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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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 & Girardeau, 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 (Gosler & 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 signalers ['Fisherman runaway' (Fisher, 1915, 1930; Lande, 1981; Kirkpatrick, 1982)]. The Fisherman model posited a runaway process in which signalers with certain extreme traits mate with receivers with matching preferences, leading to genetic coupling of trait and preference in their descendents. However, as this process can act independently of the environment, we must only exclude the Fisherman 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 signalers, 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 Moller & 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 signalers by evolving trait signals that match the sensory system of receivers, and are therefore preferred over other signalers (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 in 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
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 signalling, 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 & Slabbeekoom, 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 & Ladhich, 2007; Slabbeekoom 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.

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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 trend 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                                                                 | Increased pheromone production under urban light conditions                        | No                      | Sensory                    | Van Geffen et al. (2015b)         |
| Chemical    | Fish       | Fish               | Swordtail (Xiphophorus huchmani)                | 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. | No                      | Sensory                    | Fisher, Wong & Rosenhal (2006)    |
| Biotic      | Parasitism | Bird               | House finch (Haemorhous mexicanus)              | Visual Sender    | In rural males, larger canotenoid 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. | ?                      | Indicator                 | Sykes, Hutton & McGrav (2020)     |
| Predation   | Risk       | Amphibian          | Túngara frog (Engystoma tucidensis)             | 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)
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 flecta, 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.1.e). For example, in the túngara frog (Engystoma 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 signalers 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 matching 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 & Levinson, 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, Rodriguez & 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 (Možuraite & Buda, 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; Bati kian 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; Gruß 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). Pharmacological 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 Karraschia 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 (Tuzin, 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.2c).

(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 Geflen 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 (Vellila & 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, 2016). 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; Rischard & Brunn, 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, 2013). 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 & Shamle, 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 fulfill general energetic needs, they can fail to meet nutritional requirements imposed by reproduction (Seress et al., 2012; Peach et al., 2013). 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, Roed & Rowe, 2010; Bleu, Bessa-Gomes & Laloï, 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 moufflon (Ovis aries musimon) horns have been found to diminish in size with increasing population density (Pomfret & Knell, 2008; Kavčič et al., 2019). Male European earwigs (Forficula auricularia) from higher density populations, on the other hand, exhibit increased forceps 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.2a and II.2e.

Local population density and sex ratio can impact the production and transmission of sexual signals (Table S1), in particular in species in which the ontology 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., 2010a) 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 & Younger, 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., 2019a).

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 tree-frogs (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 tungara frog advertisement calls (Halfwerk et al., 2019a). 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 tubercles (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., 2003; 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 (Bruemm & 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 Villemerreuil 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 (Yank 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.

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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.