple, correlated physiological and behavioral traits similarly affected by urbanization?

Research in urban ecology has typically focused on one or in very rare cases, a few traits (Badyaev and others 2008; Sol and others 2013). However, an organism’s interaction with the environment is both perceived at the neuroendocrine level as well as translated into behaviors (Adkins-Regan 2005). In particular, a specific behavior might originate from a single physiological pathway, or might be the result of a suite of physiological changes (Cohen and others 2017; Ouyang and others 2016). When studying covariation between physiology and behavior, we should distinguish between correlational and causal effects. For example, cause and effect can be demonstrated as physiological mechanisms that influence behavioral traits whereas feedbacks can also occur in which physiology affects behavior, which then feeds back to affect physiology (Sih and others 2015). Thus, to fully appreciate how behavioral shifts occur in urban populations, the potential physiological pathways underlying such shifts need to be measured in conjunction. Studying how behavior and physiology feedbacks change with urbanization gives insight into ecological processes such as niche expansion, dispersal, and social organization (Réale and others 2007). Individual variation in behavioral and physiological traits affect key ecological and evolutionary processes: the pattern of phenotypic variation determines the outcome of natural selection and affects competition and the structure of ecological networks (Wolf and Weissing 2012; Wong and Candolin 2015).

In addition, recent research has highlighted that environmental change can alter the relationship between physiology and behavior. In normal conditions, physiological and behavioral responses might not be correlated with each other, but such relationships can arise when animals are exposed to environmental stressors (Killen and others 2013). The opposite can also occur (Hutton and others this issue; Killen and others 2013; Welbers and others 2017). Thus, to repeatedly measure the co-variation of physiological and behavioral traits in the same individual, for instance during different seasons or times of day, might shed light on specific ways that urbanization affect animals.

Another important aspect to consider is how urbanization affects behavioral traits that are normally correlated with each other. Indeed, recent studies suggest that organisms often exhibit behavioral syndromes, that is, suites of correlated behaviors across time and context (Sih and others 2004). The existence of these syndromes indicates that there is a limit to the range of behavioral plasticity expressed by an individual, and thus highlights the need to track individuals across space and time to capture such plasticity. In summary, we believe that the study of correlated traits across situations and biological levels (e.g., physiology and behavior) would promote a deeper understanding of how urbanization affects phenotypes. In essence, when traits are correlated, e.g., different behaviors, or behaviors with physiological traits, they should be studied together longitudinally, rather than in isolated packages, as they have mostly been thus far (but see Charmantier et al 2017).

b. What role do ontogeny, plasticity and evolution play in generating the phenotypic variation associated with urbanization?

Plasticity is the first line of response when an individual is exposed to novel environments and stimuli, such as those that exist in urban areas, and it defines the potential of an organism to acclimate to these novel environmental conditions. Such plasticity can manifest itself during development or in adulthood. Unfortunately, studies on how ontogenetic (developmental) plasticity in urban organisms may promote phenotypic differences in adulthood are very rare. An exception is the work on house finches by Badyaev and collaborators. Urban house finches in Tucson, AZ, possess larger and stronger beaks compared to their desert conspecifics (Badyaev and others 2008), which confer a fitness advantage, e.g., higher juvenile survival, because they enable them to crack open and eat the larger seeds and nuts provided in garden feeders (Badyaev 2010). The researchers studied the developmental basis of this divergence in beak morphology in adulthood, demonstrating an earlier and accelerated tissue transformation in urban versus desert house finch embryos. Indeed, the mandibular primordia of the large-beaked urban finches express bone morphogenetic proteins (BMP) earlier and at higher levels than those of the desert finches during embryonic development, leading to stronger beaks in adulthood (Badyaev and others 2008). Studies like these can shed light onto the ontogenetic basis of phenotypic differences due to urbanization. Understanding the control system that underlies trait variation can help elucidate the evolution of reaction norms. For example, control systems can impose constrains if they cannot produce the optimal reaction norm, and can create addition pressures if the system is costly (Lessells 2008).

Moreover, quantifying the extent of reversible phenotypic plasticity in adulthood is also important, as it might underlie the capacity of individuals to respond to rapid environmental changes taking place during urban development. Such plasticity can be studied via translocation studies or testing how the same individuals respond to repeated, experimental exposures to urban challenges. We can also use laboratory studies to measure plasticity in a controlled setting. It is important to note that not all plasticity is adaptive. Anthropogenic environments may be ecological traps, such as the case of dark beetles that are killed in managed forests when they are attracted to forest fuel piles that are then milled (Hedin and others 2008). Maladaptive behaviors are likely to occur when animals encounter very different conditions, e.g., urban environments, from those that shaped their traits under previous selection (Hale and others 2016). Distinguishing between adaptive and maladaptive plasticity and their degree of flexibility will be important for understanding whether urban environments act as evolutionary traps or promote adaptive evolution (Hale and others 2016; Robertson and others 2013).

It is important to recognize that without robust experimental design, plastic, non-genetic responses can be easily confounded with genetic responses. For instance, while common-garden experiments are a common way to disentangle genetic versus environmental effects on behavior and physiology, they often lack to control for the potential effect of parental and early-environmental influences on phenotypes (Dominoni and others 2013; Partecke and others 2005). Recently, Brans and others (2017) used a multi-generational common-garden experiment with *Daphnia* to ask whether urban *Daphnia* have evolved higher heat-tolerance than rural water fleas. By breeding both the parental and F1 generation in a common environment, the authors limited the effect of any potential non-genetic influence on the results. They found higher heat tolerance in animals descended from individuals collected from urban ponds compared to descendants of individuals collected from rural ponds, partly mediated by smaller body size, suggesting adaptive thermal evolution in urban *Daphnia*. Similar studies will be instrumental in disentangling genetic and non-genetic responses to urbanization.

