A comprehensive overview of the effects of urbanisation on sexual selection and sexual traits

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ABSTRACT

Urbanisation can affect mating opportunities and thereby alter inter- and intra-sexual selection pressures on sexual traits. Biotic and abiotic urban conditions can influence an individual's success in pre- and post-copulatory mating, for example through impacts on mate attraction and mate preference, fertilisation success, resource competition or rival interactions. Divergent sexual selection pressures can lead to differences in behavioural, physiological, morphological or life-history traits between urban and non-urban populations, ultimately driving adaptation and speciation. Most studies on urban sexual selection and mating interactions report differences between urban and non-urban populations or correlations between sexual traits and factors associated with increased urbanisation, such as pollution, food availability and risk of predation and parasitism. Here we review the literature on sexual selection and sexual traits in relation to urbanisation or urban-associated conditions. We provide an extensive list of abiotic and biotic factors that can influence processes involved in mating interactions, such as signal production and transmission, mate choice and mating opportunities. We discuss all relevant data through the lens of two, non-mutually exclusive theories on sexual selection, namely indicator and sensory models. Where possible, we indicate whether these models provide the same or different predictions regarding urban-adapted sexual signals and describe different experimental designs that can be useful for the different models as well as to investigate the drivers of sexual selection. We argue that we lack a good understanding of: (*i*) the factors driving urban sexual selection; (*ii*) whether reported changes in traits result in adaptive benefits; and (*iii*) whether these changes reflect a short-term ecological, or long-term evolutionary response. We highlight that urbanisation provides a unique opportunity to study the process and outcomes of sexual selection, but that this requires a highly integrative approach combining experimental and observational work.

Key words: sexual selection, urban ecology, signal evolution, adaptation, speciation, mate choice

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I. INTRODUCTION

Urban areas are projected to continue growing, both in number and size (United Nations, 2018), and urbanisation is consequently changing our planet at a rapid pace (Johnson & Munshi-South, 2017). Urbanisation typically alters a suite of environmental factors, resulting in a unique set of biotic and abiotic conditions (e.g. altered predator–prey dynamics, availability of resources and sensory pollutants), thereby forcing organisms to adapt, relocate, or go extinct (McKinney & Lockwood, 1999; McKinney, 2006). Over the past two decades, much research has documented population-level responses to urban selection pressures and has shown that many organisms can adapt to city life over ecological and evolutionary timescales (e.g. reviewed in Johnson & Munshi-South, 2017). However, most examples of urban adaptation involve responses to changes in natural selection pressures, whereas urbanisation also impacts sexual selection pressures, a process that can lead to rapid changes in animal population structures due to its close link with reproduction.

Many animals from urban areas have been reported to look, sound and behave differently than their rural counterparts, an observation that at least suggests that sexual selection is either influenced by, or operates in a different way due to urbanisation (Candolin, 2019; Candolin & Wong, 2019; Sepp, McGraw & Giraudeau, 2020). However, understanding the mechanisms involved requires detailed knowledge of specific model systems, in particular on the development and function of divergent traits involved, and how these traits in return can influence an individual's reproductive success. Furthermore, understanding changes in sexual selection pressures and in particular their consequences for associated ecological (e.g. behavioural flexibility and phenotypic plasticity) and evolutionary processes (e.g. adaptation and speciation) largely depends on the various models of sexual selection that operate on a given species.

Sexual selection in the strict sense refers to *differences in reproduction that arise from variation among individuals in traits that affect success in competition over mates and fertilisations* (Darwin, 1871; Andersson, 1994). Individuals can vary in their ability to attract and mate with members of the opposite sex (inter-sexual selection), or ability to compete for access to mates or fertilisation success (intra-sexual selection). Sexual selection therefore favours traits that increase an individual's success in rival competition (e.g. evolving bigger horns or faster swimming sperm) (Wiens & Tuschhoff, 2020) or mate choice (e.g. evolving bright colourations or complex songs to increase attractiveness). Additionally, sexual selection can favour traits in mates as well as rivals that increase their perceptual or cognitive abilities to process information on individuals (e.g. increased discrimination ability to rank courters or opponents).

Most research on intra- and inter-sexual interactions focuses on sexual traits involved in communication (Zuk, 1991), such as odours, sounds and colours used to impress rivals and potential mates. The production of these sexual signals is generally associated with one of the two sexes (most often the male), and the ability of receivers to detect and discriminate among inter-individual variations in these signals is at the core of sexual selection theory. Sexual signals are however not only detected by conspecifics, but also by unintended receivers, such as predators or parasites. The reproductive benefits of producing an attractive or competitive sexual signal can therefore be counterbalanced by the costs imposed by these eavesdroppers, and thus sexual communication systems are subject to both natural and sexual selection (Zuk & Kolluru, 1998; Zahavi & Zahavi, 1999), an important aspect in the context of urbanisation. Finally, it is important to acknowledge that sexual selection pressures are not static, but typically vary in strength, form and direction over time and space (Cornwallis & Uller, 2010), and variation in sexual selection often can be driven by environmental heterogeneity (Gosden & Svensson, 2008). Urbanisation is therefore likely to lead to changes in sexual selection pressures, affecting both senders and receivers, leading to signal divergence between urban and non-urban populations and ultimately may initiate speciation (Halfwerk, 2021).

Theoretical models on sexual selection are generally aimed at explaining the evolution of mate preference and the display of sexual signals. Fisher was the first to describe why mate choosers of certain species prefer exaggerated traits displayed by signallers ['Fisherian runaway' (Fisher, 1915, 1930; Lande, 1981; Kirkpatrick, 1982)]. The Fisherian model posited a runaway process in which signallers with certain extreme traits mate with receivers with matching preferences, leading to genetic coupling of trait and preference in their descendants. However, as this process can act independently of the environment, we will mostly exclude the Fisherian runaway model from our discussion of the effects of urbanisation in sexual selection. The other models on sexual selection can be broadly classified in two categories: (*i*) indicator models; and (*ii*) sensory models. As noted by other authors, these models are not mutually exclusive, and may operate in combination (Endler, 1992; Jones & Ratterman, 2009).

(1) Indicator models *versus* sensory models of sexual selection

Indicator models have long been seen as default models for sexual selection, since these models assume that receivers should evolve adaptive preferences for sexual traits. This group of models typically focuses on sexual signals as indicators of fitness-enhancing traits of signallers, which receivers use to their benefit (Fig. 1A). The benefits can be divided into direct (e.g. higher survival or fecundity of receiver) and indirect benefits (e.g. 'better' genotypes of offspring) (Kuijper, Pen & Weissing, 2012). Sexual signals can for example be indicators of future parental investment (reviewed in Møller & Jennions, 2001), parasitic load (Hamilton & Zuk, 1982; Milinski & Bakker, 1990), body condition (reviewed in Andersson, 2006) or 'good' or 'compatible' genes (reviewed in Achorn & Rosenthal, 2020; Mays & Hill, 2004). For receivers to benefit from signals as indicators, the link between the signal and the trait should, on average, be reliable or 'honest'.

Unlike indicator models, sensory models of sexual selection do not require traits to be indicative of sender quality. Instead, these models focus on the sensory component of sexual communication, and how it shapes the interplay between mate preference and trait evolution (Fig. 1C). The 'sensory bias' model, for example, proposes that biases in the receivers' sensory system can arise in non-reproductive contexts, like foraging, detecting predators or finding suitable habitat (Ryan & Cummings, 2013). These biases can later be exploited by signallers by evolving signal traits that match the sensory system of receivers, and are therefore preferred over other signallers (Ryan & Rand, 1990; Ryan, 1998). More broadly, the 'sensory drive' model states that environmental conditions not only drive receiver perception, but also the production and transmission of signals (Endler, 1992; Cummings & Endler, 2018). Overall, sensory models predict that signals that best match local environmental sensory conditions and the sensory propensities of mates will be favoured by selection (Boughman, 2002).

One apparent difference between indicator and sensory models is the emphasis on the role of the environment, which is explicitly considered in the latter but not the former models. For sensory models, any environmental change that influences the efficacy of signal production, transmission and perception in terms of signal detection, recognition and discrimination, will drive signal evolution. The sender that simply stands out more against the background will be easier to detect and therefore selected during for example mate choice. Under sensory models, urbanisation thus favours signals that best match the environment in terms of production, transmission and perception (Fig. 1C). Alternatively, urbanisation may relax the selective pressures imposed by the sensory environment (Fig. 1D). A change in the environment, however, can also affect the link between a sexual signal and indicator trait. Under indicator models, urbanisation may either increase (Fig. 1A) or decrease (Fig. 1B) the correlation between signal properties (e.g. hue of bird plumage) and fitness-related traits (e.g. number of offspring a male can raise).

(2) Aim and outline of the review

Our aim is to provide a comprehensive overview on a broad range of urban conditions that can influence sexual selection (and ultimately speciation). We cover a large body of literature, distinguishing between papers focusing on abiotic or biotic conditions and their divergent selection pressures on either sexual traits or receivers' responses to these traits. Most of the work we review focuses on observational data and animal communication in relation to urbanisation, although we also tried to include work covering traits and urban conditions that hypothetically could influence sexual selection (see online Supporting Information, Table S1, containing data on 108 papers, including some hypothetical case studies). Below, we review the data on divergent sexual selection pressures imposed by urbanisation and (possibly adaptive) response in sexual traits to these pressures. We focus on environmental drivers that are typically associated with urbanisation (e.g. pollution or food availability) and influence the development, functioning or evolutionary trajectory of traits involved in inter- or intra-specific sexual interactions (e.g. sexual signals, mate preferences, defence against rivals). Where possible, we indicate whether the use of specific models of sexual selection will improve our understanding of the processes operating in urban environments, specifically differentiating between the indicator and sensory models (see Section I.1). Finally, we list some key knowledge gaps and provide some exciting future directions for the field of urban sexual selection.

II. URBAN SEXUAL SELECTION AND ASSOCIATED RESPONSES IN SEXUAL TRAITS

Urban environments are characterised by many qualitative and quantitative differences in abiotic and biotic conditions
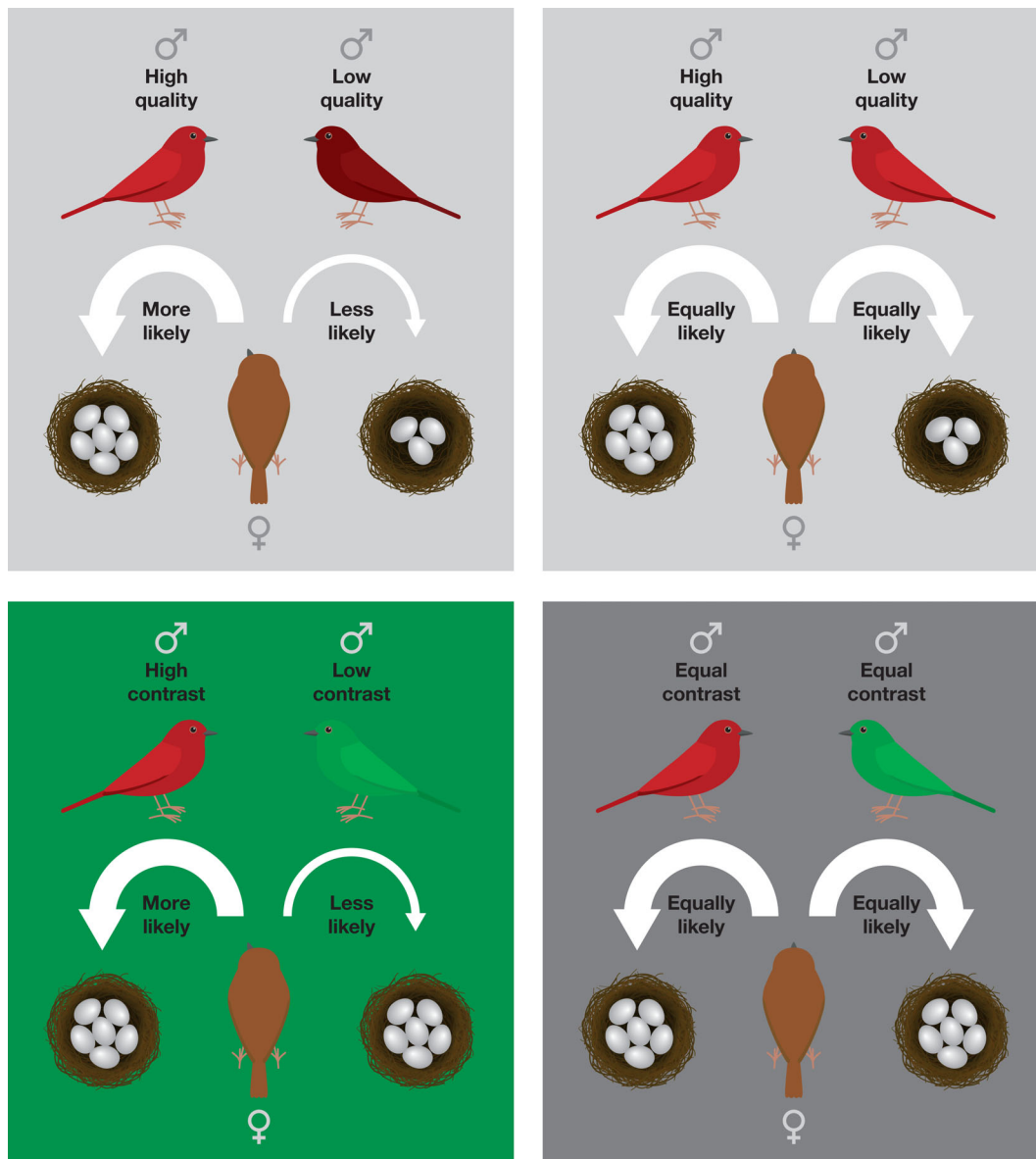
Fig. 1. Illustrations of the key concepts of the two major types of sexual selection models. The top row depicts two scenarios for which indicator models provide the best predictions with respect to changes in sexual selection pressures. In Environment A, two male birds can differ in their plumage colouration, which is linked to the benefits in terms of reproductive success they provide to females. In Environment B, this link between indicator trait (colour) and fitness is missing. Females in A will benefit from a preference for the quality-indicating signal, whereas in B this benefit is absent. Urban environments can either be representative of scenario A or B. The bottom row depicts two scenarios for which sensory models provide the best predictions. In environment C, the red male stands out most against the background and is therefore favoured by the female. In environment D, the plumage of both males contrasts equally with the environment. In both environments, females do not benefit from their choice.

when compared to other ecosystems (Niemelä *et al.*, 2011; Szulkin, Munshi-South & Charmantier, 2020). These urban conditions can influence an individual's expression of sexual traits as well as interactions among individuals that determine mating success and ultimately fitness outcomes. Predicting urban-dependent sexual selection and sexual trait divergence is therefore important, as they are likely to influence other eco-evolutionary processes (Johnson & Munshi-

South, 2017; Candolin, 2019; Svensson, 2019; Alberti *et al.*, 2020).

