Are signals of aggressive intent less reliable in urban habitats?

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Abstract

The effect of urban noise on animal communication systems is one of the best examples of how anthropogenic change affects animal social behaviour. It is well documented that urban noise drives shifts in the acoustic properties of signals but the consequences of noise for the reliability of signals – that is, how well they predict signaler behaviour, is unclear. Here we examine whether reliability of aggressive signaling in song sparrows (*Melospiza melodia*) differs between urban and rural habitats. Previous research in this species showed that urban males are more aggressive than rural males. We predicted that the main signal of aggressive intent, low-amplitude soft songs, would be less effective in urban noise and that urban birds should signal their aggressive intent via loud songs. We found that while acoustic noise was higher in urban habitats, the urban birds still sang more soft songs and rural birds. Furthermore, high rates of soft songs and lack of loud songs predicted attacks in both habitats. Finally, we found evidence for a potential but incomplete multimodal shift due to urban noise. These results indicate that urbanization, despite the well documented effects on signal structure has a limited effect on the reliability of the signals in song sparrows.

Keywords: anthropogenic change, bird song, noise, honest signaling, song sparrow, aggression

Introduction

Evolution of honesty in animal communication has been a major interest in the study of animal behaviour (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005). At the crux of the issue is the fact that when individuals with conflicting interests communicate, for example in an aggressive contest between two individuals, there is an incentive for each signaler to try to manipulate the receiver into behaving in a way that benefits the signaler (Dawkins & Krebs, 1978). This problem is particularly pronounced for signals that carry no inherent cost or can be easily faked. Signals of aggressive intent fall into this category: instead of being tied to a physical trait of the signaler, which would constrain the level of signaling, these signals are often not costly to produce and can potentially be given at any level. As such they can be used to flexibly signal aggressive intent, which can change depending on the situation, but they can also be easily faked. Indeed, initial studies were skeptical that such signals can carry information regarding the "intent" of the signaler (Caryl, 1979; Maynard Smith, 1974). More recent studies however, have shown that signals of aggressive intent reliably predict a subsequent escalation such as an attack in many species (e.g. Bachmann et al., 2017; Laidre, 2009; Searcy, Anderson, & Nowicki, 2006; Waas, 1991). The reliability of these signals appears to be maintained by the cost of social retaliation from the receivers (Anderson, DuBois, Piech, Searcy, & Nowicki, 2013; Burt, Campbell, & Beecher, 2001; Ligon & McGraw, 2016).

An implicit assumption in studies of aggressive intent has been that the signaling systems are at an evolutionary equilibrium such that signaling strategies persist over non-signaling strategies (i.e., simply attacking without signaling) (Searcy & Nowicki, 2005) . However, changes in physical and social ecology may perturb signaling systems from an equilibrium. One such change that animal populations currently experience is human-induced environmental change, in particular urbanization (Johnson & Munshi-South, 2017). Although there are a plethora of studies on the effect of urbanization on signal features, particularly with respect to acoustic noise (Brumm & Slabbekoorn, 2005; Derryberry et al., 2016; Gil & Brumm, 2014; Patricelli & Blickley, 2006; Wood & Yezerinac, 2006), the effect urbanization has on overall reliability of signaling systems has not been investigated extensively.

Here we ask whether reliability of signals of aggressive intent differs between urban and rural male song sparrows, *Melospiza melodia*, a songbird common in North America and found

in urban and rural habitats. Song sparrows have a well-studied aggressive signaling system that consists of two close-range aggressive signals: low amplitude “soft” songs and wing waves (rapid fluttering of one or both wings without getting airborne) both of which predict a subsequent attack (Akçay, Tom, Campbell, & Beecher, 2013; Nice, 1943; Searcy, Akçay, Nowicki, & Beecher, 2014; Searcy et al., 2006). Loud (broadcast) songs however, do not reliably predict attack in this species (Searcy et al., 2014).