Furthermore, we also need to stress that the emergence of specific urban phenotypes might simply be a consequence of non-random distributions of phenotypes in urban settings, pre-selected from existing rural populations during the process of urbanization. In other words, urbanization might filter species, populations, and individuals on the basis of whether or not they possess traits that make them suitable to colonize and thrive in cities. The ideas of urban habitats being “filters” has been examined largely in community ecology (Banaszak-Cibicka and Żmihorski 2012; Croci and others 2008; Maklakov and others 2011), in which species have been identified as “winners or losers.” Much less attention has been devoted to the same process acting at the individual level within a population (but see Charmantier and others 2017; Sprau and Dingemanse 2017), and we consider this as a ripe research field.

2.3 Significance and future prospects

To make strides in answering these questions, we need to not only measure phenotypic traits but we also need to measure these traits in conjunction, such that we can have information on (co)variation between and within individuals. To date, there are very few studies that have measured multiple behavioral traits (e.g., song, boldness, exploration) and multiple levels of causation (e.g., differences in physiology and morphology) within urban and rural populations and the few that have done so have been key in establishing trait covariance. To disentangle the role of parental, early developmental, environmental or genetic effects in producing organisms that avoid or exploit urban environments, we need to design robust experiments, for instance cross-fostering or common-garden experiments (Brans and others 2017; Capilla-Lasheras and others 2017; Partecke and others 2006; Kobiela and Snell-Rood this issue; Salmon et al this issue). Lastly, with the growing amount of individual-based data collected, we should integrate between different levels of organization, e.g., genetic variation, epigenetic variation, gene expression, physiology, and behavior, to form of a holistic understanding of how new behaviors and life-histories emerge in urban environments.

3. Why do urban organisms differ from their non-urban counterparts?

3.1 Background

Urban environments are relatively novel and are characterized by several anthropogenic factors, e.g., increased anthropogenic food, light and noise levels, that make them unique. Hence, cities present wildlife with novel environmental conditions that are dramatically different from those under which they have evolved. Some of these conditions might exert strong selective pressures on urban organisms

(Johnson and Munshi-South 2017). Consequently, cities can be seen as hubs of evolution in action. In fact, there has been a recent surge of interest in studying evolution in cities (see Johnson and Munshi-South 2017 for a review). Thus far, population genetic studies have been instrumental in this field. For example, Mueller and others addressed the genetic nature of behavioral adaptation of blackbirds colonizing urban areas (2013). They found evidence for consistent patterns of divergence between paired urban and rural birds at a microsatellite associated with the SERT gene. SERT has a number of hypothesized behavioral effects, including harm avoidance, which may be associated with tolerating the challenges of urban environments (Garroway and Sheldon 2013). Similarly, researchers have found that past history of urbanization of New York City is paralleled with changes in the genome and demographic history of the white-footed mouse (Harris and others 2016). Using RAD sequencing, Perrier and others found a small but significant effect of urbanization on genetic differentiation in European great tits (Perrier and others 2017). However, population genetic studies in urban ecology are still relatively rare and provide a very limited taxonomic sample. With molecular tools becoming cheaper and more accessible, much can be gained from investigating the consistency of the effects of urbanization on the spatial distribution of genetic diversity, the polygenic nature of gene–urbanization association, and potential signatures of selection in the genome of urbanized species (Bosse and others 2017).

Despite population genetics being a useful tool to highlight evidence of genetic adaptation to urban life, it does not help us to fully understand why within a species urban organisms differ from their rural counterparts. In order to achieve this, we need to integrate genetic variation data with information on the strength of selection on a particular trait and its fitness value. For instance, several urban-specific environmental factors have been proposed to explain variation in life-histories associated with urbanization: food limitation, predation, anthropogenic pollution, etc. (Sepp and others 2017). However, how these factors translate into selective pressures in urban environments is largely unknown. Moreover, how does individual fitness respond to spatio-temporal variation in such pressures along gradients of urbanization? And what traits are under selection? Quantifying selective pressures and obtaining long-term fitness data (in particular lifetime reproductive success) in urban environments remain daunting tasks, but key to understanding the evolution of urban-specialized traits.

3.2 Gaps in knowledge

a. Are behavioral/physiological changes in urban individuals adaptive?

We still do not have a clear understanding whether behavioral or physiological changes in urban individuals are adaptive or maladaptive. Repeatability, measured as the fraction of phenotypic variation that is due to differences among individuals relative to differences within an individual, can set the upper bound to heritable variation. However, for most traits we have no estimates of heritability or repeatability and no information if they change along urban gradients (Jenkins and others 2014, Salmon and others this issue; Ouyang and others 2011). To fill these gaps, we would first need repeated measures of a trait within the same urban individuals. Then, we would need to measure the relationship between this trait and individual fitness. Last, we would need to assess how such a relationship might be affected by urban-specific environmental factors, to assess the strength of selection acting on the trait (see also next section). As an alternative perspective, top-down approaches using genomic data could be used to assess signatures of selection. For example, a large genomic dataset in European great tits suggests that beak shape and size evolved rapidly as a result of domestic garden feeders (Bosse and others 2017; but see Perrier and Charmantier 2018).

b. What are the selective pressures that urban animals respond to?