Here, we define sexual selection pressures as any external condition that leads to variation in mating or fertilisation success among individuals from the same population. Below we therefore discuss the expected impact of abiotic and biotic urban conditions on sexual selection pressures, distinguishing between senders and receivers of sexual signals.

Furthermore, where possible, we aim to predict the expected change in strength and direction of sexual selection operating on sexual traits. Finally, we review documented cases of urban-dependent signal production and perception and discuss whether these cases reflect adaptive responses to urban sexual selection pressures. All of the sexual traits covered in our review are studied in the context of pre-copulatory processes, however, we hypothesise the patterns and processes to be similar for post-copulatory processes, for which we simply lack data.

Urban-associated factors have the potential to alter sexual selection pressures operating on senders and receivers in multiple ways (Fig. 1). Senders may for example directly experience changes in their signal production caused by urban factors (*cf.* indicator models), or changes in signal efficacy caused by differences in environmental transmission or detection properties (*cf.* sensory models). Receivers, on the other hand, are influenced by any condition affecting their mating preferences (*cf.* sensory models), or through changes in the link between signal characteristics and performance trait of the senders (*cf.* indicator models; see also Fig. 1). Sexual selection may also be changed in urban environments more indirectly, for example, by changes in population densities and sex ratios, which may alter the strength of selection, or by changes in predator and parasite community, influencing the balance between multiple selection pressures operating on the same sexual traits.

Sexual signals can be altered directly in response to urbanisation, through phenotypic plasticity, or incrementally over generations through (onto-)genetic mechanisms. In the case of immediate responses, sexual trait changes may provide adaptive benefits to the signaller, be neutral, or even maladaptive. Longer-term changes, on the other hand, reflect an adaptive evolutionary response to changes in selection pressures, or a neutral response, for example due to drift, but are unlikely to be maladaptive.

In this section, we review how sexual selection pressures differ in urban and non-urban environments. Furthermore, we discuss any known changes in sexual signalling observed either in urban environments, or in response to specific conditions or factors associated with urbanisation. We address whether such changes might be adaptive, and if they occur on ecological (within an individual's lifetime), or evolutionary timescales (across generations). We define 'adaptive' as any change in traits that provides a fitness benefit, irrespective of the mode of change (e.g. genetic *versus* plastic). Where possible, we link changes in sexual signalling to changes in urban-dependent selection pressures and indicate the predicted changes in signal structure under either indicator or sensory models of sexual selection (see Tables 1 and S1).

(1) Abiotic changes in sexual selection pressures

We focus primarily on abiotic factors that are known to influence either signal perception or signal production. Perception can be influenced by factors that are either external or internal to the receiver. Changes in transmission properties can, for example, influence how the signal arrives at the receiver, whereas changes in temperature can influence the sensitivity of receivers to specific signal components. In principle, urban-dependent changes in receivers can alter selection pressures operating on signals, for example by favouring signal components that transmit better in cities, or that are better at stimulating the sensory system of the receivers (*cf.* sensory models). Urban-dependent changes in senders may reflect direct changes in the physiology, morphology, or behaviour of senders, which can be an adaptive response to changes in receivers, or a non-adaptive response (possibly even reducing efficacy during intra- or inter-sexual interactions). In the latter scenario, sexual selection pressures on the sender may be altered, for example by favouring signals that can be maintained at maximum performance levels (*cf.* indicator models).

(a) Sensory pollution

Anthropogenic sensory pollutants, such as low-frequency acoustic and seismic noise (Mennitt & Fristrup, 2016), artificial light at night (Kyba *et al.*, 2015; Falchi *et al.*, 2016), and chemical pollutants (Bai *et al.*, 2017) are consistently found at elevated levels in urban environments. All of these sensory pollutants have the potential to alter the efficacy of sexual communication, and therefore the evolutionary trajectory of sexually selected signals.

The selective pressures imposed on sexual signals *via* receiver responses depend on the receiver's ability to detect and discriminate between sexual signals. Sensory pollutants typically found in cities, such as acoustic and vibrational background noise, are well known to reduce signal salience to receivers, either by directly interfering with detection (e.g. through masking) or with discrimination (e.g. by distraction; Dominoni *et al.*, 2020). Sensory pollution may also alter sexual selection pressures *via* direct effects on senders, particularly when the pollutant alters their behaviour or physiology. However, it is often difficult to separate these direct effects from indirect effects that operate *via* the interaction with receivers (e.g. through noise-dependent feedback; Halfwerk, Bot & Slabbekoorn, 2012).

Most evidence of the impact of sensory pollution on sexual selection pressures comes from the acoustic domain, where low-frequency anthropogenic noise typically masks acoustic signals, such as songs or advertisement calls (Barber, Crooks & Fristrup, 2010). Many studies have documented reduced communication efficacy across a wide range of taxa (Tables 1 and S1), including in birds (Halfwerk *et al.*, 2011; Grabarczyk & Gill, 2019), frogs (Bee & Swanson, 2007), and fish (Vasconcelos, Amorim & Ladich, 2007; Slabbekoorn *et al.*, 2010). In great tits (*Parus major*), low-frequency song features, which are important in female attraction, are masked by anthropogenic noise (Halfwerk *et al.*, 2011). Anthropogenic noise may also hinder female assessment of differences between males, especially if male variation is primarily found in frequency ranges that are masked.

Table 1. Selected examples of recent studies highlighting the potential impacts of urban-associated (abiotic or biotic) environmental conditions on sexual signalling. 'Driver' refers to the putative agent of urban change. 'Com.' is 'communication modality' and refers to the sensory channel impacted by the urban factor. 'Sender/Receiver' indicates whether the impact is predicted to affect the senders and/or receivers of sexual signals. 'Effect' summarises the observed outcome in response to the urban altered factor. 'Effect in urban environment' notes whether outcomes have been observed in urban environments. 'Potential impact(s) on sexual selection' summarises the main effects an urban altered factor may have on sexual selection. 'Expected signal change' describes a predicted impact on signallers. 'Adaptive' indicates whether the impact on signallers/receivers is likely to be adaptive or not. 'Model' refers to the model of sexual selection (sensory, indicator or both) that provides the best prediction(s) for signal change. See Table S1 for a list of all relevant studies

Driver	Taxon	Species	Com.	Sender / Receiver	Effect	Effect in urban environment	Potential impact(s) on sexual selection	Expected signal change	Adaptive	Model	Reference
Abiotic											
Noise	Bird	White-crowned sparrow (*Zonotrichia leucophrys*)	Acoustic	Sender	Males sung at lower amplitudes, and increased frequency bandwidths during a period of reduced urban noise.	Demonstrated by the study	Trade-off between signal transmission and attractiveness. Selection for increased transmission and/or detection capacity.	Increased overall frequency or trill rate to maintain signal attractiveness under noise	Yes	Both	Derryberry *et al.* (2020)
Artificial Light	Insect	Winter moth (*Operophtera brumata*)	Chemical	Receiver	Male attraction to synthetic female pheromone was reduced under artificial light.	Demonstrated by the study	Selection for increased transmission and/or detection either *via* sender (e.g. increased pheromone output), or receiver (e.g. increased sensitivity).	Increased pheromone production under urban light conditions	No	Sensory	Van Geffen *et al.* (2015b)
Chemical	Fish	Swordtail (*Xiphophorus birchmanni*)	Chemical	Receiver	Exposure to humic acid reduced female response to male pheromones, and preference for conspecific pheromones.	Hypothetical	Selection for improved signal transmission and/or detection, possibly using alternative modality.	Altered pheromone composition or increased visual signalling under urban chemical pollution	No	Sensory	Fisher, Wong & Rosenthal (2006)
Biotic											
Parasitism	Bird	House finch (*Haemorhous mexicanus*)	Visual	Sender	In rural males, larger carotenoid plumage patches were associated with smaller parasite loads, but this relationship was reversed in urban males.	Demonstrated by the study	Changes in signal honesty may alter signal attractiveness. Potential trade-off between investment in survival *versus* reproduction.	Altered visual or acoustic signals in urban areas. Novel urban signals are better correlated to parasite load	?	Indicator	Sykes, Hutton & McGraw (2020)
Predation Risk	Amphibian	Túngara frog (*Engystomops pustulosus*)	Acoustic	Sender/ Receiver	Urban male calls were more conspicuous than forest males/ Less predation in urban environments	Demonstrated by the study	Increased capacity for signal attractiveness in urban environments due to	Increased call complexity in urban areas	Yes	Sensory	Halfwerk *et al.* (2019a)

(*Continues*)

Table 1. *(Cont.)*

Driver	Taxon	Species	Com.	Sender / Receiver	Effect	Effect in urban environment	Potential impact(s) on sexual selection	Expected signal change	Adaptive	Model	Reference
Food and/or Nutrient Availability	Insect	Cabbage white (*Pieris rapae*)	Visual	Sender	Both males and females inhabiting an artificially nitrogen-rich agricultural environment allocated more resources to nitrogen-rich wing pigments.	Hypothetical	reduced predation risk. Potential disruption of relationship between ornament size and signal information content.	Altered visual or chemical signals in urban areas. Novel urban signals are better correlated to food availability	?	Indicator	Espeset *et al.* (2019)

Many studies have reported acoustic signals, such as bird songs, or frog calls, to change in relation to anthropogenic background noise levels (see also Tables 1 and S1), and these observed changes are thought to aid in auditory masking release, for example, through increasing signal amplitude (e.g. the 'Lombard Effect') (Lombard, 1911; Brumm & Zollinger, 2011), which has been observed in birds (Cynx *et al.*, 1998; Pytte, Rusch & Ficken, 2003; Brumm, 2004), mammals (Brumm *et al.*, 2004), and frogs (Halfwerk *et al.*, 2016). Similarly, increased acoustic signal frequency to circumvent masking noise has also been observed across a range of taxa (Brumm & Slater, 2006; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006; Slabbekoorn, Yeh & Hunt, 2007; Halfwerk & Slabbekoorn, 2009; Parris, Velik-Lord & North, 2009; Ripmeester, Mulder & Slabbekoorn, 2010b; Dowling, Luther & Marra, 2012). Redundancy may also be effective in this sense, with repeated signal elements allowing receivers to identify information content even if only part of the signal is recognised (Wiley, 1983). Consistent with this expectation, chaffinches (*Fringilla coelebs*) occupying noisier territories use higher redundancy by repeating the same song for longer (Brumm & Slater, 2006).

Artificial light at night (ALAN) has also been shown to alter sexual selection pressures, although far fewer cases have been documented when compared to acoustic signals. Ambient light plays a central role in temporal organisation of the biological world (Bradshaw & Holzapfel, 2010) and light pollution consequently has been associated with alterations in circadian timing of signalling, such as the dawn chorus of many songbirds (Kempenaers *et al.*, 2010; Da Silva, Valcu & Kempenaers, 2015). ALAN can also reduce the effectiveness of sexual signals in species that utilise bioluminescence (Bird & Parker, 2014). In the firefly *Aquatica ficta*, low levels of ALAN can induce males to alter their signalling, by increasing the intensity of their bioluminescent signals and simultaneously reducing the frequency of signalling (Owens & Lewis, 2018). Similar patterns are seen in female glow-worms (*Lampyris noctiluca*), which delay or even stop signalling entirely under artificial light (Elgert *et al.*, 2020).

Even in instances where female detection and discrimination abilities are maintained in urban environments, specific preferences for sexual traits may be altered, although this typically happens during cross-modal interactions (see Section II.1e). For example, in the túngara frog (*Engystomops pustulosus*), females may be more likely to select relatively unattractive calls when in artificially lit environments (Rand *et al.*, 1997).

The predicted impact of sensory pollution on the direction of selection and signal responses seems to depend on the sensory modality as well as the most likely model of sexual selection operating (indicator or sensory). Anthropogenic noise typically selects for acoustic signals that stand out best (*cf.* sensory models) and most observed changes presumably provide signallers with an adaptive advantage, although few studies have actually tested this experimentally (see also Tables 1 and S1). Indicator models can however be informative when

noise alters the link between acoustic traits and mate preferences for these traits. Female songbirds may benefit directly from low-frequency-singing males that can perhaps provide better offspring care. Choosing high-frequency-singing males (due to masking release) under noisy conditions may thus be maladaptive, and females may have to evolve alternative mating preferences to avoid possible fitness costs (Halfwerk *et al.*, 2011). Likewise, if discrimination ability is reduced in noise, then females may be less able to express their preferences, effectively reducing the strength of the sexual selective pressure on sexual signals. Consequently, noisy urban conditions may select for increased perceptual sensitivity in receivers, especially when choosing mates provides adaptive benefits (*cf.* indicator models).

So far, most documented cases of noise-dependent signalling reflect immediate responses, operating on ecological timescales, and may provide little potential for an evolutionary response (but see Reichard *et al.*, 2020). Like noise, all reported effects of ALAN on signalling reflect an immediate response, and most are presumably maladaptive, at least in the short term, as most species either decrease their signal output or conspicuousness (Table S1). The one exception seems to be changes in dawn song, which could provide males with an adaptive benefit, as early singers typically secure more extra-pair matings (Kempenaers *et al.*, 2010), although a direct (experimental) test of the effect of light pollution on male fitness is so far lacking.

(b) Urban heat islands

Urban areas typically experience a combination of higher daytime surface temperatures and higher night-time atmospheric temperatures as a result of built structures capturing solar energy and reduced evaporation by vegetation, a phenomenon known as the 'urban heat island effect' (Oke, 1982; Hibbard *et al.*, 2017). Although links between urban heat islands and sexual signalling have rarely been investigated, a number of studies have shown more general temperature effects. Ectotherm physiological processes, such as metabolic rates, are especially sensitive to environmental temperatures. Consequently, signal production in ectotherms is likely affected by urban-dependent temperatures. Fiddler crabs (*Uca pugilator*), for example, increase claw-waving (a visual signal) when thermal stress is decreased (Allen & Levinton, 2014). Many insect mating songs also show temperature-dependent temporal and spectral call parameters (Gerhardt, 1978; Fonseca & Allen Revez, 2002; Hedrick *et al.*, 2002; Arias *et al.*, 2012; Symes, Rodríguez & Höbel, 2017). Higher muscle contraction rates induced by increased temperatures may, for example, be the underlying mechanism for higher frequency calling in bush crickets (Arias *et al.*, 2012) and frogs (Parris *et al.*, 2009). Receivers may also be directly impacted due to temperature-dependent shifts in hearing sensitivity at various frequencies (Stiebler & Narins, 1990; Fonseca & Correia, 2007). Receivers may consequently hear sexual signals less well, potentially reducing

female choosiness and thereby reducing sexual selection pressure on acoustic mating displays.

Physiological processes involved in insect chemical signal generation appear similarly sensitive to temperature changes. Both pheromone production (Roeser-Mueller, Strohm & Kaltenpoth, 2010), and chemical composition (Bontonou, Denis & Wicker-Thomas, 2013; Conrad, Stöcker & Ayasse, 2017) can differ with environmental temperature. It should be noted, however, that urban heat islands do not only contrast with rural environments in terms of absolute temperatures. Ambient temperature variation is lower in urban areas, as a result of solar heat storage within the built environment (Oke, 1982). This heat is accumulated during the day, but released at night, mitigating radiative heat loss (Tam, Gough & Mohsin, 2015). As circadian patterns of pheromone release can be disrupted under less-variable temperature regimes in captivity (Mozūraitis & Būda, 2006), similar effects could occur in urban environments.

