Sexual selection and mating systems under anthropogenic disturbance.

Ken A. Otter[1], Matthew W. Reudink[2], Jennifer Foote[3], Ann McKellar[4] & Nancy Flood[2].

1. **Natural Resources and Environmental Studies, University of Northern British Columbia**
2. **Department of Biological Sciences, Thompson Rivers University**
3. **Department of Biology, Algoma University**
4. **Canadian Wildlife Service, Environment and Climate Change Canada**

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Conservation plans often focus on habitat availability and quality, population sizes, and population interconnectivity, but include little or no consideration of the sensory ecology of the animals they are managing (Lim et al. 2008, Delhey & Peters 2016). Yet, how animals perceive the world around them influences all aspects of their life history. Among these is the need to find mates, which relies upon the ability of one sex ("choosers") to assess the suitability of potential mating partners; this in turn relies upon the ability to perceive and accurately process sexual signals displayed by the other sex ("courters") (Andersson 1994, Achorn & Rosenthal 2020). Sexual selection theory is predicated on the ability of choosers (typically females) to compare the displays of courters (typically males), using them, via intersexual selection to discriminate among available suitors. Such displays can convey accurate information on the relative condition or resource holding potential of courters (Maynard-Smith and Harper 2003), which may benefit choosers in their selection of social mates or sires. As a result, any anthropogenic disturbance that alters either the production of displays or the ability of receivers to perceive them has the potential to disrupt evolved life history traits.

Much of the work on anthropogenic impacts on signaling in birds has focused on noise pollution and its capacity to mask vocalizations (see Ortega 2012 and Slabbekoorn 2013 for recent reviews). As this is a focus of Chapter 8 (Communication), we will spend little time on that topic here. Rather, we will consider how anthropogenic effects might alter other aspects of acoustic and visual signals, such as measures of signaler condition embedded within their song output and/or appearance and its impact on the ability of both courters to signal, and choosers to assess, their quality. Because many visual and auditory signals in birds used in sexual displays are condition-dependent, the honesty of the signal is maintained by a tight link between the relative condition of the signaler and the level of trait expression. Given this linkage between sexual signals and individual condition, habitat quality can indirectly influence signal expression through its effect on the condition of individuals. Here, we review literature on changes in sexual signals and the impacts on reproduction in anthropogenically disturbed landscapes, and argue that these might reflect habitat-induced impacts on individual condition. Secondly, we consider the potential for anthropogenic disturbance to affect the settlement of individuals, which could disrupt communal display arenas (leks) and/or limit the number of signalers a receiver can assess as potential mates.

Sexual selection and condition-dependent signaling.

A fundamental tenet of sexual selection theory is that there is variation among courters in mating success. This could arise through intrasexual competition to secure resources that choosers desire (e.g. direct benefits, such as nesting sites and territorial resources) or through intersexual mate choice, whereby choosers directly assess courters based on the expression of secondary sexual traits (Achorn & Rosenthal 2020). While recent reviews are correct in that choosing a particular courter based on the level of expression of a trait is not conclusive proof of 'good genes' benefits (i.e. increased genetic fitness of offspring) (Achorn & Rosenthal 2020), this does not mean that the level of trait expression doesn't convey accurate information about the condition of the signaler (Maynard Smith & Harper 2003). In fact, many signals used in courting by male birds are known to tightly co-vary with the somatic condition and resource access of the signaler. Bird song is one such trait; it serves the dual function of territorial defense and mate attraction (Catchpole and Slater 2008) and many studies have been conducted on how males structure their signaling to interact with rivals during territorial disputes (Stoddard et al. 1992, Beecher et al. 1996, Todt and Naguib 2000, Foote et al. 2008). Female birds also appear to use condition-dependent aspects of male song in mate-choice decisions, such as song output (Kempenaers et al. 1992, Otter et al. 1997, Welling et al. 1997, Mennill et al. 2002 & 2003, Poesel et al. 2004) or the performance complexity of signals themselves (Podos 2001, Ballentine 2009, Logue et al. 2019). This suggests choosers are attempting to differentiate courters on some measure of individual condition, regardless of the final benefit choosers might derive. This, however, creates a conundrum – if choosers gain an advantage by basing decisions on differences in courter “quality” (either through direct or some form of indirect benefits), how does the chooser assess underlying “quality” of another individual? Grafen (1990) suggested that choosers cannot assess courter quality directly, but have to rely on assessing overt signals that honestly co-vary with courter condition. By the use of such signals, choosers can potentially assess other qualities that will benefit either themselves (resources available within the courter’s territory, e.g. Manica et al. 2014) or their offspring (heritable components of fitness, e.g. Kempenaers et al. 1997). A key determinant in this argument is that the traits used by choosers to discriminate between courters must honestly reflect the courters condition or ability to acquire/provide resources of interest to the chooser, and that only individuals in good condition can afford (metabolically) to have high trait expression.

