



# Past and future: Urbanization and the avian endocrine system

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## ABSTRACT

Urban environments are evolutionarily novel and differ from natural environments in many respects including food and/or water availability, predation, noise, light, air quality, pathogens, biodiversity, and temperature. The success of organisms in urban environments requires physiological plasticity and adjustments that have been described extensively, including in birds residing in geographically and climatically diverse regions. These studies have revealed a few relatively consistent differences between urban and non-urban conspecifics. For example, seasonally breeding urban birds often develop their reproductive system earlier than non-urban birds, perhaps in response to more abundant trophic resources. In most instances, however, analyses of existing data indicate no general pattern distinguishing urban and non-urban birds. It is, for instance, often hypothesized that urban environments are stressful, yet the activity of the hypothalamus-pituitary-adrenal axis does not differ consistently between urban and non-urban birds. A similar conclusion is reached by comparing blood indices of metabolism. The origin of these disparities remains poorly understood, partly because many studies are correlative rather than aiming at establishing causality, which effectively limits our ability to formulate specific hypotheses regarding the impacts of urbanization on wildlife. We suggest that future research will benefit from prioritizing mechanistic approaches to identify environmental factors that shape the phenotypic responses of organisms to urbanization and the neuroendocrine and metabolic bases of these responses. Further, it will be critical to elucidate whether factors affect these responses (a) cumulatively or synergistically; and (b) differentially as a function of age, sex, reproductive status, season, and mobility within the urban environment. Research to date has used various taxa that differ greatly not only phylogenetically, but also with regard to ecological requirements, social systems, propensity to consume anthropogenic food, and behavioral responses to human presence. Researchers may instead benefit from standardizing approaches to examine a small number of representative models with wide geographic distribution and that occupy diverse urban ecosystems.

## 1. How animals persist in urban environments: the importance of endocrine flexibility

The human population has increased to an unprecedented extent over the last century and this has been accompanied by a massive exodus of rural human populations towards urban areas (United Nations, 2020). Indeed, half of humans now live in cities and this phenomenon is expected to increase until the end of the 21<sup>st</sup> century. The increase in urban human populations has been accompanied by a rapid urban sprawl and massive environmental changes (McKinney, 2002). These environmental changes are multiple, rapid, and often drastic, and cities represent the most modified environment on Earth (Grimm et al., 2008). Urbanization-associated environmental changes strongly impact

biodiversity in general, and that of wild vertebrates in particular (Chace and Walsh, 2006; Grimm et al., 2008). Whereas urban environments are often host to a similar abundance and diversity of arthropods as compared to managed agricultural areas (Turrini and Knop, 2015), urban vertebrate biodiversity is usually impoverished (Gil and Brumm, 2014; McKinney, 2006) because most vertebrate species are unable to live in this environment (urban avoiders, Blair, 1996; Fischer et al., 2015). However, some vertebrate species can adjust to cities (urban adapters) and a few even thrive in the urban environment (urban exploiters, Blair, 1996; Fischer et al., 2015). There is increasing evidence that phenotypic plasticity, defined as the ability for environmental conditions to produce varying phenotypes from an individual genotype (Pigliucci, 2001), combined with microevolutionary processes are

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important drivers of the ability of species and individuals to adjust to the urban environment (Lowry et al., 2013; Miranda et al., 2013; Thompson et al., 2021). Indeed, urban-related environmental changes are so fast and intense that they may limit the ability of urban avoiders to adapt to an urban way of life through selection processes. This may be the case especially of species with long generation times, such as most vertebrates. Therefore, phenotypic plasticity is arguably a crucial component to allow species to persist in the urban environment and for evolution to then act to further adapt species to urbanization (the concept of “buying time”, Diamond and Martin, 2021).

Endocrine mechanisms are crucial to determining whether a species is likely to persist in the urban environment. Indeed, these mechanisms are recognized as key mediators of the behavioral and physiological response to environmental changes (Ricklefs and Wikelski, 2002). They are, therefore, tightly linked to phenotypic plasticity (Hau and Goymann, 2015), and endocrine flexibility is thought to be a requisite to adapt to changes (Angelier and Wingfield, 2013; Taff and Vitousek, 2016). In addition, the functioning of endocrine mechanisms is often repeatable within individuals (Taff et al., 2018; Fanson and Biro, 2019) and somewhat heritable (e.g., Evans et al., 2006; Jenkins et al., 2014), making them likely targets for evolutionary processes in urban environments in the longer term. As the functioning of endocrine mechanisms can substantially vary between species (e.g., Romero and Gormally, 2019), interspecific differences in this functioning may explain the ability of some species to persist in urban settings.

Urban environments are often more stable than rural areas as environmental fluctuations are buffered (Ibáñez-Álamo et al., 2020). For example, urban areas are typically warmer than surrounding rural environments and may thus provide a buffer against cold temperatures (Shochat et al., 2006). Similarly, in hot climates misting systems can lower ambient temperatures and watering systems create artificial precipitation (Shochat et al., 2006). Food availability is also more predictable in urban environments (Shochat et al., 2006). Thus, it is not surprising that a review conducted by Bonier (2012) found “no clear or consistent patterns” in the endocrine responses of birds to urbanization. At that time, the authors recommended stronger research approaches to examine this relationship between and within bird taxa around the world (Bonier, 2012). Based on analyses of the literature that we present here, this remains an important call for research as inconsistencies in findings hamper efforts to form generalizations. While many biomarkers have been targeted to evaluate the influence of urbanization on individual birds (Table 1), most studies on this topic have not examined the relationship between these biomarkers and avian endocrine physiology in an urban context. Instead, most studies to date have compared hormonal levels between urban and non-urban populations without necessarily linking these hormonal levels to specific urban-related environmental modifications. In this review, we, therefore, present these biomarkers and highlight studies that have examined this link.

## 2. What are the most studied endocrine axes in urban-related research?

Several ecophysiological studies have investigated the endocrine response of vertebrates to urban challenges. The objectives of these studies were primarily to evaluate the impact of urbanization on the health of wild vertebrates and to test whether specific traits were necessary to cope with an urban way of life. Perhaps the most-often studied impact of urbanization on the endocrine physiology of wild birds is the glucocorticoid stress response (Table 2). Evidence exists that is consistent with the hypothesis that this response is related to colonization of new (potentially including urban) habitats. For example, house sparrows (*Passer domesticus*) - a species that is typically associated with human-modified environments - have undergone rapid range extension from initial introduction sites in some regions of Kenya. During the breeding season, sparrows at the edge of their range had a stronger corticosterone (CORT) response to acute stress than those at initial

**Table 1**

Published parameters used to measure the impact of urbanization on avian species.

Published parameters used to assess the effects of urbanization on birds	Examples	References
Behavior	territorial behavior and aggression, object neophobia, exploratory behavior	Atwell et al., 2012; Davies et al., 2018; Fokidis et al., 2011a; Grunst et al., 2019; Mueller et al., 2013; Riyahi et al., 2015
Biochemistry, Gene expression, Morphology, Physiology	blood biochemistry: heterophil/lymphocyte (H/L) ratio, anucleated red blood cells (RBC), protoporphyrin, methemoglobin, RBC, white blood cells (WBC) body condition, bone mineral density	Bauerová et al., 2017; Burger and Gochfeld, 1997; Siculo et al., 2009; Suárez-Rodríguez and García, 2014
	circadian, circannual	Davies et al., 2013, 2015a; Foltz et al., 2015; Giraudeau et al., 2014; Grunst et al., 2020b; Heiss et al., 2009; Injaian et al., 2018; Jimenez-Penuela et al., 2019; McGraw et al., 2020; McNew et al., 2017; Nebel et al., 2020; Ots and Hörak, 1998; Plourde et al., 2013; Sriram et al., 2018
	coloration, pigmentation, preen gland size	Davies et al., 2015a; Dominoni et al., 2013; Partecke et al., 2004; Renthlei et al., 2020, 2021; Renthlei and Trivedi, 2019; Zhang et al., 2014
	gene expression, epigenetics, RBC micronucleus, anucleated RBCs, telomeres, transcription	Giraudeau et al., 2017; Grunst et al., 2020a; Horak et al., 2001; Isaksson et al., 2005
		Andrew et al., 2019; Baesse et al., 2015, 2019; Blanco-Peña et al., 2017; Brewer et al., 2020; Ceyca-Contreras et al., 2020; Delaney et al., 2010; Evans et al., 2009; Giraudeau et al., 2020; Gonçalves et al., 2020; Grunst et al., 2020b; Ibáñez-Álamo et al., 2018; Low et al., 2018; McNew et al., 2017; Meillère et al., 2015a; Morakchi et al., 2017; Mueller et al., 2013, 2018, 2020; Ouyang et al., 2019; Renthlei et al., 2020, 2021; Riyahi et al., 2015; Salmón et al., 2021; Tan et al., 2018; Watson et al., 2017, 2020; Zhang et al., 2013
	gut microbiome oxidative stress and antioxidants	Teyssier et al., 2020
		Giraudeau and McGraw, 2014; Giraudeau et al., 2014; Herrera-Duenas et al., 2014; Isaksson et al., 2005, 2009
	reproduction and nestlings	Davies et al., 2015a, 2016a, 2018; Dominoni et al., 2013; Fokidis

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**Table 1** (continued)

