Environmental Reviews
Dossiers environnement

Sublethal consequences of urban life for wild vertebrates

Journal:	*Environmental Reviews*
Manuscript ID	er-2016-0029.R1
Manuscript Type:	Review
Date Submitted by the Author:	11-Jun-2016
Complete List of Authors:	Birnie-Gauvin, Kim; Carleton University, Department of Biology and Institute of Environmental Science Peiman, Kathryn; Carleton University, Department of Biology and Institute of Environmental Science Gallagher, Austin; Carleton University, Department of Biology and Institute of Environmental Science; Beneath the Waves; University of Miami Rosenstiel School of Marine and Atmospheric Science de Bruijn, Robert; Max Planck Institue for Ornithology; Carleton University, Department of Biology and Institute of Environmental Science Cooke, Steven; Carleton University, Department of Biology and Institute of Environmental Science
Keyword:	urban ecology, urbanization, vertebrates, sublethal consequences, synurbanization

Sublethal consequences of urban life for wild vertebrates

Accepted in Environmental Reviews

Kim Birnie-Gauvin[1*], Kathryn S. Peiman[1], Austin J. Gallagher[1,3,4], Robert de Bruijn[1,2] and Steven J. Cooke[1]

[1] Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6

[2] Max Plank Institute for Ornithology, Eberhard-Gwinner-Str., 82319 Seewiesen, Germany

[3] Beneath The Waves, Incorporated., Syracuse, NY, USA

[4] Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA

* Author for Correspondence: kimbirniegauvin@cmail.carleton.ca

Abstract

Urbanization is modifying previously pristine natural habitats and creating “new” ecosystems for wildlife. As a result, some animals now use habitat fragments or have colonized urban areas. Such animals are exposed to novel stimuli that they have not been exposed to in their evolutionary history. Some species have adapted to the challenges they face – a phenomenon known as synurbanization – while others have not. Here we present a review of the sublethal consequences of life in the city for wild vertebrates, and demonstrate that urban animals face an almost completely different set of physiological and behavioural challenges compared to their rural counterparts. We focus on the negative fitness-related impacts of urbanization, but also identify instances where there are benefits to wildlife. The effects of urbanization appear to be both species- and context-dependent, suggesting that although the field of urban ecology is far from nascent, we are still just beginning to understand how the intricacies of biodiversity on our planet are affected by our presence.

Keywords: urban ecology, urbanization, vertebrates, sublethal consequences, synurbanization

1. Introduction

The growth of cities is seen as the cornerstone achievement of human civilization (Childe 1950). In order to make a suitable living place, humans have modified natural landscapes by clearing land, moving watercourses, and building infrastructure; in essence, dominating the landscape (Vitousek et al. 1997). Today, more than half of the world's population lives in cities. By 2030, more than 60% of the population will live in urban areas (United Nations Population Fund 2007), necessitating continuing landscape modification, especially in developing countries (Cohen 2006). Humans have now spread into new landscapes and colonized natural areas or rural lands that were previously pristine (Marzluff et al. 2001). The contemporary city is home to many animal populations (Savard et al. 2000; Ditchkoff et al. 2006) that are exposed to novel stimuli and challenges that did not exist in their evolutionary past (Kowarik 2011). The extent to which animals can cope with these urban environments will affect all aspects of their fitness and survival.

Scholars have studied the ecology of urban environments for decades (McDonnell 2011) and this discipline, now known as "urban ecology" (Alberti 2008; Breuste et al. 2013), has spawned books, publications, dedicated journals (e.g., *Urban Ecosystems*, *Journal of Urban Ecology*), professional societies, and conferences. The discipline has advanced from simply documenting urban species to developing theoretical approaches (Niemela 1999) and unifying frameworks (Pickett et al. 2008). There have been nearly 500 studies investigating this topic in animals since 1971 with more than 50% of them occurring between 2000 and 2010 (Magle et al. 2012). We have detected species and behaviors in places we thought they would never exist, and we now understand that while some species suffer from urban living, others actually benefit and thrive (McKinney 2006; Bonier et al. 2007b; Lowry et al. 2013). This case is best exemplified by the grey squirrel (*Sciurus carolinensis*), which was almost eradicated following the industrial revolution in New York, only to be later reintroduced to entertain people and remind them of "nature" (Stein 2014). Today squirrels are so successful they are entrenched in our lives and people do not notice them. However, there is an increasing realization that wildlife residing in urban environments differ from rural counterparts as a result of adaptation to anthropogenic stressors – a process termed "synurbanization" (Luniak 2004).

While there have been a number of reviews on aspects of urban living in animals, they tend to focus on either a specific taxonomic group (e.g., birds [Chace and Walsh 2006]) or environmental issue or threat (e.g., road collisions [Coffin 2007], stormwater management [Walsh et al. 2005]), often with an emphasis on lethal aspects (e.g., bird strikes [Klem 1989]) or the presence or absence of species. To our knowledge, there have yet to be any reviews or syntheses that focus on the sublethal consequences (in terms of metabolism, reproduction, nutrition, etc.) of life in the city on vertebrates. This is surprising, since sublethal impacts on animals can have far-ranging effects on the viability of populations and ecosystems (Calow and Forbes 1998). Research focused on sublethal aspects of life in the city has only become popular in the last few decades and is regarded as a priority research area (Magle et al. 2012). A review of the sublethal effects of urban life on wild vertebrates would enable us to gain a deeper understanding of the effects of urbanization on biological systems across a range of taxa, which in turn may allow us to better understand how species will respond in the future to ongoing development and urbanization. Ideally, such information could enable urban planners to buffer these negative effects on wildlife. In this paper we first provide an overview of the general challenges that define life in the city for vertebrates. Next we consider how urban living negatively impacts seven biologically-relevant components of organismal function central to animal ecology and fitness: metabolism and respiration, glucocorticoids, nutrition, locomotion and activity, communication, reproduction, and disease and immune function. For all sections we attempt to integrate elements of behavior and physiology given the inherent difficulty of decoupling these concepts when dealing with wild animals (Cooke et al. 2014). We also address some of the key benefits for species that thrive in cities (i.e., synurbanization; see Figure 1). Lastly, we consider how the knowledge of these sublethal effects can help urban planners make cities more livable for wildlife. Our synthesis focuses on vertebrates that reside in urban areas including birds, mammals, fish and herpetofauna.

2. Challenges that define city life

In cities, humans purchase food at stores, select clothing geared to weather conditions, seek shelter to sleep, and use a variety of transportation methods, most notably vehicles on roads, to move ourselves and the goods that we need. Wild vertebrates need to functionally do the same things – obtain resources (goods), live safely and within their environmental tolerances (shelter), and move among areas to maximize fitness (transportation). However, an urban environment looks much different to a wild animal than it does to a human (Alberti and Marzluff 2004). We recognize that the generalities discussed here vary with climate (some areas do not receive snow, some are arid, etc.), development standards (e.g., type of infrastructure), and wealth, though in other cases patterns are evident both on a global scale (e.g., between cities in developing vs developed countries) and also within cities (e.g., between shanty-towns and suburban areas with large single-family dwellings; Alberti 1999). There can be dramatic variation in the physical footprint of an urban area as well as the density of human dwellers. What is clear is that the complexity of urban environments and anthropogenic activities make it difficult to evaluate and understand the specific mechanisms by which urbanization changes the structure of communities and function of ecosystems (Booth et al. 2004; Alberti 2005), given that these challenges posed to urban wildlife do not occur in isolation from each other. A brief overview of the complex changes urbanization creates throughout the landscape is illustrated in Figure 2.

The first step in urbanization is often land clearing followed by the installation of services such as sewer, water and electricity and associated roads. The clearing of land tends to remove shade and riparian vegetation from streambanks which decreases habitat complexity and increases erosion and water temperature (Walsh et al. 2005). Residential dwellings and other buildings (e.g., for manufacturing and service) follow. Pavement, concrete, shingles and other building materials are generally impervious to water such that precipitation rapidly moves from the built landscape into stormwater management systems. Many urban streams have been channelized and encased to be entirely subsurface (i.e., in pipes) which changes runoff patterns, a process termed the "urban stream syndrome" (Walsh et al. 2005). The hydrograph following precipitation events is often altered such that water levels rise and fall quickly with little opportunity for infiltration (Paul and Meyer 2001; Meyer et al. 2005). Runoff from roads carries a variety of substances including salt (used in winter to improve road safety), nutrients, fecal material (from wildlife and humans), and hydrocarbons and heavy metals (from combustion engines) into the stormwater system and downstream watercourses (Ball et al. 1998). Because of the historical importance of water for transportation and our continued dependence on it as a resource, most urban centers occur adjacent to estuaries, lakes, rivers or oceans such that shoreline development and water pollution are common (Grimm et al. 2008).

