



# Urban Impacts on Oxidative Balance and Animal Signals

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Though many animal ornaments and signals are sensitive to and encode information about the oxidative balance (OB) of individuals (e.g., antioxidant supplies/activity, reactive oxygen species, cellular oxidative damage/repair), often the environmental and/or physiological sources of such OB are unknown. Urban development is among the most recent, pervasive, and persistent human stressors on the planet and impacts many environmental and physiological parameters of animals. Here we review the mechanistic underpinnings and functional consequences of how *human urbanization* drives antioxidant/oxidative status in animals and how this affects signal expression and use. Although we find that urbanization has strong negative effects on signal quality (e.g., visual, auditory, chemical) and OB across a range of taxa, few urban ecophysiological studies address signals and oxidative stress in unison, and even fewer in a fitness context. We also highlight particular signal types, taxa, life-histories, and anthropogenic environmental modifications on which future work integrating OB, signals, and urbanization could be centered. Last, we examine the conceptual and empirical framework behind the idea that urban conditions may disentangle signal expression from honesty and affect plasticity and adaptedness of sexually selected traits and preferences in the city.

**Keywords:** antioxidants, animal communication, dishonest signals, oxidative stress, pro-oxidants, signal honesty, urbanization

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## GENERAL BACKGROUND

Many conspicuous traits in animals, such as songs, odorants, and bright colors, can reveal the quality of individuals and are used as signals in competition for mates or other resources (Andersson, 1994; Bradbury and Vehrencamp, 2011). The fitness-related qualities that such condition-dependent signals reveal include disease resistance (Hamilton and Zuk, 1982; Blount et al., 2003), nutrition (Walker et al., 2013), parental effort (Badyaev and Hill, 2002; Massaro et al., 2003), and oxidative stress (OS; i.e., accumulation of free-radical damage, including lipid peroxidation, protein carbonylation, and/or genotoxic damage). Recent empirical work suggests that oxidative balance (OB; i.e., balance between free-radical molecules and antioxidant defenses; Tomášek et al., 2016) integrates many aspects of individual quality/condition (e.g., disease, diet, stress) and can be an important modulator of signal production (von Schantz et al., 1999; Garratt and Brooks, 2012; Henschen et al., 2015). However, we need a deeper understanding of the extent to which oxidative challenges affect different organisms with different signals, environments, genetics, and life-histories.

A number of natural environmental factors, including heat stress and population density (Costantini, 2010; Costantini et al., 2010), are known to generate oxidative imbalance in organisms, via the accumulation of damaging pro-oxidant byproducts of cellular respiration, disruptions to the activity of endogenous antioxidants (e.g., melatonin, enzymes such as superoxide dismutase), or depletion/availability of exogenous dietary antioxidant supplies (e.g., vitamin E, carotenoids). Only recently have biologists begun to address the effects of more large-scale human-induced rapid environmental changes, such as *urbanization*, on OB and animal signals (Isaksson, 2015). Many local ecological parameters can be altered by human activities in cities and may disproportionately depress or elevate OB and environmentally sensitive sexually selected signals (Hill, 1995). Indeed, experimental research has demonstrated that many urban-associated environmental factors can cause either a reduction in antioxidant availability/expression, an increase in pro-oxidant production, and/or an increase in OS (Isaksson, 2015). Chemical contaminants (Isaksson, 2010), light pollution (Navara and Nelson, 2007), noise pollution (Demirel et al., 2009), altered diet (Isaksson and Andersson, 2007; Andersson et al., 2015), and changes in social interactions (Beaulieu et al., 2014) are candidate modulators of OB in urban animals. Alternatively, animals may experience fewer negative effects on OB in urban areas, perhaps due to increased resources or lower perceived predation threat (Janssens and Stoks, 2013). Thus, though urbanization may have positive or negative effects on OB (perhaps based on taxon-specific life-history traits, including current physiological condition or behavioral/physiological plasticity; see **Figure 1A**), we are currently unaware of the prevailing effects of urbanization on OB and signaling. Therefore, we need an overarching evaluation of the linkages between urban environmental pressures, OB, and the expression and evolution of animal signals.

Here we review literature and understudied/untested ideas surrounding three critical questions related to animal signaling and OB in urban environments: (1) How might urbanization have physiological effects on OB and signal expression?; (2) Are different organisms or signal modalities more or less prone to urban-induced change in OB and signal quality?; and (3) How might urbanization shape the links between OB and signal honesty?