Published parameters used to assess the effects of urbanization on birds	Examples	References
Infections	feather microorganisms blood and intestinal: antibiotic resistant infections, Avian influenza, Botulism, <i>Campylobacter jejuni</i> , <i>Chlamydia psittaci</i> , Coccidians, Coronaviruses, <i>Cryptococcus neoformans</i> , <i>E. coli</i> , <i>Haemoproteus</i> , Haemosporidian parasites, <i>Helicobacter</i> virus, Hematozoa parasites, <i>Leucocytozoon</i> , Microsporidia; Nematodes, <i>Neospora caninum</i> , Newcastle disease virus, <i>Plasmodium</i> , Poxvirus, <i>Salmonella</i> , <i>Sarcocystis</i> , <i>Toxoplasma gondii</i> , Trypanosomes, West Nile Virus	et al., 2011b; Fritsch et al., 2019; Morrissey et al., 2014; Partecke et al., 2004; Rowse et al., 2014; Russ et al., 2015; Schoech et al., 2004; Suárez-Rodríguez and García, 2014; Wright and Fokidis, 2016; Zhang et al., 2014 Afshari et al., 2012; Anaconda et al., 2018; Badagliacca et al., 2018; Barbosa et al., 2019; Batalha de Jesus et al., 2019; Bentz et al., 2006; Bichet et al., 2020; Blanco-Peña et al., 2017; Broomand et al., 2019; Čechová et al., 2016; Chen et al., 2015; de Sousa et al., 2010; Dolz et al., 2013; Du et al., 2019; Fecchio et al., 2021; Fox et al., 2006; Gargiulo et al., 2014; Geigenfeind et al., 2012; Gionechetti et al., 2008; Giraudeau et al., 2014, 2017; Golnar et al., 2021; Hamer et al., 2012; Hessman et al., 2018; Höfle et al., 2020; Jarma et al., 2021; Jimenez-Penuela et al., 2019; Kistler et al., 2012; Kmet et al., 2013; Konell et al., 2019; Marrow et al., 2009; Mattmann et al., 2019; McGraw et al., 2020; Morakchi et al., 2017; Naveed et al., 2019; Nebel et al., 2020; Ngaiganam et al., 2019; Ots and Hörak, 1998; Perec-Matysiak et al., 2017; Reisen and Wheeler, 2016; Ringia et al., 2004; Ruiz-Martínez et al., 2016; Sacristán et al., 2014; Schoech et al., 2004; Stephens et al., 2021; Stout et al., 2005; Urban et al., 2013; Weis et al., 2014; Wink and Bennett, 1976 Abolins-Abols et al., 2016; Atwell et al., 2012; Davies et al., 2013, 2016a, 2016b; Dominoni et al., 2021; Fokidis et al., 2009; Fokidis et al., 2011a; Foltz et al., 2015; Giraudeau and McGraw, 2014; Heiss et al., 2009; Ibáñez-Álamo et al., 2020; Meillère et al., 2016; Ouyang et al., 2019; Partecke et al., 2006; Renthlei et al.,
Stress	baseline corticosterone (CORT) levels in blood or feathers, CORT response to handling, food availability/predictability	2021; Russ et al., 2015; Schoech et al., 2004; Weaver et al., 2018; Wright and Fokidis, 2016 Brogan et al., 2017; Fernie et al., 2017; Kobayashi et al., 2005; Morrissey et al., 2014; Renthlei et al., 2021; Sun et al., 2021; Têcher et al., 2016 CORT, corticosterone; H/L, heterophil to lymphocyte ratio; RBC, red blood cells; WBC, white blood cells.

**Table 1** (continued)

Published parameters used to assess the effects of urbanization on birds	Examples	References
	thyroid	2021; Russ et al., 2015; Schoech et al., 2004; Weaver et al., 2018; Wright and Fokidis, 2016 Brogan et al., 2017; Fernie et al., 2017; Kobayashi et al., 2005; Morrissey et al., 2014; Renthlei et al., 2021; Sun et al., 2021; Têcher et al., 2016

CORT, corticosterone; H/L, heterophil to lymphocyte ratio; RBC, red blood cells; WBC, white blood cells.

**Table 2**

Some examples of the effects of urbanization on the stress physiology of birds.

Species	Stress Responses	References
Curve-billed thrashers ( <i>Toxostoma curvirostre</i> ), Tree sparrows ( <i>Passer montanus</i> ), House sparrow ( <i>Passer domesticus</i> )	Higher baseline corticosterone (CORT) in urban birds	Fokidis et al., 2011b; Zhang et al. (2011); White et al. (2022)
Common blackbirds ( <i>Turdus merula</i> )	Lower feather CORT in urban birds	Ibáñez-Álamo et al., 2020
Red-winged blackbird nestlings ( <i>Agelaius phoeniceus</i> ), Northern cardinals ( <i>Cardinalis cardinalis</i> )	Higher and lower fecal CORT in urban blackbirds and cardinals, respectively	Buxton et al., 2018; Huang et al., 2020
Juvenile house sparrows ( <i>Passer domesticus</i> ), Common blackbirds ( <i>Turdus merula</i> )	Higher feather CORT in urban birds	Beauguard et al., 2019; Meillère et al., 2016
Abert's towhees ( <i>Melospiza aberti</i> ), Song sparrows ( <i>Melospiza melodia</i> ), House sparrows ( <i>Passer domesticus</i> )	No differences in handling-induced CORT responses and/or baseline CORT	Davies et al., 2013; Foltz et al., 2015; Meillère et al. (2015b); Bokony et al. (2012)
Northern cardinals ( <i>Cardinalis cardinalis</i> ), Dark-eyed juncos ( <i>Junco hyemalis</i> ), Common blackbirds ( <i>Turdus merula</i> )	Lower baseline and/or handling-induced CORT response and behavioral stress response	Abolins-Abols et al., 2016; Partecke et al., 2006; Wright and Fokidis, 2016
House sparrows, Northern mockingbird ( <i>Mimus polyglottos</i> ), Curve-billed thrashers, Abert's towhees, Canyon towhee ( <i>Melospiza fusca</i> )	Similar baseline CORT; greater handling-induced CORT response	Fokidis et al., 2009
House finches ( <i>Haemorrhous mexicanus</i> )	Human presence increased CORT, objects and captivity did not	Weaver et al., 2018
Curve-billed thrashers, Abert's towhees, Song sparrows	More territorial and aggressive behavior that was not associated with changes in T or CORT	Davies et al., 2018; Fokidis et al., 2010
Dark-eyed juncos	Increased boldness and lower CORT	Atwell et al., 2012

introduction sites, suggesting a relationship between CORT levels and the species' ability to colonize new areas (Liebl and Martin, 2012). Overall, however, there is weak support for a consistent link between urbanization and the circulating levels of glucocorticoids in wild

vertebrates (Iglesias-Carrasco et al., 2020; Injaian et al., 2020; Table 2). Apparent discrepancies between studies may result from the complex relationship linking the hypothalamic-pituitary-adrenal (HPA) axis and stress (Romero and Beattie, 2022). In particular, the actions of glucocorticoids depend on their interactions with corticosteroid binding globulins (CBG; Breuner et al., 2013) and on feedback mechanisms (e.g., Taff et al., 2018). Furthermore, behavioral and physiological actions of glucocorticoids are mediated by several types of receptors (low affinity: glucocorticoid receptors; high affinity: mineralocorticoid receptors; Landys et al., 2006) whose densities are tissue-specific (e.g., Krause et al., 2015). In addition, glucocorticoid receptor densities are not static but as is commonly the case for endocrine systems, they are dynamically regulated. For example, these densities in some tissues change during chronic stress (Lattin and Romero, 2014) and seasonally (Lattin et al., 2013; Lattin and Romero, 2015) and they may, therefore, also change in response to urbanization although this has rarely been investigated. To our knowledge, a single recent study has examined this question in song sparrows (*Melospiza melodia*) and found that urban sparrows had fewer hippocampal CORT receptors than rural sparrows (Lane et al., 2021). The extent of seasonal modulation being tissue-dependent, glucocorticoids have the potential to selectively influence tissue types differently depending on the time of the year and/or reproductive condition of the animal. Overall, elevated CORT levels can reflect an environmental or energetic constraint, but also an animal's ability to cope successfully with stress. As a consequence of the above complexities, these levels alone are generally considered poor predictors of chronic stress (Dickens and Romero, 2013), especially when integrative and indirect measures of glucocorticoid secretion are used (i.e., feces or feathers, Romero and Beattie, 2022).

Most research on the relationships between urbanization and the avian endocrine system has focused on the HPA axis, and much less is known regarding whether urbanization influences the functioning of other endocrine axes. For example, urbanization can affect the expression of reproductive behaviors (e.g., singing and territoriality), but few studies have examined whether it affects the hypothalamic-pituitary-gonadal (HPG) axis (e.g., Davies and Sewall, 2016; Davies et al., 2015a, 2016a). Similarly, aside from associations with pollutants and pathogens, the effects of urbanization on the hypothalamus-pituitary-thyroid (HPT) axis have been largely ignored. In the following sections, we consider various environmental factors that can contribute to altering the endocrine physiology of urban birds.

### 3. Factors that may influence avian endocrine physiology in urban environments

#### 3.1. Food availability – quantity and quality

Urbanization is generally associated with dramatic qualitative and quantitative changes in the food resources that are available to urban-dwelling animals (El-Sabaawi, 2018). For example, urban vertebrates have access to anthropogenic food that is often more abundant but nutritionally inferior (e.g., energy-rich and nutrient-poor) relative to that available to corresponding non-urban animals (Coogan et al., 2018). In addition, food availability in urban areas can be reduced due to intra- and inter-specific competition for food resources (Shochat et al., 2004). Food resources can also be affected by chemical pollution and urban landscape structure (e.g., percentage of impervious surface), which affects some groups of invertebrates more than others and so has the potential to qualitatively alter the diet of organisms that depend on these invertebrates as main food source (Evans et al., 2018). A main challenge of field studies on this subject, however, is to distinguish between effects resulting from dietary differences vs. exposure to pollutants (Morrissey et al., 2014). Inversely, urbanization can in some cases facilitate access to food resources. For instance, one of the biological function-disrupting effects of artificial light at night (Boyes et al., 2021; Grubisic and van Grunsven, 2021) is to attract nocturnal insects that as a

result, may increase foraging opportunities for some insectivorous species (Rodríguez et al., 2021).