Most reported changes in relation to temperature will likely provide adaptive benefits, as receiver responses to higher signalling rates are typically stronger. In the case of indicator models, higher average signalling rates might reduce variation among males with potential consequences if signal–fitness correlations are decoupled. Under such a scenario, we predict receivers to evolve more extreme preferences, or to shift to other traits that are less sensitive to temperature changes. Urban heat islands may however also lead to heat stress, in which case we would predict a decrease in signalling effort. Although we lack data on the timescale of signal change, we predict the urban heat island effect to select for signallers that perform optimally under the local temperature regime. Furthermore, we predict species with short generation times that are heavily influenced by environmental temperatures, such as ectothermic arthropods, to respond primarily *via* evolutionary mechanisms.

(c) Chemical pollution

Urban areas generate a range of chemical pollutants, including nutrients (nitrogen and phosphorus compounds used in fertilisers), organic carbon (from street litter), toxicants (metal pollution and petroleum hydrocarbons associated with vehicle transport) and micropollutants (pharmaceuticals, pesticides and hormones) (Liu, Goonetilleke & Egodawatta, 2015; Batikian *et al.*, 2019; Xu *et al.*, 2020). Such contaminants often exert a considerable influence on biological processes, across multiple levels of organisation (Saaristo *et al.*, 2018). Chemical pollutants are known to alter physiological processes, including those integral to mate detection and discrimination. Accordingly, a range of common chemical pollutants have been found to affect sexually selected behavioural and morphological traits directly, across taxa and developmental stages (Moore & Waring, 2001; Park & Propper, 2002; Tappert *et al.*, 2017). Insect pheromone production can be amplified or diminished by pesticides (Delpuech *et al.*, 1998a; Wei & Du, 2004; Zhou, Du & Huang, 2005). Additionally, reduced

male courtship display rates have been reported in fish as a result of both embryonic (Arellano-Aguilar & Macías Garcia, 2008) and adult pesticide exposure (Baatrup & Junge, 2001; Jaensson *et al.*, 2007). In two fish species examined, behavioural changes were accompanied by depleted carotenoid ornamentation, suggesting systemic physiological impacts (Baatrup & Junge, 2001; Arellano-Aguilar & Macías Garcia, 2008). Likewise, metal pollution exposure has been linked with reduced dawn chorus singing and paler yellow breast feathers in great tits (Gorissen, Gorissen & Eens, 2006; Geens, Dauwe & Eens, 2009; Grunst *et al.*, 2020). However, responses may be species dependent, as red-legged partridges (*Alectoris rufa*) have brighter eye rings, a sexual signal, when exposed to metal pollution (Vallverdú-Coll *et al.*, 2015). Pharmaceutical contaminants also appear to exert wide-ranging effects. European starling (*Sturnus vulgaris*) exposed to oestrogen exhibit enlarged song control nuclei, and sing more complex songs (Markman *et al.*, 2008), while fluoxetine increases male guppy (*Poecilia reticulata*) coercive mating behaviour (Fursdon *et al.*, 2019).

Aside from altering sexual signalling *via* changes in physiological processes, chemical pollution can also act as a sensory pollutant, for example when the pollutant binds with chemical receptors involved in the detection of pheromones. In extreme cases, sensory pollutants can even break down species' reproductive barriers. In two sympatric swordtail fish species (*Xiphophorus birchmanni* and *X. malinche*), females select mates based on chemical and visual signals. However, species recognition using chemical signals can be disrupted by environmental pollutants (humic acid from an upstream factory binding to chemical receptors) (Fisher *et al.*, 2006). Consequently, females mate indiscriminately with males of both species, leading to increased hybridisation rates (Fisher *et al.*, 2006). Despite the potential implications of communication-disrupting chemicals, their prevalence and impact in urban ecosystems are largely unknown and merit further exploration.

Changes in response to chemical pollution are mostly expected to be maladaptive in the short term, although examples of increased song complexity and brighter eye-ring colouration suggest that changes may sometimes provide signallers with an immediate fitness benefit in terms of mate attraction (although functional explanations are lacking for both cases). Although most observed changes reflect short-term immediate responses, or longer-term developmental processes, an evolutionary response has not always been ruled out. In cases where chemical pollution influences perceptual processes, we predict sensory models of sexual selection to be the most likely underlying mechanism. Documented cases of pollutants binding specific receptors could be explored to test whether senders have adapted their chemical signals to target novel receptors, or to outcompete the pollutants at the receptor binding sites. In cases where signal production is reduced, or where the link between signal content and sender quality is decreased, we predict receivers to evolve novel preferences and senders to evolve novel signalling traits that manage to track mate

quality in chemically polluted environments (*cf.* indicator models).

(d) Physical structure

The physical structure of urbanised areas is often highly fragmented and may introduce novel microhabitats that can be exploited. However, information regarding associations between urban environmental structures and sexual signals is limited, possibly as a result of the difficulty of isolating causal effects from their urban correlates in the field (such as the urban heat island effect). Human-made structures, such as buildings, roads, streetlights or gutters can be used as substrate by signallers to display their readiness to mate or willingness to fight. For example, in the bush cricket *Anurogryllus muticus*, males can increase the active space of their sexual signals by calling from human-made objects (Erregger & Schmidt, 2018). Signalling males in the frog species *Kurixalus idiootocus* selectively choose to call from concrete roadside drainages, which both amplify and lengthen their calls, creating an acoustic "urban canyon effect" (Tan *et al.*, 2014). Such novel call sites, and the acoustic transmission properties of urban environments may help alleviate masking *via* urban noise for some species.

Physical structures may also negatively impact signal production, in particular for species that rely on a particular microhabitat for acoustic communication (Muñoz *et al.*, 2020). For example, some frogs depend on sufficient water levels to produce loud and low-frequency calls and so changes to water drainage systems may directly reduce male attractiveness to females (Smit *et al.*, 2019; Goutte *et al.*, 2020). Furthermore, high levels of impervious surfaces scatter sound waves and create reverberations that can mask, distort or cancel-out acoustic signals (Slabbekoorn *et al.*, 2007), with more pronounced effects on higher frequencies (Wiley & Richards, 1978). Signallers may avoid such impact by reducing their maximum frequencies and frequency range, as has been observed in some bird species in which song features were correlated with the proportion of impervious surfaces (Dowling *et al.*, 2012).

Compared to rural environments, urban areas are also more fragmented, often consisting of mosaics of small patches of suitable habitat (e.g. urban parks). As a consequence, traits associated with the ability to successfully traverse uninhabitable spaces to reach these patches can be selectively favoured. For example, male azure damselflies (*Coenagrion puella*) exhibit increased flight ability and different wing shapes in urban environments (Tüzün, Op de Beeck & Stoks, 2017). Both traits were found to be under directional sexual selection, but only exerted by females from urban areas.

The damselfly example appears to reflect an indicator model of sexual selection, in which receiver responses track covariances among signalling and fitness-enhancing traits in the novel environment. In other words, there is a link between urban-dependent performance (improved flight) and urban-dependent mating preferences (which is absent

in females from rural areas). The damselfly example may also provide one of the few clear examples of an adaptive evolutionary response to changes in urban sexual selection pressure, although it remains to be tested whether the performance traits are heritable and/or adapted to changes in sexual (mate preferences) or natural selection pressures (increased patch isolation). The exploitation of novel display sites that enhance acoustic signal amplitude and/or transmission may also impact signal honesty. Larger animals typically sound louder (Jakobsen *et al.*, 2021), and receivers may therefore rely on signal amplitude to decide whether they want to challenge a rival or pick them as mates. If receiver responses evolved *via* such an indicator model of sexual selection, we expect urban structures to impose novel selection pressures on the preferences of rivals and mates to ensure honest communication. If, however, sexual communication is mostly driven by a sensory model, than we expect senders simply to exploit structures that maximally increase the area over which they can be detected, as long as they avoid attracting unwanted receivers, such as predators and parasites (see Section II.2*c*).

(e) *Multisensory processes and multimodal communication*

The timing of dawn song is known to be affected by both artificial light at night and anthropogenic noise (Dominoni *et al.*, 2020; Halfwerk & Jerem, 2021), a phenomenon that has been referred to as multisensory pollution and which highlights the fact that the physical modalities through which animals communicate should not be studied independently. In addition to the complex interactive effects that can influence sexual signals when multiple sensory pollutants co-occur (a common feature of urban environments), sensory pollutants within a certain modality can modify production or perception in another sensory modality *via* so called cross-modal responses. For example, noise pollution has been shown to lead to changes in visual signals, such as vocal sac colouration in European treefrogs (*Hyla arborea*) (Troïanowski *et al.*, 2015) and cephalopod colour (Kunc *et al.*, 2014). Similarly, light pollution has been documented to alter chemical sexual signals in nocturnal female cabbage moths (*Mamestra brassicae*), which reduce pheromone output under ALAN (Van Geffen *et al.*, 2015a).

To date, most studies have examined the effects of urban factors on unimodal signals, but sexual displays that employ multiple sensory modalities are prevalent (Partan & Marler, 1999; Taylor *et al.*, 2008; Higham & Hebets, 2013; Halfwerk *et al.*, 2019b). Some species are known to switch to a different sensory modality in response to changing sensory conditions, in order to overcome masking (Gomes *et al.*, 2016; Partan, 2017). Such cross-modal masking avoidance can cause a relative shift in the importance of a particular sensory modality, and therefore has the potential to alter the selective pressures imposed on specific sensory modalities. For example, in the painted goby (*Pomatoschistus pictus*), which produces both acoustic and visual displays, females pay more attention to visual signals when in the presence of acoustic

noise (de Jong *et al.*, 2018), potentially leading to selection for brighter coloured males in noisy, urbanised environments. Anthropogenic noise may on the other hand also interfere with processing of signals and cues in other sensory modalities (most likely *via* a distraction mechanism; Halfwerk & Van Oers, 2020). Additionally, receivers paying attention to visual signals may experience increased difficulties with discriminating among senders based on subtle variation in colour or patterning under noisy urban conditions (Velilla & Halfwerk, 2019; Halfwerk *et al.*, 2019b). Considering both the prevalence of multimodal signalling, and its potential role in overcoming masking, it is important to measure all components of multimodal sexual signals. The weightings of these various components in mating decisions may shift, providing insight into the mechanisms responsible for any changing sexual signals in urban environments.

(2) Biotic changes in sexual selection pressures

Biotic conditions in urban environments may profoundly alter the strength and form of sexual selection. However, previous studies examining the impact of human activities on sexual selection have primarily focused on biotic factors in other types of human-disturbed environments, such as agriculture. The role of biotic agents in urban-altered sexual selection pressures therefore remains a highly understudied area (Candolin, 2019). Sexual selection is dependent on social interactions, and consequently biotic factors that alter the urban social environment, such as changes in demography and social competition, are likely to drive faster evolution of sexual communication systems than abiotic factors (West-Eberhard, 1983, 2014; Alberti, Marzluff & Hunt, 2017). Moreover, the biotic agents themselves may evolve, leading to complex evolutionary dynamics (Miller & Svensson, 2014; Bailey, Marie-Orleach & Moore, 2018). Here, we focus on the biotic factors in urban environments that are known, or are likely, to influence sexual selection pressures and alter signalling in urban populations.

(a) *Food and resource availability*

Available food types and abundance differ substantially between urban and natural environments (Faeth *et al.*, 2005; Shochat *et al.*, 2006; Chamberlain *et al.*, 2009; Rodewald, Kearns & Shustack., D.P., 2011a). Foods associated with natural vegetation are often restricted, while anthropogenic resources such as human food waste and bird seed can be plentiful. Relationships between food availability and several signalling components, such as amplitude, call rate, and time spent signalling, have been reported for acoustic signals in birds (Berg *et al.*, 2005; Ritschard & Brumm, 2012) and insects (Wagner & Hoback, 1999), and for claw waving in fiddler crabs (Allen & Levinton, 2014). More generally, condition-dependent signals occur across a broad range of taxonomic groups (Cotton, Small & Pomiankowski, 2006). As a result, condition-dependent signalling traits in wildlife occupying urban habitats might be

expected to contrast with that of their rural counterparts (Snell-Rood *et al.*, 2015). Under indicator models of sexual selection, food availability can influence the strength and direction of selection by altering phenotypic variance in sexually selected traits (Janicke, David & Chapuis, 2015). However, few studies have examined food-dependent sexual selection in urban environments (Oro *et al.*, 2013; Snell-Rood *et al.*, 2015).

Greater availability of energy-rich and nutritious foods in urban areas for some species may also alter the relative costs and benefits of mate choice. Previous studies have shown that mate preferences also can be condition dependent (Hunt, Brooks & Jennions, 2005; Hebets, Wesson & Shamble, 2008; Fox & Moya-Laraño, 2009), with higher quality individuals generally exhibiting stronger mate preferences (Cotton *et al.*, 2006). Therefore, greater availability of food in urban environments may enhance choosiness, leading to an increase in the strength of sexual selection on preferred sexual traits.

While anthropogenic foods may fulfil general energetic needs, they can fail to meet nutritional requirements imposed by reproduction (Seress *et al.*, 2012; Peach *et al.*, 2015). Alternatively, specific nutrients such as carotenoids, which are used in pigmentation and usually limited in natural habitats, can be more freely available in urban areas (Rodewald, Shustack & Jones, 2011b). In either scenario, any correlations between sexual signals and individual quality established in natural habitats could become weakened in human-altered environments, reducing signal indicator reliability and thereby affecting sexual selection processes that operate *via* indicator models (Snell-Rood *et al.*, 2015). One possible case of reduced signal honesty has been reported in cabbage white butterflies (*Pieris rapae*) inhabiting areas rich in anthropogenic nitrogen (Espeset *et al.*, 2019). Individuals from nitrogen-rich patches allocate more nitrogen to visual wing pigmentation, but at the same time the correlation with a proxy for male quality decreased. Similar results have been described from captivity, where elevated call rates of male field crickets (*Gryllus lineaticeps*) maintained on a high-nutrition diet were unrelated to body condition (Wagner & Hoback, 1999).

Food availability in urban areas is also likely to alter a variety of selection pressures that can act indirectly on sexual signals. Changes in diet can affect sexual selection due to concomitant changes in demography, such as population density, population age structure, and predator–prey relationships, with important consequences for sexual selection dynamics (see Section II.2b). Additionally, divergent natural selection due to food availability may even combine with sexual selection to drive population divergence and reinforce local adaptation. For example, the availability of urban bird feeders is associated with changes in beak size and song structure in urban house finches (*Haemorhous mexicanus*), which combined with courtship song learning, may have contributed to genetic divergence between urban and rural populations (Badyaev *et al.*, 2008), possibly setting the stage for urban speciation (Halfwerk, 2021).