Several studies showed that male song sparrows living in urban and rural habitats exhibit significant differences in responses to simulated territorial intrusions, with urban birds responding more strongly to simulated territory intrusions than rural birds (Davies & Sewall, 2016; Evans, Boudreau, & Hyman, 2010; Foltz et al., 2015). However, these studies did not determine if aggressive signals reliably predicted attack in each habitat. Although aggressive signals are correlated with other aggressive behaviours like approaching and attacking an opponent, signals (unlike approach and attack) have no physical function in the aggressive interaction other than the information they carry (Otte, 1974). Thus, aggressive signals and non-signaling aggressive behaviours constitute separate behavioural characters (Akçay, Campbell, & Beecher, 2015; see Araya-Ajoy & Dingemanse, 2014 for a discussion of behavioral characters). Signaling may be impacted differently by urbanization than are aggressive behaviours because ecological conditions such as noise levels impact signal transmission and detection and reduced detection could also reduce effectiveness and thus reliability of signals (Brumm & Slabbekoorn, 2005; Phillips & Derryberry, 2018; Slabbekoorn & Smith, 2002).

Soft songs and loud songs present an interesting case of how signal reliability may change with urbanization. Soft songs, due to their low amplitude, would be expected to be less effective signals given the masking effect of high anthropogenic noise levels found in urban habitats (Pohl, Slabbekoorn, Klump, & Langemann, 2009). Animals often respond to noise by vocalizing at higher amplitudes in response to higher noise levels, which is termed the Lombard effect (Brumm, 2004; Brumm & Todt, 2002; Brumm & Zollinger, 2011). Aggressive males in urban areas might use loud songs instead of soft songs in signaling their intention to escalate. In other words, under *the Lombard hypothesis* we expect to see a decrease in the frequency of use of soft songs as these would be ineffective in noisy habitats, and an increase in the frequency of use of loud songs during aggressive interactions in urban habitats compared to rural habitats.

Further, loud songs should be more strongly positively correlated with actual attack. Notice that there are two distinct predictions from this hypothesis: First, the overall rates of soft song may decrease in urban compared to rural birds while the overall rates of loud song may increase. Second, urban birds that eventually attack should sing more broadcast songs to signal their intention, with the result that the proportion of soft songs among all songs is expected to decrease in urban attackers.

While acoustic noise should affect singing behaviours, visual signals of aggressive intent should be unaffected. Indeed, males might compensate for increased acoustic noise by switching to a different modality, namely visual (Grafe et al., 2012; Partan, 2017; Patricelli & Blickley, 2006; Ríos-Chelén, Lee, & Patricelli, 2015). Under this hypothesis, urban song sparrows should switch to using wing waves to signal aggression rather than singing soft songs. Previous studies in song sparrows reported strong positive correlations between the wing waves and soft songs (Akçay, Campbell, & Beecher, 2014; Nice, 1943; Searcy et al., 2006). If urban birds increase their use of wing waves while decreasing their use of soft songs, the positive correlation between wing waves and soft songs should be weaker in the urban birds compared to rural birds.

Methods

Study site and Subjects

We studied song sparrows in in Montgomery County, VA at 2 urban and 3 rural sites. The two urban sites were the campuses of Virginia Tech (Blacksburg, VA) and Radford University (Radford, VA). The three rural sites were Heritage Park (just outside Blacksburg, VA), Kentland Farms of Virginia Tech and Stroubles Creek Stream Restoration area. These sites are shown to differ significantly in their urbanization based on quantitative measures of vegetation, paved surfaces, and buildings (Davies, Beck, & Sewall, 2018). Trials were carried out between 8th April and 13th May 2017. Most subjects tested in early spring were unbanded at the time of the trial but were captured after the simulated territory intrusion for banding and blood sampling for a different study. We tested 42 rural birds and 36 urban birds.

Noise Measurements

We measured the ambient noise levels at 12 urban and 16 rural territories using a sound meter (Radioshack Digitial Sound Level Meter model 33-2055) following the methods described

in Brumm (2004). Briefly, we pointed a sound meter, oriented horizontally, in one of the cardinal directions, picked randomly. We noted the maximum sound level measurement in a 10 second period and then rotated the sound meter clock-wise by 90 degrees and repeated the measurement. We took 2 measurements per cardinal direction and then averaged the eight values.