Such a relationship has been shown for male song in birds. The link between male condition and song output, for example, has been well established. Song output correlates with several independent measures of condition, such as dominance rank (Otter et al. 1997), parental abilities (Welling et al. 1997), age or size (Murphy et al. 2008), survival (Welling et al. 1997) and parasite loads (Møller 1991, Bischoff et al. 2009). Further, numerous studies have documented the relationship between food availability (Alatalo et al. 1990, Cuthill & Macdonald 1990, Lucas et al. 1999, Thomas 1999, Grava et al. 2009) or somatic condition (Godfrey & Bryant 2001) and these same metrics of song, establishing the link between song production and honest signaling.

Song is only one signaling modality through which male birds can provide information on their relative quality: birds also signal quality with visual signals including plumage colouration. As with song, the literature linking visual signals with male condition is extensive. One of the species in which this link has been most studied is the house finch (*Haemorhous mexicanus*). Male finches express carotenoid-based red plumage that varies with condition, and females are known to have strong preferences for certain types of males (Hill et al. 1999, Hill 2002). As carotenoids are acquired in the diet, rather than synthesized by the body (in contrast to melanin-based pigments; see below), expression of these traits in males may be more likely to convey honest signals about a male’s condition or ability to acquire resources (Hill 1995). Ample evidence shows the link between condition and trait expression in this species, with reduced expression associated with decreased condition (parasite load; Thompson et al. 1997), and increased expression associated with increased nutritional access or physical condition (Hill & Montgomerie 1994, Hill 2000). Similarly, the intensity of yellow carotenoid-based belly colouration in great tits (*Parus major*) was negatively associated with parasite load (Dufva & Allander 1995). A recent meta-analysis, however, demonstrates that though the general pattern of links between plumage coloration and quality exists, the honesty of carotenoid-based signaling is strongest for converted carotenoids (e.g., reds, oranges) rather than dietary carotenoids that do not undergo metabolic conversion (Weaver et al. 2018). In addition, the mechanism(s) maintaining signal honesty remain unclear and hotly debated (Garrat & Brooks 2012; Weaver et al. 2017).

Regardless of the mechanisms underlying signal honesty, the relationship between coloration and individual quality/condition is not restricted to carotenoid-based pigments. The blue and iridescent plumages created by structural layers of melanin in feathers (structural colours) are also condition-dependent (Keyser & Hill 1999, Siefferman & Hill 2003, Shawkey & Hill 2006, White 2020) and this expression can influence female choice (Siefferman & Hill 2005; Hill 2006). Similarly, melanin-based plumage, which is synthesized *de novo* rather than acquired from the diet, had long been considered a poor candidate for condition-dependence due to its high heritability and relatively low environmental influence. However, more recent work and comparative studies have revealed compelling evidence for the condition-dependence of melanin-based plumage (Guindre-Parker & Love 2013; Roulin 2015).

Interconnection between habitat quality, individual condition and signal expression.

Sexually-selected traits often evolved to be effective signals *because* of their dependence on the individual condition of the signalers that express them (Maynard-Smith and Harper 2003). Assessment of an individual on the basis of traits that cannot be easily faked (because the cost associated with expressing the trait at a particular level is higher for a low-quality than high-quality individual), is a central tenet of honest signaling theory. As a result, we would predict that any environmental influences that affect individual condition, such as habitat quality, also have the potential to impair or elevate the expression of the traits (Hill 1996, Godfrey 2003) and the ability of choosers to use them in assessment (Otter & Ratcliffe 2005). Thus, anthropogenic disturbance has the potential to disrupt evolved mating systems. Establishing a link between habitat quality, individual condition, and ultimately trait expression is the first step in this process.

The link between individual condition and habitat quality has been extensively considered in relation to intraspecific breeding success, with extensive work in Europe comparing populations of blue tits and great tits settling in evergreen vs deciduous oak forests (see Otter et al. 2007a for review). Deciduous oak forests have a greater proportion of their leaves replaced annually, which leads to higher abundance of caterpillar larvae in these forests – the primary prey used by tits to feed young (Blondel and Dias 1994). By comparison, evergreen oak forests found on the island of Corsica have lower prey availability, and birds in these forests tend to have lower clutch sizes and are in poorer physical condition (Blondel et al. 1993; Blondel et al. 1998; Lambrechts et al. 2004). Black-capped chickadees (*Poecile atricapillus*) occupying forests of similar composition but varying in age (mature forests vs young forests) in western Canada showed similar habitat-based effects on reproduction and condition (Otter et al. 2007a). Compared to their mature forest counterparts, chickadees in young forests have higher nest abandonment rates, which result in lower fledging success (Fort & Otter 2004a); in addition, males in young forests have poorer body condition (van Oort et al. 2007). This may be related to variation in relative food availability, which appears to differ between the two habitat types. Female chickadees solicit food from males during the egg-laying period with a particular call (*broken dees*). Otter et al. (2007b) used supplemental feeding studies to show that call rates were positively associated with relative hunger levels, and that females in young forests called at higher rates than those in mature forests. Combined, these studies suggest that variation in habitat quality can greatly impact individual condition and reproductive success; but does it also affect the expression of sexually-selected signals?