Very few studies have quantified the selection pressures that urban animals are responding to. Selective pressures in urban environments, such as temporal variation in food, water, and predation, are often relaxed (Jokimäki and others 2002; Marzluff 2017). Urban environments exhibit a range of changed ecological processes, e.g., increased primary productivity. To illustrate, although concrete surfaces in cities represent a net primary productivity of zero, city parks, gardens and golf courses elevate local productivity relative to surrounding rural areas, with these green spaces lying close to the highest end of the productivity continuum (Kaye and others 2005). These ecological processes should alter selective forces in cities, and might lead to the genetic differentiation of urban and wild populations. Alternatively or in conjunction to this, genetic changes associated with isolated wild populations due to habitat fragmentation may on one hand result from increasingly urbanized landscapes (Shochat and others 2006). On the other hand, continuous migration and gene flow, for instance in highly mobile species such as birds, might prevent the genetic differentiation of urban populations and dampen evolutionary responses.

As we highlighted above, to understand the evolutionary implications of urbanization it is imperative to obtain fitness data, preferably through experimental work in order to disentangle the fitness responses to different urban-specific environmental factors. In terms of reproductive success, food availability and quantity is often one of the characterized environmental traits, as least in avian systems (Schoech and others 2009). Higher food availability is generally associated with increased reproductive success (Verboven and others 2001) and earlier timing of reproduction (Schoech et al 2009) in urban animals. However, urbanization may also be associated with a reduction in the quality of food, for instance via reduced availability of optimal diets, and this component is not always appreciated. Recently, a reduction of food quality was linked to reduced reproductive success in birds (Pollock et al 2017) and higher disease susceptibility in coyotes (Murray et al 2015). In terms of survival, there is no study that we are aware of that has characterized both how urban animals die and what selective pressures affect their survival, so it remains a clear research gap for urban evolutionary biology.

c. Do phylogenetically related species respond similarly to urbanization?

In a review of >800 avian species across five continents, Sol and others found that most of the biodiversity loss can be attributed to a lack of appropriate adaptations for exploiting resources or avoiding risks associated with urbanized environments (2014). Importantly, closely related species tended to respond to urbanization in the same way, e.g., avoider or exploiter, possibly sharing features that affect their tolerance to urban development (La Piedra this issue). Moreover, recent work has also pointed to the reduction of avian phylogenetic uniqueness in urban habitats, which raises conservation concerns (McKinney 2006). These studies are a good start to answering this question and should be expanded to systems other than birds. In conjunction, a global network of researchers that work on the same system, e.g., house sparrows or *Anolis* lizards, may be useful to explore fundamental questions in different cities across the globe.

3.3 Significance and future prospects

These evolutionary and ultimate questions need data on life-time fitness that are often missing in field studies. In order to understand the forces of selection, we need basic information on the genetic variation of many of the behavioral or physiological traits that we are measuring. For example, we need to measure heritability and repeatability of key traits to quantify if these may constitute substrates of selection, and then measure selection coefficients. With selection coefficients, we can predict the rate of change in a trait over time and over different environmental conditions, to predict how likely a trait would be able to respond to current and future environmental change. However, it is important to note that phenotype-fitness relationships can be biased and generated by adaptive plastic responses to the environment (Bonier and Martin 2016). Moreover, we can use quantitative genomics to link genotype with phenotype. To measure evolutionary routes, we need to know which selective pressures promote trait divergence. Likely, this will include quantifying environmental factors and testing these factors using common-garden experiments in the lab. We can use phylogenetic relatedness to our advantage by comparing similar and dissimilar species pairs' responses to environmental factors that characterize cities. Lastly, comparative phylogenetic models can predict how species may respond to urbanization especially for non-avian taxa, i.e., comparing phylogenetically similar species. In summary, greater attention should be paid to urban evolutionary aspects because the type and direction of physiological, behavior, and morphological changes can indicate how selective forces in urban environments differ from those in habitats less affected by humans.

4. How do individual-level responses influence population dynamics in urban areas?

4.1 Background

We mentioned in the introduction that research in urban ecology has so far primarily focused on questions related to how urbanization affects i) population-level (urban vs rural) phenotypic responses (Alberti and others 2017) and ii) biodiversity (Aronson Myla and others 2017; Beninde and others 2015). Despite the large number of studies that have investigated these questions, there is comparatively little knowledge about if and how the two aspects are linked. Urbanization is known to affect several demographic parameters, such as reproductive success and fertility, mortality, and longevity (although examples of longevity are rare; Chamberlain and others 2009; Sepp and others 2017). However, how these demographic effects translate into changes in population dynamics and ultimately into the likelihood of a species to increase or decrease in abundance over time is a somewhat neglected aspect of urban ecology. A mechanistic appreciation of the demographic processes that regulate urban populations is imperative if we want to understand how urbanization affects species abundance and biodiversity. Thus, we believe it should be a major focus of urban ecology research in the near future. Moreover, most studies so far have utilized a cross-sectional approach, comparing demographic traits and species abundance levels across gradients of urbanization or in paired urban/rural sites. While this approach is useful to identify *patterns* of changes in demography and biodiversity associated with urbanization, its utility for understanding the *processes* underlying these changes is limited. Alternative approaches, for instance longitudinal demographic analyses during different stages of urban development, or meta-population modelling, might be much more informative of such processes, drawing from the existing tools used in the fields of invasion biology and behavioral ecology.