Urban centres are sources of heat and light pollution (Oke 1995; Longcore and Rich 2004). Furthermore, natural habitats tend to be scarce in the city, with the presence of large structures acting as barriers to the movement of animals (Cheisura 2004). The collective body of infrastructure in urban areas both stores and generates heat – a phenomenon known as the urban heat island effect where temperatures are generally several degrees warmer than in outlying areas (Oke 1995). The urban heat effect is positively correlated with city size and population density (Oke 1973; Brazel et al. 2000). At night or in low light conditions, artificial lighting is used to aid human vision which casts very directed light in some areas (e.g., head lights, street lights) and creates a more general "light haze" that surrounds urban areas – a phenomenon known as "ecological light pollution" (Longcore and Rich 2004). Although modern cities contain parks and many dwellings have yards, these are typically grass monocultures (Robbins and Sharp 2006) that lack the diversity of the native grasslands they have replaced. Extensive pesticide use is often needed to maintain lawns and other ornamental vegetation within urban areas (Robbins et al. 2001). True naturalized habitats are rare (Cheisura 2004) and where they do exist they tend to be encroached upon by non-native vegetation (e.g., ornamentals planted by humans, invasive species; Alvey 2006). The physical infrastructure also creates physical hazards or barriers to movement for fish (dams [Larinier 2001], road crossings with perched culverts [Warren and Pardew 1998]), birds (buildings; Klem 1989), and terrestrial vertebrates (buildings, roads; Coffin 2007). Human activities and infrastructure (especially from transportation) can also generate extensive noise (e.g., sirens, engines; Cunniff 1977; Zannin et al. 2006).

Pollution is a growing problem in urban areas. Emissions from combustion engines, industrial processes and burning of materials (e.g., garbage, wood, propane, natural gas or coal for cooking) generates air pollution and contributes to smog (Mage et al. 1996). The mere omnipresence of humans in urban areas also provides the opportunity for animals to be disturbed – a phenomenon that is comparatively less common in rural or natural areas. Waste generated by humans can take several forms; where sewers exist, human excrement and other inputs (e.g., pharmaceuticals, food waste, chemicals) are directed to sewage treatment plants but they are imperfect in their ability to remove all unwanted substances (Sharma and Sangi 2012). Solid waste from household and industrial sources is often collected at regular intervals and taken to central processing facilities although in some areas it is burned at source (Sakai et al. 1996). In order to maintain our function in cities, all of these processes work simultaneously, throughout the day, 365 days a year.

3. Sublethal consequences of city life on biological systems

Collectively, the various elements of urban environments have the potential to influence the biology, ecology and health of wildlife. Here we briefly summarize with representative examples the ways in which aspects of urban life influence the different components of organism function (e.g., metabolism, locomotion, etc.) related to fitness.

3.1 **Respiration and metabolism**

In wild organisms, energy resources are often limited, and must therefore be allocated efficiently to maximize fitness. Increases in respiration and metabolism lead to accelerated use of energy stores, and could potentially lower fitness. Since the physiology of free-ranging animals is directly influenced by their environment, the urban environment can drive changes in metabolic rate and respiration, which could in turn affect life-histories (Ricklefs and Wikelski 2002). There is some evidence that community respiration (total ecosystem oxygen consumption and primary production) increases as a result of increased urbanization in catchments. More specifically, it is predicted that respiration will increase for both thermoregulator and thermoconformer fish species, as well as for the platypus, *Ornithorhynchus anatinus* (Serena and

Pettigrove 2005; Walsh et al. 2005), a trend thought to be predominantly driven by urban stormwater runoff (Walsh et al. 2005).

The increased temperature from the urban heat island effect can add substantial strain on the thermoregulatory mechanisms (Kleerekoper et al. 2012) and metabolism of individuals. Metabolic rates, notably oxygen consumption and nitrogen excretion, increase as a result of elevated temperature in a variety of taxa (Morgan et al. 2001), suggesting that individuals in an urban environment would have increased metabolic rates, most prominently affecting ectothermic species. In addition, elevated temperatures can lead to an increased rate of protein degradation in the lab (e.g., Houlihan et al. 1995). Though few studies have investigated the direct impacts of heat islands on wild vertebrates, some studies have linked global climate change to impairments in energy metabolism (e.g., Sokolova and Lannig 2008), suggesting that the heat island effect will have negative consequences on the metabolism of urban wildlife.

Pollution is a growing concern in cities around the world. While many pollutants have made their way into the atmosphere and water, ammonia is the most manufactured molecule in the world and has rapidly polluted the environment (Atkins 1987). Organisms subjected to ammonia suffer metabolic costs (Calow 1991), including greater rates of protein synthesis (Reid et al. 1998), a finding generally associated with increased oxygen consumption and overall elevated metabolic rate. Maintaining an elevated metabolic rate quickly becomes costly and leads to decreased growth (Steyermark 2002). In the long-term, pollution will likely have significant negative effects on the metabolism and respiration of urban wildlife. Moreover, evidence suggests that warming temperatures and metal pollution have interactive effects on the metabolism of aquatic ectotherms, which in the long-term could have repercussions on growth, reproduction and locomotion of animals living in urban waters (reviewed in Sokolova and Lannig 2008).

3.2 Glucocorticoids

Allostasis is the process of maintaining homeostasis in the face of changing environmental and physiological conditions (McEwen and Wingfield 2003). Measures of glucocorticoids such as cortisol and corticosterone (the primary stress hormones for fish/mammals and rodents/birds/reptiles respectively) have been widely used to estimate allostatic load, defined as the current and predicted energetic demands that an organism faces (Dantzer et al. 2014). Several studies have used this approach to investigate the effects of urbanization on animals. Baseline corticosterone of non-breeding male white-crowned sparrows (*Zonotrichia leucophrys*) was higher among urban than rural individuals (Bonier et al. 2007a). However, urban European blackbirds (*Turdus merula*) (Partecke et al. 2006) and dark-eyed juncos (*Junco hyemalis*) (Atwell et al. 2012) had lower corticosterone levels after being exposed to an artificial stressor than those in rural environments, providing evidence that species may respond differently to urban stressors. For example, Nestling white-crowned sparrows (*Zonotrichia leucophrys oriantha*) near roads with traffic had increased baseline and stress-induced corticosterone levels compared to nestlings that lived further away from roads (Crino et al. 2011). However, baseline and stress-induced corticosterone levels in nestling American kestrels (*Falco sparverius*) did not vary with measures of human disturbance such as traffic speed and volume (Strasser and Heath 2011), findings which support the hypothesis that species differences in the response to urban stressors exist. Furthermore, Atwell et al. (2012) suggested that boldness and stress responsiveness through the hypothalamic-pituitary-adrenal axis were highly influenced by the urban environment, which suggests that personality and behavior may play an important role in the stress response.

While there is extensive literature on the endocrine ecology of urban avian species (review by Bonier 2012), few studies have addressed how glucocorticoid homeostasis is disturbed as a result of urbanization in non-avian animals. In squirrel gliders (*Petaurus norfolcensis*), hair-based cortisol concentrations were higher in individuals living adjacent to major roads than those residing within interior habitats (Brearley et al. 2012). In contrast, urbanized tree lizards (*Urosaurus ornatus*) in the southwestern United States exhibited lower baseline and stress-induced corticosterone concentrations than rural ones (French et al. 2008). Belanger et al. (2016) found that variation in baseline and acute cortisol concentrations in central mudminnows (*Umbra limi*) was independent of the level of urban stream degradation. This small sample of studies show a large amount of variation in stress responses among taxa, suggesting that impacts of urbanization on glucocorticoids (both baseline and stress-responsiveness) are either species or context-dependent.

3.3 Nutrition

Nutritional ecology links field ecology with animal phenotypes, as the acquisition of nutrients affects how organisms interact amongst themselves and with the environment (Raubenheimer et al. 2009; Simpson et al. 2010), especially as individuals deal with a changing world (Raubenheimer et al. 2012). Both the quality and quantity of food items have direct and indirect effects on fitness. Pollutants can often make their way into food items and may alter fitness. For example, tadpoles had reduced mass when exposed to organophosphate pesticides commonly used in urban areas, and smaller tadpole mass can lead to reduced fecundity and survival in adults (Widder and Bidwell 2008). Pollutants can also travel through the food chain.