Other resources, such as sheltering or breeding sites may also be limited or patchy in urban environments, potentially increasing (or contributing to) physiological stress. Data on associations between physiological stress and condition-dependent ornaments is however mixed (Moore, Shuker & Dougherty, 2016; Leary & Baugh, 2020). Nonetheless, relationships between glucocorticoid levels and carotenoid colouration have been observed in species known to occupy urban environments, although these can also be related to food availability or other types of stressors (Fitze *et al.*, 2009; Lendvai *et al.*, 2013).

Increasing signalling effort or intensity in response to urban-dependent changes in resource availability will in general provide adaptive benefits to senders. Receivers on the other hand may pay a cost in cases where mate choice or rival assessment is based on signal honesty, in which signalling traits are correlated to some fitness value (e.g. fighting ability or parental care; *cf.* indicator models). In these cases, we would predict receivers to evolve novel preferences for traits that still track sender quality in urban environments. For sensory models, however, we expect that preferences will be maintained or may even shift towards further trait elaboration. In cases where changes in food abundance or quality appear to have a negative effect on sexual signals, we would predict an evolutionary change at the sender's side. Most studies have so far tested for effects on ecological timescales, although it would be very interesting to test for changes on longer timescales by examining divergent populations under common garden or translocated conditions.

(b) Population density and sex ratio

The demography of urban populations may differ from rural ones due to extreme habitat fragmentation and variable resource distribution (Marzluff, 2001; Lourenço *et al.*, 2017; Schmidt *et al.*, 2020). These demographic changes are highly species specific, in particular when comparing 'urban exploiters' or 'urban avoiders' (Rodewald & Gehrt, 2014). While urban exploiters can attain densities many times higher than their rural counterparts, the reverse applies to species less suited to urban environments. Despite evidence of demographic changes linked to urbanisation, few studies have examined demographic effects on sexual selection specifically in urban environments (Ryder *et al.*, 2012). Theoretical and empirical studies carried out in other environments have, however, shown that demographic factors, such as local population density and operational sex ratio, can substantially influence the mode and intensity of sexual selection (Eshel, 1979; Jann, Blanckenhorn & Ward, 2000; Kokko & Rankin, 2006; Punzalan, Rodd & Rowe, 2010; Bleu, Bessa-Gomes & Laloi, 2012; Ryder *et al.*, 2012), some of which we will discuss below in the context of urbanisation.

In species experiencing reduced population densities, the choosing sex will encounter fewer mates and the costs of choosiness may increase due to the potential for remaining unmated and the time spent searching (Jennions & Petrie, 1997; Willis, Ryan & Rosenthal, 2011; Scott, McCann & Andrade, 2020). Species with low densities in urban areas may therefore express reduced choosiness,

which in turn may lower the selective pressures on sexual traits and thus lower the intensity of sexual selection. For 'urban exploiters' on the other hand, increased population densities may be accompanied by an increase in both competitor and mate contact rates, heightening intrasexual competition (Emlen & Oring, 1977). At extremely high densities, competition is however expected to break down, as defending mates and territories becomes prohibitively difficult (Kokko & Rankin, 2006). Such patterns may explain contrasting relationships observed between population density and competitive signalling traits. Both dung beetle and European mouflon (*Ovis aries musimon*) horns have been found to diminish in size with increasing population density (Pomfret & Knell, 2008; Kavčić *et al.*, 2019). Male European earwigs (*Forficula auricularia*) from higher density populations, on the other hand, exhibit increased forcep length, which provides them more competitive capacities (Tomkins & Brown, 2004). It is also important to note that population densities are highly likely to affect resource availability and predation or parasitism risk. As such, population density would be expected to impact sexually selected traits indirectly *via* the mechanisms described in Sections II.2*a* and II.2*c*).

Local population density and sex ratio can impact the production and transmission of sexual signals (Table S1), in particular in species in which the ontogeny of sexual signals is influenced by the social environment. For example, the density of conspecific males has been found to influence certain song components in bird species, such as temporal elements in northern cardinals (*Cardinalis cardinalis*) (Narango & Rodewald, 2016). Social conditions during ontogeny may also disrupt local signal–preference relationships and thus alter the strength and form of sexual selection (Fowler-Finn, Cruz & Rodríguez, 2017). Conspicuous sexual signals may contribute to the sensory environment, acting as cues of future conspecific density for juveniles during early development, thereby influencing investment in alternative mating strategies (Bailey, Gray & Zuk, 2010). In many cases, the impacts of an urban-altered social environment on either signalling or mate choice remain to be determined.

Few studies have linked differences in density between urban and non-urban areas to changes in signalling. Urban common blackbirds (*Turdus merula*) (Ripmeester *et al.*, 2010*a*) and great tits (Hamao, Watanabe & Mori, 2011) have been observed to change their song in relation to increased densities, although the role of confounding factors, such as variation in noise and light pollution are often difficult to assess. Whether urban-dependent changes in population density or sex ratio affect sexual selection (for either indicator or sensory models), and whether senders change their signalling (adaptively) in response (over ecological or evolutionary timescales) remains to be tested.

(c) Predation risk and parasitism

Predation risk in urban habitats is likely to be distinct from that experienced in natural environments for a number of reasons. Certain predators are generally excluded from urban areas (Randa & Yunger, 2006; Gehrt, Riley & Cypher, 2010), whereas other predator species can be more abundant closer to town or city centres than in the surrounding countryside (Sorace & Gustin, 2009; Kettel *et al.*, 2019). Even with higher predator abundances, actual predation risk may be reduced in urban environments, a process known as the "predation paradox" (Fischer *et al.*, 2012; Vincze *et al.*, 2017). Also, specialist predators tend to give way to generalists as urbanisation increases (Rodewald & Kearns, 2011; Rocha & Fellowes, 2020). Parasite abundance and diversity is generally higher in urban habitats, resulting in an increased likelihood of infection by parasites transmitted through close contact, compared to natural environments (Murray *et al.*, 2019). However, urban population densities of certain amphibian and bird parasites, as well as some parasitoids may be unaffected by, or reduced due to urbanisation (Fenoglio & Salvo, 2011; Delgado-V & French, 2012; McMahon, Rohr & Bernal, 2017; Halfwerk *et al.*, 2019*a*).

Signalling traits that enhance mating success through increased conspicuousness can simultaneously increase susceptibility to eavesdropping predators and parasites (Lima & Dill, 1990; Zuk & Kolluru, 1998). Thus, trade-offs in predation risk *versus* mate attraction may drive sexual signal evolution (Magurran & Nowak, 1991; Trillo *et al.*, 2013). Changes in the conspicuousness of both visual and acoustic signals have been related to changes in (perceived) predation risk. For example, with increasing local predation risk, male guppies showed a reduced number and size of coloured spots used by females in mate selection (Endler, 1980). Male treefrogs (*Smilisca sila*) similarly decrease the number and complexity of their advertisement calls when exposed to predatory bat models (Ryan, Tuttle & Rand, 1982). Similar results were reported in one of the few studies to link predation risk and sexually selected traits in an urban environment, where lower numbers of bat predators in urban areas were associated with more complex male túngara frog advertisement calls (Halfwerk *et al.*, 2019*a*). Signal composition may also be affected – as appears possible from changes in the chemical composition of femoral secretions in the Cyren's rock lizard (*Iberolacerta cyreni*), induced by a simulated predator attack (Aragón, López & Martín, 2008). In addition to predation acting directly on sexual signals, signals can be adjusted more indirectly *via* effects of predation on resource acquisition (e.g. foraging) (Sih, 1994), or immune function.

Relationships between parasitism and sexually selected traits have frequently been reported, albeit rarely in urban environments. Parasite load is associated with changes in the expression of a variety of morphological sexual ornaments, including deer antlers (Mulvey & Aho, 1993), bird feathers (Costa & Macedo, 2005), amphibian crests (De Lisle & Rowe, 2015), fish tubercules (Müller & Ward, 1995; Kortet & Taskinen, 2004), and insect nuptial spermatophore gifts (Lehmann & Lehmann, 2000). In some instances, parasite infection may alter expression of sexual signals due to a trade-off between host immune response and endogenous androgen production, providing a potential

mechanism underlying the relationship between signalling and parasite load (Boonekamp, Ros & Verhulst, 2008; Mougeot *et al.*, 2009; Casagrande & Groothuis, 2011; Müller *et al.*, 2013). Both risk of parasitism and parasite infection can also affect acoustic signals. In parallel with their response to predation risk, túngara frogs inhabiting urban areas with low parasitic midge prevalence use more conspicuous calls (Halfwerk *et al.*, 2019a). Similarly, male field crickets from populations inhabiting areas with low parasitoid abundance are quicker to resume calling after a disturbance (Lewkiewicz & Zuk, 2004). By contrast, actual parasite infestation can affect bird song by reducing repertoire size and consistency (Buchanan *et al.*, 1999; Müller *et al.*, 2013). Lastly, parasitism may influence the strength of signal condition dependence. The size of carotenoid-based plumage colouration patches in house finches was negatively associated with parasite load in rural populations, but this relationship was reversed in urban populations (Table 1; Sykes *et al.*, 2020). Urban environments often differ in terms of community composition, with increased rates of invasive and introduced species, which can include novel parasites. Although there is limited research of the effects of novel parasites on sexual signals, in the Pacific field cricket, *Teleogryllus oceanicus*, the presence of a novel parasite led to a rapid change in acoustic signals, and the creation of a novel acoustic sexual signal (Tinghitella *et al.*, 2021). Although this case likely provides an extreme example of the effect of novel parasites, it suggests that the introduction of novel parasites in urban environments can play a defining role in shaping sexual signals.

Differences in both predation and parasitism pressures related to urbanisation may also lead to changes in receiver behaviour and mating decisions. Real or perceived changes in predation risk may cause females to adjust their mate search behaviour or preferences. Females exposed to increased predation risk cues generally reduce mate sampling and discrimination (Hedrick & Dill, 1993; Demary, Michaelidis & Lewis, 2006; Bonachea & Ryan, 2011; but see Kim *et al.*, 2009), whereas reduced predation risk often leads to greater mate sampling and choosiness (Breden & Stoner, 1987; Godin & Briggs, 1996). Mate preferences may also be influenced by parasitism levels and the infection status of females themselves, which can impact the strength of sexual selection on condition-dependent traits (Pfennig & Tinsley, 2002). Further research is needed explicitly to examine how urbanisation reshapes predator–prey interactions and parasitism levels (Faeth *et al.*, 2005; Oro *et al.*, 2013; Start, Barbour & Bonner, 2020) to predict the impacts on sexual selection better (Snell-Rood *et al.*, 2015).

As mentioned above, few studies have directly linked predation or parasitism in urban areas to changes in signalling. In the case of túngara frogs, the reported increased call complexity could be a response to reduced predation and parasitism in cities, although the direct impact of sensory pollution on male signalling cannot be ruled out. A translocation experiment did however reveal that some differences in acoustic signalling between urban and forest males are maintained after several days, suggesting that an adaptive response to predation and parasitism is not due solely to the direct environment (Halfwerk *et al.*, 2019a).

For both indicator and sensory models, decreases in predation or parasitism pressure may select for more conspicuous signals, while simultaneously reducing the variation in these signals. This could make evaluation more difficult and potentially more costly for receivers. Over time, preference strengths for conspicuous signalling traits may therefore decrease in urban areas devoid of predators and parasites. In cases where signal traits provide reliable information on a sender's immune function (*cf.* indicator models), an absence of parasites from urban areas may influence the honesty of the communication system, which should lead to reduced preferences for these traits.

III. FUTURE DIRECTIONS

In the previous section we reviewed the literature on urban abiotic and biotic conditions that could influence sexual selection pressures and signal responses. We argue that most of the examples we have reported provide interesting cases to study adaptation and evolution in relation to sexual signalling. Below we list the most important knowledge gaps in the field of urban sexual selection and signalling and discuss some promising directions for future research.

(1) Important knowledge gaps

The majority of studies on sexual selection and signalling that focus on urban environments or urban-associated conditions report observational data (Table S1). Consequently, for many of these examples we lack understanding of whether the observed differences or correlated patterns: (*i*) are caused by urban conditions; (*ii*) reflect an adaptive change; and (*iii*) reflect an immediate or evolutionary response. Observational studies should therefore mostly serve as a starting point to explore questions related to sexual selection, and not as definitive proof. Different observational studies may however provide different starting points to assess one of these three major knowledge gaps. For example, cases of signal divergence on traits with a strong heritable component and/or known genetic bases may clearly indicate an evolutionary response, and are particularly interesting to explore in the context of urban signal evolution. For this reason, visual signals (e.g. structural colours) that are not under strong dietary influence may be a good starting point. Additionally, studying short-lived, fast-reproducing taxa is probably a better choice to screen for evolutionary changes due to urbanisation, when compared to longer-lived taxa, such as most vertebrates.

(a) Identifying the drivers of urban change

To determine which urban factors alter sexual selection pressures and signalling, experiments should first focus on conditions that directly influence key aspects of sexual

communication. Furthermore, using predictions from either indicator or sensory models of sexual selection may also determine where to start exploring. Urban factors that impact signal production, transmission and detection are generally excellent starting points. When focusing on production, research may initially focus on factors influencing sender physiology and energetics, mostly following predictions from indicator models. Thus, senders can be experimentally exposed to urban conditions, while quantifying their display performance, or assessing the links between their signal characteristics and some proxy for fitness (Fig. 1). When focusing on transmission and perception, research may initially focus on detectability, discriminability and preferences of senders following the sensory model. Studies should thus focus on various receiver responses to signals while the sensory environment is experimentally manipulated.

Studies should however always aim to focus at some point on both senders and receivers, for example when taking the role of assortative mating into account (Halfwerk, 2021). Similarly, receivers on a poor-quality urban diet may prefer to mate with senders on the same diet, to avoid having to compete for mates exposed to a high-quality diet (Holveck & Riebel, 2010). Likewise, studies of urban heat islands should investigate both temperature-dependent signalling, as well as temperature-dependent mate preferences, especially in ectothermic species (Gerhardt, 1994), as assortative mating may either enhance, or limit the strength of and responses to sexual selection.

Focusing on systems for which we have a good mechanistic understanding will also provide a useful starting point to identify drivers of urban sexual selection. Acoustic communication is, for example, well understood in terms of signal production, transmission and perception (Brumm & Slabbekoorn, 2005). Unsurprisingly, most data on urban signalling come from studies on bird song (Slabbekoorn, 2013). Although many studies so far reported behavioural flexibility in response to experimental noise exposure, a recent common garden approach revealed persistent differences in minimum song frequency use between urban and rural dark-eyed juncos (*Junco hyemalis*) (Reichard et al., 2020).

Once the direct effects of urban conditions on sexual selection have been identified or ruled out, studies could move on to testing experimentally for more indirect effects, such as changes in predation and parasitism, or population densities. Urban and rural signals could, for example, be broadcast in urban and rural environments, with approaching mates, rivals, predators and parasites scored to assess divergent selection pressures.