## OVERVIEW OF LITERATURE LINKING OB, SIGNALS, AND URBANIZATION

We surveyed the literature for studies on the relationship(s) between signal expression, OB, and/or urban conditions in animals. We found a total of 57 studies linking urbanization and signaling: consistent with the early hypothesis advanced by Hill (1995) that sexual ornaments act as indicators of environmental quality, the majority (70%) of published studies on this topic reveal that animals have reduced signal quality in urban settings (**Tables 1A,B; Figure 1B**). This suggests that urban environments

contain pervasive pressures that are stressful to animals across a range of clades and signal types. Urbanization enhanced signal expression in only 14% of studies. Interestingly, 4 of the 6 studies on melanin-based ornaments in birds show increased signal expression in the city; it is noteworthy that expression of melanin ornaments is related to resistance of both disease (Jacquin et al., 2011) and OS (Henschen et al., 2015), which may be beneficial in the pro-disease (Giraudeau et al., 2014a) and pro-oxidant urban environment. Taken together, these studies indicate that urban environments have overall strong negative impacts on the expression of animal signals, though it is not often known if these effects are plastic or adaptive (McDonnell and Hahs, 2015).

Of the nine studies that specifically tested for urban-rural differences in dietary antioxidants, 44% showed antioxidant reductions in urban compared to rural environments, and none showed an increase (**Tables 1B,C**). Urban antioxidant depletion may arise if dietary antioxidants are harder to procure in urban environments (Isaksson, 2009) and/or to maintain in the body as they are destroyed by elevated pro-oxidants (reviewed in Seifried et al., 2007). The fact that antioxidants were depleted in nearly half of the studies on urban animals is consistent with results of a large comparative study by Møller et al. (2010), who found that urban birds have lower levels of liver carotenoids and vitamin E than rural counterparts. We also found that endogenous antioxidant enzyme activity showed variable differences between urban and rural environments, as they both decreased and increased in a handful of studies (27 and 33% of total, respectively) (**Tables 1B,C**). The failure to find consistent urban-rural variation in antioxidants could reflect how organisms tend to up-regulate endogenous antioxidant activity after an oxidative challenge, but how prolonged and intense oxidative challenge may eventually overpower and deplete endogenous defenses (Finkel and Holbrook, 2000; Finkel, 2003). Alternatively, this pattern may reflect differences among studies in the timing of antioxidant measurement (e.g., due to seasonal or life-history-stage-related fluctuations; Barata et al., 2005; Falfushinska H. et al., 2008; Giraudeau and McGraw, 2014) or the use of different antioxidant tests (Beaulieu and Costantini, 2014). Therefore we stress that (1) more consistent tests of antioxidants should be conducted, all with strong biological rationale for the question(s) being asked, and (2) studies should combine measurements of past oxidative damage, current oxidative threats, as well as the actions, intake, and mobilized stores of various antioxidants, as it is difficult to interpret each independently (Beaulieu and Costantini, 2014; Costantini, 2016).

We located 15 published studies that investigated urban-rural differences in OS, 60% of which showed that urban environments have negative effects on OS (**Tables 1B,C**). These studies used a variety of OS metrics, and based on this evidence it appears that urbanization increases lipid peroxidation and genotoxic damage, but the only two studies on protein carbonylation failed to find similar trends. One exciting study shows that novel resource use can generate a trade-off between OS and parasite avoidance; although urban house finches (*Haemorrhous mexicanus*) that line nests with cigarette butts

**TABLE 1 | Summary of studies that associate urbanization with (A) animal signals, (B) both animal signals and oxidative stress and/or antioxidants, and (C) just oxidative stress and/or antioxidants.**