Studies of chickadee song would imply that it does. Song output during the dawn chorus appears to be an honest signal of condition in male chickadees, with dominant males having higher song output than their subordinate flockmates (Otter et al. 1997). Supplemental feeding studies show that this metric of song output is directly related to relative food availability (Grava et al. 2009). Females in this species have been shown to use singing behavior directly in mate choice decisions (Mennill et al. 2002 & 2003). However, van Oort et al. (2006) found that dominant males occupying young forests (low-quality habitats) had reduced song output during the dawn chorus than their counterparts in mature forests (high-quality habitats); dominant males in young forests sang at similar rates to subordinate males. This reduction of song output in otherwise dominant males would potentially put them at a disadvantage in a mating system where neighbouring females are assessing both social mates (Otter & Ratcliffe 1995, Ramsay et al. 2000) and extra-pair partners (Otter et al. 1997, Mennill et al. 2002 & 2003) based on perceived male rank, which females are partially assessing through song performance. Further, male chickadees appear to not only signal relative condition through song output, but also with how consistent successive songs are in internal frequency ratios within and between notes (Christie et al. 2004). Grava et al. (2012) found that male chickadees occupying young forest, regardless of social rank, were less able to maintain this internal consistency in their songs than were mature-forest males. Playback studies using stimuli of dominant male songs recorded in either young or mature forest further showed that mature-forest stimuli were perceived as a greater threat than young-forest stimuli, regardless of the fact that the males from which these songs were recorded were of equivalent, relative social rank. These studies strongly suggest that in this system, habitat can influence both the expression of sexually-selected traits, and how the individuals that express these are perceived by others (Grava et al. 2013).

A similar relationship between habitat quality and individual condition, and the effects these might have on female perception of relative male quality, can be found in visual signals of plumage. In an interesting early study in this area, Gustafsson et al. (1995) manipulated parental effort of collared flycatchers (*Ficedula albicollis*) by increasing or decreasing clutch size. This resulted in reduced food per nestling at enlarged nests, mimicking a poor-quality environment, but increased food per nestling at reduced nests, mimicking a higher-quality habitat. The following year, juvenile males reared in enlarged nests had smaller forehead patches (a sexually-selected plumage signal in the species - Sheldon & Ellegren 1999) compared with males reared in reduced nests. This suggests a direct link between food availability experienced as nestlings and development of secondary sexual characters. Similar links between habitat quality and expression of plumage signals occur in carotenoid-dependent plumage traits. Hill (1993) found that the extent of red plumage in house finches varied among populations, but this was not due to genetic differences between regions--birds from the different populations converged on similar plumage expression when brought into aviaries and fed on an overlapping diet. This suggests that variation in plumage colour was likely due to environmental differences in accessibility to carotenoids in the diet. These studies suggest that relationships between individual condition and expression of sexually-selected traits can be influenced by the linkage between individual condition and habitat quality. In poor-quality habitat, the ability of signalers to express condition-dependent traits may be so generally depressed that these traits no longer allow discrimination amongst individuals, even if there are underlying differences in individual signaler quality. As a result, choosers in lower-quality habitats may be less able to discriminate among available courters. This could result, at best, in the loss or relaxation of mate choice decisions in these habitats or, at worst, in maladaptive decisions. The above studies have focused on variation in condition/signal expression in habitats that are still largely natural. However, anthropogenic disturbances and their effects on habitat quality might exacerbate these effects.

Anthropogenic influences on signal expression and condition.

There are two ways that we envision anthropogenic disturbance might affect sexually selected signals; 1) it may affect the signaling environment, resulting in altered signal transmission; or 2) it may impact the condition of the signalers and so alter their ability to fully express the signals. Transmission issues in acoustic signals have been heavily studied in relation to noise pollution (for additional detail see Chapter 8). We will focus on anthropogenic disturbances on acoustic and visual signals and how these disturbances may impact the ability to fully express secondary sexual characters.

Light environment and visual signals

Delhey & Peters (2016) make a strong case that alteration of habitats may impact the light environments in which signals evolved. This occurs either through altering the vegetative structure of the environment or via the introduction of artificial light that differs in emphasized wavelengths from natural light. Much of the work in this field has focused on alterations of aquatic environments and the consequent impacts this has had on visual signaling in fish. However, similar impacts may be seen in birds. Endler & Théry (1996) found that Cock-of-the-Rock males prefer to display in forest patches that have sunlight beams breaking through the canopy, particularly when display perches allow them to move in and out of light beams that emphasize their bright orange feathers. Although other studies on lekking manakin species have found less evidence for the generality of this filtered-light effect (Anciães & Prum 2008), it may still influence locations of leks in some species, particularly those with greater emphasis on long-wavelength orange/red signals, like Cock-of-the-Rocks, compared to the blue-black plumage of many manakin species. Disruption to vegetation that alters the frequency/nature of these natural light gaps could in turn disrupt the suitability of the site for leks.