Multiple studies have investigated relationships between food availability (quality and quantity), whether provided intentionally or not intentionally, and the avian endocrine system, and several of these studies have been conducted in an urban context. Food supplementation (i.e., food for birds) to rural (“wildland”) Florida scrub-jays (*Aphelocoma coerulescens*) is associated with earlier breeding as well as lower CORT in both sexes, and with higher plasma testosterone in males but no change in plasma estradiol in females (Schoech et al., 2004). In this species, food supplementation to suburban birds also results in earlier breeding and lower plasma CORT relative to jays inhabiting natural habitats (Schoech, 2009). These effects of food availability on the timing of breeding could be mediated by CORT and its effects on the HPG axis (Lattin et al., 2016), a hypothesis that is supported by the observation that early-breeding supplemented jays had lower plasma CORT than control birds (Schoech, 2009). The generality of these findings is, however, not established because in the male northern cardinal (*Cardinalis cardinalis*), food supplementation did not impact dehydroepiandrosterone (DHEA) or CORT concentrations (Wright and Fokidis, 2016). Other studies did likewise not identify an unambiguous link between food supplementation and endocrine axes in birds. For example, Davies et al. (2016a) found no differences in either hypothalamic (gonadotropin releasing and inhibitory hormones, GnRH and GnIH) or plasma (testosterone (T) and luteinizing hormone (LH)) hormones between urban and rural Abert's towhees (*Melospiza aberti*). Rather, in this species seasonal testicular growth occurred earlier in urban birds, but this difference was not associated with food abundance, which did not differ between locations (Davies et al., 2016a). Heiss et al. (2009) also found in suburban American crows (*Corvus brachyrhynchos*) that food supplementation resulted in larger nestlings, but CORT concentrations did not differ in urban and rural nestlings. These studies illustrate the need for additional research aimed at clarifying functional relationships between the HPA axis and the reproductive system in situations of fluctuating food abundance.

In contrast to food supplementation, food restriction can decrease the HPG axis activity (Hahn, 1995; O'Brien and Hau, 2005; Perfito et al., 2008; Davies et al., 2015b; Valle et al., 2015, 2019, 2020). This decrease appears to result from effects at multiple levels including the hypothalamus and gonads (Davies et al., 2015b; Valle et al., 2015, 2020), but the mechanisms by which nutritional signals influence the reproductive system of wild birds remain poorly understood. Indeed, food restriction may inhibit reproductive functions by decreasing the animal's overall energy stores and thereby disrupting energy homeostasis. Alternatively, and/or additionally, food restriction may limit the availability of specific metabolic substrates and interfere with the activity of specific metabolic pathways, such as those involved in gonadal steroidogenesis (Valle et al., 2020).

Urban birds often have access to relatively abundant food in the form of handouts, refuse, pet food, etc., but anthropogenic food generally is of lower nutritional quality than natural food (Coogan et al., 2018). Surprisingly, however, most experimental endocrine research on wild birds to date has manipulated the food abundance while ignoring the food composition, even though tantalizing cues indicate the potentially important physiological role of the latter. For example, free-living Florida Scrub-Jays with access to high fat and high protein food supplement had lower plasma CORT either than birds with access to high fat and low protein food supplement or than non-supplemented (control) jays (Schoech et al., 2004). The result of a study on captive white ibis (*Endocimus albus*) nestlings receiving an anthropogenic diet (addition of white bread and reduction in seafood content) suggested that this diet decreases the birds' ability to fight pathogens (Cummings et al., 2019). Finally, captive mourning doves (*Zenaidura macroura*) from a wild population that were fed white bread for four weeks had elevated hepatic glycogen but did not differ from control doves with regard to their plasma glucose and other indicators of metabolic physiology (Basile



et al., 2020). These studies vividly illustrate the potential for anthropogenic food to disrupt physiological homeostasis, but also highlight how underexplored this topic is despite its relevance to our understanding of the consequences of urbanization to avian populations.

The gut microbiome is increasingly recognized as a significant contributor to the health of wild vertebrates (Bodawatta et al., 2022). Interestingly, a few studies found that urbanization can affect the gut microbiome of wild birds and mammals (e.g., Berlow et al., 2021). For example, the gut microbiome of urban house sparrows is less diverse than that of rural sparrows (Teyssier et al., 2020), and urban sparrows host a greater abundance of Proteobacteria, which are associated with illnesses (Gadau et al., 2019). However, few studies have examined the gut microbiome of urban birds with a focus specifically on diet or endocrine physiology (Stothart et al., 2019). Nogeura et al. (2018) administered CORT to yellow-legged gull (*Larus michahellis*) chicks and found that this treatment decreases the abundance of pathogenic gut bacteria, suggesting that elevated CORT may reduce the risk of infection. Despite these recent and significant advances, our current knowledge of the link between endocrine traits and gut microbiota is scarce and future studies are definitely needed to better understand how the functioning of endocrine axes and gut microbiome are inter-connected.

### 3.2. Water availability

Few data are available to assess whether urbanization affects water availability to wild birds. On the one hand, urban areas, in particular those in arid regions, can be associated with year-round water sources such as fountains, urban ponds, and remaining water in gutters (Larson and Perrings, 2013). Such water availability can have a cooling effect by decreasing surface temperature (e.g., Wang et al., 2021), and it may benefit urban birds (i.e., decreased thermoregulatory cost) during periods of intense heat. On the other hand, impervious surfaces absorb solar radiation and, combined with the urban heat island effect (section 3.6), this may increase evaporation and water runoff leading to a quick disappearance of water sources in urban areas (Arnfield, 2003). The influence of water availability on the endocrine physiology of birds has been rarely investigated, especially in the context of urbanization. In a few studies examining avian hormonal levels of urban birds in a desert area, water has been suggested to potentially explain differences between rural and urban birds (Fokidis et al., 2009). Recently, Brischoux et al. (2020) found in captive house sparrows that a short period (~ 6 h during daylight time) of water restriction can result in increased baseline CORT levels. Other studies reported that water restriction can also disrupt reproduction and reduce circulating LH and testosterone levels in zebra finches (*Taeniopygia guttata*; Perfito et al., 2006; Prior et al., 2013). Similarly, the absence of bathing water can affect circulating hormone levels that are linked to stress (increased CORT levels, Krause and Ruploh, 2016) or reproduction (e.g., LH, Wingfield et al., 2012). Some of these results may be specific to zebra finches, a desert-adapted species, but the studies emphasize that water availability should be considered when comparing hormonal titers between urban and rural bird populations.

### 3.3. Light and noise pollution

Birds rely heavily on light cues to regulate their circadian and circannual rhythms (Cassone and Westneat, 2012). For this reason, much attention has focused on the potential endocrine-disrupting effects of artificial light at night (ALAN) in birds (Table 3). Similar to light, city noises have attracted the attention of scientists because singing is regulated by the endocrine system and urban noise may alter the way birds vocally communicate with each other (Slabbekoorn and den Boer-Visser, 2006): Noisy environments may require birds to change their song or to sing at a higher frequency in order to be heard by conspecifics (Nemeth and Brumm, 2009; Luther and Baptista, 2010). Furthermore, birds in different neighborhoods have different 'dialects' whereas songs

**Table 3**

Effects of light, noise, and EMF pollution on endocrine responses in wild birds.

Urban stressor	Species	Endocrine outcomes	References
Artificial light at night (ALAN)	Tree sparrows ( <i>Passer montanus</i> ) and Great tits ( <i>Parus major</i> )	<ul style="list-style-type: none"> <li>Tree sparrows: advances luteinizing hormone (LH) secretion</li> <li>Tree sparrows: lower peak LH, estradiol (E2), and testosterone (T)</li> <li>Sparrows and great tits: lower melatonin and/or pineal gland AANAT gene expression (synthesis of melatonin)</li> </ul>	Renthlei and Trivedi, 2019; Zhang et al., 2014; Ziegler et al., 2021
	Great tits	<ul style="list-style-type: none"> <li>More active at night</li> </ul>	Ouyang et al., 2017
	Great tits	<ul style="list-style-type: none"> <li>increased mRNA transcripts related to germ cell development, testes growth, and steroid synthesis</li> <li>larger testes and upregulated spermatogenesis</li> </ul>	Dominoni et al., 2018
	Great tit nestlings	<ul style="list-style-type: none"> <li>higher feather corticosterone (CORT)</li> <li>not associated with telomere length or fledgling success</li> </ul>	Grunst et al., 2020c
	Blue tit nestlings ( <i>Cyanistes caeruleus</i> )	<ul style="list-style-type: none"> <li>Urban: higher feather CORT with ALAN; positively associated with fledgling success</li> <li>Rural: higher overall plasma CORT than urban birds (irrespective of ALAN); lower feather CORT with ALAN</li> </ul>	Dominoni et al., 2021
	European blackbirds ( <i>Turdus merula</i> )	<ul style="list-style-type: none"> <li>Advanced reproductive development and molting</li> <li>Females: Positively correlated with CORT and negatively with E2</li> <li>Males: No association with T</li> </ul>	Dominoni et al., 2013; Russ et al., 2015
	Tree swallow nestlings ( <i>Tachycineta bicolor</i> )	<ul style="list-style-type: none"> <li>No change in body condition or fledgling success</li> </ul>	Injaian et al., 2021
	Zebra finches ( <i>Taeniopygia guttata</i> )	<ul style="list-style-type: none"> <li>more active at night</li> <li>elevated CORT</li> <li>no change in body condition or food intake</li> </ul>	Alaasam et al., 2018
	Zebra finches ( <i>Taeniopygia guttata</i> )	<ul style="list-style-type: none"> <li>loss of normal pattern of circulating CORT, cytokine, and melatonin concentrations</li> </ul>	Mishra et al., 2019; Moaraf et al., 2020a, 2020b, 2021
	Black swans ( <i>Cygnus atratus</i> )	<ul style="list-style-type: none"> <li>Annual Formula One Grand Prix: Higher baseline CORT prior to event and decreased during event; Handling-</li> </ul>	Payne et al., 2012

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Table 3 (continued)

Urban stressor	Species	Endocrine outcomes	References
	Tree swallows	<ul style="list-style-type: none"> <li>induced CORT peaked during event</li> <li>Traffic noise: negative correlation with handling-induced CORT in adult females; positive association with baseline CORT and negative association with body condition in nestlings</li> </ul>	Injaian et al., 2018
	Adult house wrens ( <i>Troglodytes aedon</i> )	<ul style="list-style-type: none"> <li>Higher baseline CORT in urban than rural birds</li> <li>urban: noise had no effect on circulating CORT</li> <li>Rural: CORT increased with noise exposure</li> </ul>	Davies et al., 2017
	House sparrows ( <i>Passer domesticus</i> )	<ul style="list-style-type: none"> <li>No changes in body condition, growth, fledgling success, or CORT responses</li> </ul>	Angelier et al., 2016
	Japanese quail ( <i>Coturnix coturnix japonica</i> ) chicks	<ul style="list-style-type: none"> <li>No significant effect on CORT stress response</li> </ul>	Flores et al., 2019
	Western bluebird ( <i>Sialis mexicana</i> )	<ul style="list-style-type: none"> <li>No effect on clutch or brood size, fledgling numbers, or nest success</li> </ul>	Mulholland et al., 2018
	Zebra finches ( <i>Taenopygia guttata</i> )	<ul style="list-style-type: none"> <li>Breeding birds: lower baseline CORT with noise</li> <li>Nestlings: reduced body mass</li> </ul>	Zollinger et al., 2019
Electromagnetic Fields (EMF)	Various	<ul style="list-style-type: none"> <li>Inconsistent changes in behavior, reproductive success, endocrinology, growth and development</li> </ul>	For review: Fernie and Reynolds, 2005

ALAN, artificial light at night; CORT, corticosterone; E2, estradiol; LH, luteinizing hormone; T, testosterone.

vary less in rural environments (Luther and Baptista, 2010). Urban noise and ALAN can also affect multiple stress-coping endocrine mechanisms because these types of pollution can be perceived as stressful by animals living in the urban environment (e.g., noise, Davies et al., 2017; Angelier, 2022; light: Dominoni et al., 2021).