<b>A</b>				
<b>Class</b>	<b>Common name</b>	<b>Scientific name</b>	<b>Ornamentation</b>	<b>Reference</b>
Amphibia	Common eastern froglet	<i>Crinia signifera</i>	–A (voc)	Parris et al., 2009
	European tree frog	<i>Hyla arborea</i>	–V (car); 0A (voc)	Troianowski et al., 2015
	Southern brown tree frog	<i>Litoria ewingii</i>	–A (voc)	Parris et al., 2009
Aves	American robin	<i>Turdus migratorius</i>	–A (voc)	Seeger-Fullam et al., 2011
	American robin	<i>Turdus migratorius</i>	+ A (voc)	Dowling et al., 2012
	Black-capped chickadee	<i>Poecile atricapillus</i>	–A (voc)	Lazerte et al., 2015
	Carolina wren	<i>Thyrothorus ludovicianus</i>	0A (voc)	Dowling et al., 2012
	Comparative analysis	–	–A (voc)	Hu and Cardoso, 2010
	Dark-eyed junco	<i>Junco hyemalis</i>	–V (struct)	Yeh, 2004
	Dark-eyed junco	<i>Junco hyemalis</i>	? Olf (gland) <sup>a</sup>	Whittaker et al., 2010
	Dark-eyed junco	<i>Junco hyemalis</i>	–A (voc)	Slabbekoorn et al., 2007
	Eastern bluebird	<i>Sialia sialis</i>	–A (voc)	Kight and Swaddle, 2015
	Eurasian wren	<i>Troglodytes troglodytes</i>	0A (voc)	Yang and Slabbekoorn, 2014
	European blackbird	<i>Turdus merula</i>	–A (voc)	Ripmeester et al., 2010
	Florida scrub-jay	<i>Aphelocoma coerulescens</i>	–V (struct)	Tringali and Bowman, 2015
	Gray catbird	<i>Dumetella carolinensis</i>	–A (voc)	Dowling et al., 2012
	Great tit	<i>Parus major</i>	–V (car)	Hörak et al., 2000
	Great tit	<i>Parus major</i>	–V (car)	Hörak et al., 2001
	Great tit	<i>Parus major</i>	–V (mel)	Senar et al., 2014
	Great tit	<i>Parus major</i>	–A (voc)	Halfwerk et al., 2011
	Great tit	<i>Parus major</i>	–A (voc)	Mockford and Marshall, 2009
	House finch	<i>Haemorhous mexicanus</i>	+ V (car)	Hill, 1993
	House finch	<i>Haemorhous mexicanus</i>	–V (car)	Hasegawa et al., 2014
	House finch	<i>Haemorhous mexicanus</i>	+ A (voc)	Badyaev et al., 2008
	House finch	<i>Haemorhous mexicanus</i>	–A (voc)	Fernández-Juricic et al., 2005
	House finch	<i>Haemorhous mexicanus</i>	–A (voc)	Giraudeau et al., 2014b
	House wren	<i>Troglodytes aedon</i>	0A (voc)	Dowling et al., 2012
	House wren	<i>Troglodytes aedon</i>	–A (voc)	Redondo et al., 2013
	Mountain chickadee	<i>Poecile gambeli</i>	–A (voc)	Lazerte et al., 2015
	Noisy miner	<i>Manorina melanocephala</i>	–A (voc)	Lowry et al., 2012
	Northern cardinal	<i>Cardinalis cardinalis</i>	–V (car)	Jones et al., 2010
	Northern cardinal	<i>Cardinalis cardinalis</i>	–A (voc)	Dowling et al., 2012
	Northern cardinal	<i>Cardinalis cardinalis</i>	–A (voc)	Narango and Rodewald, 2016
	Northern cardinal	<i>Cardinalis cardinalis</i>	–A (voc)	Seeger-Fullam et al., 2011
	Red-winged blackbird	<i>Agelaius phoeniceus</i>	0 V (dis); –A (voc)	Ríos-Chelén et al., 2015
	Rock dove	<i>Columba livia</i>	+ V (mel)	Jacquin et al., 2011
	Rock dove	<i>Columba livia</i>	+ V (mel)	Obukhova, 2007
	Rock dove	<i>Columba livia</i>	+ V (mel)	Obukhova, 2011
	Saffron finch	<i>Sicalis flaveola</i>	–A (voc)	Leon et al., 2014
	Silvereye	<i>Zosterops lateralis</i>	M A (voc) <sup>b</sup>	Potvin and Parris, 2012
	Silvereye	<i>Zosterops lateralis</i>	+ A (voc)	Potvin et al., 2014
	Silvereye	<i>Zosterops lateralis</i>	–A (voc)	Potvin and Mulder, 2013
	Song sparrow	<i>Melospiza melodia</i>	0A (voc)	Dowling et al., 2012

(Continued)