More generally, artificial light and air pollution have the potential to change the nature of light (Gaston et al. 2013), which in turn could alter the perception of colour. Much of the work in disruption of visual signaling in fish centers on alteration of the light environment, which in turn may alter colour perception in receivers (reviewed in Delhey & Peters 2016). Such alteration of the light environment can decrease the information content of visual cues to receivers and lead to increased interspecific matings and hybridization, as species-specific colour markers are lost. While this likely would not be the case in birds, which also rely upon species-specific auditory signals in recognition, disruption of perceived colours could easily occur through changes in light environments, but the relative importance of perceived color in promoting hybridization is unknown. Some artificial lights have restricted wavelengths, and can alter the perception of colour in plumage. This could decrease the reflectance of visual cues, including those presented by ultraviolet plumage, which are important in the sexual displays of some species (Bennett et al. 1997). Similarly, increased amounts of fine particles in the air, such as those arising from air pollution, can refract light and alter the perceived reflectance of plumage. This may even dampen perceived colour via simple accumulation of industrial grime on plumage (DuBay & Fuldner 2017). Griggio et al. (2011) exposed throat feathers from taxidermied starling specimens to atmospheric pollutants (dust/smoke, pollution etc) in one of the most polluted valleys in Italy and compared them to feathers kept in sealed plastic bags. The exposed feathers had significantly decreased transmission, particularly in the UV light range, over 3-6 weeks. Control (bagged) feathers had no such reduction in light transmission. Light transmittance continued to decrease over time, and was most strongly affected in the UV and shorter wavelengths, which correspond to known sexual signals in starling plumage (Bennett et al. 1998). Birds, however, are likely to use multiple signals in mate assessment (Otter & Ratcliffe 2006), and transmission of one signal may simply shift reliance onto other signals. Further, some forms of this kind of anthropogenic impact, such as accumulated grime on feathers, may even be mitigated by the birds themselves, by increased preening behavior (Griggio et al. 2011).

Urbanization and signalling

For most species, urban environments are generally considered poorer habitat than rural environments. A meta-analysis of studies comparing urban vs rural breeding populations of multiple species (Chamberlain et al. 2009) found a general pattern of earlier laying, but with smaller clutch sizes, reduced fledging success and smaller nestling mass in urban landscapes. Similar patterns continue to emerge, suggesting that many species considered “urban adapters” (Blair 1996) have lower productivity when breeding in urban environments (Bailly et al. 2015, Meyrier et al. 2017). There are multiple explanations for these types of patterns (Seress & Liker 2015, Isaksson 2018), but perhaps two of the best explored are the effects of altered food availability and industrial toxicity.

Winter food supplementation, as well as slightly warmer temperatures offered by the heat-island effect in cities, may explain advanced laying dates (Chamberlain et al. 2009, Seress & Liker 2015, Bailly et al. 2015), but the food types typically used in winter are not those used to feed nestlings; indeed, insect prey limitation may be one source of reduced nestling condition in cities (Chamberlain et al. 2009, Seress & Liker 2015, Bailly et al. 2015, Meyrier et al. 2017). A recent detailed study showed that the density of caterpillars, preferred for nestling provisioning, was lower in urban versus forested areas, and resulted in reduced nestling provisioning and survival in blue tits (Pollock et al. 2017). Further, supplementation of insect prey during nestling provisioning alleviated some of the negative effects on nestlings (Meyrier et al. 2017), pointing to resource availability as one of the major factors affecting differences in habitat quality in urban vs rural environments.

Additional consequences of living in highly industrialized landscapes is exposure to toxic chemicals. Eens et al. (1999) found that levels of heavy metals in the feathers of both blue and great tits were correlated with proximity to industrial pollution sources. Although neither Dauwe et al. (2006) or Snoeijs et al. (2004) found differences in the morphology or haematocrit levels of great tits relative to the source of pollution, Snoeijs et al. (2004) did find that humoral response to an immune challenge was highest among birds living farthest from contamination sites. This suggests that chemical pollutants may decrease the immunological condition of birds, and could exacerbate differences across habitats already created by differences in relative prey availability.