Some evidence appears to point towards altered endocrine physiology in urban birds exposed to environmental disturbances (Table 1). However, a comprehensive review conducted by Injaian et al. (2020) found no general pattern between plasma CORT and urban characteristics such as noise, roadways, human presence, ALAN, and level of urbanization. In addition, Foltz et al. (2015) found no clear effects of habitat alone on body condition in a 4-year longitudinal study of song sparrows. Casasole et al. (2017) additionally found no relationship between measures of oxidative stress and road pollution, anthropogenic noise, or ALAN in great tit (*Parus major*) nestlings. In fact, the amount of oxidative stress varied more within nestlings in a nest as opposed to between nests (Casasole et al., 2017). Much of the research on the effects of ALAN, however, has involved experimental manipulations of ALAN exposure, which may have limited relevance to urban settings wherein birds may have a choice regarding exposure levels. In fact, when given a choice, both urban and forest great tits chose to sleep under ALAN instead of in darkness (Ulgezen et al., 2019).

Experimental exposure of urban blue tit (*Cyanistes caeruleus*) as well

as great tit nestlings to ALAN after hatching increased feather CORT (Dominoni et al., 2021; Grunst et al., 2020c), whereas a reduction in feather CORT was seen when rural blue tit nestlings were exposed to ALAN (Dominoni et al., 2021). Rural blue tit nestlings additionally had higher circulating CORT concentrations regardless of ALAN exposure (Dominoni et al., 2021). Similarly, Injaian et al. (2021) concluded that ALAN exposure did not have negative effects on tree swallow (*Tachycineta bicolor*) nestlings as it did not alter body condition or fledgling success. Other studies illustrate the diversity of relationships between ALAN and the avian endocrine system. Zebra finches exposed to ALAN had altered eating patterns, lower melatonin, and higher glucose at nighttime, along with lower circulating thyroxine ( $T_4$ ) and triglycerides during the daytime (Batra et al., 2019). Furthermore, in this species the normal nocturnal pattern of melatonin and diel pattern of CORT secretion were lost in response to ALAN exposure (Mishra et al., 2019; Moaraf et al., 2020a, 2020b, 2021). Zebra finches exposed to light in the blue range (5000 K) were more active at night and had elevated CORT although body condition and food intake were not altered (Alaasam et al., 2018). Similarly, Indian house crows (*Corvus splendens*) exposed to ALAN developed sleep loss, reduced melatonin, and depressive-like symptoms, although changes in diurnal CORT were not observed (Taufique et al., 2018). Adult great tits exposed to white light at night were more active at night and more likely to be infected with malaria (Ouyang et al., 2017). In contrast, Saini et al. (2019) observed an increase in plasma bactericidal activity against *E. coli*. Dominoni et al. (2018) found that exposure to ALAN altered mRNA transcripts including increases in mRNA related to germ cell development, testis growth, and steroid synthesis consistent with larger testes and upregulated spermatogenesis, suggesting that ALAN affects the HPG axis. Supporting this hypothesis, ALAN was associated with activation of the reproductive endocrine axis (GnRH transcription, LH, and estradiol levels) in Eurasian tree sparrows (*Passer montanus*), although this effect was reversed after exposure to high-intensity ALAN (Zhang et al., 2019). Although studies of mammals show a decline in oxalate concentrations with sleep debt, great tit nestlings instead showed a rise in oxalate in response to ALAN exposure, again suggesting that the effects of ALAN in birds may not be comparable to those in mammals (Raap et al., 2018).

Urban noise can affect reproductive behavior, such as the timing and intensity of singing (e.g., Brumm, 2004), or territoriality in birds (e.g., Fokidis et al., 2011a). Limited information indicates that it can also affect aspects of avian reproduction (Table 3). For example, zebra finch nestlings exposed to traffic noise weighed less than controls (Zollinger et al., 2019). A negative effect of noise exposure on reproduction was also found in the ash-throated flycatcher (*Myiarchus cinerascens*), in which exposure of nests to noise led to nest abandonment (Mulholland et al., 2018). In contrast, exposing western bluebird (*Sialis mexicana*) nests to traffic noise did not affect clutch or brood size, fledgling numbers, or nest success (Mulholland et al., 2018). Overall, the link between urban noise and the reproductive endocrine axis remains understudied and poorly understood.

Little information is also available about relationships between ambient noise and the CORT stress response. The meta-analysis by Injaian et al. (2020) did not report any strong link between these variables. Similarly, Angelier et al. (2016) found no changes in body condition, growth, fledgling success, or CORT responses in an urban exploiter, the house sparrow, experimentally exposed to traffic noise. Likewise, while black swans (*Cygnus atratus*) had higher baseline CORT prior to a Formula One Grand Prix event, levels actually decreased during the event, although handling-induced CORT peaked at this time (Payne et al., 2012). And while urban adult house wrens (*Troglodytes aedon*) had higher baseline CORT than rural birds, exposure to traffic or pink noise had no effect on circulating CORT in urban birds, but increased the hormone levels in rural birds (Davies et al., 2017). Studies on the effects of noise exposure on circulating CORT in young birds also yielded conflicting results. On the one hand, Kleist et al. (2018) reported that chronic anthropogenic noise was associated with reduced baseline

CORT levels in the chicks of multiple urban species. Interestingly, they also found that the CORT stress response of these chicks increased in response to such noise, suggesting that noise can have complex effects on the HPA axis. On the other hand, Flores et al. (2019) found no effect of exposing Japanese quail (*Coturnix coturnix japonica*) chicks to traffic noise on stress responses. However, exposed birds had higher glutathione levels, suggesting upregulated antioxidant defenses. To our knowledge, the impact of urban noise on other endocrine systems has rarely been investigated. A few studies have shown that urban noise could affect whole-organism metabolism (Brischoux et al., 2017), which is tightly linked to the HPT axis activity (Chastel et al., 2003). These topics certainly represent promising research avenues for future studies. Together, the lack of consistent relationships between what we would consider anthropogenic stressors and physiological stress responses in birds (Casasole et al., 2017; Foltz et al., 2015; Injaian et al., 2020) suggests that birds adapted to life in urban areas may be quite resilient.

### 3.4. Electromagnetic fields

Organisms residing in urban environments are continuously exposed to electromagnetic fields (EMF) generated by electrical lines, radio and personal communication devices, and other forms of technology. Access to power lines, electrical towers, and poles is useful to birds in terms of providing structures on which to perch, nest, and hunt. However, utilization of these structures exposes birds to EMFs (Ferne and Reynolds, 2005), and there is evidence for detrimental effects of this exposure (Table 3). For example, EMF exposure in birds generally lowers their melatonin secretion, which may affect circadian as well as circannual rhythms (Ferne and Reynolds, 2005). In the American kestrel (*Falco sparverius*), EMF exposure caused changes in reproductive behaviors, although not in egg laying or clutch size (Ferne et al., 2000). In another study, experimental exposure of turkeys (*Meleagris gallopavo*) to extremely low frequency EMF reduced norepinephrine activation of the  $\beta$ -adrenoceptor (Laszlo et al., 2018). Besides secreting melatonin, the avian pineal gland functions as a magnetic sensor for navigation (Demaine and Semm, 1985). Thus, exposure to EMF in birds has the potential to disrupt multiple behavioral and physiological processes (Demaine and Semm, 1985; Kishkinev et al., 2021; Balmori, 2021). Mammalian studies also show the potential for negative effects of EMF exposure, which can alter cellular function through several mechanisms: Increased calcium influx into cells, inhibition of cell growth and proliferation, elevated oxidative stress, DNA damage, and misfolding of proteins (Gye and Park, 2012). In mammals, EMF exposure can also impact the release of melatonin from the pineal gland, which can in turn alter gonadotropin release and function (Gye and Park, 2012). As reviewed by Ferne and Reynolds (2005), a majority of avian studies at the time concerned adverse effects of EMF exposure on growth and development, and few studies had investigated relationships between this exposure and endocrine systems. Given the relatively few current studies examining the effects of EMF on the endocrine physiology of birds and that many urban species are likely exposed to EMF, much research is needed in this area.

### 3.5. Chemical pollution and toxins

In recent years, there has been an intense focus on assessing biomarkers of avian exposure to urban environmental pollutants including heavy metals, flame retardants, chemicals, and pesticides (Table 4). While some urban pollutants, such as cigarette butts, may offer benefits in the form of warding off ectoparasites (Suárez-Rodríguez and García, 2014), others have been shown to harm the endocrine physiology of urban birds. As evidenced in Table 4, many studies show that heavy metals are found at higher concentrations in birds captured from urban areas. Some studies have shown an association between the amount of heavy metals found in birds and traffic or leaded gasoline (Schilderman et al., 1997) as well as air pollution (Grunst et al., 2020a) and

contamination of food sources, such as earthworms (Scheifler et al., 2006). For insectivorous and carnivorous species such as Anna's hummingbirds (*Calypte anna*), black-chinned hummingbirds (*Archolochus alexandri*), vultures (*Gyps bengalensis*), barn owls (*Tyto alba*), and red-tailed hawks (*Buteo jamaicensis*), consumption of prey exposed to pesticides and rodenticides may contribute to higher levels of these chemicals in urban animals (Huang et al., 2016; Nair and Pillai, 1992; Okoniewski et al., 2021). Studies of common eiders (*Somateria mollissima*) in the Norwegian Oslofjord demonstrate the birds are exposed to marine pollution (Thorstensen et al., 2021). Erythroplastids, an indicator of pollution damage, are also more prevalent in helmeted manakins (*Antilophia galeata*) living in close proximity to urbanized areas in Brazil (Goncalves et al., 2020).