TABLE 1 | Continued

<b>A</b>						
Class	Common name	Scientific name	Ornamentation		References	
	Song sparrow	<i>Melospiza melodia</i>	–A (voc)		Wood and Yezerinac, 2006	
	Vermillion flycatcher	<i>Pyrocephalus rubinus</i>	–A (voc)		Ríos-Chelén et al., 2013	
Gastropoda	–	<i>Cepea vindobonensis</i>	? V (unk) <sup>C</sup>		Kramarenko et al., 2007	
Insecta	Fruit fly	<i>Drosophila kikkawai</i>	–V (mel)		Costa et al., 2003	
	Grasshopper	<i>Chorthippus biguttulus</i>	–A (strid)		Lampe et al., 2012	
	Grasshopper	<i>Chorthippus biguttulus</i>	–A (strid)		Lampe et al., 2014	
	Meadow froghopper	<i>Philaenus spumarius</i>	+ V (mel)		Stewart and Lees, 1996	
	Taiwanese cicada	<i>Cryptotympana takasagona</i>	0 A (strid)		Shieh et al., 2012	
	Tree cricket	<i>Oecanthus spp.</i>	–A (strid)		Costello and Symes, 2014	
Mammalia	Indian gerbil	<i>Tatera indica</i>	–Olf (gland)		Prakesh et al., 1998	
<b>B</b>						
Class	Common name	Scientific name	Antioxidants	Oxidative stress	Ornamentation	References
Aves	House finch	<i>Haemorhous mexicanus</i>	M car <sup>d</sup>	+ lip	–V (car)	Giraudeau et al., 2015
	Great tit	<i>Parus major</i>	0 GSH	+ G:G	–V (car)	Isaksson et al., 2005
	Great tit	<i>Parus major</i>	0 car; 0 VA; 0 VE		–V (car)	Hörak et al., 2004
<b>C</b>						
Class	Common name	Scientific name	Antioxidants	Oxidative stress	References	
Actinopterygii	Fathead minnow	<i>Pimphales promelas</i>	0 CAT; 0 GPx; + GST; + GR; –SOD	+ G:G	Jasinska et al., 2015	
	Fathead minnow	<i>Pimphales promelas</i>	+ GST		Crago et al., 2011	
	Red mullet	<i>Mullus barbatus</i>	0 CAT; –GPx		Lionetto et al., 2003	
Amphibia	Eurasian marsh frog	<i>Rana ridibunda</i>	0 CAT; + GSH; –SOD	–lip; –pro	Falfushinska H. I. et al., 2008	
	Eurasian marsh frog	<i>Rana ridibunda</i>	0 CAT; 0 GSH; 0 SOD	0 pro; + lip	Falfushinska H. et al., 2008	
Aves	Comparative analysis	–	–car; –VE		Møller et al., 2010	
	European blackbird	<i>Turdus merula</i>	–GPx; –OXY	0 lip	Costantini et al., 2014	
	European blackbird	<i>Turdus merula</i>	–melatonin		Dominoni et al., 2013	
	Great tit	<i>Parus major</i>	0 car		Isaksson et al., 2007b	
	Great tit	<i>Parus major</i>	0 car; + TAA		Isaksson et al., 2007a	
	Great tit	<i>Parus major</i>	–car; –VE		Hörak et al., 2002	
	Great tit	<i>Parus major</i>	0 car		Isaksson et al., 2008	
	Herring gull	<i>Larus argentatus</i>		+ gen	Skarphedinsdottir et al., 2010	
	House finch	<i>Haemorhous mexicanus</i>	0 VE; –car; –VA	0 lip	Giraudeau and McGraw, 2014	
	House finch	<i>Haemorhous mexicanus</i>		+ gen	Suárez-Rodríguez and Macías García, 2014	
	House sparrow	<i>Passer domesticus</i>	0 CAT; 0 SOD; –TAA	0 G:G; 0 lip; 0 pro	Herrera-Dueñas et al., 2014	
	White stork	<i>Ciconia ciconia</i>	–melatonin		Kulczykowska et al., 2007	
Bivalvia	Freshwater mussel	<i>Pyganodon grandis</i>	0 GST	–lip	Jasinska et al., 2015	
	Mediterranean mussel	<i>Mytilus galloprovincialis</i>	0 CAT; 0 GPx		Lionetto et al., 2003	
Insecta	–	<i>Hydropsyche exocellata</i>	0 SOD; + CAT; + GST; –GPx	+ lip	Barata et al., 2005	
	Comparative analysis	Order: <i>Lepidoptera</i>	–car		Isaksson and Andersson, 2007	
Mammalia	Human	<i>Homo sapiens sapiens</i>		+ lip	Bono et al., 2014	

(Continued)