Aggression assays

We carried out the simulated territory intrusions at the estimated territory center of a male by placing a speaker (VictSing model C6) connected to a smartphone via Bluetooth and a taxidermic model of a song sparrow on a natural perch. We adjusted speaker volume to be approximately 80 dB SPL, measured at 1m (with the same sound meter as above), which corresponds to normal loud song volume in song sparrows. Song stimuli were recorded around Blacksburg from birds that were at least 1 km separated from our subjects using a Marantz PMD 660 or PMD 661 Solid State recorder and a Sennheiser ME66/K6 directional microphone. Two observers standing about 20m from the speaker narrated the trial using the same recording equipment as above.

After setting up the equipment, we started to play a song sparrow song at a rate of 1 song every ten seconds with the taxidermic model covered. We recorded aggressive and signaling behaviours for three minutes after the first response of the focal male. After the three-minute period, we paused the playback and one experimenter removed the cover to reveal the taxidermic model. We resumed the playback for another 10 minutes or until the subject attacked.

Response Measures

Attacks were defined as the subject physically touching the mount. If an attack occurred, we stopped the playback and retrieved the mount before it was destroyed. During the trial, the observer narrating the trial noted the following behaviours: flights (with distance to the speaker after each flight), soft songs, loud songs and wing waves (all divided by trial duration and reported as rates). Soft and loud song determination was made in the field by experienced observers (CA or MLB) which has been shown to produce a clear cut-off point when validated with actual amplitude measurements (Anderson, Searcy, Peters, & Nowicki, 2008). The trial recordings were scanned with the software Syrinx (John Burt, Portland, OR). From the trial recordings we extracted the counts of flights, loud songs, soft songs and wing waves for both the

initial 3-minute period as well as the mount period. We also calculated the proportion of time spent within 5 m of the speaker and noted the closest approach for the initial three minutes and time spent within 1 m of the speaker and latency for the subject to fly within 5 m of the speaker (subjects flew away when the experimenter approached the speaker to remove the cover on the mount) for the duration of the period when the mount was uncovered (10 minutes or until attack). Flights, proportion of time spent within 5 or 1 m of the speaker and latency to approach are considered aggressive behaviours, whereas the loud songs, soft songs and wing waves are considered signaling behaviours (Akçay, Campbell, et al., 2015).

Data analyses

Because aggressive behaviours were correlated with each other (see supplementary material), we carried out principal component analyses (PCA) for the three-minute pre-mount period and the 10-minute mount period as in (Akçay et al., 2013). The first PCA for the pre-mount period contained the variables flight rate (number of flights divided by duration of playback period), proportion of time spent within 5m and closest approach to the speaker. The first component in this PCA explained 67.3% of variance and was taken as aggression score for the pre-mount period (see Table 1 for loading coefficients). For the mount period, the PCA included the variables flight rates, time spent within 1m of the mount and latency to arrive at 5m after the first playback with mount uncovered (all of these variables were correlated with each other, all p's< 0.0009). The first component of this PCA explained 64.9% of variance and was taken as aggression score for the mount period (see Table 1 for loading coefficients).

Table 1. Loading coefficients for principle component analyses (PCA) aggression scores. There were two separate PCAs.

Variable	**PCA pre-mount**	**Variable**	**PCA mount period**
Flight rate	0.52	**Flight Rate**	0.58
Proportion of time within 5 m	0.61	**Proportion of time within 1m**	0.61
Closest Approach	-0.60	**Latency to 5 m**	-0.54

Our first analysis addressed whether there were any differences between aggressive behaviours and signaling behaviours of rural and urban birds. We compared the aggression scores of urban and rural birds with independent sample t-tests and used a Chi-square test to

determine whether attack rates differed between urban and rural birds. The rates of signaling behaviours were all distributed non-normally and we used Mann-Whitney U tests to test differences between urban and rural birds.