How, then, do these consequences of living in urban environments impact trait expression? Gorissen et al. (2004) found that great tits living near pollution sources had smaller repertoires and lower song output than those living farther from contaminates. Other work has shown that song structure and/or brain areas associated with song complexity are related to levels of specific pollutants including polychlorinated biphenyls (PCBs) (DeLeon et al. 2013), mercury (Hallinger et al. 2010; but see also Greene et al. 2018), and brominated flame retardants (Eng et al. 2018). Similarly, Geens et al. (2009) found that the chroma (purity of colour) and hue (colour) of carotenoid-based breast plumage was reduced in more polluted sites among both adults and nestlings. Perez et al (2010) concluded that contaminants found in oil pollution correlated with a reduction in the size of the sexually-selected, carotenoid-based red bill spot in gulls. Recently, Grunst et al. (2020) found similar effects, with UV chroma lower in birds closer to pollution sources, and carotenoid chroma lowest in birds settling closest to roads; in this study both the proximity to roads and the pollution source (smelter) were associated with higher heavy metal levels in feathers. There is also evidence of colour disruption in species with structural colouration; for example, mercury contamination affects plumage on belted kingfishers (White and Cristol 2014). In this case, the effect -- brightening of blue back feathers and dulling of white breast feathers-- may be due to interference by mercury in the melanin production pathway. Melanin organization is essential for the colouration of structural blue feathers (Shawkey & Hill 2006), and the chemical pathway for the body to produce melanin requires the activation of the enzyme tyrosinase to catalyze the reaction; tyrosinase is activated when the element copper (a co-factor to the enzyme) binds to tyrosinase. Because of its similarity in chemical structure, the element mercury can bind competitively to the activation site on tyrosinase instead of copper; mercury, though, does not activate tyrosinase and so the enzyme cannot catalyze its normal reaction when mercury binds to it, thus impairing the melanin production pathway. The result is that contaminants can disrupt the normal production of melanin, which in turn can disrupt the microstructure of the feathers, altering the scattering of white light and resulting in changes to the brightness and hues of feathers. It is currently untested how much these colours affect mate choice in kingfishers, but colour dimorphism between males and females may suggest the structural colours are sexually selected.

These changes in song and colours may point to toxin-induced differences in condition, but could also be compounded by general differences in prey availability in urban landscapes. Carotenoid-based plumage colouration relies on acquisition of these pigments through diet, and availability may be reduced in urban sites either through lower overall food availability or lower carotenoid-bearing food. Hõrak et al. (2000) found that great tits reared in urban sites had lower yellow carotenoid levels in breast feathers than those in rural nests. Moreover, while rural nestlings transplanted to urban nests showed a reduction in feather colour compared to their siblings reared in the original home nest, the reciprocal was not the case--urban birds transplanted to rural nests remained similarly depressed in expressing yellow plumage as their non-transplanted siblings. Biard et al (2017) studied the colour of nestling great tits in two rural and two urban locations in France. While the brightness of nestlings' yellow feathers did not vary between the types of sites, chroma was significantly higher in woodlands; Biard et al. suggested that this was due a reduced ability on the part of parents to deposit carotenoids in eggs and/or feed chicks carotenoid rich food in urban environments. Similarly, Giraudeau et al. (2018) measured carotenoid based plumage in house finches at multiple sites that differed in a continuum from urban center to desert in Arizona. Males were reddest and heaviest in the less industrialized sites. These findings suggest that birds may be in poorer overall condition in urban areas, and this is expressed in their plumage. This effect is sufficiently widespread that some have suggested using trait expression as a proxy for assessing the relative quality of different habitats (Hill 1995, Godfrey 2003). However, as with most aspects of urbanization studies, there may be subtleties to such generalizations.

Some species may benefit from resources available in urban environments; for example, abundance of carotenoid-containing berry bushes may increase with ornamental plants in suburban landscapes (Jones et al.

2010). The red plumage of northern cardinals (*Cardinalis cardinalis*) is tightly correlated with body condition, but while city birds had overall duller plumages, the relationship between condition and trait expression was depressed (Jones et al. 2010). This suggests that general availability of carotenoid-bearing plants may allow males in poorer condition to express traits at similar levels to those in better condition, making the signal less reliable in urban areas. Indeed, Rodewald & Arcese (2017) found female selection pressure seemed to be relaxed in urban habitats, likely due to greater homogeneity among males/territories in such environments. Similarly, some urban populations of house finches may not be as greatly hampered by the overall pattern of reduced carotenoids in plumage as others. Giraudeau et al. (2018) tested females from three populations for preferences for male colours. They used carotenoid diet-deprived males, who were artificially coloured with marker pens to manipulate colour independent of male condition; females from two of the three populations tested preferred the reddest males, even if males in their population were not on average this red. One population of females, however, preferred yellower males; interestingly, males in their population were much yellower on average. This indicates that sexually preferred traits may also shift in some habitats, depending on what females' experience. This adaptation, however, would require low levels of gene flow among populations.