TABLE 1 | Continued

C					
Class	Common name	Scientific name	Antioxidants	Oxidative stress	References
Reptilia	Blue spiny lizard	<i>Sceloporus serrifer</i>	–GST; –SOD		Aguilera et al., 2012
	Geoffrey's toadhead turtle	<i>Phrynops geoffroanus</i>	+ GST; + TAA	+ lip	Venancio et al., 2013
	Side-blotched lizard	<i>Uta stansburiana</i>		0 OS <sup>e</sup>	Lucas and French, 2012

Included were studies that compare signal or oxidative balance/stress components along an urban gradient or between urban and rural environments. We excluded studies that met the prior criterion, but did not have some feasible mechanism by which oxidative balance would alter signal expression. Studies of oxidative dynamics may have included studies of dietary and/or endogenously produced antioxidants, pro-oxidants, or current oxidative stress. However, we found only a single study for which pro-oxidants were measured *in vitro*<sup>e</sup> and therefore only present columns for antioxidants and oxidative stress. For ornament expression (A,B), symbols denote whether ornament quality increased (+) or decreased (–) in quality in the city, or whether there was no effect (0). Letters are used to indicate the modality of the signal, whether visual (V), auditory (A), or olfactory (Olf). Here, ornament quality is defined on a taxon-by-taxon basis in terms of known mate preference patterns in ex-urban environments. For example, in house finches, females prefer red over yellow males as mates and therefore redder males have greater ornament quality. "Unknown effects" is used when ornament quality could not be evaluated because ornament preference for a taxon was unavailable or unclear. In (B,C), symbols show whether urbanization increased (+), decreased (–), or had no effect (0) on antioxidants or OS. For further clarification see Beaulieu and Costantini (2014). Additional abbreviations for signals: car, carotenoids or carotenoid pigmentation; dis, visual motor display; gland, glandular excretion; mel, melanin; struct, structural color or shade; strid, stridulations; voc, vocalizations. Additional abbreviations for oxidative balance and stress: car, carotenoids; CAT, catalase; gen, genotoxic damage; G:G, reduced to oxidized glutathione ratio; GPx, glutathione peroxidase; GR, glutathione reductase; GSH, glutathione; GST, glutathione-S-transferase; lip, lipid peroxidation; OXY, non-enzymatic antioxidant capacity; pro, protein carbonylation; SOD, sodium oxide dismutase; TAA, total antioxidant activity; VA, vitamin A; VE, vitamin E.

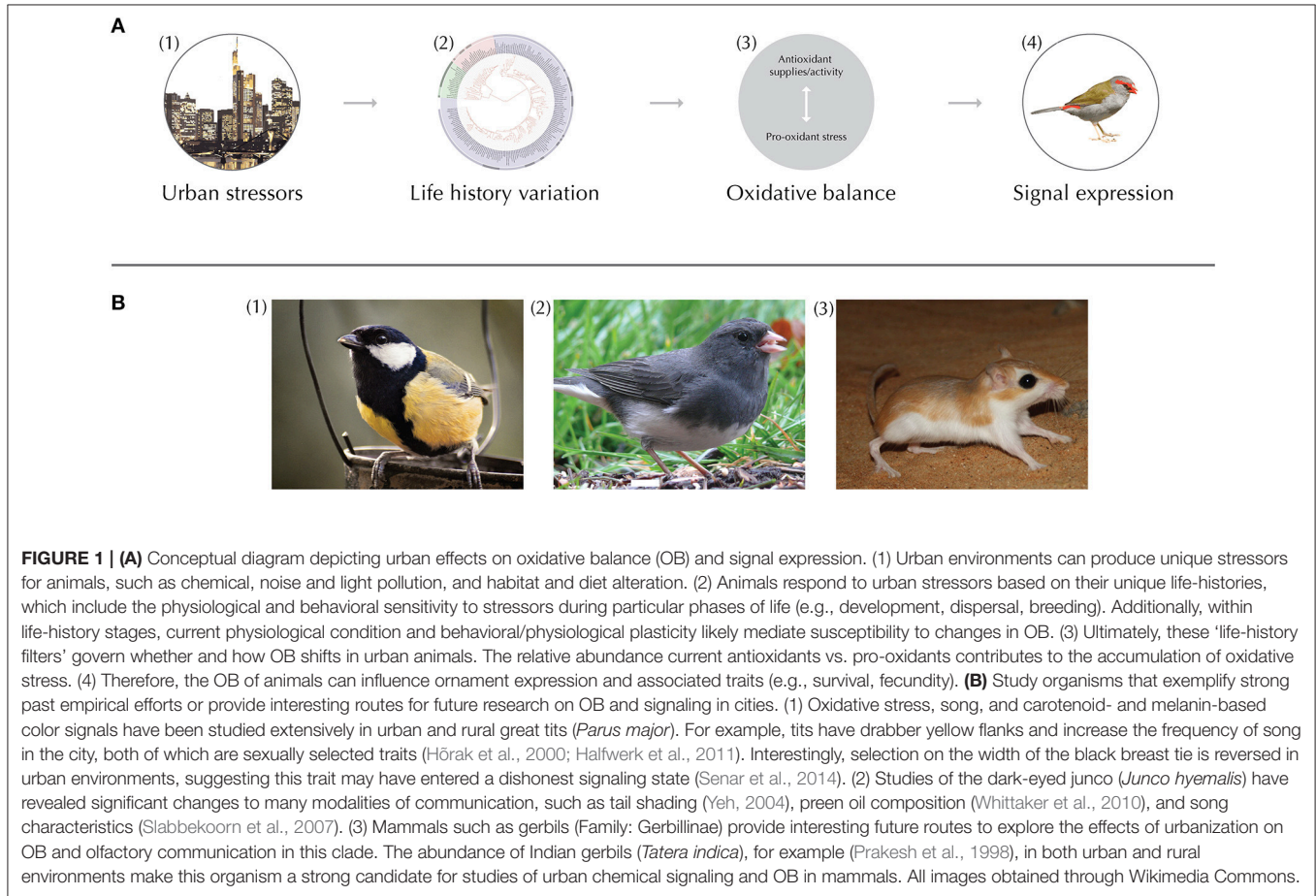
<sup>a</sup>Mate preference, and therefore effect of urbanization on signal quality is unknown.