4.2 Gaps in knowledge

a. What is the impact of urbanization on components of fitness?

The need to obtain accurate demographic data is imperative to assess not only the impact of urbanization on fitness, but also the selective forces acting on urban populations (see section 3), and the consequences of such demographic changes for the persistence of wild species in urban areas. For instance, there is mounting evidence that passerine birds have reduced reproductive success in urban areas. This is partly due to reduced investment in clutch size (Chamberlain and others 2009; Sepp and others 2017), but also to poor diet and health in early life which may reduce both pre- and post-fledging survival (Bailly and others 2016; Capilla-Lasheras and others 2017; Pollock and others 2017; Rodewald and others 2013; Salmón and others 2017; Smith and others 2016). However, most of these studies were limited to one or few years, whereas studies that have measured lifetime reproductive success (the most compelling fitness measure) in urban populations are non-existent. Similarly, there are very few examples of urban populations in which survival and especially longevity are measured accurately for most individuals (but see Sepp and others 2017). A key challenge is therefore to move towards long-term monitoring of urban populations in order to obtain high quality data on individual reproduction and survival.

b. How are such changes in individual fitness linked to population dynamics in urban areas?

Very few studies have assessed population dynamics of species in urban areas (but see Balogh and others 2011; Harveson and others 2007; Riley and others 2003). Such lack of knowledge limits our capacity to understand the drivers of change in population abundance associated with urbanization, as well as whether urban populations are sources or sinks. Likewise, evolutionary traps and range shifts are likely to interact as animals respond to rapid urbanization (Hale and others 2016). If colonizers are more likely to encounter traps as they explore novel urban environments, what happens to these phenotypes and would they be removed from these environments? Perhaps the phenotypic traits that make an urban colonizer successful are not those that would persist in urban environments. Hence, it will be important to measure range shifts and dispersal strategies. In a recent study, Smith and co-authors (2016) have used a three-year dataset on reproductive success and annual survival to build a stochastic demographic model and estimate population growth rate for spotted towhees (*Pipilo maculatus*) in four parks in Portland, OR, USA. Their model revealed that despite high levels of annual reproductive output, post-fledging survival can be very low. This pattern suggests that some urban populations might be sinks and must rely on immigration from source areas to be sustained. However, immigration as well as dispersal rates were not measured in this study. To obtain such estimates in urban areas where populations are likely to be distributed within a mosaic of small to large patches of remnant habitat can be daunting, but nevertheless essential for the understanding of population dynamics and the ecological connectivity of urban landscapes (LaPoint and others 2015). Biotelemetry studies conducted in urban areas are increasing in number and scope (LaPoint and others 2015), and we advocate more use of these tools to assess movements between sub-populations and thus inform metapopulation models with emigration and immigration rates. Alternatively, genetic information can be used to assess the direction and strength of gene flow and demographic history (Andreasen Alyson and others 2012; Gaggiotti and others 2009).

c. When are changes in individual fitness reflected in demographic changes during progressive urbanization?

An important aspect to consider when assessing the demographic consequences of urbanization, and thus its effects on biodiversity, is not only *how* and *why*, but also *when* during the different stages of urban development a species begins to show changes in demographic parameters that can lead to changes in abundance. It is important to also assess population density and land-use changes in areas surrounding cities as these areas can also develop at different time scales. Longitudinal analyses have been instrumental in elucidating the mechanisms underlying population dynamics in other study systems (Ewald and others 2015; Haddad and others 2015; Potts and others 1980; Reed and others 2013). However, as mentioned earlier, long-term ecological studies are rare in urban habitats. In this context, data obtained through citizen science projects can play a crucial role. Indeed, such data is intrinsically linked to the presence of humans and is therefore often collected within urban areas of different size and age (Bates and others 2015; Bradsworth and others 2017). Such data are increasingly used to assess long-term population trends and their underlying causes, and could be further exploited to understand early warning symptoms of demographic change linked to increasing urbanization.

4.3 Significance and future prospects

The widespread species loss associated with urbanization does not only happen during its first stages, but also during the complex process of urban sprawl, which creates a mosaic of different urban sub-habitats, from concrete-heavy business districts to greener suburban areas, that may or may not become unsuitable for certain species. Understanding when during this process species may cease to be able to cope with urban development is a research challenge that, if met, it will provide us with unique knowledge about how urbanization affects biodiversity. We believe that meeting this challenge will require a mechanistic comprehension of this process that relies on long-term data on individual fitness, population growth, and habitat change.

Conclusions

There is a compelling need to expand and integrate different components of urban ecology to reach an integrative mechanistic understanding of how organisms respond to, cope with, and adapt to urbanization (French and others this issue; Isaksson 2015). Urban sprawl has profound impacts on wild organisms, and the resulting disruption of physiology, behavior, and life history has major conservation implications (Kernbach and others this issue; Kleist and others 2018; Knop and others 2017; Ouyang and others 2017). In this context, there is a need to develop amelioration plans for species affected by urbanization, with the ultimate goal of designing environmentally sustainable cities with minimal ecological footprints. Despite the fact that the field of urban ecology is moving fast and attracting increasing scientific and public attention, we still lack a framework that can help us understand individual and population-level responses to urbanization.