To date, the potential impact of these multiple contaminants on the endocrine systems of urban birds is relatively overlooked. Table 4 presents some evidence regarding the relationship between heavy metal exposure and endocrine physiology of wild birds. Whereas experimental exposure of birds to lead or zinc did not alter CORT, prolactin, or testosterone-mediated behaviors (Chatelain et al., 2018), heavy metals are associated with increased hematopoiesis in great tits (Bauerová et al., 2017) and with changes in circulating hormonal levels in other studies. For example, there is some evidence that lead can affect the functioning of the HPA axis in birds (Angelier, 2022) with increased CORT levels in contaminated urban birds (feather CORT levels: Meillère et al., 2016; stress-induced plasma CORT levels: Baos et al., 2006). In contrast, PCBs (polychlorinated biphenyl) and PDBE (polybrominated diphenyl ether) chemicals have been negatively associated with thyroid hormone concentrations in Cooper's hawks (*Accipiter cooperii*; Brogan et al., 2017) and Eurasian dippers (*Cinclus cinclus*; Morrissey et al., 2014). Inversely, various PFAA (perfluoroalkyl acid) chemicals have been associated with increased thyroid gland activity in peregrine falcons (*Falco peregrinus*; Sun et al., 2021) and dioxins have been shown to alter thyroid gland histology in wild jungle crows (*Corvus macrorhynchos*) in urban areas (Kobayashi et al., 2005). Further field and experimental studies are required to better understand not only the disruption of these endocrine axes resulting from exposure to urban contaminants, but also the fitness consequences of this exposure.

Because environmental pollutants can induce oxidative stress, several studies have examined diverse measures of oxidative status in urban birds. One study showed no differences in oxidized lipoproteins (TBARS) between urban and rural great tits (Isaksson et al., 2009), but another study by the same researchers found a higher ratio of oxidized to reduced glutathione in urban great tits, an indication of oxidative stress (Isaksson et al., 2005). Isaksson et al. (2009) also measured higher levels of antioxidants in urban than rural great tits, which may protect urban birds from oxidative stress. In contrast, Herrera-Duenas et al. (2014) measured reductions in total antioxidant capacity and hemoglobin concentrations in urban house sparrows. Similarly, a study of house finches found decreased carotenoids in urban birds (Giraudeau and McGraw, 2014). Oxidative stress and dietary antioxidants may alter avian endocrine responses. For example, supplementing European starlings (*Sturnus vulgaris*) with anthocyanin-enriched food attenuated post-flight elevations in CORT compared to control birds (Casagrande et al., 2020). Haussmann et al. (2012) administered CORT to domestic chicks (*Gallus domesticus*) *in ovo* and found that CORT-treated chicks had higher levels of oxidative stress and shorter telomeres, indicative of higher mortality risk, as compared to untreated birds. As well, Vagasi et al. (2020) observed an increase in oxidative damage in house sparrows when levels of CORT, glucose as well as insulin-like growth factor-1 (IGF-1) were elevated.

### 3.6. Ambient temperature

A main consequence of urbanization is a local increase in air temperature relative to surrounding non-urbanized areas (Tzavali et al., 2015), a phenomenon called the urban heat island. The urban heat

**Table 4**  
Exposure of urban birds to heavy metals and other urban pollutants.

Urban pollutant	Species	Findings	References
Heavy Metals	Great tits ( <i>Parus major</i> )	<ul style="list-style-type: none"> <li>Higher lead content in nestlings and aged birds (7+ years)</li> <li>Feather heavy metals: significant association with heterophil/lymphocyte (H/L) ratio</li> <li>Blood heavy metals: males with higher levels had lower H/L ratio, decreased absolute erythrocyte count and increased hematopoiesis</li> <li>Higher feather heavy metals associated with lower carotenoid coloration but no association with melanin coloration</li> </ul>	Bauerova et al., 2020; Grunst et al., 2020b Bauerová et al., 2017
	Pigeons ( <i>Columba livia</i> )	<ul style="list-style-type: none"> <li>Femur lead levels positively associated with traffic</li> </ul>	Drasch et al., 1987
	Common blackbirds ( <i>Turdus merula</i> )	<ul style="list-style-type: none"> <li>Cd not associated with life history traits</li> <li>Survival probability increased with higher levels</li> </ul>	Fritsch et al., 2019
	Acadian flycatcher ( <i>Empidonax virescens</i> ), Common blackbirds ( <i>Turdus merula</i> )	<ul style="list-style-type: none"> <li>Female blackbirds: Lead negatively associated with lifetime breeding success</li> <li>Flycatcher: Mercury associated with lower number of fledglings; obtained from insect diet</li> </ul>	Fritsch et al., 2019; Rowse et al., 2014
	Bald eagle ( <i>Haliaeetus leucocephalus</i> ) nestlings, Common blackbirds ( <i>Turdus merula</i> ), Cattle egret ( <i>Bubulcus ibis</i> ), North Island Kaka ( <i>Nestor meridionalis septentrionalis</i> ), Adult and nestling Peregrine falcons ( <i>Falco peregrinus</i> ), Pigeons ( <i>Columba livia</i> ), Red-shouldered hawks ( <i>Buteo lineatus</i> ); House sparrows ( <i>Passer domesticus</i> )	<ul style="list-style-type: none"> <li>Detected heavy metals in feathers, feces, blood, and/or tissues</li> <li>Associated with more DNA damage in pigeons</li> <li>Associated with feather CORT and plasma CORT in common blackbirds and house sparrows, respectively</li> <li>Associated with higher traffic areas</li> </ul>	Bruggeman et al., 2018; Ceyca-Contreras et al., 2020; DeMent et al., 1986; Meillère et al., 2016; Pyzik et al., 2021; Roux and Marra, 2007; Scheifler et al., 2006; Schilderman et al., 1997; Slabe et al., 2019; Sriram et al., 2018; Yasmeen et al., 2019; White et al., 2022
	Common eider ( <i>Somateria mollissima</i> ), Red-winged blackbirds ( <i>Agelaius phoeniceus</i> )	<ul style="list-style-type: none"> <li>Detected lower mercury in urban than rural red-winged nestlings; higher in adults than nestlings</li> <li>High mercury in common eider indicative of marine pollution</li> </ul>	Gillet and Seewagen, 2014; Thorstensen et al., 2021
	Northern goshawk ( <i>Accipiter gentilis</i> )	<ul style="list-style-type: none"> <li>No association with urbanization</li> </ul>	Dolan et al., 2017
	House sparrows ( <i>Passer domesticus</i> )	<ul style="list-style-type: none"> <li>Detected 12 genes associated with exposure to lead including 2 metal transporters</li> </ul>	Andrew et al., 2019
	Ring-billed gulls ( <i>Larus delawarensis</i> )	<ul style="list-style-type: none"> <li>Negatively correlated with bone mineral density</li> <li>Levels in liver positively correlated with (thyroxine) T4 and lower retinol</li> <li>Liver levels negatively correlated with thyroid gland deiodinase type 3, thyroid peroxidase, and thyroid hormone receptor beta</li> </ul>	Desjardins et al., 2019; Plourde et al., 2013; Técher et al., 2016
	Cooper's hawks ( <i>Accipiter cooperii</i> ), Eurasian dipper ( <i>Cinclus cinclus</i> ) nests, Peregrine falcon ( <i>Falco peregrinus</i> ) nestlings	<ul style="list-style-type: none"> <li>Urban peregrine falcon nestlings had lower polybrominated diphenyl ethers (PBDEs), higher T4, triiodothyronine (T3), lower T3:T4 ratio, lower retinol compared to rural</li> <li>PDBEs negatively correlated with T3</li> </ul>	Brogan et al., 2017; Fernie et al., 2017; Morrissey et al., 2014
Other chemicals: Insecticides, Rodenticides, PCBs, PDBEs, PFAAs, Organohalogen compounds, Dioxins	Anna's hummingbirds ( <i>Calypte anna</i> ), Barn owls ( <i>Tyto alba</i> ), Black-chinned hummingbirds ( <i>Archilochus alexandri</i> ), Black harrier ( <i>Circus maurus</i> ), Common eider ( <i>Somateria mollissima</i> ), Cooper's hawk ( <i>Accipiter cooperii</i> ), Eurasian dipper ( <i>Cinclus cinclus</i> ) nests, Herring gull ( <i>Larus argentatus</i> ), Jungle crows ( <i>Corvus macrorhynchos</i> ), Peregrine falcons ( <i>Falco peregrinus</i> ), Red-tailed hawks ( <i>Buteo jamaicensis</i> ), vultures ( <i>Gyps bengalensis</i> )	<ul style="list-style-type: none"> <li>Black harrier: Detected polychlorinated diphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT); PCBs related to number of electrical transformers near nest</li> <li>Detected organohalogen compounds in common eider – indicates marine pollution</li> <li>PCBs correlated with urbanization in Cooper's hawk and Eurasian dipper nests; PCBs negatively associated with thyroid hormones</li> <li>Dioxins higher in urban jungle crows and associated with changes in thyroid gland histology</li> <li>Detected neonicotinoid insecticides in Anna's hummingbird and black-chinned hummingbird feathers</li> <li>Detected anticoagulant rodenticide in red-tailed hawks and barn owls</li> <li>Perfluoroalkyl acids (PFAAs) associated with thyroid hormone and thyroid gland activity in peregrine falcon nestlings; detected in blood and eggs</li> <li>DDT and hexachlorocyclohexane (HCH) detected in pigeons and vultures</li> <li>Higher short-chained chlorinated paraffins and cyclic volatile methyl siloxane (CVMS) deca-methylcyclopentasiloxane in urban female herring gulls</li> <li>Substituted diphenylamine higher in urban double crested cormorants</li> </ul>	Brogan et al., 2017; Garcia-Heras et al., 2018; Graves et al., 2019; Huang et al., 2016; Knudtson et al., 2021; Kobayashi et al., 2005; Lu et al., 2019; Morrissey et al., 2014; Nair and Pillai, 1992; Okoniewski et al., 2021; Sun et al., 2020, 2021; Thorstensen et al., 2021



island results from the influence of many factors including air pollution, the release of heat by human activities, the physical configuration of urban spaces (e.g., geometry, light-reflecting surfaces), the lack of green spaces, and local meteorological and climatic characteristics. Even though the magnitude and temporal particularities of the urban heat island vary across cities, it is a worldwide phenomenon (Tzavali et al., 2015).