In urban sites, both common blackbirds (*Turdus merula*) and their earthworm prey had higher lead concentrations than in rural areas (Scheifler et al. 2006). Six of seven species of passerine birds exhibited higher lead in their blood in urban compared to rural environments; nestlings of two of the species also had higher lead in urban than rural environments, and for one species this was correlated with reduced body condition (Roux and Marra 2007). Interestingly, ground feeders had higher levels of lead than canopy feeders, possibly due to leaded gasoline leaching into the soil and concentrating in the ground-based food chain (Roux and Marra 2007). Poisoning is an unintended consequence of urban prey selection, such as when anticoagulant rodenticides are ingested by mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*) making them more susceptible to mange (Riley et al. 2007). In general, the presence of pollutants in food items negatively impacts wild vertebrates, through both direct and indirect consumption.

Predictable anthropogenic food sources (dumps, middens, fishing discards, etc.) affect many individual and population level parameters (reviewed in Oro et al. 2013). This food provisioning can lead to problems such as increased aggression at feeding sites and malnutrition (e.g., Newsome and Rodger 2008). Provisioned feeding can also have long-lasting consequences by negatively affecting the following year's reproduction (Grieco et al. 2002; Plummer et al. 2013). Food pulses can also increase competition if more individuals of ecologically similar species stay to breed (Jansson et al. 1981) and predation if more predatory individuals are attracted to the food source (Marzluff and Neatherlin 2006; Morris 2005). The indirect effects of supplementation are less studied. For instance, Saggese et al. (2011) found that supplemented male great tits delayed their dawn chorus, which negatively affects mate acquisition. Other indirect effects include shifts in peak insect abundance due to altered vegetative phenologies driven by the urban heat island effect, which may result in a mismatch between chick rearing and food supply for birds (Penuelas and Filella 2001). Thus, both the quantity and quality of food is affected by human activities, and their negative effects may vary by sex, age and personality (reviewed in Oro et al. 2013).

Increases in nocturnal illumination from urban areas has also led to changes in foraging behavior and predator-prey interactions. For instance, artificial light was shown to create shadows in the night which hinder the visibility of surrounding predators, making prey more vulnerable to predation (reviewed in Rich and Longcore 2013). These findings suggest that light can affect the nutrition of wildlife through impacts on behavior.

3.4 Locomotion and activity

Spatially, urbanized habitats are complex mosaics with an altered availability and structure of pathways and corridors that affects an organism's ability to access resources and mates (Alberti 2005). Many studies have investigated how the locomotor activity and movement patterns of vertebrates differ between urban and rural habitats. Both bat (Chiroptera) (Gehrt and Chelsvig 2003) and coyote (*Canis latrans*) (McClennen et al. 2001; Grinder and Krausman 2001) activity levels were higher in urbanized landscapes than in rural areas. These findings suggest that due to the presence of artificial lighting in urban areas, these animals can prey into the night (McClennen et al. 2001). In the marine realm, bull sharks (*Carcharhinus leucas*) throughout a developed coastal ecosystem off Australia avoided areas of high modification (Werry et al. 2012), providing evidence that the effects of urbanization go beyond the boundaries of the city. Animals can adapt their activity levels to urbanization in different ways. Fragmented urban habitats can cause arboreal species to modify their movement. For example, Siberian flying squirrels (*Pteromys volans*) avoided urbanized habitats by moving through them more quickly (Mäkeläinen et al. 2016). Alternatively, some animals shift the timing of their activity.

For example, coyotes and bobcats decrease their activity levels during daylight hours (Tigas et al. 2002). In general, linear features associated with urbanization such as transportation corridors inhibit the mobility of many species of birds (Crooks 2002, Tremblay and St. Clair 2009), freshwater fish (Coutant and Whitney 2000), and large mammals (bobcats, Poessel et al. 2014).

Artificial light is altering natural light cycles extensively (reviewed in Gaston et al. 2014). Light now continues into the night, affecting the normal locomotion activities of many animals such as foraging (Lebbin et al. 2007) and migration (reviewed in Navara and Nelson 2007). For example, many migratory animals (e.g., birds, turtles) can become attracted to or disoriented by artificial illumination (reviewed in Longcore and Rich 2004), demonstrating that important aspects of the life cycle of animals can be altered as a consequence of urbanization.

It appears that the locomotor activities of generalist species are not drastically affected by urbanization, probably due to the fact that the availability of human-provisioned resources offsets fitness-related costs associated with prey-searching (Oro et al. 2013). However, fragmentation can be lethal or create significant costs to movement if urbanization occurs within the entire home range of certain species (i.e., specialists). In these cases, there are likely to be more dramatic changes such as restricted movement which could lead to decreased condition and fitness. This is especially relevant for developing countries in the tropics that contain a greater proportion of specialists, as maintaining natural areas around urbanized fragments will provide greater conservation benefits.

3.5 Communication

Anthropogenic noise is ubiquitous in its effects across the globe and in the taxonomic diversity of animals affected, and has been the subject of numerous reviews (Shannon et al 2015). It can be a source of stress for urban animals, as erratic sounds are perceived as threats and chronic sounds can lead to acoustic interference (i.e., acoustic masking, Francis and Barber 2013). To reduce the masking effects of anthropogenic noise, acoustically plastic individuals can change the frequency, amplitude, or timing of their calls (Slabberkoorn 2013; Laiolo 2010; Patricelli and Blickley 2006).Traffic noise is also associated with a reduction in the abundance and diversity of avian migrants (McClure et al. 2013) and with decreased body condition of those that stay (Ware et al. 2015), indicating that even among plastic species that remain in the presence of noise there may be sublethal effects. Noise pollution can affect an individual's ability to identify predators, defend against rivals, find mates, and identify offspring. For instance, female house sparrows showed increased vigilance when exposed to chronic noise (Meillere et al. 2015); anthropogenic noise led to ineffective parent-offspring communication and lower body mass in house sparrow chicks (Schroeder et al. 2012); and noise impaired the ability of larval fishes to locate suitable habitat (Simpson et al 2008). Noise pollution additionally impairs the ability of animals to locate food, either directly in sonar-producing animals or indirectly through reduced ability to communicate with group members. For example, greater mouse-eared bats (*Myotis myotis*) reduced their foraging time and effort due to traffic noise (Jones 2008).

There are numerous examples of species modifying their vocalizations in noisy environments (Sol et al 2013 and refs therein). These modifications may be energetically costly (Oberweger and Goller 2001) and can have unanticipated effects on communities (Naguib 2013), such as when traffic noise indirectly increased the calling rate of the frog *Rana nigrovittata* due to heterospecifics reducing their calling rate under noisy conditions (Sun and Narins 2005). Whether other forms of communication, such as visual and chemical cues, are also affected by anthropogenic changes have rarely been investigated (Candolin and Wong 2012). Nonetheless, it is clear that urbanization has extensive consequences on the communication of urban wildlife, effects which can have negative repercussions on reproduction (mating calls), foraging (food location) and population dynamics (acoustic interference).

3.6 Reproduction

Reproduction is often incompatible with a stressed state and successful reproductive investment can only occur when there are sufficient resources available to devote to it. Landscape alterations likely contribute to the higher breeding densities and longer breeding seasons observed in a variety of urban wildlife (e.g., Walcott 1974; Cramp 1972). However, urbanization does not have reproductive benefits for all wildlife. For example, female English sole (*Parophrys vetulus*) from areas with high levels of water contaminants adjacent to urban areas in Puget Sound, Washington, had more reproductive impairments and produced a lower proportion of normal larvae compared to fish from non-polluted areas (Casillas et al. 1991). Similarly, a study by Partecke et al. (2005) revealed that urban European blackbirds showed earlier gonadal growth, secretion of luteinizing hormone (LH) and testicular development than their rural counterparts. Pollutants are not the only source of alterations in reproductive activity for urban wildlife. Artificial night light, which birds from urban centres are exposed to, appears to cause early reproductive development (Dominoni et al. 2013). Furthermore, the same study showed that city birds responded differently to light than their rural counterparts, exemplifying once again that urbanization can change the physiological phenotype of organisms (Dominoni et al. 2013).