The four questions we have raised here provide a framework and a pathway for an integrative understanding of urban ecology through a focus on mechanisms. We stress that we will need a combination of laboratory studies with controlled conditions, field studies that characterize fitness and the environment, and comparative and meta-analyses with global approaches for broad-scale patterns to form a holistic view of urban ecology. First, with clear definitions of the different factors that characterize a city, we can measure the socio-economic and ecological factors that influence the observable traits in animals, and their interactive effects. Second, we need to understand how urban animals differ from their rural counterparts through common garden and genomic studies that disentangle the genetic, epigenetic, and phenotypic contributions from development to adult phenotype. This will require us to not only focus on one trait but also on correlated traits. Next, to explore why individuals differ, we need to understand the evolutionary potential for adaptive change in traits of urban organisms. We will need to measure selection coefficients and use population genomic studies to explore global patterns. Lastly, to facilitate crosstalk between studies of individual-level phenotypic traits and biodiversity, we will need measures of lifetime fitness and links to population dynamics. With the expansion of the urban human population, having a concurrent increase in studies that address these knowledge gaps will help us build greener cities that maintain biodiversity and ecosystem function.

Funding

This work was supported by the Society of Integrative and Comparative Biology (SICB), the National Science Foundation (NSF OIA-1738594 to JQO), the National Institutes of Health (NIH- P20 GM103650 to JQO), the Swedish Research Council (VR; C0361301 to CI).

Acknowledgments

We wish to acknowledge the intellectual contributions of the participants in the Behavioral and Physiological Adaptations to Urban Environments workshop and symposium during the SICB 2018 meeting in San Francisco, CA. Lori Strong, Brett Burk, Ruedi Birenheide, and Richard Blob provided technical and administrative support.

References

Adkins-Regan E. 2005. Hormones and animal social behavior. Princeton, NJ, USA: Princeton University Press.

Alberti M. 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol Evol 30(2):114-26.

Alberti M, Correa C, Marzluff JM, Hendry AP, Palkovacs EP, Gotanda KM, Hunt VM, Apgar TM, Zhou Y. 2017. Global urban signatures of phenotypic change in animal and plant populations. Proceedings of the National Academy of Sciences.

Andreasen Alyson M, Stewart Kelley M, Longland William S, Beckmann Jon P, Forister Matthew L. 2012. Identification of source ‐ sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21(23):5689-5701.

Arnfield AJ. 2003. Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. International Journal of Climatology 23(1):1-26.

Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarkson B et al. . 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B: Biological Sciences 281(1780).

Aronson Myla FJ, Lepczyk Christopher A, Evans Karl L, Goddard Mark A, Lerman Susannah B, MacIvor JS, Nilon Charles H, Vargo T. 2017. Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15(4):189-196.

Audet J-N, Ducatez S, Lefebvre L. 2016. The town bird and the country bird: problem solving and immunocompetence vary with urbanization. Behavioral Ecology 27(2):637-644.

Badyaev AV. 2010. The beak of the other finch: coevolution of genetic covariance structure and developmental modularity during adaptive evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365(1543):1111-1126.

Badyaev AV, Young RL, Oh KP, Addison C. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. Evolution 62(8):1951-1964.

Bailly J, Scheifler R, Berthe S, Clément-Demange V-A, Leblond M, Pasteur B, Faivre B. 2016. From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. Journal of Ornithology 157(2):377-392.

Balogh AL, Ryder TB, Marra PP. 2011. Population demography of Gray Catbirds in the suburban matrix: sources, sinks and domestic cats. Journal of Ornithology 152(3):717-726.

Banaszak-Cibicka W, Żmihorski M. 2012. Wild bees along an urban gradient: winners and losers. Journal of Insect Conservation 16(3):331-343.

Bates AJ, Lakeman Fraser P, Robinson L, Tweddle JC, Sadler JP, West SE, Norman S, Batson M, Davies L. 2015. The OPAL bugs count survey: exploring the effects of urbanisation and habitat characteristics using citizen science. Urban Ecosystems 18(4):1477-1497.

Beninde J, Veith M, Hochkirch A, Haddad N. 2015. Biodiversity in cities needs space: a meta ‐ analysis of factors determining intra ‐ urban biodiversity variation. Ecology Letters 18(6):581-592.

Blair RB. 1996. Land Use and Avian Species Diversity Along an Urban Gradient. Ecological Applications 6(2):506-519.

Bonier F. 2012. Hormones in the city: Endocrine ecology of urban birds. Hormones and Behavior 61(5):763-772.

Bonier F, Martin PR. 2016. How can we estimate natural selection on endocrine traits? Lessons from evolutionary biology. Proceedings of the Royal Society B: Biological Sciences 283(1843).

Bosse M, Spurgin LG, Laine VN, Cole EF, Firth JA, Gienapp P, Gosler AG, McMahon K, Poissant J, Verhagen I et al. . 2017. Recent natural selection causes adaptive evolution of an avian polygenic trait. Science 358(6361):365-368.

Bradsworth N, White JG, Isaac B, Cooke R. 2017. Species distribution models derived from citizen science data predict the fine scale movements of owls in an urbanizing landscape. Biological Conservation 213:27-35.

Brans KI, Jansen M, Vanoverbeke J, Tüzün N, Stoks R, Meester LD. 2017. The heat is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size. Global Change Biology 23(12):5218-5227.