Temperature may alter the endocrinology of wild birds and investigating these alterations in urban birds is relevant given the urban heat island effect (Ruuskanen et al., 2021). On average, birds maintain relatively high body temperatures of around 38.5 °C at rest, 41 °C while active, and 43.9 °C during high levels of activity (Prinzinger et al., 1991). Elevated ambient temperatures may impact birds more so than mammals given their naturally higher body temperatures and metabolic rates (Ruuskanen et al., 2021). Thermoregulatory responses to increasing temperatures can be both physiological (increased body temperatures, metabolism, evaporative cooling; see review: McKechnie et al., 2021) and behavioral (moving towards shady, cooler areas, taking a bath, panting, fluffing feathers). Some urban animals may even take advantage of anthropogenic resources to maintain body temperature. For example, rosy-faced lovebirds (*Agapornis roseicollis*) living in Phoenix, Arizona capitalize on microclimates created by air conditioning relief vents to cool off from the summer heat (Mills and McGraw, 2021).

As mentioned above, increasing environmental temperatures prompt a rise in metabolic rate in animals (Ruuskanen et al., 2021; McKechnie et al., 2021). The HPT axis is primarily responsible for regulating body temperature in response to cold-induced hypothermia through activation of non-shivering thermogenesis via increased metabolic activity (Ruuskanen et al., 2021). Temperature may in some cases alter CORT levels which may in turn participate in thermoregulation by providing fuels for metabolism (Ruuskanen et al., 2021). Supporting a role of the HPA axis in the ability of birds to cope with change in ambient temperature, recent studies have demonstrated that temporary cooling increases feather CORT levels in chicks of several species (Crino et al., 2020; Lynn et al., 2022). Importantly, another recent study found that heat waves increase CORT concentrations in a passerine and so are presumably perceived as an acute stressor (Moagi et al., 2021). The generality of this effect is not established: zebra finches, for example, did not increase their baseline plasma CORT levels during heat waves, provided that drinking water was available (Cooper et al., 2020). With increasing heat in urban environments, birds will likely rely increasingly on evaporative water loss to dissipate heat, which requires the regulation of water balance to prevent excessive fluid loss and dehydration. Alternatively, some species may adjust to high ambient temperatures by shifting their thermoneutral zones to higher temperatures, thereby decreasing their metabolic heat production and evaporative water loss (Cooper et al., 2020). Arginine vasotocin (the avian homologue of mammalian vasopressin) may play an important role in these processes as it can inhibit thyroid hormones and lower heart rate and activity, in addition to decreasing shivering and body temperature (Ruuskanen et al., 2021). Overall, few avian studies have linked environmental temperature to endocrine functions (reviewed by de Bruijn and Romero, 2018), especially in the context of urbanization. Thus, further research comparing urban and rural birds is necessary to better assess how the endocrine system is influenced by, and facilitates adjustments to, high environmental temperatures.

The heat island effect may amplify and become geographically more widespread in the future due to more widespread urbanization combined with global climate change. In addition to influencing thermoregulatory processes as described above, could the heat island effect, and more generally ambient temperature, alter the avian reproductive system? Several lines of evidence support this idea and in particular that ambient temperature can impact the initiation and termination of the annual reproductive period (Davies and Deviche, 2014). Correlative and experimental studies demonstrate that an increase in ambient

temperature is associated with an earlier timing of breeding in birds (Visser et al., 2009; Schaper et al., 2012; Caro et al., 2013; Martin et al., 2020). Consistent with the hypothesis that temperature is causally involved in this effect, captive photostimulated great tits developed their testes earlier when exposed to high (20 °C) as compared to low (4 °C) temperature (Silverin et al., 2008). Also, in agreement with these findings, exposure to elevated ambient temperature (30 °C) enhanced follicular development in photostimulated white-crowned sparrows (*Zonotrichia leucophrys*), although this treatment did not influence photoinduced male testicular development (Wingfield et al., 1997). Studies on other species confirm and extend these findings. For example, gonadal development, the initiation of breeding, as well as LH and testosterone levels are associated with spring temperatures in Asian short-toed larks (*Alaudala cheleensis*), in which an experimental increase in ambient temperature (3 °C) resulted in an earlier increase in LH, testosterone, and estradiol levels (Zhang et al., 2017). It should, however, be pointed out that elevated temperature does not increase the HPG axis activity in all bird species and/or populations. For instance, ambient temperature affected plasma LH levels in Eurasian skylarks (*Alauda arvensis*) but not in great tits (Gao et al., 2018). In the latter species in captivity, elevated ambient temperature promoted testicular development in photostimulated birds from southern (Italy) but not northern (Scandinavia) populations (Silverin et al., 2008). In addition, ambient temperature can under some circumstances be disconnected from LH, testosterone, and estradiol levels (Wingfield et al., 2003; Caro et al., 2013), suggesting a role for gonadotropin-independent mechanisms. It should finally be noted that an increase in ambient temperature above a certain threshold (“heat wave”) can have the opposite effect to a moderate increase, i.e., it inhibits reproductive functions. This was the case in the male house finch (*Haemorrhous mexicanus*), in which experimental exposure to a simulated “heat wave” inhibited the endocrine reproductive axis including the testicular expression of 17 $\beta$ -hydroxysteroid dehydrogenase (Valle et al., 2020). Besides altering the initiation of seasonal reproductive processes, ambient temperature can modulate the timing of the reproductive system involution that takes place at the end of the breeding season, thereby potentially affecting the duration of this season. Indeed, captive male great tits regressed their gonads later when exposed to 4 °C than to 20 °C (Silverin et al., 2008). Similarly, low temperature delayed seasonal gonadal regression in the European starling (Dawson, 2018). Future research should thus consider comparing the overall duration of the reproductive period (i.e., the time between gonadal development and regression) in conspecific urban vs. non-urban birds with particular attention to the potential role of the heat island effect: Either a temporal shift in this period or a change in its duration may have considerable implications for the reproductive success and, therefore, the fitness of urban birds.

### 3.7. Pathogens

Urbanization is classically associated with multiple biotic and abiotic changes that affect the occurrence and the transmission of pathogens (Bradley and Altizer, 2007). As a result, urban birds commonly carry a variety of pathogens such as *Campylobacter jejuni* in pigeons (*Columba livia*) and crows (*Corvus sp.*; Du et al., 2019; Gargiulo et al., 2014; Weis et al., 2014), *Cryptococcus neoformans* in pigeons (Afshari et al., 2012; Anaconda et al., 2018), microsporidia in rooks (*Corvus frugilegus*; Perec-Matysiak et al., 2017), and *Chlamydia psittaci* in pigeons (Čechová et al., 2016; Mattmann et al., 2019). Furthermore, some studies found differences in microorganisms carried by urban vs. non-urban birds. For example, the nests and feathers of urban mountain chickadees (*Poecile gambeli*) contained higher bacterial community richness compared to rural birds (Stephens et al., 2021). Likewise, a study found that urban house finches have a higher abundance of feather-degrading bacteria and larger preen glands than rural conspecifics (Giraudeau et al., 2017), the latter likely to compensate for higher loads of these bacteria.

Not all pathogens are more prevalent in urban than rural birds,

however. For instance, avian malaria parasite infections did not differ between urban and rural house sparrows (Bichet et al., 2020). As well, urban Common blackbirds (*Turdus merula*) and blue-black grassquits (*Volatinia jacarina*) have a lower haemosporidian prevalence than rural conspecifics (Bentz et al., 2006; Fecchio et al., 2021). Whereas intestinal coccidians and poxvirus were found to be more prevalent among urban house finches (Giraudeau et al., 2014; McGraw et al., 2020), no spatial pattern was found for house sparrows (Ruiz-Martínez et al., 2016). Other research found a more complex relationship between urbanization and prevalence of parasitic infections. For example, this relationship in house sparrows differed depending on the fecal *Yersinia* species considered (Rouffauer et al., 2017). Pathogens not only activate the immune system, but may also alter the HPA activity via cytokines. Indeed, the immune system is tightly connected to multiple endocrine systems (e.g., HPA axis, Martin, 2009). Moreover, studies have shown that urban great tits and those infected with hemoparasites have reduced carotenoid-based coloration (Horak et al., 2001; Isaksson et al., 2005). A study by McGraw et al. (2020) also found elevated glucose in urban house finches infected with poxvirus. Few studies have examined the potential link between pathogens and endocrine axes in wild birds. Recently, Names et al. (2021) found in a Hawaiian passerine that malaria-infected birds had lower prolactin levels than uninfected birds although no such difference was found for CORT and testosterone. Similarly, Bichet et al. (2020) did not find any difference in the functioning of the HPA axis between malaria-infected and uninfected house sparrows in both urban and rural areas. Finally, Schoenle et al. (2017) experimentally demonstrated that malaria had no effect on circulating CORT levels in the red-winged blackbird (*Agelaius phoeniceus*). However, a recent meta-analysis reported that parasite infection is associated with an increase in the plasma levels of glucocorticoids in vertebrates (O'Dwyer et al., 2020). Interestingly, experimental immune studies also suggest that pathogens may induce important endocrine changes in birds. For example, several studies have used lipopolysaccharide (LPS) injections to mimic an acute infection and reported that this treatment inhibits the HPG axis (e.g., GnRH, Lopes et al., 2012; LH, Owen-Ashley et al., 2006; testosterone, Needham et al., 2017), activates the HPA axis (e.g., CORT, Owen-Ashley et al., 2006), and affects metabolic processes that may be linked to endocrine axes (Scafì et al., 2019).