To address our main question of whether reliability of signaling differs between urban and rural habitats, we carried out separate logistic regressions on attacking behaviour (attack or non-attack) with the following predictor variables: habitat and soft songs (or wing waves or loud songs,), and the interaction effect. The main effects and interaction effects were entered sequentially, representing 2 contrasts we were interested in: 1) Does a signal (soft song, loud song or wing waves) predict attack after taking into account the effect of habitat and 2) Is there an interaction between habitat and signal in predicting attack? Because the Lombard hypothesis predicts the relative use of soft songs by attackers will decrease in urban habitats, we compared the proportion of soft songs among all songs of attackers and non-attackers in a similar logistic regression model.

Finally, to ask whether the relationship between wing waves and soft song is weakened in urban birds relative to rural birds, we used out a general linear mixed model (GLMM) with wing wave count as the response variable, and soft song rates, habitat and their interaction as predictor variables. We included the duration of the mount period as an offset variable to account for unequal trial durations. Because of significant overdispersion we used a quasipossion model using the 'glm' function in R (Zeileis, Kleiber, & Jackman, 2008). We also ran non-parametric correlations (Spearman's ρ) on the urban and rural birds separately to assess the relationship between soft song and wing wave rates.

Results

Ambient noise levels were significantly higher by approximately 8 decibels in the urban territories (M±SD: 71.22±3.11 dB; n=12) than the rural territories (M±SD: 64.37±5.54 dB, n=16; independent samples t-test: t_{26}=3.84, p=0.0007). The noise levels at urban habitats correspond to the higher end of noise measurements reported in a study that documented effects of urban noise on the acoustic properties of song sparrow song (2006). Urban birds were significantly more aggressive than rural birds (independent samples t-tests; pre-mount: t_{76}=2.65, p= 0.01; mount: t_{76}= 2.78, p= 0.007, Figure S1a). More urban birds (14 out of 36, 38.9%) attacked the mount than rural birds (4 out of 46, 8.7%; χ^2= 9.42; p= 0.002).