Capilla-Lasheras P, Dominoni DM, Babayan SA, O'Shaughnessy PJ, Mladenova M, Woodford L, Pollock CJ, Barr T, Baldini F, Helm B. 2017. Elevated Immune Gene Expression Is Associated with Poor Reproductive Success of Urban Blue Tits. Frontiers in Ecology and Evolution 5(64).

Chace JF, Walsh JJ. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74(1):46-69.

Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ. 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151.

Chapple DG, Simmonds SM, Wong BBM. 2012. Can behavioral and personality traits influence the success of unintentional species introductions? Trends in Ecology & Evolution 27(1):57-64.

Charmantier A, Demeyrier V, Lambrechts M, Perret S, Grégoire A. 2017. Urbanization Is Associated with Divergence in Pace-of-Life in Great Tits. Frontiers in Ecology and Evolution 5(53).

Cohen AA, Isaksson C, Salguero-Gómez R. 2017. Co-existence of multiple trade-off currencies shapes evolutionary outcomes. PLOS ONE 12(12):e0189124.

Corsini M, Dubiec A, Marrot P, Szulkin M. 2017. Humans and Tits in the City: Quantifying the Effects of Human Presence on Great Tit and Blue Tit Reproductive Trait Variation. Frontiers in Ecology and Evolution 5(82).

Croci S, Butet A, Clergeau P. 2008. Does Urbanization Filter Birds on the Basis of Their Biological Traits. The Condor 110(2):223-240.

Da Silva A, Samplonius JM, Schlicht E, Valcu M, Kempenaers B. 2014. Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. Behavioral Ecology.

Davies S, Haddad N, Ouyang JQ. 2017. Stressful city sounds: glucocorticoid responses to experimental traffic noise are environmentally dependent. Biology Letters 13(10).

Dominoni DM, Carmona-Wagner EO, Hofmann M, Kranstauber B, Partecke J. 2014. Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. J Anim Ecol 83(3):681-92.

Dominoni DM, Greif S, Nemeth E, Brumm H. 2016. Airport noise predicts song timing of European birds. Ecology and Evolution 6(17):6151-6159.

Dominoni DM, Quetting M, Partecke J. 2013. Artificial light at night advances avian reproductive physiology. Proc Biol Sci 280.

Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ. 2011. What makes an urban bird? Global Change Biology 17(1):32-44.

Evans KL, Gaston KJ, Sharp SP, McGowan A, Simeoni M, Hatchwell BJ. 2009. Effects of urbanisation on disease prevalence and age structure in blackbird Turdus merula populations. Oikos 118(5):774-782.

Ewald JA, Wheatley CJ, Aebischer NJ, Moreby SJ, Duffield SJ, Crick HQP, Morecroft MB. 2015. Influences of extreme weather, climate and pesticide use on invertebrates in cereal fields over 42 years. Global Change Biology 21(11):3931-3950.

Fokidis HB, Orchinik M, Deviche P. 2009. Corticosterone and corticosteroid binding globulin in birds: relation to urbanization in a desert city. Gen Comp Endocrinol 160(3):259-70.

Foltz SL, Ross AE, Laing BT, Rock RP, Battle KE, Moore IT. 2015. Get off my lawn: increased aggression in urban song sparrows is related to resource availability. Behavioral Ecology 26(6):1548-1557.

Gaggiotti OE, Bekkevold D, Jørgensen HBH, Foll M, Carvalho GR, Andre C, Ruzzante DE. 2009. Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: Atlantic herring as a case study. Evolution 63(11):2939-2951.

Garroway CJ, Sheldon BC. 2013. Urban behavioural adaptation. Molecular Ecology 22(13):3430-3432.

Giraudeau M, Mousel M, Earl S, McGraw K. 2014. Parasites in the City: Degree of Urbanization Predicts Poxvirus and Coccidian Infections in House Finches (Haemorhous mexicanus). PLOS ONE 9(2):e86747.

Goddard MA, Dougill AJ, Benton TG. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology & Evolution 25(2):90-98.

Greaver TL, Sullivan TJ, Herrick JD, Barber MC, Baron JS, Cosby BJ, Deerhake ME, Dennis RL, Dubois J-JB, Goodalee CL et al. . 2012. Ecological effects of nitrogen and sulfur air pollution in the US: what do we know? Frontiers in Ecology and the Environment 10(7):365-372.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD et al. . 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1(2).

Hale JD, Davies G, Fairbrass AJ, Matthews TJ, Rogers CDF, Sadler JP. 2013. Mapping Lightscapes: Spatial Patterning of Artificial Lighting in an Urban Landscape. PLOS ONE 8(5):e61460.

Hale R, Morrongiello JR, Swearer SE. 2016. Evolutionary traps and range shifts in a rapidly changing world. Biology Letters 12(6).

Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences 108(35):14549-14554.

Halfwerk W, Slabbekoorn H. 2013. The impact of anthropogenic noise on avian communication and fitness. In: Gil D, Brumm H, editors. Avian Urban Ecology: Behavioral and Physiological Adaptations. Oxford, UK: Oxford University Press. p. 84-97.

Harris SE, Xue AT, Alvarado-Serrano D, Boehm JT, Joseph T, Hickerson MJ, Munshi-South J. 2016. Urbanization shapes the demographic history of a native rodent (the white-footed mouse, Peromyscus leucopus) in New York City. Biology Letters 12(4).