Importantly, the behavioral and physiological response of birds to infection can vary depending on the type of pathogen (Coon et al., 2011), making it difficult to generalize the results from these former studies. In addition, the environmental context and, therefore, urbanization, may also affect these behavioral and physiological responses to infection. Whether and how these pathogens alter the endocrine physiology of urban birds has largely been ignored in the scientific literature and is a topic that definitely deserves further work.

### 3.8. Predation

The risk of predation can affect the endocrine system and particularly the HPA axis. For instance, Great Tits rapidly increased their CORT secretion when exposed to a stuffed Tengmalm's Owl, *Aegolius funereus*, but not to a non-predatory bird (Cockrem and Silverin, 2002). As well, European Starlings witnessing a brief (< 10 s.) predator attack responded by increasing their plasma CORT (Jones et al., 2016). The importance of these effects to wild animal populations remains poorly understood for several reasons. First, urban environments have high populations of predators but predation is sometimes lower than in corresponding rural environment (the *Predation Paradox*: Fischer et al., 2012; Rodewald et al., 2010; Shochat, 2004). Second, urban animals can modify their behaviors to avoid predation (Moller and Ibanez-Alamo, 2012), and in some cases can also adjust physiologically to the risk of predation by attenuating their endocrine response to stressors, thereby presumably decreasing the potential for developing chronic stress (Nelson et al., 2015). Thus, whether predator-prey interactions chronically alter the endocrine physiology of urban birds (Iglesias-Carrasco

et al., 2020; Injaian et al., 2020; Romero and Beattie, 2022) remains largely unknown. Furthermore, interactions between predators and prey in urban environments may be disrupted by the high availability of anthropogenic food resources (Rodewald et al., 2010). Much research is warranted in this field given the current paucity of studies relating predation and the endocrine physiology of wild birds.

### 3.9. Genetic and epigenetic adaptations

Mounting, albeit currently limited, evidence indicates that genetic modifications may contribute to avian adaptations to urbanization. This is the case in dark-eyed juncos (*Junco hyemalis*), in which colonization of urban environments by some populations was apparently associated with genetically driven plumage differentiation from non-urban populations (Yeh, 2004, but see Friis et al., 2022). A study of invasive Javan mynas (*Acridotheres javanicus*) identified low buildings as barriers to gene flow (Low et al., 2018), while Delaney et al. (2010) implicated roadways in reduced gene flow in wrentits (*Chamaea fasciata*). Contrasting with these findings, a study of tree sparrows identified only weak genetic differences between urban and rural birds (Zhang et al., 2013) and a study of song sparrows found comparable genetic diversity among study sites (Brewer et al., 2020). In contrast, Evans et al. (2009) found less genetic diversity in urban common blackbirds (*Turdus merula*) while Mueller et al. (2018) found reduced gene flow in urban burrowing owls (*Athene cunicularia*). Expanding upon this work, Andrew et al. (2019) used house sparrows to identify 12 genes that are associated with exposure to environmental lead, with two of these genes being involved in metal transporters. Moreover, recent studies have identified genes associated with antimicrobial resistance in fecal samples collected from urban rock pigeons (Blanco-Peña et al., 2017; Morakchi et al., 2017). Adding to the idea that urban and non-urban birds differ genetically, a polymorphism in the serotonin transporter (SERT) gene was found in urban common blackbirds (Mueller et al., 2013). Furthermore, Renthlei et al. (2020) identified genes, including Bmal1, Npas2, Per2, and Cry1, whose expression peaked earlier during development in urban Eurasian tree sparrows, while expression of the Clock gene was delayed in these birds. Similarly, genes associated with neuronal connectivity, motivation and cognitive function were enriched in urban burrowing owls (Mueller et al., 2020). Transcriptomics also revealed that genes related to stress responses are more highly expressed in urban great tits (Watson et al., 2017). As already mentioned, other work suggests that aspects of the avian CORT response to stress involves a genetic component (Jenkins et al., 2014). Thus, it cannot be dismissed that differences in gene expression as described by Watson et al. (2017) contribute to establishing this differential pattern of CORT secretion. Overall, therefore, the above studies support the hypothesis that urban environments can cause genetic changes. It should, however, be noted that limited evidence is yet available demonstrating that these changes contribute to endocrine differences between urban and non-urban birds, a topic that awaits further research.

Gene expression can also be regulated epigenetically, e.g., through DNA methylation. There is evidence for differences in DNA methylation between Darwin's finches (*Geospiza fortis* and *Geospiza fuliginosa*) residing in urban vs. rural areas (McNew et al., 2017) and it has been suggested that DNA methylation in house sparrows contributes to the phenotypic plasticity that this species exhibits in relationship to colonization of new environments (Liebl et al., 2013). Riyahi et al. (2015) found 1–4% higher methylation of SERT and DRD4 genes in urban great tits that were associated with exploratory behavior and novelty seeking. In the same species, Watson et al. (2020) found differentially methylated genes associated with steroid biosynthesis and transport of cholesterol (among other processes) and they isolated diet and exposure to reactive oxygen species as factors driving these changes. A few studies examined telomere length in relationship to urbanization, but insufficient data are currently available to draw firm conclusions. For example, urban common blackbirds were found to have shorter telomeres (Ibáñez-Álamo

et al., 2018) and Meillère et al. (2015a) found in house sparrows that exposure to traffic noise shortens telomeres. In addition, Salmon et al. (2016) experimentally showed that the urban environment was associated with shorter telomeres in great tit nestlings. However, Dorado-Correa et al. (2018) observed no such shortening in zebra finches, although they reported negative effects of ambient noise in post fledgling birds. Similarly, Biard et al. (2017) studied four populations of great tits and did not find any relationship between telomere length and the degree of urbanization. Together, these data offer tantalizing evidence for epigenetic mechanisms affecting the avian endocrine phenotype. However, it is generally difficult to differentiate between phenotypic differences resulting from (epi)genetic changes vs. from other developmental processes (Miranda et al., 2013; Ouyang et al., 2019) and so considerably more work is necessary to fully understand the physiological implications of urbanization-related epigenetic changes.

#### 4. Challenges and opportunities in urban endocrine research

A considerable amount of information is now available concerning relationships between urbanization and the avian endocrine system. Studies demonstrate, in particular, that multiple aspects of urbanization ranging from anthropogenic noise, ALAN, chemical pollution, food and water quality and availability, temperature, and pathogens affect endocrine systems or have the potential to do so at all life stages and in a wide range of taxa. These studies also reveal that such effects occur across cities around the world. However, results are often inconsistent and fail to follow predictions such that findings can be difficult to interpret, to extrapolate across taxa and locations, and, therefore, to generalize. In addition, most studies to date have focused on few endocrine systems, especially the HPA and HPG axes. Little information is consequently available on associations or causal relationships between urbanization and many hormones including those that play critical metabolic roles (e.g., thyroid hormones, growth hormone, and glucagon; Renthlei et al., 2021), regulate blood osmolality, volume, and pressure (e.g., vasotocin and angiotensin; (Fokidis and Deviche, 2012)), govern the expression of parental behavior (prolactin; Angelier and Chastel, 2009), and control digestive physiology (e.g., cholecystokinin and vasoactive intestinal polypeptide). Additionally, few studies have examined either genetic or epigenetic endocrine-related adaptations to urban environments. Thus, we lack clear and unequivocal answers to many fundamental questions regarding the impact of urbanization on avian endocrine systems. Answering these questions will continue to pose challenges (Table 5) but despite, and in fact due to the above limitations, many opportunities exist for significant progress.

##### 4.1. Correlative vs. causative research

Urban ecosystems vary greatly with respect to many of their physical characteristics including size, geography and climate, type and expanse of infrastructure and green spaces, water availability, history, and growth rate. Furthermore, some of these characteristics often co-vary in time and/or space, making it difficult to disentangle the relative impacts of multiple urban environmental factors on endocrine systems. For example, urban centers often have higher air pollution levels but also more ALAN, higher temperature, and more ambient noise than peripheral areas. Another challenge to researchers is that these factors may affect organisms not only by themselves but also additively, and/or synergistically. As a result, much of the work done to date on the biological effects of urbanization has yielded correlative information, and relatively few, mechanistic, causative studies on free-living organisms have aimed at establishing a role for specific features of the urban environment (e.g., Davies et al., 2017; Dominoni et al., 2013, 2018, 2021; Injaian et al., 2018; Mulholland et al., 2018). Furthermore, many studies compare only a couple of study sites (e.g., rural vs. urban; e.g., Abolins-Abols et al., 2016; Atwell et al., 2012; McNew et al., 2017; Yasmeen et al., 2019), or investigate only birds residing in the urban

**Table 5**

Current challenges and recommendations for research aimed at elucidating the effects of urbanization on avian wildlife.