Rubbo and Kiesecker (2005) investigated the effects of urbanization on the breeding distribution of amphibians across wetlands along an urban gradient in Pennsylvania, USA. Urban wetlands had lower larval amphibian species richness than rural areas. This was due to fewer wood frogs (*Rana sylvatica*) and salamanders (*Ambystoma maculatum* and *A. jeffersonianum*) breeding and/or offspring survival in urban areas, suggesting that these species are highly sensitive to urban development, while other species (*Anura* spp. [toads], *Rana catesbeiana* [American bullfrog], *Hyla versicolor* [grey tree frog] and *Notophthalmus viridescens* [Eastern newt]) appeared to be more resilient to the altered landscape. Big brown bats (*Eptesicus fuscus*) and red bats (*Lasirus borealis*) from rural areas in Detroit, Michigan USA had fewer offspring and lower population size in urban parks (Kurta and Teramino 1992). Taken together, these findings suggest that life in the city affects the reproductive capabilities of some species but not others, highlighting variation in the sensitivity of wildlife to urban development.

3.7 Disease and immune function

There is increasing interest in studying the relationship between urban life and the emergence of wildlife diseases as urbanization may create shifts in host geographical ranges and densities, interspecific interactions and contamination via pathogens (Daszak et al. 2000). In coastal Florida, a pathogenic nematode in wading birds was only present in sites disturbed by stream engineering and nutrient fluxes (Coyner et al. 2002). Similarly, in a study by Saldiva et al. (1992), rats that were exposed to the urban air pollution of São Paulo, Brazil, for six months developed inflammatory complications in their breathing airways, resulting in increased respiratory failure, when compared to control rats kept in a clean city. These negative repercussions on the health of wildlife as a result of urbanization have also been observed in aquatic ecosystems. Helms et al. (2005) revealed that fish health (measured by the proportion of fish with eroded fins, lesions and tumors) declined with increasing urbanization. In all of these cases, pathogens and illnesses appear to be a direct result of developing urban areas.

In the context of epidemiology, cities function as first points of entry for novel pathogens, and provide opportunities for rapid amplification and cross-species contamination (ecology of wildlife diseases review by Bradley and Altizer 2006). For example, grey squirrels were introduced to the United Kingdom where they competed with native red squirrels (*Sciurus vulgaris*). The gray squirrels also carried *paramyxovirus* and through these interspecific interactions infected red squirrels, leading to a decline of the latter (Wauters and Grunell 1999; Tompkins et al. 2002). In another example, the poultry bacterium *Mycoplasma gallisepticum* infected wild songbirds in 1994, and may be spread when birds interact at feeders (Dhondt et al. 2014). Human interactions can also affect the immunity of wildlife. In the Southern sea otter (*Enhydra lutris nereis*), infection with meningoencephalitic disease was greater in regions associated with high human density (Miller et al. 2002). Thus, cities provide both the ideal conditions for the spread of pathogens and diseases, and make animals more susceptible to those diseases by lowering their immune function.

3.8 Synthesis

It is obvious that no two species are affected in the same manner by the process of urbanization, and in fact, these effects likely differ even across sexes, life-stages, or ecomorphs. Nevertheless, there do appear to be overall patterns in how key biological systems are affected, although we did not rank the vulnerability of these systems. Some differences may also shift with time-scale focus (i.e., physiology is acutely affected, fitness is chronically affected). Furthermore, it is important to note that landscapes can vary, each bringing their own set of challenges and affecting wildlife in different ways. For example, aquatic organisms are more likely to be affected by stormwater runoff than birds, while skyscrapers are more likely to influence birds than solely ground-dwelling or aquatic organisms. This suggests that the consequences of urban life on animals are both species- and context-dependent.

While the urban life poses various challenges to core biological systems, the effects of such challenges are not independent of each other, and their additive or synergistic effects are rarely studied. For example, the city may cause an animal to spend more time foraging due to habitat fragmentation, with success mediated by light pollution and the urban heat island effect, which in turn lowers investment in offspring. There can also be inter-generational nature and nurture effects which have yet to be explored in detail. Parents in poor condition may have offspring with lower body condition, leading to increased susceptibility to pathogens and decreased future reproductive success. Additionally, selection on foraging time may lead to food specialization and a loss of ability to respond to future environmental changes if those changes were to cause a decrease in food availability. Quite simply, life in the city for vertebrates means exposure to a wide range of conditions and stressors that differ dramatically from what organisms living in more pristine settings (e.g., rural environments, wilderness).

4. Making cities more liveable

Habitat loss, fragmentation, and degradation are the major threats to organisms living in urban environments (McKinney 2002), and attenuating these threats are obvious first choices for making cities more liveable for all vertebrates. Margules and Pressey (2000) suggested the "node, buffer, corridor" principle for landscape-scale conservation. *Nodes* are high quality habitats with little to no anthropogenic disturbances. Nodes are surrounded by *buffer zones* in which human activity decreases with proximity to nodes. *Corridors* connect the nodes to create a more accessible habitat network. This approach has been successful for many ungulates and large predators in suburban areas, especially in the context of highway crossings, but there are few examples where this technique has been integrated directly into urban centres.

It is important to note that land use planning can be approached at local, regional, and global scales. The addition of a green space (e.g., parks, nature reserves) within an urban environment can have substantial benefits for many regional organisms such as squirrels and birds (e.g., Flores et al. 1998; Chiesura 2004). The implementation of wild gardens in a yard (Goddard et al. 2010) or living roof or living wall components (Francis and Lorimer 2011) can enhance the fitness of local animals and increase biodiversity. However, the needs of animals can vary extensively and must be accounted for when making land use planning or urban design decisions. For example, some birds need mature forests to breed, while larger predators tend to need large undisturbed habitats, and so planning should ideally also include natural areas of various size and with various levels of disturbance.

Important actions to consider for restoration and the mitigation of urbanization effects on wildlife include maintaining native vegetation and nesting structures, increasing foliage height diversity, integrating urban parks in the native habitat system, reducing urban effects on remote natural areas, and developing monitoring programs (Marzluff and Ewing 2001). Collaborative planning and the spread of knowledge to appropriate stakeholders can provide significant advantages for making cities more liveable. Addressing issues with water conveyance to promote infiltration rather than stormwater runoff are sorely needed. In addition, there is a need to reduce sources of pollution including light and noise. Furthermore, outreach programs about urban wildlife and biodiversity may go a long way to educate city dwellers and instill a sense of environmental stewardship in light of people’s daily choices and the future threats facing urban animals (Andersson et al. 2014). We present successful approaches to making cities more livable in Figure 3.

5. Conclusion and research needs

As the knowledge base expands, it is apparent that, given the many challenges that urban animal face, they can be severe consequences on their fitness. Certainly some aspects of urban life are lethal (e.g., vehicle collisions and bird strikes) but the sublethal effects are even more pervasive. The sublethal consequences are not independent of one another reflecting the diversity of stressors and diversity of organismal responses. The core biological systems described in this paper can be altered in complex, sometimes unexpected ways, making it difficult to precisely predict how wildlife will respond to urban life and emerging stressors. Based on our review, it became apparent that future research needs to consider the spatial, temporal and biological (e.g., individual, population, community, ecosystem) scale of their study to ensure that findings are relevant to planners and managers. In addition, many studies face challenges with identifying appropriate "controls". The use of urban gradients (rather than true controls) can be problematic because often the most sensitive species are already extirpated, forcing studies to rely on the more available species, which are often generalists (e.g., Sorace and Gustin 2009). There is little documentation on the evolutionary consequences of this ecological sorting. Even for species that can tolerate life in the city, the majority of studies have taken an ecological approach, with only a few investigating whether acclimatization to urbanization occurs via phenotypic plasticity or whether it is a function of evolutionary dynamics (Lowry et al. 2013). Urban environments tend to be more homogeneous in biotic and abiotic variables than the natural environments they replace (plant composition, temperature, humidity etc.; Hall et al. 2016). This homogeneity may lead to a loss in genetic diversity and individual variation, which is the basis for natural selection. Synurbanization is an increasingly recognized phenomenon (Figure 1) yet it is unclear what the long-term consequences of it are on organismal fitness and the evolutionary trajectory of populations. In many cases, human population growth and development is happening at such a rapid rate that the research community will lag in their understanding of how species are affected by new stressors such as emergency exposures (oil spills, nuclear power plant meltdowns, etc.), or other developing, synergistic changes.