Such restricted movement and differential selection within different environments has been suggested in house finches, where Badyaev et al. (2008) compared the bill morphology of desert-dwelling vs urban-dwelling house finches, finding that harder seeds in urban sites appear to select for larger bills. However, larger bills can also constrain the motor ability of birds to sing rapidly while simultaneously spanning broad frequency bandwidths (Podos 2001), which is considered a performance constraint upon which female birds may assess males (Ballentine 2009, Logue et al. 2019). Indeed, Badyaev et al. (2008) also found that urban birds had slower trill rates and fewer notes in their songs than rural birds. This could be viewed as compromised song performance. This examination of change in song structure was coupled with genetic analysis that showed high differentiation between the urban and rural populations, suggesting reproductive isolation may be occurring and allowing divergence. Job et al. (2016) found a similar compromise associated with urban song; house wrens in more urban habitats reduced the overall frequency bandwidth of their songs in response to urban noise, but did not correspondingly increase their trill rates. This could lower perception of the urban male's song performance relative to rural males. Indeed, when noise broadcasts were played to unpaired vs paired male house wrens, paired males shifted their songs up to a higher, but narrower, frequency bandwidth to compensate. Unpaired males did not shift their songs, suggesting that unpaired males may be constrained to sing songs preferred by females even if these may have reduced transmission (Grabarczyk et al. 2018). Similar changes in song structure in cardinals (Narango & Rodewald 2018) and white-crowned sparrows (Luther et al. 2016, Derryberry et al. 2016) suggest that attempting to compensate for urban noise may compromise perceived song performance. In contrast, male European starlings exposed to endocrine disrupting chemicals (EDCs) had enlarged HVC volumes (*High Vocal Center*; a brain region associated with song complexity), and longer and more complex songs, which were preferred by females (Markman et al. 2008). However, exposure to EDCs also caused reduced immune response in these males. Thus, exposure to pollutants in this case made a sexually selected signal of male quality less honest, which could have population-level consequences if mating with immunocompromised males decreased female fitness.

As mentioned previously, nutrition is another contributor to singing performance, particularly to song rates or output over extended periods. As urban areas are typically associated with lower food availability, one might expect reduced song output in urban vs rural settling birds. However, this has not necessarily been the case. Kempenaers et al. (2010) reported higher song output rates of male blue tits living in close proximity to artificial light sources. While they equate this to the direct impact of light inducing increased dawn singing, our own studies have found that when controlling for the dominance ranks of male chickadees, males singing near street lamps begin chorusing earlier, but do not sing for longer or at higher rates (K.A. Otter, unpublished data). This suggests that light pollution is more likely to clock-shift the chorus than it is to increase overall song output, the latter of which may instead be more limited by food availability. Blue tits that sing near street lights are also likely to be in closer proximity to artificial food sources, which may not only advance breeding in urban-dwelling birds, but could also influence the relative condition of males early in the breeding season when song output is typically highest. In our own studies on mountain chickadees, we found an increased song output during the early-season dawn chorus in urban vs rural birds; this was not only associated with singing earlier, but also with singing for longer and at higher rates of songs/minute (Marini et al. 2017a). In this context, the song output of urban-dwelling males may help compensate for potential differences in other sexual signals (e.g., plumage), and allow some degree of phenotypic plasticity for mate choice decisions among birds settling in urban landscapes. Despite being considered a habitat specialist, mountain chickadees breeding in urban sites have comparable fledging rates and nestling growth rates to those characteristic of rural birds (Marini et al. 2017b), suggesting that it is possible to adjust to some of the challenges of urban living.

An interesting facet of anthropogenic impacts on signaling is that living in proximity to humans may facilitate aspects of signals that do not occur in more natural settings. Various bird species make use of anthropogenic features in their signals, including the many vocal mimics that incorporate car alarms and other city sounds into their repertoires (Marx 2018). For species where the diversity of sounds produced is under directional sexual selection, the addition of novel stimuli to integrate into their repertoire may enhance attractiveness as a potential mate. Similarly, the extended phenotype that males of some species use to attract females can also be affected by humans. For example, male bower birds decorate with both natural and artificial objects (e.g. bits of glass and plastic) collected from their environments, the colour of the materials selected varying by species (Marshall 1954). Satin bowerbirds (*Ptilonorhynchus violaceus*) prefer blue. The number of blue objects in a bower is positively related to female visitation rate, while the availability of such objects in the environment is negatively related to theft of decorations by other males (Hunter and Dwyer 1997). Rosenthal and Stuart-Fox (2012) note that if human disturbance greatly increased availability of blue objects in the environment, this might reduce variation among males in their ability to collect suitable decorations, compromising the reliability of this as an honest signal and leading to reduced sexual selection on this trait. In contrast, integration of human-made items into displays may enhance perception of quality in other species; black kites (*Milvus migrans*), which use nest decoration as an honest signal of territory quality and social status, preferentially collect white, especially artificial (e.g., plastic) objects. Birds with more of these objects in their nests are in better condition, and although they suffer from fewer territorial intrusions, birds with more decorations were more successful at repelling intruders than birds with few decorations (Sergio et al. 2011). This stresses the complexity of determining whether anthropogenic disturbance will enhance or detract from the perceived signal value of traits, as this is highly context-dependent and specific to how the life-history of individual species interacts with the changes associated with anthropogenic disturbance.