<sup>b</sup>Urbanization had varying effects on quality of different song components.

<sup>c</sup>Shell coloration of unknown mechanism, and mate preference and therefore effect of urbanization on signal quality is unknown.

<sup>d</sup>Urbanization had varying effects on different circulating plasma carotenoids.

<sup>e</sup>Oxidative stress calculated as difference between standardized reactive oxygen species and OXY.



experience reduced parasitism, they suffer increased genotoxic damage, presumably due to chemical contaminant exposure (Suárez-Rodríguez and Macías García, 2014). In addition to the aforementioned evidence that cities disrupt signal quality, the fact that cities affect overall OS provides deeper evidence that urban environments alter environmental and physiological conditions that are key for the production and maintenance of quality signals. Still, there may be taxon- or life-history-specific effects of urbanization, given that not all studies found urban impacts on OS.

Surprisingly, we found only three studies (all on carotenoid color signals of birds) that simultaneously tested urban-rural differences in OB and signals (Hörak et al., 2004; Isaksson et al., 2005; Giraudeau et al., 2015) (Table 1B). Both Isaksson et al. (2005) and Giraudeau et al. (2015) report drabber plumage coloration and increased levels of OS in Swedish great tits (*Parus major*) and house finches, respectively. In breeding Estonian great tits, Hörak et al. (2004) found a strong trend that city birds are drabber in color, but no urban-rural difference in levels of dietary antioxidants. This limited dataset also suggests that OB is a potential critical constraint on signal production in the city. Taken altogether, studies testing urban effects on OB and signals both independently and simultaneously reveal the general pattern that urban animals experience both impaired OB and signal expression. However, we urge more comprehensive testing of this idea across animal clades and signaling modalities (see more below).

## SIGNAL MODALITIES AND TAXONOMIC PERSPECTIVES

Urban environments are inhabited by a diversity of animals that have different communication modalities, life-history traits, developmental histories, and adaptabilities. Thus, cities may present unique oxidative and signaling challenges to specific taxa or ornament types. In other words, urban stressors ‘filter’ through taxon-specific life-history variation (e.g., metamorphosis, home-range size, current physiological state, behavioral/physiological plasticity) before ultimately influencing OB and signal quality (Figure 1A). Based on such differences in oxidative susceptibility, some animals may inherently rely more on either endogenous or exogenous antioxidants or suffer more oxidative damage. In the same vein, some ornament modalities may be more sensitive to cities and OB disruptions than others, and one hypothesis is that those signals that are both directly (e.g., song masking by noise; Gil et al., 2015) and indirectly (i.e., OS) affected by urban environmental conditions will be most disrupted.