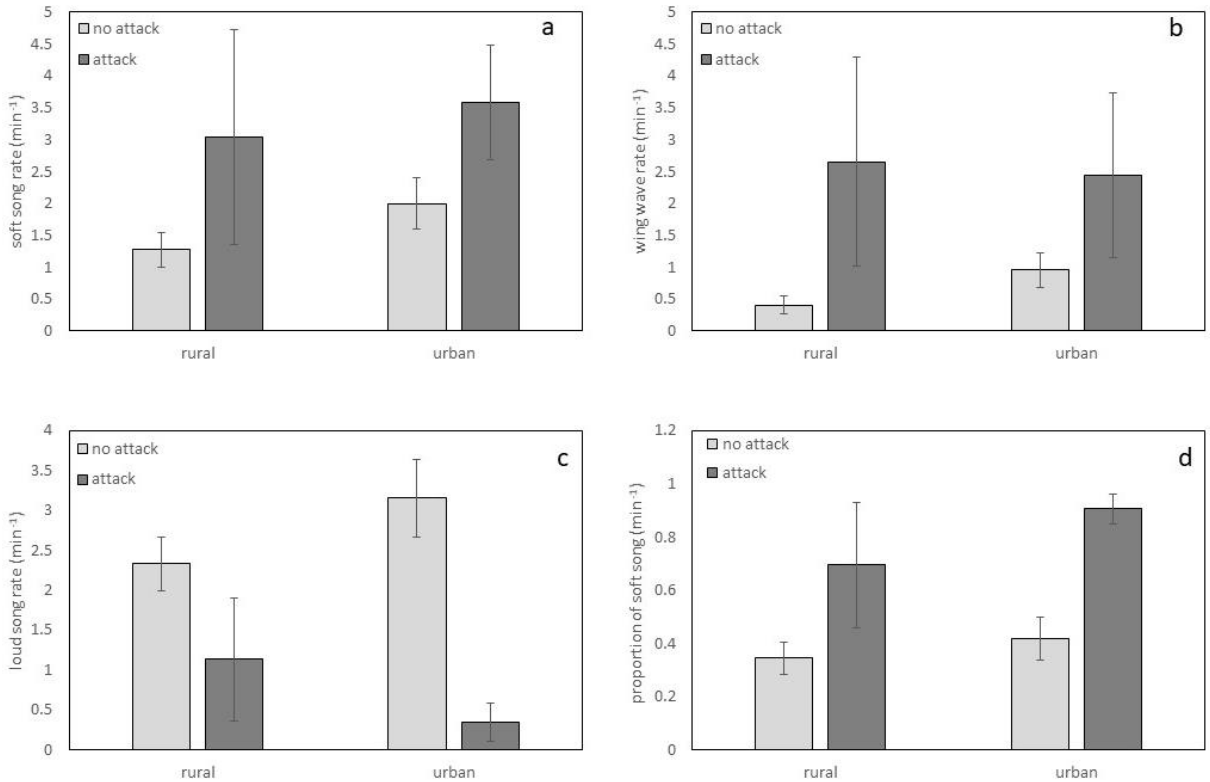

Figure 1. Mount period (a) soft song rates, (b) wing wave rates, (c) loud song rates and (d) proportion of soft songs of attacking and non-attacking birds by habitat. The bars denote the means and the errors denote standard error.

Table 2. Logistic regression models with habitat and soft songs, wing waves, loud songs or proportion of soft songs as predictor variables. A separate model for each signal was run. The cells report χ^2 values (p-values, alpha <0.05 indicated with bold text) from a forward sequential logistic regression. Note that habitat was entered first in all models followed by the signal and their interaction. Six subjects did not sing any songs (soft or loud) and were excluded from the model with proportion of soft songs (rightmost column).

Model:	*Soft song model*	*Wing wave model*	*Loud song model*	*Proportion of soft songs*
Habitat	9.74 (**0.002**)	9.74 (**0.002**)	9.74 (**0.002**)	5.18 (**0.022**)
Signal	5.45 (**0.019**)	5.37 (**0.020**)	17.82 (**0.000002**)	15.51 (**0.000008**)
Habitat*Signal	0.27 (0.61)	2.43 (0.12)	1.26 (0.26)	1.48 (0.22)

During the pre-mount period, urban birds sang more soft songs (U=397, p=0.0003) and gave more wing waves (U= 385, p=0.000009) than rural birds. Rates of loud songs did not differ between rural and urban birds during the pre-mount period (U=645, p=0.27). During the mount period, urban birds sang more soft songs (U=548.5, p=0.036, Figure S1b) and gave more wing waves (U=524, p=0.015, Figure S1c) than rural birds. Loud song rates did not differ significantly between urban and rural birds during the mount period (U=835, p=0.43, Figure S1d).

Logistic regression models on attacks as the response variable showed that the main effect of habitat and each of soft song (Figure1a), wing wave (Figure 1b) and loud song (Figure 1c) was significant (Table 2). The two-way interaction between the signal and habitat was not significant in any of the models. The proportion of soft songs was also a highly significant predictor of attack among both urban and rural birds (Figure 1d, Table 2).

The quasipoisson GLM showed that while there was significant positive relationship between soft songs and wing waves, this relationship was modified by a significant interaction with habitat type (Table 3). In the urban habitat, the relationship between soft songs and wing waves was weaker than in rural habitats as evidenced by a negative interaction term. The correlation between soft song and wing wave rates were positive and significant in both habitat types but it was stronger in rural habitats compared to urban habitats (rural: Spearman's ρ=0.71, p=0.0000001, n=42; urban: Spearman's ρ=0.53, p=0.0008, n=36).

Table 3. Model coefficients, t-values and associated p-values (Wald test) in the GLM using quasipoisson distribution. Wing wave counts are the response variable; habitat and soft song rates (soft songs per minute) and their interaction are predictor variables, with trial duration (in log) as offset variable.