Disruption to reproduction and mating systems from anthropogenic disturbance

The expression-level of signals may be impacted by anthropogenic disturbance, but this is only one aspect of signal assessment in sexual selection. Any land change that impacts density and spacing of birds may also disrupt mate choice. For choosers, the ability to directly compare the quality of potential mates is an important feature of most mating systems, but is perhaps most acute in lek-based mating systems. Changes in habitat quality due to anthropogenic disturbance, including oil and gas or wind development, forestry and agricultural practices, and urban development, can influence the spacing of leks and the density of lek attendants (Blickley et al. 2012, Hess & Beck 2012, Kouffeld et al. 2013, Hovik et al. 2015, Winder et al. 2015). While these effects are often considered from a population monitoring standpoint, their impact on mating systems is often overlooked, despite mating systems and mate choice being clearly linked to density (reviewed by Kokko and Rankin 2006). In lek-based mating systems, reproductive success is often limited to one or several males (e.g. Kokko et al. 1998), which provide females with only indirect benefits (Petrie 1994). Females visit leks to assess males, mating with males that have the best visual displays or plumage traits (Petrie et al. 1991, Petrie 1994) and in some cases, females are more likely to visit (and mate at) larger leks (reviewed in Hutchison 2005). When density is reduced due to anthropogenic disturbance, how does this influence male mating skew in leks and the intensity of sexual selection? Models suggest that as the availability of mates declines, so too may female selectivity, and indiscriminate mating may result (Kokko & Rankin 2006). However, it is also possible that mate choice errors may be reduced at lower density; for example, the frequency of “spillover copulations” that occur when less suitable males crowd near dominant males in a lek may be lower at lower densities (Rintamaki et al. 1995, Johnstone and Earn 1999; Hutchison 2005). At very low density, selection could be relaxed leading to the reduction of ornaments (Kokko and Rankin 2006). Thus, the impacts of land change on lek mating systems is difficult to predict a priori, and requires study of the specific system under investigation.

In territorial species with social monogamy, anthropogenic changes to habitat can also influence density and, as a consequence, sexual selection through both primary mate choice and extra-pair mate choice (Westneat & Sherman 1997; Petrie & Kempenaers 1998). For example, in gray catbirds (*Dumatella carolinensis*), eastern bluebirds (*Sialia sialis*), blue tits, American redstarts (*Setophaga ruticilla*) and reed buntings (*Emberiza schoeniclus*), rates of extra-pair paternity were higher at higher breeding densities (Charmantier & Perret 2004; Stewart et al. 2009; Ryder et al. 2012; Mayer and Pasinelli 2013; McKellar et al. 2014). In tree swallows, an interaction between density and colouration on determining extra-pair mating success suggests that successful males had different colour attributes when they occurred in either high vs low density (Van Wijk et al. 2016). In addition to altering breeding density, variation in habitat quality can also affect territorial behavior; Fort & Otter (2004b) found chickadees that occupy young forest (lower-quality habitat) had much greater territorial overlap and lower levels of defense of territorial boundaries than males in mature forests (high-quality habitats). Could this in turn suggest there are higher opportunities for extra-pair copulations (EPCs) in such habitats due to increased contact rates between non-mated males and females? Where anthropogenic alteration of the landscape influences breeding density or intersexual contact rates, there may be potential for changing the strength and direction of, or opportunity for, sexual selection.

There are few studies that have directly compared mating tactics, such as extra-pair paternity rates, between urban and rural populations within the same species. However, the few that have find contrasting patterns among the different species tested. In some species, urbanization may increase mating opportunities due to increased resources and/or breeding density. Urban Cooper’s Hawks (*Accipiter cooperi*) had high rates of extra-pair young in nests (19.3%) compared to the low rates typically found in raptors (0-11%) (Rosenfeld et al. 2015). Rosenfeld et al. suggest that because Coopers hawks tend to copulate when the male returns with food during pre-nesting, that females might accept or solicit EPCs from other males in this food-rich, high breeding-density setting. Smith et al. (2016) found higher extra-pair paternity rates among Spotted Towhee (*Piilo maculatus*) nests on the edges of urban parks; the authors proposed that anthropogenic food sources available near these edge habitats may attract individuals, increasing encounter rates between females and potential extra-pair sires. Blue tits in areas lit by artificial street lights (which may also have been closer to urban food sources) experience elevated success in extra-pair matings (Kempenaers et al. 2010). However, other studies have found little evidence that paternity is disrupted in anthropogenic habitats. Bonderud et al. (2018) found no difference in extra-pair paternity rates between urban and rural nesting mountain chickadees. Similarly, despite urban populations having higher nesting densities, Rodriguez-Martínez et al. (2014) did not find this affected either the extra-pair paternity rates or intra-specific brood parasitism rates of burrowing owls (*Athene cunicularia*). Perhaps the differences in the studies above reflect how disturbance affects the habitat quality as perceived by different species. If anthropogenic disturbance provides increased resource availability and alters condition-dependent signaling, it may affect not only density but the propensity of females to assess males worthy of extra-pair matings. In other species, anthropogenic landscapes do not appear to promote these alternate mating tactics. It is interesting to note that, despite limited research on the topic, none of the species studied experienced reduced extra-pair behavior in urban areas. This is an area of research that is worthy of further investigation.