Birds and small mammals continue to be the best-studied taxonomic groups with respect to sublethal consequences on urban vertebrates. Other taxonomic groups continue to be less studied, despite the recognition of this imbalance (Luniak and Pisarski 1994). Fish have received relatively little attention (Magle et al. 2012); future work on aquatic organisms is sorely needed as over half of the world's population lives near a coastline. Electronic tagging tools that enable researchers to track the spatial movements and survival of wildlife combined with sensors (e.g., acceleration, heart rate, body temperature; see Wilson et al. 2015) and cameras/video will provide researchers with important information on how urban wildlife interact with their environment and other organisms (including humans; see O'Connell et al. 2010). Similarly, the use of non-lethal sampling techniques and biomarkers (e.g., blood samples, fur and feathers for glucocorticoids, scats for disease screening) provide us with new tools for connecting individual-level condition and state with behaviour and other metrics of relevance to population-level processes (Sheriff et al. 2011). Indeed, this integration of behavior and physiology (see Cooke et al. 2014) is at the very core of urban ecology and will help us truly understand the long-term fitness-related impacts on animals, making it an exciting, timely, and extremely collaborative field of study.

We have clearly shown that life in the city is not without sublethal consequences. Despite the potential for synurbanization, the reality is that most urban wildlife experiences negative effects compared to conspecifics in more rural/pristine locations, and that presumably sensitive species have been replaced by generalists that are more robust to sublethal disturbances. There are many ways in which urban life can alter the biology and ecology of vertebrates and we encourage urban planners to create developments that support biodiversity and minimize disturbance (Savard et al. 2000). Humans value urban wildlife (Alberti et al. 2003), particularly vertebrates (Soule 1991), and urban wildlife generates numerous ecosystem services (Gómez-Baggethun and Barton 2013). Therefore, there is a pressing need for understanding and mitigating the sublethal consequences of urban life on wild vertebrates.

Acknowledgements: S.J.C. is supported by the Natural Sciences and Engineering Research Council of Canada (E.W.R. Steacie Fellowship, the Discovery Grant Program and the Strategic Grant Program) and the Canada Research Chairs Program. Additional support is provided by Carleton University and the US Fish and Wildlife Foundation through the United States Fish and Wildlife Service Fish Enhancement, Mitigation and Research Fund for the St. Lawrence River. R.dB. is supported by a Marie Curie Fellowship and the Max Plank Institute for Ornithology.

Literature Cited:

Alberti, M. 1999. Urban patterns and environmental performance: what do we know?. J. Plan. Edu. Res. **19**: 151-163.

Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C., Zumbrunnen, C. 2003. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. BioSci. **53**: 1169-1179.

Alberti, M., Marzluff, J.M. 2004. Ecological resilience in urban ecosystems: linking urban patterns to human and ecological functions. Urban Ecosyst. **7**: 241-265.

Alberti, M. 2005. The effects of urban patterns on ecosystem function. Int. Reg. Sci. Rev. **28**: 168-192.

Alberti, M. 2008. Advances in urban ecology: integrating humans and ecological processes in urban ecosystems. Springer, New York.

Alvey, A.A. 2006. Promoting and preserving biodiversity in the urban forest. Urban Forest. Urban Green. **5**: 195-201.

Andersson, E., Barthel, S., Borgström, S., Colding, J., Elmqvist, T., Folke, C., Gren, Å. 2014. Reconnecting cities to the biosphere: Stewardship of green infrastructure and urban ecosystem services. Ambio. **43**: 445-453.

Atkins, P.W. 1987. Molecules. Page 197. Freeman, New York.

Atwell, J.W., Ketterson, E.D. 2012. Boldness and stress physiology in a novel urban environment suggest rapid evolutionary adaptation. Behav. Ecol. **23**: 960-969.

Ball, J.E., Jenks, R., Aubourg, D. 1998. An assessment of the availability of pollutant constituents on road surfaces. Sci. Total Environ. **209**: 243-254.

Belanger, C.B., Vera-Chang, M.N., Moon, T.W., Midwood, J.D., Suski, C.D., Cooke, S.J. 2016. Seasonal variation in baseline and maximum whole-body cortisol concentrations in small-bodied stream fish independent of habitat quality. Comp. Biochem. Physiol. A: in press.

Bonier, F., Martin, P.R., Sheldon, K.S., Jensen, J.P., Foltz, S.L., Wingfield, J.C. 2007a. Sex-specific consequences of life in the city. Behav. Ecol. **18**: 121-129.

Bonier, F., Martin, P.R., Wingfield, J.C. 2007b. Urban birds have broader environmental tolerance. Biol. Lett. **3**: 670-673.

Bonier, F. 2012. Hormones in the city: Endocrine ecology of urban birds. Horm. Behav. **61**: 763-772.

Booth, D.B., Karr, J.R., Schauman, S., Konrad, C.P., Morley, S.A., Larson, M.G., Burges, S.J. 2004. Reviving urban streams: land use, hydrology, biology, and human behavior. J. Am. Water Resour. Assoc. **40**: 1351-1364.

Bradley, C.A., Altizer, S. 2006. Urbanization and the ecology of wildlife diseases. Trends Ecol. Evol. **22**: 95-102.

Brazel, A., Selover, N., Vose, R., Heisler, G. (2000). The tale of two climates – Baltimore and Phoenix urban LTER sites. Climate Res. **15**: 123-135.

Brearley, G., McAlpine, C., Bell, S., Bradley, A. (2012). Influence of urban edges on stress in an arboreal mammal: a case study of squirrel gliders in southeast Queensland, Australia. Landsc. Ecol. **27**: 1407-1419.

Breuste, J., Feldmann, H., Uhlmann, O. 2013. Urban Ecology. Springer Science & Business Media.

Brown, R.R., Farrelly, M.A., Loorbach, D.A. 2013. Actors working the institutions in sustainability transitions: the case of Melbourne's stormwater management. Global Environ. Change **23**: 701-718.

Calow, P. 1991. Physiological costs of combating chemical toxicants: ecological implications. Comp. Biochem. Physiol. **100**: 3-6.

Calow, P., Forbes, V.E. 1998. How do physiological responses to stress translate into ecological and evolutionary processes?. Comp. Biochem. Physiol. A. **120**: 11-16.

Candolin, U., Wong, B.B.M. 2012. Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press.

Castillas, E., Misitano, D., Johnson, L.L., Rhodes, L.D., Collier, T.K., Stein, J.E., McCain, B.B., Varanasi, U. 1991. Inducibility of spawning and reproductive success of female English sole (*Parophrys vetulus*) from urban and nonurban areas of Puget Sound, Washington. Mar Environ. Res. **31**: 99-122.

Chace, J.F., Walsh, J.J. 2006. Urban effects on native avifauna: a review. Landsc. Urban Plan. **74:** 46-69.

Chiesura, A. 2004. The role of urban parks for the sustainable city. Landsc. Urban Plan. **68**: 129-138.

Childe, V.G. 1950. The urban revolution. Town Plan. Rev. **21**: 3–17.

Coffin, A.W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. J. Transp. Geog. **15**: 396-406.

Cohen, B. 2006. Urbanization in developing countries: Current trends, future projections, and key challenges for sustainability. Tech. Soc. **28**: 63-80.

Cooke, S.J., Blumstein, D.T., Buchholz, R., Caro, T., Fernández-Juricic, E., Franklin, C.E., Metcalfe, J., O'Connor, C.M., St. Clair, C.C., Sutherland, W.J., Wikelski, M. 2014. Physiology, behaviour and conservation. Physiol. Biochem. Zool. **87**: 1-14.

Coutant, C.C., Whitney, R.R. 2000. Fish behavior in relation to passage through hydropower turbines: a review. Trans. Am. Fish. Soc. **129**: 351-380.

Coyner, D.F., Spalding, M.G., Forrester, D.J. 2002. Epizootiology of Eustrongylides ingotus in Florida: distribution, density, and natural infections in intermediate hosts. J. Wildl. Dis. **38**: 483–499.

Cramp, S. 1972. The breeding of urban woodpigeons. Intern. J. Avian Sci. **114**: 163-171.

Crino, O.L., Klaassen Van Oorschot, B., Johnson, E.E., Malisch, J.L., Breuner, C.W. 2011. Proximity to a high-traffic road: Glucocorticoid and life history consequences for nestling white-crowned sparrows. Gen. Comp. Endocrin. **173**: 323-332.

Crooks, K.R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv. Biol. **16**: 488-502.

Cunniff, P.F. 1977. Environmental noise pollution. John Wiley & Sons Inc.

Dantzer, B., Fletcher, Q.E., Boonstra, R., Sheriff, M.J. 2014. Measures of physiological stress: a transparent or opaque window into the status, management and conservation of species?. Conserv. Physiol. **2**: cou023.

Daszak, P., Cunningham, A.A., Hyatt, A.D. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. Science. **287**: 443–449.

