Are signals of aggressive intent less honest in urban habitats?

Çağlar Akçay, a,b,c Michelle L. Beck, b,c and Kendra B. Sewall b

aDepartment of Psychology, Koç University, Rumelifeneri Kampusu, Sariyer 34450 Istanbul, Turkey, bDepartment of Biological Sciences, Virginia Tech, 2125 Derring Hall, Blacksburg, VA 24061, USA, and cDepartment of Biology, Rivier University, Nashua, NH 03060, USA

Received 12 April 2019; revised 7 September 2019; editorial decision 13 September 2019; accepted 23 September 2019.

How anthropogenic change affects animal social behavior, including communication is an important question. Urban noise often drives shifts in acoustic properties of signals but the consequences of noise for the honesty of signals—that is, how well they predict signaler behavior—is unclear. Here we examine whether honesty of aggressive signaling is compromised in male urban song sparrows (Melospiza melodia). Song sparrows have two honest close-range signals: the low amplitude soft songs (an acoustic signal) and wing waves (a visual signal), but whether the honesty of these signals is affected by urbanization has not been examined. If soft songs are less effective in urban noise, we predict that they should predict attacks less reliably in urban habitats compared to rural habitats. We confirmed earlier findings that urban birds were more aggressive than rural birds and found that acoustic noise was higher in urban habitats. Urban birds still sang more soft songs than rural birds. High rates of soft songs and low rates of loud songs predicted attacks in both habitats. Thus, while urbanization has a significant effect on aggressive behaviors, it might have a limited effect on the overall honesty of aggressive signals in song sparrows. We also found evidence for a multimodal shift: urban birds tended to give proportionally more wing waves than soft songs than rural birds, although whether that shift is due to noise-dependent plasticity is unclear. These findings encourage further experimental study of the specific variables that are responsible for behavioral change due to urbanization.

Key words: anthropogenic change, bird song, honest signaling, multimodal signaling, song sparrow, urban noise.

INTRODUCTION

When individuals with conflicting interests communicate (e.g., during an aggressive interaction) there is an incentive for each signaler to try to manipulate the receiver into behaving in a way that benefits the signaler, thus jeopardizing the honesty of the signal (Dawkins and Krebs 1978). This problem is particularly pronounced for signals of aggressive intent (or threat signal), which are by definition not tied to a physical trait of the signaler. Instead, they are thought to predict future behavior or intention of the signaler (Andersson 1980). These signals are usually not costly to produce and can potentially be given at any level. A good example of this is bird song: singing seems to carry little or no metabolic cost compared to other activities birds have to carry out during an aggressive interaction (Zollinger et al. 2011).

Although early ethological literature assumed these signals of intent had to be honest—otherwise they would not exist— theoretical and empirical treatments of these signals in the 1970s were more skeptical (Maynard Smith 1974; Dawkins and Krebs 1978; Caryl 1979). The problem seemed to be that if signals are only indicative of aggressive “intent” of the signaler and not tied to a physical cost, then the signals would be easy to cheat for “bluffers” who would threaten without any intention to follow through with an attack. Therefore these signals were viewed mostly as attempts at manipulation by the signaler instead of carrying information regarding future behavior (Dawkins and Krebs 1978). More recently, however, a multitude of studies have shown that signals of aggressive intent can honestly predict a subsequent escalation such as an attack in many species (e.g., Waas 1991; Scarcy et al. 2006; LaLonde 2009; Akçay et al. 2013; Bachmann et al. 2017). Often, the mechanism that ensures the honesty of these signals seem to be the subsequent risk of retaliation from receivers (Molles and Vehrencamp 2001; Anderson et al. 2012; Anderson et al. 2013; Bachmann et al. 2017).

An implicit assumption in the studies of honest signaling has been that the signaling systems are at an evolutionary equilibrium such that signaling strategies persist over non-signaling strategies (Scarcy and Nowicki 2005). Changes in physical and social ecology, however, may disrupt this equilibrium. One such change that animal populations currently experience is human-induced environmental change, in particular, urbanization (Johnson and Munshi-South 2017). While there are a number of studies on
the effect of urbanization on signal features, for example, how noise affects the frequency characteristics of bird song (Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Wood and Yeyerinac 2006; Halfwerk and Slabbekoorn 2009; Gill and Brumm 2014; Derryberry et al. 2016), we do not know of any studies that examined the overall honesty of signals, particularly aggressive signals, in relation to urbanization.