	Coefficient (SE)	t	*p*
intercept	-1.89 (0.44)	-4.22	**0.000007**
Habitat (urban)	1.39 (0.57)	2.42	**0.02**
Soft song rate	0.49 (0.09)	5.37	**<0.0000001**
Habitat (urban)*Soft song rate	-0.33 (0.12)	-2.63	**0.01**

Discussion

We aimed to test the hypothesis that low amplitude songs in urban song sparrows may be a less reliable signal of aggression than loud songs due to anthropogenic noise in urban habitats.

We predicted, based on the Lombard hypothesis, that urban birds would sing fewer soft songs and more loud songs, and loud songs and not soft songs would predict attacks in urban habitats. We also predicted the urban birds would change their multimodal signaling and use wing waves rather than soft song to signal intent to attack, such that the correlation between wing waves and soft songs should weaker in urban habitats. Contrary to these predictions. the relationship between signaling and actual attack did not interact with the habitat type, suggesting that there are no differences in reliability of soft songs, wing waves, or loud songs across habitats (Figure 1). The most reliable signal of attack was loud songs, but the number of loud songs was inversely related to attack (attackers sang fewer loud songs), which was again contrary to the prediction of the Lombard hypothesis. Consequently, a high proportion of soft songs among all songs was still significantly predictive of attack in urban as well as rural birds. Finally, we did find a weaker relationship between soft songs and wing waves in urban habitats, although the relationship remained significant among urban birds. Below we discuss these results in the context of previous research on signal honesty in this and other songbirds.

Use of soft songs persists in urban noise

Even under noisy conditions of the urban habitats, male song sparrows seemed to use soft songs as a reliable signal of aggressive intent. Given the decrease in amplitude in soft song (relative to loud song), it seems reasonable to suppose that soft song will be less effective in urban habitats as an aggressive signal. However, it remains to be seen whether that is indeed the case. Previous studies found that animals can engage in strategies (other than increase in amplitude) to compensate for the effect of noise, including adjustment of frequencies. Most studies found that urban birds sing songs with higher minimum frequencies (but see Potvin, Mulder, & Parris, 2014; for an interesting exception), although this may be in part due to the Lombard effect itself, as signal frequency increase as amplitude increases (Nemeth et al., 2013).

Indeed, song sparrows are reported to change the acoustic properties of loud songs by singing fewer low frequency notes in urban habitats and putting less energy in the low frequency parts of the songs (Wood & Yezerinac, 2006), although no study has so far looked at whether they also vary the acoustic properties of soft songs depending on the noise levels. It is worth noting that there are two types of soft songs which differ in their acoustic structure: crystallized soft songs, which are quiet renditions of the broadcast repertoire songs, and warbled soft songs,

which are songs not found in the broadcast repertoire (Anderson, Nowicki, & Searcy, 2007; Anderson et al., 2008). The latter type of soft songs tend to have the lowest amplitude and contain alternating sequences of low and high frequency elements covering a broader frequency range (1539-9118 Hz for warbled songs, 1762-8081 for crystallized soft songs and 2038-7999 Hz for broadcast songs, see Table 1 of Anderson et al. 2008). Although usually assumed that the acoustic structure of soft song is selected for minimizing transmission distance (which would exacerbate the difficulty of their detection under urban noise), the evidence for this is as yet lacking for song sparrows (Akçay, Anderson, Nowicki, Beecher, & Searcy, 2015; Akçay & Beecher, 2012; Searcy & Yasukawa, 2017). In fact, a recent study found that soft songs (both crystallized and warbled) transmitted slightly better than broadcast songs when played at low amplitudes from a speaker and remeasured at different distances (Niederhauser, DuBois, Searcy, Nowicki, & Anderson, 2018). Thus, at least over the short distances in which soft song is given, urban noise may have little or no effect, and in fact soft song may be favored over loud song because of its better transmissibility.