Dhondt, A.A., DeCoste, J.C., Ley, D.H., Hochachka, W.M. 2014. Diverse wild bird host range of *Mycoplasma gallisepticum* in Eastern North America. PLoS ONE **9**, e103553.

Ditchkoff, S., Saalfeld, S., Gibson, C. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. Urban Ecosyst. **9**: 5-12.

Dominoni, D., Quetting, M., Partecke, J. 2013. Artificial light at night advances avian reproductive physiology. Proc. R. Soc. B **280**: 20123017.

Flores, A., Pickett, S.T., Zipperer, W.C., Pouyat, R.V., Pirani, R. 1998. Adopting a modern ecological view of the metropolitan landscape: the case of a greenspace system for the New York City region. Landsc. Urban Plan. **39**: 295-308.

Francis, C.D., Barber, J.R. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. **11**: 305-313.

Francis, R.A., Lorimer, J. 2011. Urban reconciliation ecology: the potential of living roofs and walls. J. Environ. Manage. **92**: 1429-1437.

French, S.S., Fokidis, H.B., Moore, M.C. 2008. Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban-rural gradient. J. Comp. Physiol. B **178**: 997-1005.

Gehrt, S.D. 2007. Ecology of coyotes in urban landscapes. In Nolte, DL, Arjo, WM, Stalman, DH, editors. Proceedings of the 12th Wildlife Damage Management Conference.

Gehrt, S.D., Chelsvig, J.E. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecol. Appl. **13**; 939-950.

Gehrt, S.D., Brown, J.L., Anchor, C. 2011. Is the urban coyote a misanthropic synanthrope? The case from Chicago. Cities Environ. **4**.

Goddard, M.A., Dougil, A.J., Benton, T.G. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. **25**: 90-98.

Gómez-Baggethun, E., Barton, D.N. 2013. Classifying and valuing ecosystem services for urban planning. Ecol. Econ. **86**: 235-245.

Grieco, F., van Noordwijk, A.J., Visser, M.E. 2002. Evidence for the effect of learning on timing of reproduction in blue tits. Science. **296**: 136-138.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M. 2008. Global change and the ecology of cities. Science. **319**: 756-760.

Grinder, M.I., Krausman, P.R. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. J.Wildl. Manage. **65**: 887-898.

Grubbs, S.E., Krausman, P.R. 2009. Use of urban landscape by coyotes. Southwest. Nat. **54**: 1-12.

Hall, S.J., Learned, J., Ruddell, B., Larson, K.L., Cavender-Bares, J., Bettez, N., Groffman, P.M., Grove, J.M., Heffernan, J.B., Hobbie, S.E., Morse, J.L., Neill, C., Nelson, K.C., O'Neil-Dunne, J.P.M., Ogden, L., Pataki, D.E., Pearse, W.D., Polsky, C., Chowdhury, R.R., Steele, M.K., Trammell, T.L.E. 2016. Convergence of microclimate in residential landscapes across diverse cities in the United States. Landsc. Ecol. **31**: 101-117.

Helms, B.S., Feminella, J.W., Pan, S. 2005. Detection of biotic responses to urbanization using fish assemblages from small streams of western Georgia, USA. Urban Ecosyst. **8**: 39-57.

Houlihan, D.F., Carter, C.G., McCarthy, I.D. 1995. Protein synthesis in fish. Pages 191-220 in: Hochachka, P., Mommsen, T., editors. Biochemistry and Molecular Biology of Fishes. Elsevier, Amsterdam.

Jansson, C., Ekman, J., von Bromssen, A. 1981. Winter mortality and food supply in tits *Parus spp*. Oikos **37**: 313-322.

Jones, G. 2008. Sensory ecology: noise annoys foraging bats. Curr. Biol. **18**: R1098-1100.

Kleerekoper, L., van Esch, M., Baldiri Salcedo, T. 2012. How to make a city climate-proof, addressing the urban island heat effect. Resour. Conserv. Recy. **64**: 30-38.

Klem Jr, D. 1989. Bird: Window Collisions. The Wilson Bulletin, 606-620.

Kowarik, I. 2011. Novel urban ecosystems, biodiversity, and conservation. Environ. Pollut. **159**: 1974-1983.

Kurta, A., Teramino, J.A. 1992. Bat community structure in an urban park. Ecograph. **15**: 257-261.

Laiolo, P. 2010. The emerging significance of bioacoustics in animal species conservation. Biol. Conserv. **143**: 1635-1645.

Larinier, M. 2001. Environmental issues, dams and fish migration. FAO Fish. Tech. Paper **419**: 45-89.

Longcore, T., Rich, C. 2004. Ecological light pollution. Front. Ecol. Environ. **2**: 191-198.

Lowry, H., Lill, A., Wong, B.B.M. 2013. Behavioural responses of wildlife to urban environments. Biol. Rev. **88**: 537-549.

Luniak, M. 1996. Synurbanization of animals as a factor increasing diversity of urban fauna. Pages 566-575 in di Castri, F., Younes, T., editors. Biodiversity, science, and development: toward a new partnership. CAB International.

Luniak, M. 2004. Synurbization–adaptation of animal wildlife to urban development. Pages 50-55 in Proceedings of the 4th International Symposium Urban Wildlife Conservation of Tucson.

Luniak, M., Pisarski, B. 1994. State of research into the fauna of Warsaw (up to 1990). Memorabilia Zool. **49**: 155-165.

Mage, D., Ozolins, G., Peterson, P., Webster, A., Orthofer, R., Vandeweerd, V., Gwynne, M. 1996. Urban air pollution in megacities of the world. Atmos. Environ. **30**: 681-686.

Magle, S.B., Hunt, V.M., Vernon, M., Crooks, K.R. 2012. Urban wildlife research: past, present, and future. Biol. Conserv. **155**: 23-32.

Mäkeläinen, S., de Knegt, H.J., Ovaskainen, O., Hanski, I.K. 2016. Home-range use patterns and movements of the Siberian flying squirrel in urban forests: Effects of habitat composition and connectivity. Mov. Ecol. **4**: 1.

Margules, C.R., Pressey, R.L. 2000. Systematic conservation planning. Nature. **405**: 243-253.

Marzluff, J.M., Bowman, R., Donnelly, R.E. 2001. A historical perspective on urban bird research: trends, terms and approaches. Pages 1-18 in Marzluff JM, Bowman R, Donnelly RE, editors. Avian conservation and ecology in an urbanizing world. Kluwer, New York.

Marzluff, J.M., Ewing, K. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restor. Ecol. **9**: 280-292.

Marzluff, J.M., Neatherlin, E. (2006). Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biol. Conserv. **130**: 301-14.

McClennen, N., Wigglesworth, R.R., Anderson, S.H., Wachob, D.G. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). Am. Midl. Nat. **146**: 27-36.

McClure, C.J.W., Ware, H.E., Carlisle, J., Kaltenecker, G., Barber, J.R. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc. R. Soc. B **280**.

McDonnell, M.J. 2011. The history of urban ecology: an ecologist's perspective. Pages 5-13 in Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N.E., editors. Urban Ecology: Patterns, Processes and Applications. Oxford University Press, Oxford.

McEwen, B.S., Wingfield, J.C. 2003b. The concept of allostasis in biology and biomedicine. Horm. Behav. **43**: 28-30.

McKinney, M.L. 2002. Urbanization, biodiversity and conservation: the impacts of urbanization on native species are poorly studies, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. BioSci. **52**: 883-890.

McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. **127**: 247-260.

Meillere, A., Brischoux, F., Angelier, F. 2015. Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows. Behav. Ecol.: in press.

Meyer, J.L., Paul, M.J., Taulbee, W.K. 2005. Stream ecosystem function in urbanizing landscapes. Journal of the North American Benthol. Soc. **24**: 602-612.

Miller, M.A., Gardner, I.A., Kreuder, C., Paradies, D.M., Worcester, K.R., Jessup, D.A., Dodd, E., Harris, M.D., Ames, J.A., Packham, A.E., Conrad, P.A. 2002. Coastal freshwater runoff is a risk factor for Toxoplasma gondii infection of southern sea otters (*Enhydra lutris nereis*). Int. J. Parasitol. **32**: 997–1006.

Miranda, A.C., Schielzeth, H., Sonntag, T., Partecke, J. 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Glob. Change Biol. **19:** 2634-2644.

Morgan, I.J., McDonald, D.G., Wood, C.M. 2001. The cost of living for freshwater fish in a warmer, more polluted world. Glob. Change Biol. **7**: 345-355.