(b) Testing for adaptive changes in signalling

Few studies on urbanisation have related changes in signalling to changes in sexual selection pressures, or tested for adaptive changes in other ways. Comparing the performance of urban *versus* rural phenotypes under urban and rural conditions would be a good start to assess the adaptive benefits of signal change (Halfwerk et al., 2011). Experiments should expose senders to different conditions to test whether they change their signalling in the predicted (presumably adaptive) direction (Halfwerk & Slabbekoorn, 2009). Furthermore, receivers should be exposed to divergent signals under divergent conditions (ideally using stimuli of senders from the same system) to assess habitat-dependent signal efficacy (Dingle et al., 2010; Halfwerk et al., 2011). Systems that allow experimental stimulus control under field conditions are ideal to assess the performance of different signals under divergent conditions. Acoustic signals can, for example, be manipulated before playback, chemical compounds synthesised before release and visual courtship rituals displayed with state-of-the art techniques, such as robotics or holographic representations (Taylor et al., 2008; Varkevisser et al., 2021).

The underlying assumptions about whether sensory or indicator models of sexual selection apply to a study system may also affect the predicted patterns of adaptive signalling changes. Sensory models would typically predict urban conditions to influence receiver sensitivities, which in turn would select for signals with properties best matching these sensitivities. Experimental studies should first document a shift in sensitivities due to urban conditions; for example, in the case of great tits, receivers are better able to detect higher frequency songs when exposed to low-frequency noise (Pohl et al., 2009). Next, studies should predict and test signal changes in response to these perceptual shifts. For great tits, urban birds sing higher frequency sounds compared to rural birds, which appears to be a within-individual adaptive response to avoid masking by noise (Slabbekoorn & Peet, 2003; Halfwerk & Slabbekoorn, 2009).

Indicator models would typically predict an urban condition to influence the link between a signal component and a measure of performance or fitness. The link between indicator and performance trait could either be weakened (Fig. 1), in which case we would predict receivers to evolve reduced preferences for these indicator signals, or the link becomes stronger, in which case we would predict the opposite. Urban receivers should thus be compared to non-urban receivers in terms of their preference strengths. In the case of a stronger link, senders may not be able to produce the preferred indicator signal any more and would have to adapt their signalling effort or strategy. Experiments should therefore compare how urban and rural senders deal with urban conditions influencing the production or expression of a trait. Urban individuals may, for example, be better at producing diet-based visual signals in the city, compared to rural individuals.

(c) Assessing the underlying mechanism of change

Observed population-level changes in signalling and receiver responses can be the result of a within- or between-individual change. Mechanisms that lead to within-individual changes include behavioural flexibility, habituation, developmental plasticity or learning. Between-individual changes, on the other hand, can be the result of maternal effects, copying

behaviour and epigenetics, or be the outcome of (random or directional) selection of specific genotypes. Experiments should expose individuals directly to urban and non-urban conditions to assess whether reported changes reflect a within-individual response. In case of developmental plasticity, such direct exposure has to start early in an individual's life. Alternatively, individuals and/or their offspring can be translocated between urban and non-urban areas and monitored throughout their lifetime. Common garden breeding experiments are typically used to assess potentially heritable differences between populations. Population-level differences in tail feather colouration of dark-eyed juncos persist, for example, when raising urban and rural populations in the laboratory (Yeh, 2004). Follow-up studies, borrowing sophisticated breeding designs from the field of quantitative genetics (De Villemereuil *et al.*, 2016), could distinguish further whether these differences are caused by epigenetic or maternal effects, or reflect genomic or genetic variation. Finally, in cases of heritable genetic traits, studies could relate phenotypic variation to genotypic variation using whole-genome sequencing data to focus on potential genomic regions of interest that may underlie a documented case of urban adaptive evolution in a sexual trait (Lambert *et al.*, 2020).

(2) Promising topics

(a) *Potential cases of adaptive evolution in response to urban sexual selection*

Although there is an increasing focus on urban evolutionary ecology, clear examples of adaptive evolution are still quite rare, and even rarer still in response to changes in sexual selection (Lambert *et al.*, 2020). Abiotic factors have been studied more thoroughly thus far, and acoustic signalling in birds remains one of the best-studied examples of divergence in urban populations. One recent example highlighting urban-altered sexual selection pressures occurred in response to the ongoing COVID-19 pandemic and its dramatic impact on the urban soundscape. By studying the same urban and forest populations of white-crowned sparrows (*Zonotrichia leucophrys*) before and during the pandemic, with high and low levels (respectively) of anthropogenic noise, Derryberry *et al.* (2020) demonstrated that urban shifts in song characteristics, particularly increasing amplitude, represented a way to overcome background noise (Table 1). They also report however that such an adaptive response comes at the cost of decreased trill performance, a potential male-quality indicator. Most studies that document acoustic shifts in urban populations, including the one on white-crowned sparrows, are indicative of behavioural flexibility rather than due to genetic changes. It would be interesting to test whether urban-adapted individuals can adjust their signalling flexibly, while maintaining high performance and/or attractiveness under urban noisy conditions. Studies of other urban abiotic factors also often document temporary shifts (Van Geffen *et al.*, 2015a). However, a recent study by

Reichard *et al.* (2020) was able to use a common garden approach to show that song differences persist between urban and non-urban populations raised in the same environment, thus suggesting that even in the acoustic domain, these song differences in birds may have some genetic bases, and may thus be evolving (see also Tables 1 and S1).

The role of biotic changes in urban-altered signalling remains largely understudied, likely due to the increased difficulty of disentangling biotic interactions. However, one recent example that supports a role for urban biotic factors in promoting adaptive changes in sexual signalling comes from the túngara frog. Comparing male mating calls from urban and forest populations, Halfwerk *et al.* (2019a) showed that urban males exhibit more complex calls. Using a translocation experiment, urban males were also found to display greater signalling flexibility in response to environmental conditions. Playback experiments indicated that urban-altered calling behaviour may be an adaptive response to the joint effects of relaxed natural selection, as predation and parasitism were lower in urban environments, and increased sexual selection pressures due to lower female encounter rates. Taken together, this study provides strong evidence for adaptive changes in sexual signalling *via* changes in urban biotic conditions, although clearly disentangling the relative role of abiotic and biotic factors remains a challenge. Additional studies have also documented shifts in the relationships between sexual signals and other fitness measures in urban *versus* rural environments, for example, due to food availability (Sykes *et al.*, 2020), but it remains to be seen whether these differences are demonstrative of adaptive changes in urban environments. Using some of the various experimental techniques mentioned above, we anticipate that forthcoming studies will greatly improve our understanding of adaptive responses to urban abiotic and biotic factors.

(b) *Neutral processes influencing sexual selection*

Neutral processes are likely to interact with and impact sexual selection pressures in urban environments. Habitat fragmentation leading to small/isolated urban populations may enhance genetic drift and constrain gene flow, reducing genetic diversity (Munshi-South & Richardson, 2020; Schmidt *et al.*, 2020). So, even when a clear case of a change in sexual selection pressure due to urbanisation is documented, a reduction in genetic diversity may limit the opportunity subsequently to select for favourable sexual traits. Other neutral processes, such as a founder effect, may actually enhance population-level responses to urban sexual selection pressures, for example, when only specific phenotypes end up in urban areas. Theoretically, a neutral process may even induce novel sexual selection pressures that are fully independent of environmental variation. A genetic linkage between preference and trait loci may, for example, increase as a result of altered gene flow, or founder effects, inducing a Fisherian-like runaway process, leading to increasingly conspicuous urban sexual signals, and increasingly extreme mate

choice preferences (Lande, 1981; Kirkpatrick, 1982). Finally, mutation rates may be elevated in urban areas thereby increasing the availability of beneficial and deleterious mutations (Yauk *et al.*, 2000; Somers, 2004). Studying the importance of neutral evolutionary processes in urban adaptation and sexual traits thus requires linking genetic and phenotypic data, as well as changes in selective pressures.

(c) Eco-evolutionary dynamics

Urban altered mate choice can influence multiple hierarchical levels from the individual or population to the community resulting in complex feedback and evolutionary dynamics. For example, habitat fragmentation can increase mate search costs, which can reduce population sizes and concomitantly reduce predator populations, culminating in the reduction of costs of conspicuous sexual signals (Candolin, 2019). Understanding the impact of urbanisation on sexual selection and eco-evolutionary dynamics will therefore be vital for predicting the long-term influence of urban environments on populations (Svensson, 2019; Alberti *et al.*, 2020).

IV. CONCLUSIONS

(1) Urban environments have the potential to alter the efficacy of sexual communication and the outcomes of mating or fertilisation decisions.

(2) Divergent selective pressures are expected to drive divergence in sexual traits in all cases, which may even initiate or advance a speciation process, although this would typically require the subsequent evolution of assortative mating.

(3) Most documented cases of urban sexual selection are related to sexual advertisement signals or other traits that influence an individual's pre-copulatory success. We predict however that post-copulatory processes will also play a role in urban adaptation and evolution, but we stress that we simply lack clear data on this topic.

(4) Future research should clearly identify the biotic and abiotic drivers of urban-associated changes in sexual traits, explicitly test if changes represent adaptive responses, and assess whether urban changes are plastic responses, or if they have genetic bases.

(5) The use of common garden experiments, experimental manipulations of urban factors, and transplant experiments provide promising avenues to examine thoroughly how urbanisation impacts sexual signalling and sexual selection.

(6) Establishing broad, taxonomically wide, directional patterns of sexual selection on specific traits is difficult at this stage, due in part to species-specific responses to urban (a)biotic factors. Further research in diverse taxa and multiple factors, abiotic and biotic, is thus required to identify trends and make reliable

predictions about how the urban environment may alter the selection operating on secondary sexual traits.

V. REFERENCES

Achorn, A. M. & Rosenthal, G. G. (2020). It's not about him: mismeasuring 'good genes' in sexual selection. *Trends in Ecology and Evolution* **35**, 206–219.

Alberti, M., Marzluff, J. & Hunt, V. M. (2017). Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160029.

Alberti, M., Palkovacs, E. P., Roches, S. D., De Meester, L., Brans, K. I., Govaert, L., Grimm, N. B., Harris, N. C., Hendry, A. P., Schell, C. J., Szulkin, M., Munshi-South, J., Urban, M. C. & Verrelli, B. C. (2020). The complexity of urban Ecco-evolutionary dynamics. *Bioscience* **70**, 772–793.

Allen, B. J. & Levinton, J. S. (2014). Sexual selection and the physiological consequences of habitat choice by a fiddler crab. *Oecologia* **176**, 25–34.

Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.

Andersson, M. (2006). Condition-dependent indicators in sexual selection. In *Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour* (eds J. R. Lucas and L. W. Simmons), pp. 253–267. Academic Press, Cambridge.

Aragón, P., López, P. & Martín, J. (2008). Increased predation risk modifies lizard scent-mark chemicals. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* **309**, 427–433.

Arellano-Aguilar, O. & Macías Garcia, C. (2008). Exposure to pesticides impairs the expression of fish ornaments reducing the availability of attractive males. *Proceedings of the Royal Society B: Biological Sciences* **275**, 1343–1350.

Arias, A., Márquez, R., Llusia, D., Beltrán, J. F., Slimani, T., Radi, M., Fattah, A. & El Mouden, E. H. (2012). Effects of temperature on the song parameters of the Moroccan bushcricket *Eugaster spinulosa* (Orthoptera, Tettigoniidae). *Bioacoustics* **21**, 225–238.

Baatrup, E. & Junge, M. (2001). Antiandrogenic pesticides disrupt sexual characteristics in the adult male guppy (*Poecilia reticula*). *Environmental Health Perspectives* **109**, 1063–1069.

Badyaev, A. V., Young, R. L., Oh, K. P. & Addison, C. (2008). Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* **62**, 1951–1964.

Bai, X., McPhearson, T., Cleugh, H., Nagendra, H., Tong, X., Zhu, T. & Zhu, Y. G. (2017). Linking urbanization and the environment: conceptual and empirical advances. *Annual Review of Environment and Resources* **42**, 215–240.

Bailey, N. W., Gray, B. & Zuk, M. (2010). Acoustic experience shapes alternative mating tactics and reproductive investment in male field crickets. *Current Biology* **20**, 845–849.

Bailey, N. W., Marie-Orleach, L. & Moore, A. J. (2018). Indirect genetic effects in behavioral ecology: does behavior play a special role in evolution? *Behavioral Ecology* **29**, 1–11.

Barber, J. R., Crooks, K. R. & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution* **25**, 180–189.

Batikian, C. M., Lu, A., Watanabe, K., Pitt, J. & Gersberg, R. M. (2019). Temporal pattern in levels of the neonicotinoid insecticide, imidacloprid, in an urban stream. *Chemosphere* **223**, 83–90.

Bee, M. A. & Swanson, E. M. (2007). Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour* **74**, 1765–1776.

Bent, A. M., Ings, T. C. & Mowles, S. L. (2021). Anthropogenic noise disrupts mate choice behaviors in female *Gryllus bimaculatus*. *Behavioral Ecology* **32**, 201–210.

Berg, M. L., Beintema, N. H., Welbergen, J. A. & Komdeur, J. (2005). Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. *Journal of Avian Biology* **36**, 102–109.

Berglund, A. (1993). Risky sex: male pipefishes mate at random in the presence of a predator. *Animal Behaviour* **46**, 169–175.

Bertram, M. G., Saaristo, M., Baumgartner, J. B., Johnstone, C. P., Allinson, M., Allinson, G. & Wong, B. B. (2015). Sex in troubled waters: widespread agricultural contaminant disrupts reproductive behaviour in fish. *Hormones and Behavior* **70**, 85–91.

Bird, S. & Parker, J. (2014). Low levels of light pollution may block the ability of male glow-worms (*Lampyris noctiluca* L.) to locate females. *Journal of Insect Conservation* **18**, 737–743.

Bleu, J., Bessa-Gomes, C. & Laloi, D. (2012). Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio. *Animal Behaviour* **83**, 131–136.

Bonachea, L. A. & Ryan, M. J. (2011). Predation risk increases permissiveness for heterospecific advertisement calls in túngara frogs, *Physalaemus pustulosus*. *Animal Behaviour* **82**, 347–352.

BONTONOU, G., DENIS, B. & WICKER-THOMAS, C. (2013). Interaction between temperature and male pheromone in sexual isolation in *Drosophila melanogaster*. *Journal of Evolutionary Biology* **26**, 2008–2020.

BOONEKAMP, J. J., ROS, A. H. F. & VERHULST, S. (2008). Immune activation suppresses plasma testosterone level: a meta-analysis. *Biology Letters* **4**, 741–744.

BOUGHMAN, J. W. (2002). How sensory drive can promote speciation. *Trends in Ecology and Evolution* **17**, 571–577.

BRADSHAW, W. E. & HOLZAPFEL, C. M. (2010). Light, time, and the physiology of biotic response to rapid climate change in animals. *Annual Review of Physiology* **72**, 147–166.

BREDEN, F. & STONER, G. (1987). Male predation risk determines female preference in the Trinidad guppy. *Nature* **329**, 831–833.

BRUMM, H. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *Journal of Experimental Biology* **207**, 443–448.

BRUMM, H. & SLABBEKOORN, H. (2005). Acoustic communication in noise. In *Advances in the Study of Behavior* (ed. M. NAGUIB), pp. 151–209. Academic Press, Cambridge.