Despite the potential ecological and evolutionary insights gained by studying urban effects on signaling and OB in diverse taxa, studies have overwhelmingly been performed on the ornaments and OB of birds (73% of total), with a notable paucity of studies on mammals, reptiles, fish, and invertebrates. Moreover, among the various animal-signaling modalities (e.g., visual, auditory, olfactory), studies of acoustic signals (68%

of total) and colors (32% of total; some studies include multiple ornaments and therefore sum >100%) dominate the types of ornaments studied in relation to urbanization and OB to date (see Figure 1B for breakdown of strong past and future study systems). Only a handful of studies were performed on other modalities, such as motor displays (Ríos-Chelén et al., 2015) or olfactory (Whittaker et al., 2010) communication.

Studies of some signaling modalities have better considered the impacts of OB than others. As referenced above, studies of plumage coloration in birds like house finches and great tits have best wrapped together both signals and OB (Isaksson et al., 2007a; Giraudeau and McGraw, 2014), perhaps because of the natural links between carotenoid nutrition, OB, and plumage coloration (Blount, 2004; Svensson and Wong, 2011). Conversely, despite the large proportion of urban studies on auditory communication, the majority are considered in the context of short-term behavioral plasticity in noisy environments, few are in the context of individual quality, and none are from an OB perspective (Narango and Rodewald, 2016). Therefore, we stand to gain from reciprocally testing the current knowledge gaps for each modality: the behavioral/physiological plasticity of color ornaments (e.g., combined use in behavioral display, rapidly changeable bare parts) and how acoustic signals covary with urban oxidative conditions. For example, song learning and quality may be disrupted in the city, due to oxidative damage suffered to brain or vocal musculature during development (von Schantz et al., 1999; Nowicki et al., 2002; Buchanan et al., 2004) or adulthood (Garratt and Brooks, 2012).

Relatively little attention has been paid to other important signal modalities that may also be affected by cities and OB, such as chemical and electrical signals. The rare studies to date of this sort serve as exciting building-blocks; for example both male and female Indian gerbils (*Tatera indica*) are far less likely to express mature scent-marking glands in urban environments (Prakesh et al., 1998), perhaps due to increased gregariousness and reliance on close-quarters communication. The unique chemoscape of the city (e.g., chemical masking) may provide heretofore unconsidered selective pressures for animals that rely on chemical communication. Moreover, only in lab studies have links been made between OB and chemical signaling; Garratt et al. (2014) showed that both the mass of preputial glands and molecular composition of urine is depressed in knockout mice for superoxide dismutase, an endogenous antioxidant. We must now put this work in urban-ecological context and consider natural co-variation in OB and olfactory signals. Another understudied but exciting direction for future research is urban effects on OB and electrical signals of aquatic animals (Stoddard, 2002). Electrical signals may be anthropogenically altered via oxidative-stress pathways either through disruption of Ca<sup>2+</sup> ionic homeostasis (van der Vliet and Bast, 1992) or man-made electro-magnetic fields (Consoles et al., 2012). However, whether sexually selected electrical signals are sensitive to OB or electromagnetic pollution has yet to be tested in an ecological or urban context.

## FUTURE DIRECTIONS: BROAD IMPLICATIONS FOR UNDERSTANDING URBAN EVOLUTION OF HONEST SIGNALS

Honest communication requires that a signal provide fitness benefits to both sender and receiver (Maynard Smith and Harper, 2003). However, if environmental conditions change rapidly, then signals of mate quality may become uncoupled from individual quality and animals may choose low-quality mates as a result (Robinson et al., 2008; Bro-Jørgensen, 2010; Robertson et al., 2013). A classic example of this is the high rates of parasitism and mortality experienced by calling males (and females that prefer calling males) in newly introduced Polynesian field crickets (*Teleogryllus oceanicus*) in Hawaii (Zuk et al., 2006; Tinghitella and Zuk, 2009); this eventually led to the rapid loss of a sexually selected trait in this species. Rapid environmental alterations in cities may also perturb conditions, including via OB, in a way that leads to dishonest signaling systems.