Morris, D.W. 2005. Paradoxical avoidance of enriched habitats: have we failed to appreciate omnivores? Ecol. **86**: 2568-2577.

Naguib, M. 2013. Living in a noisy world: indirect effects of noise on animal communication. Behav. **150**: 1069-1084.

Navara, K.J., Nelson, R.J. 2007. The dark side of light at night: physiological, epidemiological and ecological consequences. J. Pineal Res. **43**: 215-224.

Newsome, D., Rodger, K. 2008. To feed or not to feed: a contentious issue in wildlife tourism. Pages 255-270 in Lunney D, Munn A, Meikle W, editors. Too close for comfort: contentious issues in human-wildlife encounters. Royal Zoological Society of New South Wales, Mosman, Australia.

Niemelä, J. 1999. Is there a need for a theory of urban ecology?. Urban Ecosyst. **3**: 57-65.

Oberweger, K., Goller, F. 2001. The metabolic cost of birdsong production. J. Exp. Biol. **204**: 3379-3388.

O'Connell, A.F., Nichols, J.D., Karanth, K.U., editors. 2010. Camera traps in animal ecology: methods and analyses. Springer Science & Business Media.

Oke, T.R. 1973. City size and the urban heat island. Atmos. Environ. **7**: 769-779.

Oke, T.R. 1995. The heat island of the urban boundary layer: characteristics, causes and effects. Pages 81-107 in Wind Climate in Cities. Springer, Netherlands..

Onorato, D.P., Belden, C., Cunningham, M., Land, D., McBride, R., Roelke, M. 2010 Long-term research on the Florida panther (*Puma concolor coryi*): historical findings and future obstacles to population persistence. Pages 453-469 in Macdonald, D., Loveridge, A., editors. Biology and Conservation of Wild Felids. Oxford University Press, Oxford, UK.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martinez-Abrain, A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. **16**: 1501-1514.

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

Partecke, J., Schwabl, I., Gwinner, E. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecol. **87**: 1945-1952.

Patricelli, G.L., Blickley, J.L. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk **123**: 639-649.

Paul, M.J., Meyer, J.L. 2001. Streams in the urban landscape. Pages 207-231 in Urban Ecology. Springer: USA.

Penuelas, J., Filella, I. 2001. Responses to a warming world. Science. **294**: 793-794.

Pickett, S.T., Cadenasso, M.L., Grove, J.M., Groffman, P.M., Band, L.E., Boone, C.G., Law, N.L. 2008. Beyond urban legends: an emerging framework of urban ecology, as illustrated by the Baltimore Ecosystem Study. BioSci. **58**: 139-150.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E., Blount, J.D. 2013. Winter food provisioning reduces future breeding performance in a wild bird. Sci. Rep. **3**: 1-6.

Poessel, S.A., Burdett, C.L., Boydston, E.E., Lyren, L.M., Alonso, R.S., Fisher, R.N., Crooks, K.R. 2014. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biol. Conserv. **180**: 224-232.

Prange, S., Gerht, S.D., Wiggers, E.P. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. J. Wildl. Manage. **67**: 324-333.

Raubenheimer, D., Simpson, S.J., Mayntz, D. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Funct.Ecol. **23**: 4-16.

Raubenheimer, D., Simpson, S.J., Tait, A.H. 2012. Match and mismatch: conservation physiology, nutrition ecology and the timescales of biological adaptation. Phil. Trans. R. Soc. B. **367**: 1628-1646.

Reid, S.D., Linton, T.K., Dockray, J.J., McDonald, D.G., Wood, C.M. 1998. Effects of chronic sublethal ammonia and a simulated summer global warming scenario: protein synthesis in juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **55**: 1534-1544.

Rich, C., Longcore, T. 2013. Ecological consequences of artificial night lighting. Island Press, Washington D.C.

Ricklefs, R.E., Wikelski, M. 2002. The physiology/life-history nexus. Trends. Ecol. Evol. **17**: 462-468.

Riley, S.P.D., Bromley, C., Poppenga, R.H., Uzal, F.A., Whited, L., Sauvajot, R.M. 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. J. Wildl. Manage. **71**: 1874-1884.

Robb, G.N., McDonald, R.A., Chamberlain, D.E., Bearhop, S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front. Ecol. Environ. **6**: 476-484.

Robbins, P., Sharp, J. 2006. Turfgrass subjects: the political economy of urban monoculture. Pages 106-123 in Heynen, N., Kaika, M., Swyngedouw, E., editors. The Nature of Cities: Urban political ecology and the politics of urban metabolism. Routledge, London, UK.

Robbins, P., Polderman, A., Birkenholtz, T. 2001. Lawns and toxins: an ecology of the city. Cities. **18**: 369-380.

Rodewald, A.D., Kearns, L.J., Shustack, D.P. 2011. Anthropogenic resource subsidies decouple predator-prey relationships. Ecol. Appl. **21**: 936-943.

Roux, K.E., Marra, P.P. 2007. The presence and impact of environmental lead in passerine birds along an urban to rural land use gradient. Arch. Environ. Contam. Toxicol. **53**: 261-268.

Rubbo, M.J., Kiesecker, J.M. 2005. Amphibian breeding distribution in an urbanization landscape. Conserv. Biol. **19**: 504-511.

Saggese, K., Korner-Nievergelt, F., Slagsvold, T., Amrhein, V. 2011. Wild bird feeding delays start of dawn singing in the great tit. Anim, Behav. **81**: 361-365.

Sakai, S., Sawell, S.E., Chandler, A.J., Eighmy, T.T., Kosson, D.S., Vehlow, J., Hjelmar, O. 1996. World trends in municipal solid waste management. Waste Manag. **16**: 341-350.

Saldiva, P.H.N., King, M., Delmonte, V.L.C., Macchione, M., Parada, M.A.C., Daliberto, M.L., Sakae, R.S., Criado, P.M.P., Silveira, P.L.P., Zin, W.A., Böhm, G.M. 1992. Respiratory Alterations due to urban air pollution: an experimental study in rats. Environ. Res. **57**: 19-33.

Savard, J.P.L., Clergeau, P., Mennechez, G. 2000. Biodiversity concepts and urban ecosystems. Landsc. Urban Plan. **48**: 131-142.

Scheifler, R., Coeurdassier, M., Morilhat, C., Bernard, N., Faivre, B., Flicoteaux, P., Giraudoux, P., Noel, M., Piotte, P., Rieffel, D., de Vaufleury, A., Badot, P.M. 2006. Lead concentrations in feathers and blood of common blackbirds (*Turdus merula*) and in earthworms inhabiting unpolluted and moderately polluted urban areas. Sci. Total Environ. **371**: 197-205.

Schroeder, J., Nakagawa, S., Cleasby, I.R., Burke, T. 2012. Passerine birds breeding under chronic noise experience reduced fitness. PLoS ONE **7**: e39200.

Serena, M., Pettigrove, V. 2005. Relationship of sediment toxicants and water quality to the distribution of platypus in urban streams. J. North Am. Benthol. Soc. **24**: 679-689.

Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S., Wittemyer, G. 2015. A synthesis of two decades of research documenting the effects of noise on wildlife. Biol. Rev. in press.

Sharma, S.K., Sanghi, R., editors. (2012). Advances in water treatment and pollution prevention. Springer Science & Business Media.

Sheriff, M.J., Dantzer, B., Delehanty, B., Palme, R., Boonstra, R. 2011. Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecol. **166**: 869-887.

Sih, A., Cote, J., Evans, M., Fogarty, S., Pruitt, J. 2012. Ecological implications of behavioural syndromes. Ecol. Lett. **15**: 278-289.

Simpson, S.J., Raubenheimer, D., Charleston, M.A., Clissold, F.J. 2013. Modelling nutritional interactions: from individuals to communities. Trends Ecol. Evol. **25**: 53-60.

Simpson, S.D., Meekan, M.G., Jeffs, A., Montgomery, J.C, McCauley, R.D. 2008. Settlement-stage coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef noise. Anim. Behav. **75**: 1861-1868.

Slabbekoorn, H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim. Behav. **85**: 1089-1099.

Smith, B.R., Blumstein, D.T. 2008. Fitness consequences of personality: a meta-analysis. Behav. Ecol. **19**: 448-455.

Solokova, I.M., Lannig, G. 2008. Interactive effects of metal pollution and temperature on metabolism in aquatic ectotherms: implications of global climate change. Clim. Res. **37**: 181-201.