BRUMM, H. & SLATER, P. J. B. (2006). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology* **60**, 475–481.

BRUMM, H. & ZOLLINGER, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**, 1173–1198.

BUCHANAN, K. L., CATCHPOLE, C. K., LEWIS, J. W. & LODGE, A. (1999). Song as an indicator of parasitism in the sedge warbler. *Animal Behaviour* **57**, 307–314.

CANDOLIN, U. (2019). Mate choice in a changing world. *Biological Reviews* **94**, 1246–1260.

CANDOLIN, U. & WONG, B. B. M. (2019). Mate choice in a polluted world: consequences for individuals, populations and communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180055.

CASAGRANDE, S. & GROOTHUIS, T. G. G. (2011). The interplay between gonadal steroids and immune defence in affecting a carotenoid-dependent trait. *Behavioral Ecology and Sociobiology* **65**, 2007–2019.

CHAMBERLAIN, D. E., CANNON, A. R., TOMS, M. P., LEECH, D. I., HATCHWELL, B. J. & GASTON, K. J. (2009). Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* **151**, 1–18.

CONNER, J. (1989). Density-dependent sexual selection in the fungus beetle, *Bolitotherus cornutus*. *Evolution* **43**, 1378–1386.

CONRAD, T., STÖCKER, C. & AYASSE, M. (2017). The effect of temperature on male mating signals and female choice in the red mason bee, *Osmia bicornis* (L.). *Ecology and Evolution* **7**, 8966–8975.

CORNWALLIS, C. K. & ULLER, T. (2010). Towards an evolutionary ecology of sexual traits. *Trends in Ecology & Evolution* **25**, 145–152.

COSTA, F. J. V. & MACEDO, R. H. (2005). Coccidian oocyst parasitism in the blue-black grassquit: influence on secondary sex ornaments and body condition. *Animal Behaviour* **70**, 1401–1409.

COTTON, S., SMALL, J. & POMIANKOWSKI, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology* **16**, R755–R765.

CUMMINGS, M. E. & ENDLER, J. A. (2018). 25 years of sensory drive: the evidence and its watery bias. *Current Zoology* **64**, 471–484.

CYNX, J., LEWIS, R., TAVEL, B. & TSE, H. (1998). Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Animal Behaviour* **56**, 107–113.

DA SILVA, A., VALCU, M. & KEMPENAERS, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common european songbirds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**, 20140126.

DARWIN, C. R. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

DE JONG, K., AMORIM, M. C. P., FONSECA, P. J. & HEUBEL, K. U. (2018). Noise affects multimodal communication during courtship in a marine fish. *Frontiers in Ecology and Evolution* **6**, 1–8.

DE LISLE, S. P. & ROWE, L. (2015). Parasitism and the expression of sexual dimorphism. *Ecology and Evolution* **5**, 961–967.

DE VILLEMEREUIL, P., GAGGIOTTI, O. E., MOUTERDE, M. & TILL-BOTTRAUD, I. (2016). Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity* **116**, 249–254.

DELGADO-V, C. A. & FRENCH, K. (2012). Parasite-bird interactions in urban areas: current evidence and emerging questions. *Landscape and Urban Planning* **105**, 5–14.

DELPUECH, J. M., FROMENT, B., FOUILLET, P., POMPANON, F., JANILLON, S. & BOULÉTREAU, M. (1998a). Inhibition of sex pheromone communications of *Trichogramma brassicae* (hymenoptera) by the insecticide chlorpyrifos. *Environmental Toxicology and Chemistry* **17**, 1107–1113.

DELPUECH, J. M., GAREAU, E., TERRIER, O. & FOUILLET, P. (1998b). Sublethal effects of the insecticide chlorpyrifos on the sex pheromonal communication of *Trichogramma brassicae*. *Chemosphere* **36**, 1775–1785.

DEMARY, K., MICHAELIDIS, C. I. & LEWIS, S. M. (2006). Firefly courtship: behavioral and morphological predictors of male mating success in *Photinus greeni*. *Ethology* **112**, 485–492.

DERRYBERRY, E. P., PHILLIPS, J. N., DERRYBERRY, G. E., BLUM, M. J. & LUTHER, D. (2020). Singing in a silent spring: birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science* **370**(6516), 575–579.

DINGLE, C., POELSTRA, J. W., HALFWERK, W., BRINKHUIZEN, D. M. & SLABBEKOORN, H. (2010). Asymmetric response patterns to subspecies-specific song differences in allopatry and parapatry in the gray-breasted wood-wren. *Evolution* **64**, 3537–3548.

DOMINONI, D. M., HALFWERK, W., BAIRD, E., BUXTON, R. T., FERNÁNDEZ-JURICIC, E., FRISTRUP, K. M., MCKENNA, M. F., MENNITT, D. J., PERKIN, E. K., SEYMOURE, B. M., STONER, D. C., TENNESSEN, J. B., TOTH, C. A., TYRRELL, L. P., WILSON, A., et al. (2020). Why conservation biology can benefit from sensory ecology. *Nature Ecology and Evolution* **4**, 502–511.

DOWLING, J. L., LUTHER, D. A. & MARRA, P. P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology* **23**, 201–209.

ELGERT, C., HOPKINS, J., KAITALA, A. & CANDOLIN, U. (2020). Reproduction under light pollution: maladaptive response to spatial variation in artificial light in a glowworm. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20200806.

EMLEN, S. T. & ORING, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

ENDLER, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.

ENDLER, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist* **139**, S125–S153.

ERREGGER, B. & SCHMIDT, A. K. D. (2018). Anthropogenic calling sites boost the sound amplitude of advertisement calls produced by a tropical cricket. *Animal Behaviour* **142**, 31–38.

ESHEL, I. (1979). Sexual selection, population density, and availability of mates. *Theoretical Population Biology* **16**, 301–314.

ESPESET, A., KOBIELA, M. E., SIKKINK, K. L., PAN, T., ROY, C. & SNELL-ROOD, E. C. (2019). Anthropogenic increases in nutrients alter sexual selection dynamics: a case study in butterflies. *Behavioral Ecology* **30**, 598–608.

FAETH, S. H., WARREN, P. S., SHOCHAT, E. & MARUSSICH, W. A. (2005). Trophic dynamics in urban communities. *Bioscience* **55**, 399–407.

FALCHI, F., CINZANO, P., DURISCOE, D., KYBA, C. C. M., ELVIDGE, C. D., BAUGH, K., PORTNOV, B. A., RYBNIKOVA, N. A. & FURGONI, R. (2016). The new world atlas of artificial night sky brightness. *Science Advances* **2**, 1–26.

FENOGLIO, M. S. & SALVO, A. (2011). Urbanization and parasitoids: an unexplored field of research. *Advances in Environmental Research* **11**, 163–176.

FISCHER, J. D., CLEETON, S. H., LYONS, T. P. & MILLER, J. R. (2012). Urbanization and the predation paradox: the role of trophic dynamics in structuring vertebrate communities. *Bioscience* **62**, 809–818.

FISHER, H. S., WONG, B. B. M. & ROSENTHAL, G. G. (2006). Alteration of the chemical environment disrupts communication in a freshwater fish. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1187–1193.

FISHER, R. A. (1915). The evolution of sexual preference. *Eugenics Review* **7**, 184–191.

FISHER, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.

FITZE, P. S., COTE, J., SAN-JOSE, L. M., MEYLAN, S., ISAKSSON, C., ANDERSSON, S., ROSSI, J.-M. & CLOBERT, J. (2009). Carotenoid-based colours reflect the stress response in the common lizard. *PLoS One* **4**, e5111.

FONSECA, P. & ALLEN REVEZ, M. (2002). Temperature dependence of cicada songs (Homoptera, Cicadoidea). *Journal of Comparative Physiology A* **187**, 971–976.

FONSECA, P. J. & CORREIA, T. (2007). Effects of temperature on tuning of the auditory pathway in the cicada *Tettigetta josei* (Hemiptera, Tibicinidae). *Journal of Experimental Biology* **210**, 1834–1845.

FORSGREN, E. (1992). Predation risk affects mate choice in a gobiid fish. *The American Naturalist* **140**, 1041–1049.

FOWLER-FINN, K. D., CRUZ, D. C. & RODRÍGUEZ, R. L. (2017). Local population density and group composition influence the signal-preference relationship in *Enchenopa* treehoppers (Hemiptera: Membracidae). *Journal of Evolutionary Biology* **30**, 13–25.

FOX, C. W. & MOYA-LARAÑO, J. (2009). Diet affects female mating behaviour in a seed-feeding beetle. *Physiological Entomology* **34**, 370–378.

FURSDON, J. B., MARTIN, J. M., BERTRAM, M. G., LEHTONEN, T. K. & WONG, B. B. M. (2019). The pharmaceutical pollutant fluoxetine alters reproductive behaviour in a fish independent of predation risk. *Science of the Total Environment* **650**, 642–652.

GALVÁN, I. & RODRÍGUEZ-MARTÍNEZ, S. (2018). Females mate with males with diminished pheomelanin-based coloration in the Eurasian nuthatch *Sitta europaea*. *Journal of Avian Biology* **49**, e01854.

GEENS, A., DAUWE, T. & EENS, M. (2009). Does anthropogenic metal pollution affect carotenoid colouration, antioxidative capacity and physiological condition of great tits (*Parus major*)? *Comparative Biochemistry and Physiology - C Toxicology and Pharmacology* **150**, 155–163.

GEHRT, S. D., RILEY, S. P. D. & CYPHER, B. L. (2010). Carnivore behavior and ecology, and relationship to urbanization. In *Urban Carnivores: Ecology, Conflict, and Conservation* (eds S. GEHRT, S. RILEY and B. CYPHER), pp. 13–19. John Hopkins University Press, Baltimore.

GERHARDT, H. C. (1978). Temperature coupling in the vocal communication system of the gray tree frog, *Hyla versicolor*. *Science* **199**, 992–994.

GERHARDT, H. C. (1994). The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics* **25**, 293–324.

GODIN, J. G. J. & BRIGGS, S. E. (1996). Female mate choice under predation risk in the guppy. *Animal Behaviour* **51**, 117–130.

GOMES, D. G. E., PAGE, R. A., GEIPEL, I., TAYLOR, R. C., RYAN, M. J. & HALFWERK, W. (2016). Bats perceptually weight prey cues across sensory systems when hunting in noise. *Science* **353**, 1277–1280.

GOODCHILD, C. G., BECK, M. L., VANDIEST, I., CZESAK, F. N., LANE, S. J. & SEWALL, K. B. (2021). Male zebra finches exposed to lead (Pb) during development have reduced volume of song nuclei, altered sexual traits, and received less attention from females as adults. *Ecotoxicology and Environmental Safety* **210**, 111850.

GORISSEN, L., GORISSEN, M. & EENS, M. (2006). Heterospecific song matching in two closely related songbirds (*Parus major* and *P. caeruleus*): great tits match blue tits but not vice versa. *Behavioral Ecology and Sociobiology* **60**, 260–269.

GORISSEN, L., SNOEIJS, T., VAN DUYSE, E. & EENS, M. (2005). Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Behavioral Ecology* **145**, 504–509.

GOSDEN, T. P. & SVENSSON, E. I. (2008). Spatial and temporal dynamics in a sexual selection mosaic. *Evolution* **62**, 845–856.

GOSDEN, T. P. & SVENSSON, E. I. (2009). Density-dependent male mating harassment, female resistance, and male mimicry. *The American Naturalist* **173**, 709–721.

GOUTTE, S., MUÑOZ, M. I., RYAN, M. J. & HALFWERK, W. (2020). Floating frogs sound larger: environmental constraints on signal production drives call frequency changes. *The Science of Nature* **107**, 41.

GRABARCZYK, E. E. & GILL, S. A. (2019). Anthropogenic noise masking diminishes house wren (*Troglodytes aedon*) song transmission in urban natural areas. *Bioacoustics* **29**, 518–532.

GRUNST, M. L., GRUNST, A. S., PINXTEN, R., BERVOETS, L. & EENS, M. (2020). Carotenoid- but not melanin-based plumage coloration is negatively related to metal exposure and proximity to the road in an urban songbird. *Environmental Pollution* **256**, 113473.

GWYNNE, D. T. & SIMMONS, L. W. (1990). Experimental reversal of courtship roles in an insect. *Nature* **346**, 172–174.

HALFWERK, W. (2021). How should we study urban speciation? *Frontiers in Ecology and Evolution* **8**, 573545.

HALFWERK, W., BLAAS, M., KRAMER, L., HIJNER, N., TRILLO, P. A., BERNAL, X. E., PAGE, R. A., GOUTTE, S., RYAN, M. J. & ELLERS, J. (2019a). Adaptive changes in sexual signalling in response to urbanization. *Nature Ecology and Evolution* **3**, 374–380.

HALFWERK, W., BOT, S., BUIKX, J., VAN DER VELDE, M., KOMDEUR, J., TEN CATE, C. & SLABBEKOORN, H. (2011). Low-frequency songs lose their potency in noisy urban conditions. *Proceedings of the National Academy of Sciences* **108**, 14549–14554.

HALFWERK, W., BOT, S. & SLABBEKOORN, H. (2012). Male great tit song perch selection in response to noise-dependent female feedback. *Functional Ecology* **26**, 1339–1347.

HALFWERK, W. & JEREM, P. (2021). A systematic review of research investigating the combined ecological impact of anthropogenic noise and artificial light at night. *Frontiers in Ecology and Evolution* **9**, 9.

HALFWERK, W., LEA, A. M., GUERRA, M. A., PAGE, R. A. & RYAN, M. J. (2016). Vocal responses to noise reveal the presence of the Lombard effect in a frog. *Behavioral Ecology* **27**, 669–676.

HALFWERK, W. & VAN OERS, K. (2020). Anthropogenic noise impairs foraging for cryptic prey via cross-sensory interference. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192951.

HALFWERK, W. & SLABBEKOORN, H. (2009). A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour* **78**, 1301–1307.

HALFWERK, W., VARKEVISSER, J., SIMON, R., MENDOZA, E., SCHARFF, C. & RIEBEL, K. (2019b). Toward testing for multimodal perception of mating signals. *Frontiers in Ecology and Evolution* **7**, 2013–2019.

HAMAO, S., WATANABE, M. & MORI, Y. (2011). Urban noise and male density affect songs in the great tit *Parus major*. *Ethology Ecology and Evolution* **23**, 111–119.

HAMILTON, W. D. & ZUK, M. M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

HEBETS, E. A., WESSON, J. & SHAMBLE, P. S. (2008). Diet influences mate choice selectivity in adult female wolf spiders. *Animal Behaviour* **76**, 355–363.

HEDRICK, A. V. & DILL, L. M. (1993). Mate choice by female crickets is influenced by predation risk. *Animal Behaviour* **46**, 193–196.

HEDRICK, A. V., PEREZ, D., LICHTI, N. & YEW, J. (2002). Temperature preferences of male field crickets (*Gryllus integer*) alter their mating calls. *Journal of Comparative Physiology A* **188**, 799–805.