Finally, it is also possible that divergent sexual selection due to urbanization could facilitate speciation events, although there is a dearth of research on the subject. Most relevant is a study on dark-eyed juncos (*Junco hyemalis*), which found a decrease in the amount of white in tail feathers - a sexually selected signaling trait - in a recently established urban population compared to nonurban populations (Yeh 2004). Changes in tail white were suggested to be caused by an increase in length of the breeding season in the urban environment (Price et al. 2008). Such a divergence could potentially contribute to premating isolation between urban and nonurban populations, but more research is needed into this subject (Thompson et al. 2016).

Recommendations for Management.

Making general recommendations for management of anthropogenic disruption to sexual selection is difficult. Unlike noise pollution, which has a somewhat general masking impact on organisms that signal within a particular band-width, how the expression of sexually selected signals is impacted by anthropogenic disturbance is somewhat dependent on how disturbance affects the quality of the habitat as it is experienced by the birds. If disturbance reduces food availability, as appears to be the case with many insectivorous species occupying urban habitats, there may be reduced capacity for courters to produce condition-dependent signals and this could reduce the quality of mating displays. This in turn can disrupt mate choice, and lead to overall reductions in mating success. Supplemental provisioning of food may alleviate some of these impacts, but typical supplementation via seed feeders could have undesired effects. For example, song sparrow (*Melospiza melodia*) pairs that were provided with extra food produced sons with repertoires that were smaller than those of their fathers and smaller than those of unfed pairs nesting in the same area, due to fed pairs producing more, but smaller, offspring (Zanette et al. 2009). Winter feeding may elevate male condition and increase condition-dependent signalling early in the season, but it may also fail to provide resources necessary for successful nestling provisioning later in the season, leaving urban landscapes as potential ecological traps (Schlaepfer et al. 2002). Perhaps a better long-term strategy for creating positive urban landscapes is to increase the density of deciduous trees that provide foraging habitat, but we recommend these plans focus on tree species typical of the region rather than non-native ornamentals. Retention or restoration of insect-producing shrub/grasslands (again focusing on native vegetation) may also supplement food supplies, particularly for edge-associated or grassland species occupying urban landscapes. Carotenoid-rich exotics can result in courters expressing elevated signals in urban landscapes, but which do not necessarily reflect the courter's true condition or the suitability of their territory for breeding (Rodewald et al. 2011). However, urban landscapes can also result in depressed expression of carotenoid-dependent plumage in other species, so even increasing green spaces containing natural food sources within cities may only partially alleviate negative impacts. Reducing pollution (e.g. particulates) and toxin exposure may not only increase individual condition, but may also help alleviate the impact these have on obscuring light transmission or soiling plumage. Thus, the best means of creating urban environments that allow for evolved systems of sexual selection is to simply focus on making our urban landscapes as naturalistic as possible.

A recent study has highlighted the potential that altering our landscapes to alleviate pressures on sexual signaling can have, as well as the resilience of birds to respond to such changes. Derryberry et al. (2020) recorded white-crowned sparrows in the reduced noise-scapes of San Francisco during the COVID-19 shutdown. The reduction in traffic during spring 2020 shutdowns resulted in a reduction to noise levels not seen since the 1950s. This not only made birds more audible, but males responded to the noise relief by decreasing the minimum frequencies of the trills at the end of their songs. The result was that the terminal trills of males had broader bandwidths in urban areas than they had had pre-COVID lockdown. As noted previously, performing rapid trills with broad bandwidth is considered a performance constraint on song (Ballentine 2009, Logue et al. 2019). Previous studies on this species (Luther et al. 2016) suggested that urban males constrained to produce lower bandwidths to avoid being masked by noise pollution may have potentially compromised signals, as perceived by choosing females. Derryberry et al. (2020) showed that within a single year, the alleviation of this masking noise pollution resulted in urban males producing songs with lower minimum frequencies and larger bandwidths than males in these same areas in preceding years. More importantly, the songs of urban males in 2020 also did not differ from those of rural males in the years both preceding and during COVID. This suggests that urban planning that reduces noise (or other impediments to signaling), could result in rapid rebound effects.

Even if noise and other sources of pollution addressed, the variability in spacing of birds in urban areas relative to wild spaces may impact mating systems. Low densities and irregular inter-individual spacing could decrease the ability of choosers to assess the signals of multiple courters, thus decreasing discriminate mate choice. However, concentrated settlement into small patches of suitable, available habitat may have the alternate effect of promoting increased density for some species, and make assessment of multiple courters easier. The ideal solution may be to plan cities with retention of sufficient native vegetation to create regular and even settlement of species, rather than either clumped or scattered settlement. Even if the settlement densities are lower than native habitat, even spacing may allow better opportunities for maintaining signal transmission and assessment in a network-like fashion than either clumping or scattering populations. This in turn may alter mating tactics, such as the rate of extra-pair matings. Thus, understanding how urbanization impacts urban-settling species will require research into how changes to urban landscapes interact with individual species' life history traits, and whether this allows them to adjust to the challenges of city life. This is what makes this field interesting.

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