Sol, D., Lapeidra, O., Gonzalez-Lagos, C. 2013. Behavioural adjustments for a life in the city. Anim. Behav. **85**: 1101-1112.

Sorace, A., Gustin, M. 2009. Distribution of generalist and specialist predators along urban gradients. Landsc. Urban Plan. **90**: 111-118.

Soule, M.E. 1991. Land use planning and wildlife maintenance: guidelines for conserving wildlife in an urban landscape. J. Am. Plan. Assoc. **57**: 313-323.

Stein, S. 2014. Alien Squirrel. New York Magazine, New York.

Steyermark, A.C. 2002. A high standard metabolic rate constrains juvenile growth. J. Zool. **105**: 147-151.

Stracey, C.M. 2011. Resolving the urban nest predator paradox: the role of alternative foods for nest predators. Biol. Conserv. **144**: 1545-1552.

Strasser, E.H., Heath, J.A. 2011. Effects of developmental conditions on nestling American kestrel (*falco sparverius*) corticosterone concentrations. Gen. Comp. Endocrin. **173**: 164-170.

Sun, J.W.C., Narins, P.M. 2005. Anthropogenic sounds differentially affect amphibian call rate. Biol. Conserv. **121**: 419-427.

Tigas, L.A., Van Vuren, D.H., Sauvajot, R.M. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biol. Conserv. **108**: 299-306.

Tompkins, D., Sainsbury, A.W., Nettleton, P., Buxton, D., Gurnell, J. 2002 Parapoxvirus causes a deleterious disease of red squirrels associated with UK population declines. Proc. R. Soc. B. **269**: 529–533.

Tremblay, M.A., St Clair, C.C. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. J. Appl. Ecol. **46**: 1314-1322

United Nations Population Fund. (2007). State of the world population 2007: unleashing the potential of urban growth. United Nations Population Fund, New York.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M. 1997. Human domination of earth's ecosystems. Science. **277**: 494-499.

Walcott, C.F. 1974. Changes in bird life in Cambridge, Massachusetts from 1860 to 1964. Auk. **91**: 151-160.

Walsh, C.J., Roy, A.H., Feminella, J.W., Cottingham, P.D., Groffman, P.M., Morgan II, R.P. 2005. The urban stream syndrome: current knowledge and the search for a cure. J. North. Am. Benthol. Soc. **24**: 706-723.

Ware, H.E., McClure, C.J.W., Carlisle, J.D., Barber, J.R. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proc. Nat. Acad. Sci. **112**: 12105-12109.

Warren Jr, M.L., Pardew, M.G. 1998. Road crossings as barriers to small-stream fish movement. Trans. Am. Fish. Soc. **127**: 637-644.

Wauters, L.A., Grunell, J. 1999. The mechanism of replacement of red by grey squirrels: a test of the interference competition hypothesis. Ethology. **105**: 1053–1071.

Werry, J.M., Lee, S.Y., Lemckert, C.J., Otway, N.M. 2012. Natural or artificial? Habitat-use by the bull shark, *Carcharhinus leucas*. PloS ONE **7**: e49796.

Widder, P.D., Bidwell, J.R. 2009. Tadpole size, cholinesterase activity, and swim speed in four frog species after exposure to sub-lethal concentrations of chlorpyrifos. Aquat. Toxicol. **88**: 9-18.

Wilson, A.D.M., Wikelski, M., Wilson, R.P., Cooke, S.J. 2015. Utility of biological sensor tags in animal conservation. Conserv. Biol. **29**:1065–1075.

Zannin, P.H.T., Ferreira, A.M.C., Szeremetta, B. 2006. Evaluation of noise pollution in urban parks. Environ. Monit. Asses. **118**: 423-433.

Figure Captions

Figure 2. Overview of the potential challenges that urbanization poses on wild vertebrates. City lights can greatly affect migratory species and circadian rhythms. Large factories can participate in generating heat islands and pollution. Vehicles and boats pollute the surrounding environment through exhaust. Stream water runoff can severely impact the water quality of streams, having effects on fish populations. Noise can impair intraspecific communication.

Figure 1 – Synurbanization

Synurbanization refers to the adaptation of wildlife to urban environments (reviewed by Luniak 2004). The study of synurbanization has grown recently, as we try to tease apart the degree to which phenotypic plasticity and microevolutionary processes leading to divergent selection contribute to changes in animals under human-altered conditions. The creation of a new urban ecosystem has benefitted some animals, namely small mammals and birds. These species have adjusted to urban pressures through higher population densities, reduced migratory behavior, prolonged breeding seasons, greater longevity, prolonged circadian rhythms, and changes in feeding behavior (as listed in Luniak 1996). For example, many birds benefit from supplementary feeding in urban areas, leading to earlier lay dates, larger clutches and chicks, and higher hatching and fledging success (reviewed in Robb et al. 2008). Top-down processes may also affect these species, as predation pressure may be reduced when predators shift their diet to anthropogenic sources (Rodewald et al. 2011; Stracey 2011). More omnivorous species can mitigate the costs of searching for and killing live prey by modifying their behavior to depend on anthropogenic food, a trend that is becoming increasingly apparent for coyotes, raccoons, and black bears (Prange et al. 2003; Gehrt 2007). Urban populations also tend to be more aggressive, take more risks, are less neophobic, are more exploratory/bold and have reduced escape behaviors compared to rural populations (Miranda et al 2013; Sih et al 2012). These personality traits can be linked to fitness: bolder and more aggressive individuals have greater reproductive success, and exploratory individuals have higher survival (Smith and Blumstein 2008), suggesting these personality traits are beneficial when inhabiting a novel and risky urban environment. The home ranges of both bats (Gehrt and Chelving 2003) and coyotes (*Canis latrans*) (McClennen et al. 2001, Grubbs and Krausman 2009) did not differ between fragmented and unfragmented habitats, and both species used human-generated corridors during travel, suggesting that species which can persist in urban environments (i.e., synanthropes, Gerht et al. 2011) are able to adjust their behavior to habitat fragmentation and human activities. Studies integrating bottom-up and top-down ecological interactions with behaviour and physiology and linking these traits with fitness are sorely needed, as the sublethal consequences of urban modifications are both acute and chronic. 1a) A fox (*Vulpes vulpes*) is walking in a residential area at night, and 1b) a grey heron (*Ardea cinerea*) has acquired food from a local street vendor in Amsterdam. *Images by Sam Hobson*

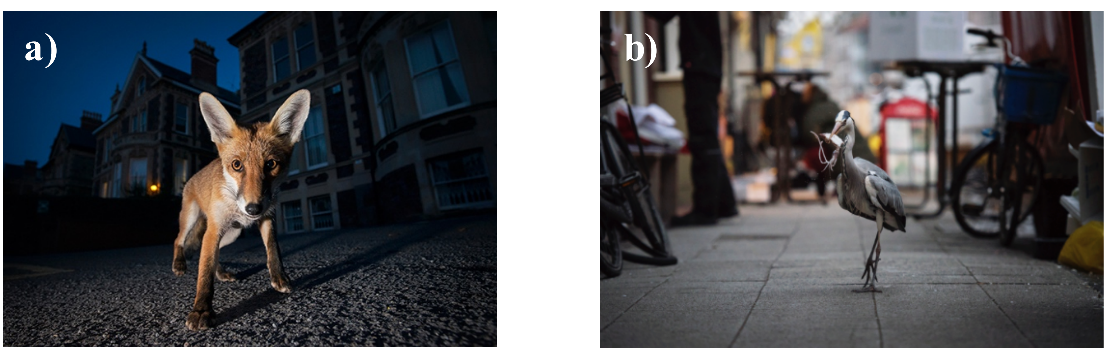

Figure 3 – Making cities more liveable: success stories

3a) Every year, billions of birds migrate north in the spring and south in the fall. Many species will do so at night, when the presence of lights from buildings and other structures can cause severe disturbances to bird's navigation as they fly over. *Lights Out* is a national effort in the USA that aims to reduce this issue by simply convincing building owners and managers to turn off excess lighting at night during the months that birds are migrating. *Image by NASA*

3b) Discouraging open lawns on public and private property was successful in restoring some wildlife habitat in King County, Washington. The many layers of undisturbed habitat provide a complex and favorable environment for small mammals and birds. *Image by Wave Hill*

3c) In Melbourne, Australia, stormwater infrastructure was altered over the course of almost two decades to improve the city's waterways. They used community members, environmental scientists and policy-makers to establish a plan to make a smoother transition to a more sustainable infrastructure (Brown et al. 2013). *Image by Storm Water Systems*