Harveson PM, Lopez RR, Collier BA, Silvy NJ. 2007. Impacts of urbanization on Florida Key deer behavior and population dynamics. Biological Conservation 134(3):321-331.

Hedin J, Isacsson G, Jonsell M, Komonen A. 2008. Forest fuel piles as ecological traps for saproxylic beetles in oak. Scandinavian Journal of Forest Research 23(4):348-357.

Hope D, Gries C, Zhu W, Fagan WF, Redman CL, Grimm NB, Nelson AL, Martin C, Kinzig A. 2003. Socioeconomics drive urban plant diversity. Proceedings of the National Academy of Sciences 100(15):8788-8792.

Ibáñez-Álamo JD, Rubio E, Bitrus Zira K. 2017. The Degree of Urbanization of a Species Affects How Intensively It Is Studied: A Global Perspective. Frontiers in Ecology and Evolution 5(41).

Isaksson C. 2010. Pollution and Its Impact on Wild Animals: A Meta-Analysis on Oxidative Stress. EcoHealth 7(3):342-350.

Isaksson C. 2015. Urbanization, oxidative stress and inflammation: a question of evolving, acclimatizing or coping with urban environmental stress. Functional Ecology 29(7):913-923.

Järup L. 2003. Hazards of heavy metal contamination. British Medical Bulletin 68(1):167-182.

Jenkins BR, Vitousek MN, Hubbard JK, Safran RJ. 2014. An experimental analysis of the heritability of variation in glucocorticoid concentrations in a wild avian population. Proceedings of the Royal Society B: Biological Sciences 281(1790).

Johnson MTJ, Munshi-South J. 2017. Evolution of life in urban environments. Science 358(6363).

Jokimäki J, Clergeau P, Kaisanlahti-Jokimäki M-L. 2002. Winter bird communities in urban habitats: a comparative study between central and northern Europe. Journal of Biogeography 29(1):69-79.

Kalnay E, Cai M. 2003. Impact of urbanization and land-use change on climate. Nature 423(6939):528-531.

Kaye JP, McCulley RL, Burke IC. 2005. Carbon fluxes, nitrogen cycling, and soil microbial communities in adjacent urban, native and agricultural ecosystems. Global Change Biology 11(4):575-587.

Killen SS, Marras S, Metcalfe NB, McKenzie DJ, Domenici P. 2013. Environmental stressors alter relationships between physiology and behaviour. Trends in Ecology & Evolution 28(11):651-658.

Kinzig AP, Warren P, Martin C, Hope D, Katti M. 2005. The Effects of Human Socioeconomic Status and Cultural Characteristics on Urban Patterns of Biodiversity. Ecology and Society 10(1).

Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD. 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proceedings of the National Academy of Sciences.

Knop E, Zoller L, Ryser R, Gerpe C, Hörler M, Fontaine C. 2017. Artificial light at night as a new threat to pollination. Nature 548(7666):206-209.

LaPoint S, Balkenhol N, Hale J, Sadler J, Ree R, Evans K. 2015. Ecological connectivity research in urban areas. Functional Ecology 29(7):868-878.

Lessells CM. 2008. Neuroendocrine control of life histories: what do we need to know to understand the evolution of phenotypic plasticity? Philosophical Transactions of the Royal Society B-Biological Sciences 363:1589-1598.

Liker A, Papp Z, Bókony V, Lendvai ÁZ. 2008. Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. Journal of Animal Ecology 77(4):789-795.

Maklakov AA, Immler S, Gonzalez-Voyer A, Rönn J, Kolm N. 2011. Brains and the city: big-brained passerine birds succeed in urban environments. Biology Letters 7(5):730-732.

Marzluff JM. 2017. A decadal review of urban ornithology and a prospectus for the future. Ibis 159(1):1-13.

McIntyre NE. 2000. Ecology of Urban Arthropods: A Review and a Call to Action. Annals of the Entomological Society of America 93(4):825-835.

McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127(3):247-260.

McMahon TA, Rohr JR, Bernal XE. 2017. Light and noise pollution interact to disrupt interspecific interactions. Ecology 98(5):1290-1299.

Moller AP. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159(4):849-58.

Mueller JC, Partecke J, Hatchwell BJ, Gaston KJ, Evans KL. 2013. Candidate gene polymorphisms for behavioural adaptations during urbanization in blackbirds. Molecular Ecology 22(13):3629-3637.

Nations U. 2014. World urbanization prospects. In: Affairs DoEaS, editor.

Ouyang JQ, Davies S, Dominoni D. 2018. Hormonally mediated effects of artificial light at night on behavior and fitness: linking endocrine mechanisms with function. The Journal of Experimental Biology 221(6).

Ouyang JQ, de Jong M, van Grunsven RHA, Matson KD, Haussmann MF, Meerlo P, Visser ME, Spoelstra K. 2017. Restless roosts: Light pollution affects behavior, sleep, and physiology in a free-living songbird. Global Change Biology.

Ouyang JQ, Hau M, Bonier F. 2011. Within seasons and among years: When are corticosterone levels repeatable? Hormones and Behavior 60(5):559-564.

Ouyang JQ, Lendvai ÁZ, Moore IT, Bonier F, Haussmann MF. 2016. Do Hormones, Telomere Lengths, and Oxidative Stress form an Integrated Phenotype? A Case Study in Free-Living Tree Swallows. Integrative and Comparative Biology 56(2):138-145.