To date, the majority of studies on signals in urban settings operate under the assumption that signals remain condition-dependent. To ask whether signal honesty persists or degrades in urban environments, we must know if and how ornament expression is related to condition of the signal sender (i.e., OB) or fitness in both rural and urban environments, how signal receivers base mate choice on ornaments, and their resulting fitness consequences. Thus, if signal honesty degrades in urban environments, we predict that (1) ornament expression will be positively related to condition only in natural/rural environments, and there will be either no relationship or a negative relationship in urban environments, and (2) signal receivers retain a preference for the exaggerated trait, a choice that (3) ultimately impairs fitness. The mechanisms that generate dishonesty may be diverse in nature. For example, Candolin (1999) showed that three-spined sticklebacks (*Gasterosteus aculeatus*) in extremely poor condition invested heavily into ornamentation, perhaps as a last-ditch effort to acquire a mate before dying; a similar scenario may occur given that urban environments generally have negative effects on OB. Alternatively, low-quality males may produce elaborate ornaments if they exploit urban-specific resources that provide surplus mate-choice currency (e.g., carotenoid-rich human-provided foods) but no real benefit to viability or ultimately do not reflect genetic quality.

The few published studies that address this question indeed point to dishonest signaling as a potential consequence of urbanization. Perhaps the best evidence comes from work on plumage coloration of Florida scrub-jays (*Aphelocoma coerulescens*). Prior to breeding, suburban and rural jays immigrate to the same location, allowing for pairing amongst jays of urban and ex-urban origin. Suburban jays had UV-shifted plumage relative to rural jays, and suburban jays were more likely to achieve breeder status, suggesting that UV-rich plumage is preferred (Tringali and Bowman, 2015). Importantly, reproductive success was lower per unit effort in nests of suburban than rural immigrants, thereby suggesting that suburban jays dishonestly exaggerated signals of quality. Senar

et al. (2014) showed that rural great tits with large melanin-based ornaments (width of the ventral black tie) were more likely to survive, whereas large-tied great tits in urban settings were less likely to survive. Though this suggests that the condition-dependent expression of tie width is altered in the city, further work is necessary to test whether urban female great tits that choose males with large black ties experience reduced fitness, and if so, whether females adaptively (or plastically; Qvarnström et al., 2000) reverse mate selection for ornament size. Unlike in these previous two cases, urbanization may also *prevent* the formation of dishonest signaling. For example, Amur honeysuckle (*Lonicera maackii*) is an invasive nest- and food-plant for both urban and rural populations of Northern cardinal (*Cardinalis cardinalis*) and substantially increases plumage brightness of birds that nest in and forage from it, but amplifies nest predation, ultimately lowering reproductive output of females that choose “high-quality” males. However, only in rural, but not urban landscapes do redder males prefer to nest in honeysuckle (Rodewald et al., 2011). Therefore, in the city, females that choose red males tend to avoid amplified predation rates imposed by honeysuckle. Though these few examples highlight potential dishonest signaling systems, further work is clearly needed within these systems to meet the full criteria we outlined, and to expand the diversity of modalities and taxa studied.

We have previously established that few studies investigate the mechanistic role of OB for signal production in the city. One major utility of these and future studies will be for examining the relationship between individual quality, signal quality, and signal use in both urban and rural environments. To investigate the potential for dishonest signaling systems, future studies should examine the covariation between OB and signals at the time of both ornament production and ornament use (i.e., during mate choice). For example, in urban environments, ornaments may honestly reflect individual quality at the time of production, but become dishonest before/during mate selection if the costs of bearing high-quality ornaments are disproportionately high in the city. These studies perhaps make best sense in the framework of relatively non-labile signals (e.g., dead integumentary ornaments, skeletal armaments like horns/antlers), whereas rapidly changeable signals may be less prone to dishonesty (e.g., song, bare part coloration, odorants; Hutton et al., 2015). Long-term studies of ornamentation, OB, and mate choice on species that advertise dishonestly in the city will be extremely productive for understanding urban plasticity and evolution of mate choice tactics. Additionally, species that bear multiple signals may flexibly choose mates based on those signal components/modalities that retain their reliability in the city (Troianowski et al., 2015).

Finally, the most robust urban-ecological studies on OB and signal expression/honesty will consider the variability and heterogeneity of the cities themselves (i.e., “not all cities and their oxidative stressors are created equal”). Urban stressors and selective pressures may differ in type, timing, and intensity across diverse urban-rural landscape gradients (e.g., desert city, forest city) and within individual cities based on spatiotemporal changes in development and infrastructure, and therefore we will

benefit greatly from increasingly global perspectives. Ultimately, urban environments serve as excellent, long-term and continuing “natural experiments” for understanding basic ecological, physiological, and evolutionary mechanisms underlying signal honesty, and the evolution and plasticity of mate preferences as a function of signal honesty/dishonesty (Hahs and Evans, 2015).

## AUTHOR CONTRIBUTIONS

Both PH and KJM drafted and intellectually contributed to the work and approved it for publication.

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