Challenges	Recommendations
Varied physiological responses to urbanization	<ul style="list-style-type: none"> <li>● Consider interspecific variations in experimental designs (species specific outcomes)</li> <li>● Consider intraspecific variations in experimental designs (individual variations in outcomes)</li> <li>● Consider urbanization gradients within and between cities (ex: pollution, ALAN, temperature, noise, green spaces, built environment) and how these factors may act alone, additively, or synergistically</li> </ul>
Variations between species limit generalization	<ul style="list-style-type: none"> <li>● Consider standardized approaches that include a small number of representative models with wide geographic distribution in diverse urban ecosystems (ex: house sparrows, rock pigeon, starlings)</li> <li>● Continue to investigate less widespread species and those that do not adapt well to urbanization to identify adaptive and maladaptive characteristics of birds as well as unusual or extreme adaptations</li> <li>● Assess underlying mechanisms as well as gauge generalization of the findings.</li> </ul>
Potential for altering the genotype and thus evolution of species	<ul style="list-style-type: none"> <li>● Consider phenotypic plasticity vs genomic or epigenetic adaptations</li> <li>● Identify specific environmental factors to which animals respond behaviorally and physiologically to identify causal relationships and those that may alter phenotype</li> <li>● Consider mechanistic experiments that manipulate singly and additively variables of interest such as light, temperature, noise, food, social environment, etc.</li> </ul>
Accurate physiological indicators of stress	<ul style="list-style-type: none"> <li>● Consider alternative measures of stress (in addition to, or in place of, CORT) such as behavior, epinephrine/norepinephrine (E/NE), etc.</li> <li>● Identify specific environmental factors to which animals respond behaviorally and physiologically to identify potential stressors and stress responses</li> <li>● Consider whether stressors and outcomes may occur alone, additively, or synergistically</li> <li>● Consider long-term studies to assess desensitization</li> </ul>
Observational studies often lack mechanistic insights	<ul style="list-style-type: none"> <li>● Incorporate mechanistic, manipulative approaches to identify specific environmental factors that shape phenotypic responses</li> <li>● Identify neuroendocrine and metabolic bases of responses</li> </ul>
Potential influence of confounding factors and their interactions is often lacking	<ul style="list-style-type: none"> <li>● Identify factors that may affect responses to urbanization such as sex, age, developmental profile, reproductive status, season, spatial and temporal resource requirements, social system, mobility, and metabolism</li> <li>● Identify cumulative or synergistic interactions</li> </ul>

environment (e.g., Baesse et al., 2019; Bauerová et al., 2017; Bauerova et al., 2020; Burt et al., 2021; Casasole et al., 2017). As the physical characteristics of areas within a city (e.g., number, size, and connectivity of green spaces; socioeconomic status; open sources of water; proportion of residential vs. industrial buildings; ambient noise level) can vary considerably at the microscale level, the correlative nature of many studies, together with the lack of replicates, can limit the ability to draw general conclusions. New studies are, therefore, warranted to further



identify the specific environmental factors to which urban organisms respond behaviorally and physiologically, to characterize the mechanisms of action of these factors at the organismal, tissue, and cellular levels, and to determine whether they act alone, additively, or synergistically. Field studies on this subject will continue to serve as essential tools. These studies will gain from the inclusion, when feasible, of manipulative experiments in which variables of interest (e.g., light, temperature, noise, food, and social environment; see above examples) are modulated in a controlled manner and within ecologically relevant limits.

#### 4.2. Integration across space, expertise, and species

In order to obtain a more comprehensive picture of the link between urbanization and endocrine systems, we believe that field studies will benefit from an integration in national, continental and international networks (see Beaugéard et al., 2019; Ibáñez-Álamo et al., 2020; Salmón et al., 2021 for some examples). Such networks would allow the scientific community not only to replicate field studies along a wide variety of urban sites with contrasted characteristics (land use, climate, degree of urbanization, etc.), but also to benefit from the expertise of each research group in specific endocrine systems. Given the complexity of the urban environment and multitude of endocrine axes of interest, such networks seem crucial to obtain a better understanding of the influence of urbanization on the endocrinology of birds, and to a larger extent on the ecology of birds. These networks could focus on a few species that are widely studied at the continental scale (e.g., great tits and common blackbirds in Europe; Eurasian tree sparrow in Asia; song sparrows, northern cardinals, and house finch in North America) or even at a planetary scale (e.g., house sparrows and feral pigeons), and allow us to generalize findings. In addition, they could also allow us to obtain robust endocrine data on a wide range of bird species, and thus, to better understand the role of endocrine mechanisms in determining the ability of species to adjust to the urban environment.

#### 4.3. A call for standardized methodological approaches

The above approach alone will often not suffice to establish causal relationships between environmental factors and physiological processes, and progress in this area will be facilitated by integrating research on free-ranging subjects with work in captive settings. Researchers will, however, need to bear in mind that captive settings do generally not replicate the richness and diversity of biotic and abiotic stimuli to which free-ranging organisms are naturally exposed. Captive settings can also be stressful to study animals and consequently modify their normal physiology and behavior (Romero and Wingfield, 1999; Fischer et al., 2018; Dickens and Romero, 2009; Dickens et al., 2009). In addition, many captive studies are conducted on domesticated bird species, which can dramatically differ in their endocrine physiology in comparison to wild urban birds. Thus, the extension of conclusions reached from captive studies to free-ranging organisms should always be asserted carefully and conservatively, keeping in mind the biological peculiarities of the species including its natural ecology, behavior, and physiology.

A main challenge facing avian urban endocrinologists is that the diversity of organisms used in studies of urbanization and the heterogeneity of urban environments make it difficult to identify generalized patterns. Within the same vertebrate class (i.e., birds), taxa vary greatly with regard to their biological characteristics including spatial and temporal resource requirements, metabolism, developmental profile, and life history (e.g., social system, seasonality, and mobility). Not surprisingly, these differences are associated with varied responses to urbanization which can, therefore, appear to be taxon-specific. This is the case for the reproductive system. For instance, Renthlei et al. (2021) observed delayed seasonal testicular development in free-ranging urban Eurasian tree sparrows, along with lower transcription of GnRH. In

contrast, LH secretion increased and testicular development occurred earlier in the year in urban than rural captive-raised common blackbirds (Partecke et al., 2004) and in free-ranging Abert's towhees (Davies et al., 2015b). In both species, these differences were observed in the wild as well as in captivity (Partecke et al., 2004; Davies et al., 2015b), indicating that findings in captive birds were not the result of captive conditions. Studies on relationships between urbanization and CORT, by far the most commonly measured hormone in studies on the avian stress response, similarly reveal extensive species differences. For example, feather CORT is lower in urban than rural male common blackbirds but no such relationship is observed in conspecific females (Ibáñez-Álamo et al., 2020). By contrast, feather CORT in juvenile house sparrows is positively correlated with the level of urbanization (Beaugéard et al., 2019). The origin and ecological significance of these apparent inter-specific differences are unclear. It is possible that urbanization does, indeed, inherently affect birds physiologically in a taxon-specific manner. Alternatively, limited data and many of the experimental methodologies used to date may contribute to producing apparent discrepancies between studies. For example, feather CORT in the house sparrow is negatively related to the degree of urbanization as determined at the individual home range, but not at the city-level scale (Strubbe et al., 2020). Furthermore, CORT in birds may in fact not constitute an accurate biomarker of stress (Romero and Beattie, 2022). If this hypothesis is correct, a lack of consistency between studies on the relationships between urbanization (e.g., human population density, ambient noise, or nocturnal illumination; Injaian et al., 2020) and the stress response as determined by CORT would not be unexpected. Researchers investigating relationships between urbanization and stress should, therefore, consider measuring alternate and/or additional indicators of physiological stress, such as thyroid hormones, heat shock proteins, markers of oxidative stress, and immune parameters such as the blood heterophil to lymphocyte (H/L) ratio. To facilitate the comparison and integration of results across studies, it would also be greatly beneficial to establish a standard and representative number of such parameters that, when possible, will be measured across studies.

#### 4.4. Model species vs. comparative approaches

Most avian studies on the endocrine effects of urbanization have been carried out on a relatively small number of widespread and easily accessible model species, in particular house sparrows, tree swallows, great tits, European kestrels (*Falco tinnunculus*), and song sparrows. Further research on these species in diverse urban environments and climatic conditions is essential as it minimizes the need to address some above-mentioned complications and may reveal generalizations in the endocrine responses to urbanization. Comparative studies using less well-studied species, including those belonging to various taxonomic groups, that adjust to various degrees to urbanization, use various types of resources, and differ with respect to their life histories, are also of great importance in order to test the generality of findings in better investigated species. Finally, examination of species that avoid urban environments, or whose populations are declining in urban environments, is important in formulating generalizations and understanding exceptions in the responses to urbanization. In addition to urban adapters and urban exploiters, these urban avoiders are crucial to study in order to better understand how endocrine mechanisms may affect the ability of avian species to exploit and persist in the urban environment.

#### 4.5. Phenotypic adjustments vs. adaptations

Another challenge results from the difficulty of assigning behavioral differences to phenotypic plasticity vs. adaptation. For instance, the flight initiation distance of many birds decreases following repeated contact with humans, but whether this decrease reflects habituation or non-random distribution of individuals differing in heritable personality traits is not established (Botsch et al., 2018). Phenotypic plasticity



extends to some aspects of the endocrine system. Ouyang et al. (2019) found in adult free-ranging urban house wrens that urban birds have higher baseline CORT than rural conspecifics. This difference is already observed at the time of hatching in captive-raised birds, but rural offspring increase plasma CORT when moved to urban environments. Thus, the observed difference in adult hormone levels in this study was apparently due to phenotypic plasticity. Increasing evidence also supports the existence of genetic and epigenetic differences between rural and conspecific urban avian populations (section 3.9).

## 5. Concluding remarks

In this review, we have attempted to summarize the current literature examining the impact of urbanization on the endocrine physiology of wild birds. While some relatively widespread responses to urbanization have emerged, such as earlier development of reproductive systems in seasonally breeding urban birds, these responses do not appear to be associated with corresponding differences in the endocrine physiology of urban birds, such that generalizations regarding the endocrine response to urbanization have failed to emerge as noted a decade ago by Bonier (2012). Similarly, the impacts of presumed urban stressors related, e.g., to food and water availability, temperature, noise, ALAN, and pollution on avian endocrine physiology show little consistency across taxa. We suggest that these dissimilarities arise in part from the heterogeneity of study species, experimental designs, and outcomes. Moreover, many studies included in this review were correlative in nature, thus limiting the ability to determine causal relationships. Looking to the future, we recommend prioritizing mechanistic approaches to identify environmental factors unique to urban environments as well as animal-specific factors (species, behavior, age, sex, reproductive status, mobility, seasonality, etc.) that alone or together may shape phenotypic responses of organisms to their environment. Standardizing approaches with regard to experimental models, systems, and study design should help identify generalizable patterns in the endocrine response of birds to urbanization. However, we recognize the critical role of explorative studies that examine unique species, study systems, and patterns of adaptation. As noted here and throughout this review, much remains to be learned about avian adaptations to urban environments, and the study of endocrine physiology can definitely contribute to a better understanding of these adaptations. Moreover, elucidating the bases of these adaptations may have profound implications for understanding the determinants of urban biodiversity as well as the composition and dynamics of urban wildlife communities. This understanding will become increasingly important as urbanization continues to expand worldwide and it may serve as an important tool in the design and renovation of urban spaces to facilitate the accommodation of both human activities and wildlife.

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## Author contributions

All authors contributed equally.

## Data availability

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