Partecke J, Gwinner E, Bensch S. 2006. Is urbanisation of European blackbirds (Turdus merula) associated with genetic differentiation? Journal of Ornithology 147(4):549-552.

Partecke J, J. Van't Hof T, Gwinner E. 2005. Underlying physiological control of reproduction in urban and forest-dwelling European blackbirds Turdus merula. Journal of Avian Biology 36(4):295-305.

Perrier C, Charmantier A. 2018. On the timing of bill length evolution in British great tits: A comment on Bosse et al. 2017. bioRxiv.

Perrier C, Lozano del Campo A, Szulkin M, Demeyrier V, Gregoire A, Charmantier A. 2017. Great tits and the city: Distribution of genomic diversity and gene–environment associations along an urbanization gradient. Evolutionary Applications 0:1-21.

Pollock CJ, Capilla-Lasheras P, McGill RAR, Helm B, Dominoni DM. 2017. Integrated behavioural and stable isotope data reveal altered diet linked to low breeding success in urban-dwelling blue tits (Cyanistes caeruleus). Scientific Reports 7(1):5014.

Potts GR, Coulson JC, Deans IR. 1980. Population Dynamics and Breeding Success of the Shag, Phalacrocorax aristotelis, on the Farne Islands, Northumberland. Journal of Animal Ecology 49(2):465-484.

Ramalho CE, Hobbs RJ. 2012. Time for a change: dynamic urban ecology. Trends in Ecology & Evolution 27(3):179-188.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82(2):291-318.

Reed TE, Jenouvrier S, Visser ME. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol 82(1):131-44.

Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, Wayne RK. 2003. Effects of Urbanization and Habitat Fragmentation on Bobcats and Coyotes in Southern California. Conservation Biology 17(2):566-576.

Robertson BA, Rehage JS, Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. Trends in Ecology & Evolution 28(9):552-560.

Rodewald AD, Kearns LJ, Shustack DP. 2013. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. Biological Conservation 160:32-39.

Salmón P, Nilsson JF, Watson H, Bensch S, Isaksson C. 2017. Selective disappearance of great tits with short telomeres in urban areas. Proceedings of the Royal Society B: Biological Sciences 284(1862).

Salmon P, Stroh E, Herrera-Duenas A, von Post M, Isaksson C. 2018. Oxidative stress in birds along a NOx and urbanisation gradient: An interspecific approach. Sci Total Environ 622-623:635-643.

Schoech SJ, Rensel MA, Bridge ES, Boughton RK, Wilcoxen TE. 2009. Environment, glucocorticoids, and the timing of reproduction. General and Comparative Endocrinology 163(1-2):201-207.

Sepp T, McGraw KJ, Kaasik A, Giraudeau M. 2017. A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? Global Change Biology.

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21(4):186-191.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19(7):372-378.

Sih A, Mathot KJ, Moirón M, Montiglio P-O, Wolf M, Dingemanse NJ. 2015. Animal personality and state-behaviour feedbacks: a review and guide for empiricists. Trends in Ecology & Evolution 30(1):50-60.

Slabbekoorn H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17(1):72-83.

Smith SB, McKay JE, Richardson JK, Shipley AA, Murphy MT. 2016. Demography of a ground nesting bird in an urban system: are populations self-sustaining? Urban Ecosystems 19(2):577-598.

Sol D, González-Lagos C, Moreira D, Maspons J, Lapiedra O. 2014. Urbanisation tolerance and the loss of avian diversity. Ecology Letters 17(8):942-950.

Sol D, Lapiedra O, González-Lagos C. 2013. Behavioural adjustments for a life in the city. Animal Behaviour 85(5):1101-1112.

Spoelstra K, van Grunsven RHA, Ramakers JJC, Ferguson KB, Raap T, Donners M, Veenendaal EM, Visser ME. 2017. Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. Proc Biol Sci 284(1855).

Sprau P, Dingemanse NJ. 2017. An Approach to Distinguish between Plasticity and Non-random Distributions of Behavioral Types Along Urban Gradients in a Wild Passerine Bird. Frontiers in Ecology and Evolution 5(92).

Sprau P, Mouchet A, Dingemanse NJ. 2017. Multidimensional environmental predictors of variation in avian forest and city life histories. Behavioral Ecology 28(1):59-68.

Swaddle JP, Francis CD, Barber JR, Cooper CB, Kyba CCM, Dominoni DM, Shannon G, Aschehoug E, Goodwin SE, Kawahara AY et al. . 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends in Ecology & Evolution 30(9):550-560.

Tinbergen N. 1963. On aims and methods of Ethology. Zeitschrift für Tierpsychologie 20(4):410-433.

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, Ali AH, Allen AM, Attias N, Avgar T et al. . 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359(6374):466-469.

Verboven N, Tinbergen JM, Verhulst S. 2001. Food, reproductive success and multiple breeding in the Great Tit Parus major. Ardea 89(2):387-406.

Welbers AAMH, van Dis NE, Kolvoort AM, Ouyang J, Visser ME, Spoelstra K, Dominoni DM. 2017. Artificial Light at Night Reduces Daily Energy Expenditure in Breeding Great Tits (Parus major). Frontiers in Ecology and Evolution 5(55).

While A, Whitehead M. 2013. Cities, Urbanisation and Climate Change. Urban Studies 50(7):1325-1331.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution 27(8):452-461.

Wong BBM, Candolin U. 2015. Behavioral responses to changing environments. Behavioral Ecology 26(3):665-673.