HEUSCHELE, J., SALMINEN, T. & CANDOLIN, U. (2012). Habitat change influences mate search behaviour in three-spined sticklebacks. *Animal Behaviour* **83**, 1505–1510.

HIBBARD, K., HOFFMAN, F. M., HUNTZINGER, D. & WEST, T. O. (2017). Changes in land cover and terrestrial biogeochemistry. In *Climate Science Special Report: Fourth National Climate Assessment, Volume I* (eds D. J. WUEBBLES, D. W. FAHEY, K. A. HIBBARD, D. J. DOKKEN, B. C. STEWART and T. K. MAYCOCK), pp. 405–442. U.S. Global Change Research Program, Washington.

HIGHAM, J. P. & HEBETS, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology* **67**, 1381–1388.

HOLVECK, M. J. & RIEBEL, K. (2010). Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B: Biological Sciences* **277**, 153–160.

HUNT, J., BROOKS, R. & JENNIONS, M. D. (2005). Female mate choice as a condition-dependent life-history trait. *American Naturalist* **166**, 79–92.

JAENSSON, A., SCOTT, A. P., MOORE, A., KYLIN, H. & OLSÉN, K. H. (2007). Effects of a pyrethroid pesticide on endocrine responses to female odours and reproductive behaviour in male parr of brown trout (*Salmo trutta* L.). *Aquatic Toxicology* **81**, 1–9.

JAKOBSEN, L., CHRISTENSEN-DALSGAARD, J., JUHL, P. M. & ELEMANS, C. P. H. (2021). How loud can you go? Physical and physiological constraints on producing high sound pressures in animal vocalizations. *Frontiers in Ecology and Evolution* **9**, 9.

JANICKE, T., DAVID, P. & CHAPUIS, E. (2015). Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability. *The American Naturalist* **185**, 756–768.

JANN, P., BLANCKENHORN, W. U. & WARD, P. I. (2000). Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scathophaga stercoraria*. *Journal of Evolutionary Biology* **13**, 927–938.

JENNIONS, M. D. & PETRIE, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* **72**, 283–327.

JOHNSON, M. T. J. & MUNSHI-SOUTH, J. (2017). Evolution of life in urban environments. *Science* **358**, eaam8327.

JOHNSON, T. L., SYMONDS, M. R. & ELGAR, M. A. (2017). Anticipatory flexibility: larval population density in moths determines male investment in antennae, wings and testes. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20172087.

JONES, A. G. & RATTERMAN, N. L. (2009). Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences* **106**, 10001–10008.

KAVČIĆ, K., CORLATTI, L., SAFNER, T., GLIGORA, I. & ŠPREM, N. (2019). Density-dependent decline of early horn growth in European mouflon. *Mammalian Biology* **99**, 37–41.

KEMPENAERS, B., BORGSTRÖM, P., LOËS, P., SCHLICHT, E. & VALCU, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology* **20**, 1735–1739.

KETTEL, E. F., GENTLE, L. K., YARNELL, R. W. & QUINN, J. L. (2019). Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes. *Urban Ecosystem* **22**, 117–125.

KIM, T. W., CHRISTY, J. H., DENNENMOSER, S. & CHOE, J. C. (2009). The strength of a female mate preference increases with predation risk. *Proceedings of the Royal Society B: Biological Sciences* **276**, 775–780.

KIRKPATRICK, M. (1982). Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.

KOKKO, H. & RANKIN, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 319–334.

KORTET, R. & TASKINEN, J. (2004). Parasitism, condition and number of front head breeding tubercles in roach (*Rutilus rutilus* L.). *Ecology of Freshwater Fish* **13**, 119–124.

KUIJPER, B., PEN, I. & WEISSING, F. J. (2012). A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics* **43**, 287–311.

KUNC, H. P., LYONS, G. N., SIGWART, J. D., MCLAUGHLIN, K. E. & HOUGHTON, J. D. R. (2014). Anthropogenic noise affects behavior across sensory modalities. *American Naturalist* **184**, E93–E100.

KYBA, C. C. M., TONG, K. P., BENNIE, J., BIRRIEL, I., BIRRIEL, J. J., COOL, A., DANIELSEN, A., DAVIES, T. W., DEN OUTER, P. N., EDWARDS, W., EHLERT, R., FALCHI, F., FISCHER, J., GIACOMELLI, A., GIUBBILINI, F., et al. (2015). Worldwide variations in artificial skyglow. *Scientific Reports* **5**, 8409.

LAMBERT, M. R., BRANS, K. I., DES ROCHES, S., DONIHUE, C. M. & DIAMOND, S. E. (2020). Adaptive evolution in cities: progress and misconceptions. *Trends in Ecology and Evolution* **36**, 239–257.

LAMPE, U., SCHMOLL, T., FRANZKE, A. & REINHOLD, K. (2012). Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. *Functional Ecology* **26**, 1348–1354.

LANDE, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences* **78**, 3721–3725.

LEARY, C. J. & BAUGH, A. T. (2020). Glucocorticoids, male sexual signals, and mate choice by females: implications for sexual selection. *General and Comparative Endocrinology* **288**, 113354.

LEHMANN, G. U. C. & LEHMANN, A. W. (2000). Spermatophore characteristics in bushcrickets vary with parasitism and remating interval. *Behavioral Ecology and Sociobiology* **47**, 393–399.

LEMMEN, J. & EVENDEN, M. (2015). Environmental conditions terminate reproductive diapause and influence pheromone perception in the long-lived moth *Caloptilia fraxinella*. *Physiological Entomology* **40**, 30–42.

LENDVAI, Á. Z., GIRAUDEAU, M., NÉMETH, J., BAKÓ, V. & McGRAW, K. J. (2013). Carotenoid-based plumage coloration reflects feather corticosterone levels in male house finches (*Haemorhous mexicanus*). *Behavioral Ecology and Sociobiology* **67**, 1817–1824.

LENGAGNE, T. (2008). Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation* **141**, 2023–2031.

LEWKIEWICZ, D. A. & ZUK, M. (2004). Latency to resume calling after disturbance in the field cricket, *Teleogryllus oceanicus*, corresponds to population-level differences in parasitism risk. *Behavioral Ecology and Sociobiology* **55**, 569–573.

LIMA, S. L. & DILL, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–640.

LIPKOWSKI, K., PLATH, M., KLAUS, S. & SOMMER-TREMBO, C. (2019). Population density affects male mate choosiness and morphology in the mate-guarding amphipod *Gammarus roeselii* (Crustacea: Amphipoda). *Biological Journal of the Linnean Society* **126**, 899–911.

LIU, A., GOONETILLEKE, A. & EGODAWATTA, P. (2015). Urbanisation and Stormwater quality. In *Role of Rainfall and Catchment Characteristics on Urban Stormwater Quality* (eds A. LIU, A. GOONETILLEKE and P. EGODAWATTA), pp. 1–14. Springer, Singapore.

LOMBARD, E. (1911). Le signe de l'élévation de la voix. *Annales des Maladies de l'Oreille et du Larynx* **37**, 101–119.

LOURENÇO, A., ÁLVAREZ, D., WANG, I. J. & VELO-ANTÓN, G. (2017). Trapped within the city: integrating demography, time since isolation and population-specific traits to assess the genetic effects of urbanization. *Molecular Ecology* **26**, 1498–1514.

LÜPOLD, S., JIN, L. & LIAO, W. B. (2017). Population density and structure drive differential investment in pre-and postmating sexual traits in frogs. *Evolution* **71**, 1686–1699.

MAGURRAN, A. E. & NOWAK, M. A. (1991). Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, *Poecilia reticulata*. *Proceedings of the Royal Society B: Biological Sciences* **246**, 31–38.

MARKMAN, S., LEITNER, S., CATCHPOLE, C., BARNSLEY, S., MÜLLER, C. T., PASCOE, D. & BUCHANAN, K. L. (2008). Pollutants increase song complexity and the volume of the brain area HVC in a songbird. *PLoS One* **3**, e1674.

MARTIN, O. Y. & HOSKEN, D. J. (2003). The evolution of reproductive isolation through sexual conflict. *Nature* **423**, 979–982.

MARZLUFF, J. M. (2001). Worldwide urbanization and its effects on birds. In *Avian Ecology and Conservation in an Urbanizing World* (eds J. M. MARZLUFF, R. BOWMAN and R. DONNELLY), pp. 19–47. Springer, Boston.

MAYS, H. L. & HILL, G. E. (2004). Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution* **19**, 554–559.

McKINNEY, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**, 247–260.

McKINNEY, M. L. & LOCKWOOD, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453.

McMAHON, T. A., ROHR, J. R. & BERNAL, X. E. (2017). Light and noise pollution interact to disrupt interspecific interactions. *Ecology* **98**, 1290–1299.

MENNITT, D. J. & FRISTRUP, K. M. (2016). Influential factors and spatiotemporal patterns of environmental sound levels in the contiguous United States. *Noise Control Engineering Journal* **64**, 342–353.

MILINSKI, M. & BAKKER, T. C. M. (1990). Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**, 330–333.

MILLER, C. W. & SVENSSON, E. I. (2014). Sexual selection in complex environments. *Annual Review of Entomology* **59**, 427–445.

MØLLER, A. & JENNIONS, M. (2001). How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88**, 401–415.

MOORE, A. & WARING, C. P. (2001). The effects of a synthetic pyrethroid pesticide on some aspects of reproduction in Atlantic salmon (*Salmo salar* L.). *Aquatic Toxicology* **52**, 1–12.

MOORE, F. R., SHUKER, D. M. & DOUGHERTY, L. (2016). Stress and sexual signaling: a systematic review and meta-analysis. *Behavioral Ecology* **27**, 363–371.

MOUGEOT, F., MARTÍNEZ-PADILLA, J., WEBSTER, L. M. I., BLOUNT, J. D., PÉREZ-RODRÍGUEZ, L. & PIERTNEY, S. B. (2009). Honest sexual signalling mediated by parasite and testosterone effects on oxidative balance. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1093–1100.

MOZŪRAITIS, R. & BŪDA, V. (2006). Pheromone release behaviour in females of *Phyllonorycter junoniella* (Z.) (Lepidoptera, Gracillariidae) under constant and cycling temperatures. *Journal of Insect Behavior* **19**, 129–142.

MÜLLER, G. & WARD, P. I. (1995). Parasitism and heterozygosity influence the secondary sexual characters of the European minnow, *Phoxinus phoxinus* (L.) (Cyprinidae). *Ethology* **100**, 309–319.

MÜLLER, W., HEYLEN, D., EENS, M., RIVERA-GUTIERREZ, H. F. & GROOTHUIS, T. G. G. (2013). An experimental study on the causal relationships between (ecto-)parasites, testosterone and sexual signalling. *Behavioral Ecology and Sociobiology* **67**, 1791–1798.

MULVEY, M. & AHO, J. M. (1993). Parasitism and mate competition: liver flukes in white-tailed deer. *Oikos* **66**, 187.

MUÑOZ, M. I., GOUTTE, S., ELLERS, J. & HALFWERK, W. (2020). Environmental and morphological constraints interact to drive the evolution of communication signals in frogs. *Journal of Evolutionary Biology* **33**, 1749–1757.

MUNSHI-SOUTH, J. & RICHARDSON, J. L. (2020). Landscape genetic approaches to understanding movement and gene flow in cities. In *Urban Evolutionary Biology* (eds M. SZULKIN, J. MUNSHI-SOUTH and A. CHARMANTIER), pp. 54–73. Oxford University Press, Oxford.

MURRAY, M. H., SÁNCHEZ, C. A., BECKER, D. J., BYERS, K. A., WORSLEY-TONKS, K. E. L. & CRAFT, M. E. (2019). City sicker? A meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment* **17**, 575–583.

NARANGO, D. L. & RODEWALD, A. D. (2016). Urban-associated drivers of song variation along a rural-urban gradient. *Behavioral Ecology* **27**, 608–616.

NIEMELÄ, J., BREUSTE, J. H., GUNTENSPERGEN, G., McINTYRE, N. E., ELMQVIST, T. & JAMES, P. (eds) (2011). *Urban Ecology*. Oxford University Press, Oxford.

OKE, T. R. (1982). The energetic basis of the urban heat Island. *Quarterly Journal of the Royal Meteorological Society* **108**, 1–24.

ORCI, K. M., PETRÓCZKI, K. & BARTA, Z. (2016). Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*. *Animal Behaviour* **112**, 187–194.

ORO, D., GENOVART, M., TAVECCHIA, G., FOWLER, M. S. & MARTÍNEZ-ABRAÍN, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* **16**, 1501–1514.

OWENS, A. C. S. & LEWIS, S. M. (2018). The impact of artificial light at night on nocturnal insects: a review and synthesis. *Ecology and Evolution* **8**, 11337–11358.

PARK, D., HEMPLEMAN, S. C. & PROPPER, C. R. (2001). Endosulfan exposure disrupts pheromonal systems in the red-spotted newt: a mechanism for subtle effects of environmental chemicals. *Environmental Health Perspectives* **109**, 669–673.

PARK, D. & PROPPER, C. R. (2002). Endosulfan affects pheromone detection and glands in the male red-spotted newt, *Notophthalmus viridescens*. *Bulletin of Environmental Contamination and Toxicology* **69**, 609–616.

PARRIS, K. M., VELIK-LORD, M. & NORTH, J. M. A. (2009). Frogs call at a higher pitch in traffic noise. *Ecology and Society* **14**, 25.

PARTAN, S. & MARLER, P. (1999). Communication Goes Multimodal. *Science* **283**, 1272–1273.

PARTAN, S. R. (2017). Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Animal Behaviour* **124**, 325–337.

PEACH, W. J., MALLORD, J. W., OCKENDON, N., ORSMAN, C. J. & HAINES, W. G. (2015). Invertebrate prey availability limits reproductive success but not breeding population size in suburban house sparrows *Passer domesticus*. *Ibis* **157**, 601–613.

PFENNIG, K. S. & TINSLEY, R. C. (2002). Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *Journal of Evolutionary Biology* **15**, 399–406.

POHL, N. U., SLABBEKOORN, H., KLUMP, G. M. & LANGEMANN, U. (2009). Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. *Animal Behaviour* **78**, 1293–1300.

POMFRET, J. C. & KNELL, R. J. (2008). Crowding, sex ratio and horn evolution in a South African beetle community. *Proceedings of the Royal Society B: Biological Sciences* **275**, 315–321.

PUNZALAN, D., RODD, F. H. & ROWE, L. L. (2010). Temporally variable multivariate sexual selection on sexually dimorphic traits in a wild insect population. *American Naturalist* **175**, 401–414.

PYTTE, C. L., RUSCH, K. M. & FICKEN, M. S. (2003). Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*. *Animal Behaviour* **66**, 703–710.

RAND, A. S., BRIDAROLLI, M. E., DRIES, L. & RYAN, M. J. (1997). Light levels influence female choice in túngara frogs: predation risk assessment? *Copeia* **1997**, 447–450.

RANDA, L. A. & YUNGER, J. A. (2006). Carnivore occurrence along an urban-rural gradient: a landscape-level analysis. *Journal of Mammalogy* **87**, 1154–1164.