Several studies showed that birds 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 (Evans et al. 2010; Davies and Sewall 2016; Fokilis et al. 2011; Foltz et al. 2013; Hardman and Dalesman 2018). However, these studies did not determine if aggressive signals also differed in their honesty between habitats. It is worth noting that although honest aggressive signals are correlated with other aggressive behaviors like approaching and attacking an opponent, these 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 behaviors constitute separate behavioral characters and may respond differently to changes associated with urbanization (Akçay et al. 2015b; see Araya-Ajoy and Dingemanse 2014 for a discussion of behavioral characters). To our knowledge, no previous study assessed the honesty of aggressive signals in urban and rural habitats.

Here we ask whether the honesty of multimodal signals of aggressive intent differs between urban and rural male song sparrows, Melospiza melodia, a songbird common in North America and found abundantly in urban and rural habitats. Urban song sparrows have been found to exhibit higher levels of aggression than their rural counterparts in several studies that include sites from a range of latitudes and ranges of human habitat impact (Evans et al. 2010; Foltz et al. 2015; Davies and Sewall 2016). 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 (Nice 1943; Searcy et al. 2006; Akçay et al. 2013; Searcy et al. 2014). Loud (broadcast) songs, however, do not reliably predict attack in this species (Searcy et al. 2014). This difference in honesty between soft songs and loud songs seems to hold for several other species. Whereas soft songs reliably predict attack in several species, loud songs generally do not (Searcy and Beecher 2009; Akçay et al. 2015a).

Soft songs represent an interesting potential case of how acoustic signaling changes in urban habitats (Halfwerk and Slabbekoorn 2015). The defining feature of soft song is the low amplitude compared to the loud broadcast songs, which would decrease the transmission distance of the signal to limit eavesdropping by unintended receivers other than the opponent (presumed to be the intended receiver). In some species, soft song also differs in acoustic structure from broadcast songs (Dabelsteen et al. 1998; Vargas-Castro et al. 2017) although whether these differences are adaptations to further decrease transmission distances and thereby minimize eavesdropping is currently unclear (Akçay and Beecher 2012; Vargas-Castro et al. 2017; Niederhauser et al. 2018). In the case of song sparrows in particular, soft song differs from loud song in that it has a lower minimum frequency (1500 to 1700 Hz for soft songs vs. ca. 2000 for loud songs, Anderson et al. 2008). Furthermore, in a study completed in a rural habitat, birds tended to put relatively more energy into the lower frequencies of soft song, which overlap with urban noise (Anderson et al. 2000). At the same time, Wood and Yeyerinac (2006) found that most of the acoustic noise in urban habitats was present at 1–4 kHz range and that urban song sparrows living in noisy habitats put relatively less energy into this frequency range of their songs when singing loud songs, although they did not record soft songs in their study. Considered together, these findings suggest that the frequency and amplitude characteristics of soft songs should make them less effective compared to loud songs due to the masking effect of high anthropogenic noise levels commonly found in urban habitats (Pohl et al. 2009).

One solution to the presence of urban noise is to sing loudly. Indeed, animals often respond to noise by vocalizing at higher amplitudes in response to higher noise levels, which is termed the Lombard effect (Cynx et al. 1998; Brumm and Todt 2002; Brumm 2004; Brumm and Zollinger 2011). The Lombard effect is particularly strong if noise overlaps the frequency range of the vocalizations (Manabe et al. 1998; Brumm and Todt 2002). If song sparrows show a Lombard effect in urban areas, they may sing loud songs instead of soft songs to signal their aggressive intent. Under this prediction, we expect more loud songs in the urban habitats compared to rural habitats particularly by those birds who end up attacking their opponent.

Another solution for the problem introduced by noise would be to sing at a closer distance to their opponent in order to ensure transmission of low amplitude signals in the urban habitats (Halfwerk et al. 2012). Getting closer to the intended receiver would increase the signal-to-noise ratio of the signal at the point of reception and, therefore, would ensure reliable transmission. Approaching simply to ensure transmission may come at a cost to the receiver during an aggressive interaction, as the proximity to the opponent potentially increases the risk of retaliation (Anderson et al. 2012; Templeton et al. 2012).