An alternative possibility is that while signalers are using soft songs at high rates in urban habitats, receivers may still be less responsive to them. In two out of three previous studies on receiver response to soft song, soft song elicited stronger responses than loud song (Anderson et al., 2007; Anderson, Searcy, Hughes, & Nowicki, 2012; Templeton, Akçay, Campbell, & Beecher, 2012), but no previous study compared the responses of urban and rural song sparrows to soft songs. If it is the case that soft song is a less efficient signal, the receivers should respond less strongly to soft songs than loud songs, even when they are presented at close range.

Finally, it is also possible that urban song sparrows may be showing a subtler Lombard effect. Although we (and other researchers in the field) classify soft and loud songs categorically, soft songs are given at a wide range of amplitudes: Anderson and colleagues (2008) found that songs classified as soft ranged from 77 to about 50 dB SPL (measured at 1m with a calibrated microphone). This continuous variation in soft song means that song sparrows might be adjusting the amplitude of their song slightly and still sing what experimenters consider soft song. Nonetheless such a shift wouldn’t affect reliability of soft song unless it’s strong enough that soft songs turn into loud songs (e.g. have amplitudes > 77 dB SPL). The fact that loud songs are

almost never sung by the most aggressive signalers in urban habitats suggests that aggressive birds don't show a significant Lombard effect for soft songs.

Multimodal signaling in urban habitats

Although urban noise did not seem to have an overall effect on soft songs to make them less used or reliable, we found tentative evidence that the signaling behaviours of urban song sparrows are affected. Namely, among urban birds, the well-documented correlation between wing waves and soft song appears to be weakened (Table 3), although it was still significant and positive. This finding is consistent with a modest multi-modal shift in signaling in response to acoustic noise (Partan, 2017; Partan, Fulmer, Gounard, & Redmond, 2010).

It is important to note that if a multi-modal shift is occurring in urban song sparrows it is incomplete: the urban birds still sing more soft songs than rural birds and soft song is still a reliable signal of aggressive intent in urban birds. Whether wing waves are a more effective signal compared to soft songs in urban habitats from a receiver perspective is an open question. An experiment displaying the visual (wing wave) and acoustic (soft song) signal separately and together with a robotic model (Anderson et al., 2013) could answer this question (see [50] for such a study in gray squirrels).

Although the acoustic response of songbirds to the noise in urban habitats has been the subject of considerable amount of research, whether acoustic noise leads to multi-modal shifts to other channels is less studied. In the most direct test of this hypothesis with songbirds, red-winged blackbirds showed no evidence that they switch to visual displays from acoustic signals under noise conditions (Ríos-Chelén et al., 2015). Given the present results, which only provide qualified support for a multi-modal shift, it is still an open question whether multi-modal shifts in response to acoustic noise occur regularly in songbirds.

Another visual signal that might be used more efficiently under acoustic noise is the melanin-based spotting on the chest. An earlier study in our population found that chest spotting differs in its association with aggression across urban and rural habitats (Beck, Davies, & Sewall, 2018): the brightness of the melanin-based spotting on the breasts of males correlated positively with aggression in urban but not in rural habitats. In contrast, the extent of the breast spotting correlated negatively with aggression in rural but not in urban habitats. We are currently

investigating how plumage signaling and signaling via song and wing waves are related to each other across urban and rural habitats, experimentally.

In summary, we found that acoustic noise does not seem to affect the use of soft songs as a reliable aggressive signal in song sparrows, although it may affect multi-modal displays by inducing some males to switch to a visual display (wing waves) instead of soft songs. We believe that the song sparrow signaling system is an excellent model to ask how multi-modal signaling evolves under anthropogenic habitat change.

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Ethics

All procedures in the study reported here were conducted under the appropriate State (Virginia Department of Game and Inland Fisheries permit #058685) and U.S. Federal permits (US Fish and Wildlife Service Banding Permit # 23818) and approved by the Virginia Tech Institutional Animal Care and Use Committee (protocol # 16-176).

Data, code and materials

The data and R-script required to reproduce the results are available with the manuscript as supplementary files.

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