REICHARD, D. G., ATWELL, J. W., PANDIT, M. M., CARDOSO, G. C., PRICE, T. D. & KETTERSON, E. D. (2020). Urban birdsongs: higher minimum song frequency of an urban colonist persists in a common garden experiment. *Animal Behaviour* **170**, 33–41.

RIPMEESTER, E. A. P., KOK, J. S., VAN RIJSSEL, J. C. & SLABBEKOORN, H. (2010a). Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. *Behavioral Ecology and Sociobiology* **64**, 409–418.

RIPMEESTER, E. A. P., MULDER, M. & SLABBEKOORN, H. (2010b). Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behavioral Ecology* **21**, 876–883.

RITSCHARD, M. & BRUMM, H. (2012). Zebra finch song reflects current food availability. *Evolutionary Ecology* **26**, 801–812.

ROCHA, E. A. & FELLOWES, M. D. E. (2020). Urbanisation alters ecological interactions: ant mutualists increase and specialist insect predators decrease on an urban gradient. *Scientific Reports* **10**, 1–8.

RODEWALD, A. D. & GEHRT, S. D. (2014). Wildlife population dynamics in urban landscapes. In *Urban Wildlife* (eds R. A. MCCLEERY, C. E. MOORMAN and M. N. PETERSON), pp. 117–147. Springer, Boston.

RODEWALD, A. D. & KEARNS, L. J. (2011). Shifts in dominant nest predators along a rural-to-urban landscape gradient. *Condor* 113, 899–906.

RODEWALD, A. D., KEARNS, L. J. & SHUSTACK, D. P. (2011a). Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications* 21, 936–943.

RODEWALD, A. D., SHUSTACK, D. P. & JONES, T. M. (2011b). Dynamic selective environments and evolutionary traps in human-dominated landscapes. *Ecology* 92, 1781–1788.

ROESER-MUELLER, K., STROHM, E. & KALTENPOTH, M. (2010). Larval rearing temperature influences amount and composition of the marking pheromone of the male beewolf, *Philanthus triangulum*. *Journal of Insect Science* 10, 1–16.

RYAN, M. J. (1998). Sexual selection, receiver biases, and the evolution of sex differences. *Science* 281, 1999–2003.

RYAN, M. J. & CUMMINGS, M. E. (2013). Perceptual biases and mate choice. *Annual Review of Ecology, Evolution, and Systematics* 44, 437–459.

RYAN, M. J. & RAND, A. S. (1990). The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44, 305–314.

RYAN, M. J., TUTTLE, M. D. & RAND, A. S. (1982). Bat predation and sexual advertisement in a neotropical anuran. *The American Naturalist* 119, 136–139.

RYDER, T. B., FLEISCHER, R. C., SHRIVER, W. G. & MARRA, P. P. (2012). The ecological–evolutionary interplay: density-dependent sexual selection in a migratory songbird. *Ecology and Evolution* 2, 976–987.

SAARISTO, M., BRODIN, T., BALSHINE, S., BERTRAM, M. G., BROOKS, B. W., EHLMAN, S. M., MCCALLUM, E. S., SIH, A., SUNDIN, J., WONG, B. B. M. & ARNOLD, K. E. (2018). Direct and indirect effects of chemical contaminants on the behaviour, ecology and evolution of wildlife. *Proceedings of the Royal Society B: Biological Sciences* 285, 20181297.

SCHMIDT, C., DOMARATZKI, M., KINNUNEN, R. P., BOWMAN, J. & GARROWAY, C. J. (2020). Continent-wide effects of urbanization on bird and mammal genetic diversity. *Proceedings of the Royal Society B: Biological Sciences* 287, 20192497.

SCOTT, C. E., MCCANN, S. & ANDRADE, M. C. B. (2020). Black widows as plastic wallflowers: female choosiness increases with indicators of high mate availability in a natural population. *Scientific Reports* 10, 1–9.

SEPP, T., MCGRAW, K. J. & GIRAUDEAU, M. (2020). Urban sexual selection. In *Urban Evolutionary Biology* (eds M. SZULKIN, J. MUNSHI-SOUTH and A. CHARMANTIER), pp. 234–252. Oxford University Press, Oxford.

SERESS, G., BÓKONY, V., PIPOLY, I., SZÉP, T., NAGY, K. & LIKER, A. (2012). Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. *Journal of Avian Biology* 43, 403–414.

SHOCHAT, E., WARREN, P. S., FAETH, S. H., MCINTYRE, N. E. & HOPE, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution* 21, 186–191.

SIH, A. (1994). Predation risk and the evolutionary ecology of reproductive behaviour. *Journal of Fish Biology* 45, 111–130.

SIH, A. & KRUPA, J. J. (1992). Predation risk, food deprivation and non-random mating by size in the stream water strider, *Aquarius remigis*. *Behavioral Ecology and Sociobiology* 31, 51–56.

SLABBEKOORN, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour* 85, 1089–1099.

SLABBEKOORN, H. & DEN BOER-VISSER, A. (2006). Cities change the songs of birds. *Current Biology* 16, 2326–2331.

SLABBEKOORN, H., BOUTON, N., VAN OPZEELAND, I., COERS, A., TEN CATE, C. & POPPER, A. N. (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology and Evolution* 25, 419–427.

SLABBEKOORN, H. & PEET, M. (2003). Birds sing at a higher pitch in urban noise. *Nature* 424, 267.

SLABBEKOORN, H., YEH, P. & HUNT, K. (2007). Sound transmission and song divergence: a comparison of urban and forest acoustics. *The Condor* 109, 67–78.

SMIT, J. A. H., LONING, H., RYAN, M. J. & HALFWERK, W. (2019). Environmental constraints on size-dependent signaling affects mating and rival interactions. *Behavioral Ecology* 30, 724–732.

SMOTT, S., MONCZAK, A., MILLER, M. E. & MONTIE, E. W. (2018). Boat noise in an estuary soundscape–a potential risk on the acoustic communication and reproduction of soniferous fish in the May River, South Carolina. *Marine Pollution Bulletin* 133, 246–260.

SNELL-ROOD, E., COTHRAN, R., ESPESET, A., JEYASINGH, P., HOBBIE, S. & MOREHOUSE, N. I. (2015). Life-history evolution in the anthropocene: effects of increasing nutrients on traits and trade-offs. *Evolutionary Applications* 8, 635–649.

SOMERS, C. M. (2004). Reduction of particulate air pollution lowers the risk of heritable mutations in mice. *Science* 304, 1008–1010.

SORACE, A. & GUSTIN, M. (2009). Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning* 90, 111–118.

START, D., BARBOUR, M. A. & BONNER, C. (2020). Urbanization reshapes a food web. *Journal of Animal Ecology* 89, 808–816.

STIEBLER, I. B. & NARINS, P. M. (1990). Temperature-dependence of auditory nerve response properties in the frog. *Hearing Research* 46, 63–81.

SUHONEN, J., ILVONEN, S., DUNN, D. W., DUNN, J., HÄRMÄ, O., ILVONEN, J. J., KAUNISTO, K. M. & KRAMS, I. (2018). Parasitism affects variation in a male damselfly sexual ornament. *Ethology Ecology & Evolution* 30, 256–266.

SVENSSON, E. I. (2019). Eco-evolutionary dynamics of sexual selection and sexual conflict. *Functional Ecology* 33, 60–72.

SWADDLE, J. P. & PAGE, L. C. (2007). High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. *Animal Behaviour* 74, 363–368.

SYKES, B. E., HUTTON, P. & MCGRAW, K. J. (2020). Sex-specific relationships between urbanization, parasitism, and plumage coloration in house finches. *Current Zoology* 67, 237–244.

SYMES, L. B., RODRÍGUEZ, R. L. & HÖBEL, G. (2017). Beyond temperature coupling: effects of temperature on ectotherm signaling and mate choice and the implications for communication in multispecies assemblages. *Ecology and Evolution* 7, 5992–6002.

SZULKIN, M., MUNSHI-SOUTH, J. & CHARMANTIER, A. (eds) (2020). *Urban Evolutionary Biology*. Oxford University Press, Oxford.

TAM, B. Y., GOUGH, W. A. & MOHSIN, T. (2015). The impact of urbanization and the urban heat Island effect on day to day temperature variation. *Urban Climate* 12, 1–10.

TAN, W. H., TSAI, C. G., LIN, C. & LIN, Y. K. (2014). Urban canyon effect: storm drains enhance call characteristics of the Mientien tree frog. *Journal of Zoology* 294, 77–84.

TAPPERT, L., POKORNY, T., HOFFERBERTH, J. & RUTHER, J. (2017). Sublethal doses of imidacloprid disrupt sexual communication and host finding in a parasitoid wasp. *Scientific Reports* 7, 42756.

TAYLOR, R. C., KLEIN, B. A., STEIN, J. & RYAN, M. J. (2008). Faux frogs: multimodal signalling and the value of robotics in animal behaviour. *Animal Behaviour* 76, 1089–1097.

TINGHITELLA, R. M., BRODER, E. D., GALLAGHER, J. H., WIKLE, A. W. & ZONANA, D. M. (2021). Responses of intended and unintended receivers to a novel sexual signal suggest clandestine communication. *Nature Communications* 12, 797.

TOMKINS, J. L. & BROWN, G. S. (2004). Population density drives the local evolution of a threshold dimorphism. *Nature* 431, 1099–1103.

TRILLO, P. A., ATHANAS, K. A., GOLDHILL, D. H., HOKE, K. L. & FUNK, W. C. (2013). The influence of geographic heterogeneity in predation pressure on sexual signal divergence in an Amazonian frog species complex. *Journal of Evolutionary Biology* 26, 216–222.

TROÏANOWSKI, M., DUMET, A., CONDETTE, C., LENGAGNE, T. & MONDY, N. (2015). Traffic noise affects colouration but not calls in the European treefrog (*Hyla arborea*). *Behaviour* 152, 821–836.

TÜZÜN, N., OP DE BEECK, L. & STOKS, R. (2017). Sexual selection reinforces a higher flight endurance in urban damselflies. *Evolutionary Applications* 10, 694–703.

UNITED NATIONS, DEPARTMENT OF ECONOMIC AND SOCIAL AFFAIRS, P.D. (2018). The World's Cities in 2018 - Data Booklet (ST/ESA/SER.A/417).

VALLVERDÚ-COLL, N., ORTIZ-SANTALIESTRA, M. E., MOUGEOT, F., VIDAL, D. & MATEO, R. (2015). Sublethal Pb exposure produces season-dependent effects on immune response, oxidative balance and investment in carotenoid-based coloration in red-legged partridges. *Environmental Science & Technology* 49, 3839–3850.

VAN GEFFEN, K. G., GROOT, A. T., VAN GRUNSVEN, R. H. A., DONNERS, M., BERENDSE, F. & VEENENDAAL, E. M. (2015a). Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology* 40, 401–408.

VAN GEFFEN, K. G., VAN ECK, E., DE BOER, R. A., VAN GRUNSVEN, R. H., SALIS, L., BERENDSE, F. & VEENENDAAL, E. M. (2015b). Artificial light at night inhibits mating in a geometrid moth. *Insect Conservation and Diversity* 8, 282–287.

VARKEVISSER, J. M., SIMON, R., MENDOZA, E., HOW, M., VAN HIJLKEMA, I., JIN, R., LIANG, Q., SCHARFF, C., HALFWERK, W. H. & RIEBEL, K. (2021). Adding colour-realistic video images to audio playbacks increases stimulus engagement but does not enhance vocal learning in zebra finches. *Animal Cognition* 2021, 1–26.

VASCONCELOS, R. O., AMORIM, M. C. P. & LADICH, F. (2007). Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. *Journal of Experimental Biology* 210, 2104–2112.

VELILLA, E. & HALFWERK, W. (2019). Adjustments to facilitate communication in noisy environments. In *Encyclopedia of Animal Behavior* (ed. J. C. CHOE), pp. 598–605. Academic Press, Cambridge.

VERGARA, P., MOUGEOT, F., MARTÍNEZ-PADILLA, J., LECKIE, F. & REDPATH, S. M. (2012). The condition dependence of a secondary sexual trait is stronger under high parasite infection level. *Behavioral Ecology* 23, 502–511.

VINCZE, E., SERESS, G., LAGISZ, M., NAKAGAWA, S., DINGEMANSE, N. J. & SPRAU, P. (2017). Does urbanization affect predation of bird nests? A meta-analysis. *Frontiers in Ecology and Evolution* 5, 1–12.

WAGNER, W. E. & HOBACK, W. W. (1999). Nutritional effects on male calling behaviour in the variable field cricket. *Animal Behaviour* 57, 89–95.

WEI, H. Y. & DU, J. W. (2004). Sublethal effects of larval treatment with deltamethrin on moth sex pheromone communication system of the Asian corn borer, *Ostrinia furnacalis*. *Pesticide Biochemistry and Physiology* **80**, 12–20.

WEST-EBERHARD, M. J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**, 155–183.

WEST-EBERHARD, M. J. (2014). Darwin's forgotten idea: the social essence of sexual selection. *Neuroscience and Biobehavioral Reviews* **46**, 501–508.

WIENS, J. J. & TUSCHHOFF, E. (2020). Songs versus colours versus horns: what explains the diversity of sexually selected traits? *Biological Reviews* **95**, 847–864.

WILEY, R. H. (1983). The evolution of communication: information and manipulation. In *Animal Behaviour, Vol. 2, Communication* (eds T. R. HALLIDAY and P. J. B. SLATER), pp. 156–189. Blackwell Scientific Publications, Oxford.

WILEY, R. H. & RICHARDS, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* **3**, 69–94.

WILLIS, P. M., RYAN, M. J. & ROSENTHAL, G. G. (2011). Encounter rates with conspecific males influence female mate choice in a naturally hybridizing fish. *Behavioral Ecology* **22**, 1234–1240.

WOOD, W. E. & YEZERINAC, S. M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* **123**, 650–659.

XU, L., GRANGER, C., DONG, H., MAO, Y., DUAN, S., LI, J. & QIANG, Z. (2020). Occurrences of 29 pesticides in the Huangpu River, China: highest ecological risk identified in Shanghai metropolitan area. *Chemosphere* **251**, 126411.

YAUK, C. L., FOX, G. A., MCCARRY, B. E. & QUINN, J. S. (2000). Induced minisatellite germline mutations in herring gulls (*Larus argentatus*) living near steel mills. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis* **452**, 211–218.

YEH, P. J. (2004). Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution* **58**, 166–174.

ZAHAVI, A. & ZAHAVI, A. (1999). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford University Press, Oxford.

ZHOU, H., DU, J. & HUANG, Y. (2005). Effects of sublethal doses of malathion on responses to sex pheromones by male Asian corn borer moths, *Ostrinia furnacalis* (Guenée). *Journal of Chemical Ecology* **31**, 1645–1656.

ZUK, M. (1991). Sexual ornaments as animal signals. *Trends in Ecology and Evolution* **6**, 228–231.

ZUK, M. & KOLLURU, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology* **73**, 415–438.

VI. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Comprehensive overview of studies examining the potential impacts of urban-associated (abiotic or biotic) environmental conditions on sexual signalling.