A further strategy to ensure transmission of soft songs would be to increase repetition rate or serial redundancy (Brumm and Slater 2006). Under this strategy, we expect the rate of soft songs to increase in urban habitats, whereas rates of loud songs should not change given the latter do not reliably signal aggression. These strategies (singing more loud songs, decreasing distance and increasing serial redundancy) are not mutually exclusive strategies; however, they would affect the overall honesty of the signal, measured as the statistical association between the signal and subsequent attack in different ways. If urban song sparrows increase the amplitude of their aggressive songs, we expect that they would sing more loud songs compared to rural song sparrows, and attackers would give significantly more loud songs, making loud songs the more honest signal. If song sparrows decrease the distance to the mount while singing soft songs, we expect that the distance at which soft song is sung will be lower in urban than rural habitats, whereas the distance at which loud songs are sung would not differ between urban and rural habitats. The latter prediction assumes that the intended audience of the loud songs is not the immediate intruder but other neighbors, since loud songs do not reliably predict attack on the immediate intruder. Finally, if song sparrows increase the repetition rates for soft songs in urban habitats, we expect that birds will sing more soft songs in urban habitats, and this difference will be particularly pronounced for attackers. In this case, soft songs would reliably predict attacks in urban habitats.

Given that song sparrows also have a visual signal of aggression, wing waves, that is positively correlated with soft songs, urban song sparrows may also shift their signaling effort to the visual modality (Halfwerk and Slabbekoorn 2015). Only a few studies have examined whether acoustic noise drives such a multimodal shift to visual
signals and evidence for this remains absent in birds (Patricelli and Blickley 2006; Grafe et al. 2012; Ríos-Chelen et al. 2015; Partan and Burt, Portland, OR). From the trial recordings, we extracted the distance at which each loud and soft song were delivered (as noted above, distance information was given with each flight during the trial).

Aggression assays
We carried out the simulated territory intrusions at a location that was estimated to be a central location in the male’s territory based on observation of singing perches. We placed a speaker (VictSing model C6 connected to a smartphone via Bluetooth) and a taxidermic model of a song sparrow (initially covered by a piece of cloth) on a natural perch. We adjusted speaker volume to be approximately 80 dB SPL, measured at 1 m (with the same sound meter and settings as above), which corresponds to loud song volume in song sparrows. Two observers standing about 20 m from the speaker narrated the trial with the same recording equipment.

After setting up the equipment, we started to play a song at a rate of one song every 10 s with the taxidermic model covered. Song sparrow songs last an average of 3 s and we presented stimuli at a rate of one song per 10 s for the duration of the trial, which approximates typical song sparrow singing rate. Each male received only a single rendition of one song type during the trial repeated every 10 s. This is consistent with the fact that song sparrows repeat a single song type for several minutes during their natural singing (eventual variety singing), and does not lead to any habituation at even longer durations than used in this experiment (Akçay et al. 2013). We recorded behaviors for 3 min after the first response of the focal male (the pre-mount period). After the pre-mount period, we paused the playback and one experimenter removed the piece of cloth to reveal the taxidermic model. We then restarted the playback at the same song rate as before and continued for another 10 min or until the subject attacked (i.e., physically touched the mount), at which point we stopped the playback and retrieved the mount before it was destroyed (the mount period).

Response measures
During the trial, the observer narrating the trial noted attacks and the following behaviors: 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). Song amplitude in song sparrows varies continuously between 55 dB to 85 dB, and our determination of soft versus loud song reduces this continuous variation into a categorical decision. This method has been validated by Anderson et al. (2008), who showed that an expert observer produces a clear cutoff point with soft versus loud determinations made in the field when these are validated with actual amplitude measurements from a fixed distance. Several studies using soft song categorization in this way in this species found that it reliably predicts attack whereas loud songs do not (e.g., Searcy et al. 2006; Akçay et al. 2013). Thus, this categorization captures biologically meaningful variation in amplitude.

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 and proportion of time spent within 1 m for both the initial pre-mount period and the mount period. Additionally, we noted the closest approach distance for the pre-mount period. We did not use closest approach for the mount period as a response variable because there was little variation in that measure for the mount period (an overwhelming majority of the subjects approached to within 1 m). Finally, we also extracted from the recordings the distance at which each loud and soft song were delivered (as noted above, distance information was given with each flight during the trial).
Data analyses

Our first analysis addressed whether there were any differences between aggressive behaviors and signaling behaviors of rural and urban birds. We used Mann-Whitney $U$ tests for all aggressive behaviors and signaling behaviors as these were non-normally distributed. We report effect sizes (Hedges’ $g$, computed with the R package “efsize”; Torchiano 2018) and confidence intervals for the urban-rural comparisons in all of the response variables. We carried out a Chi-square test to determine whether attack rates differed between urban and rural birds.

To address our main question of whether honesty of signaling differs between urban and rural habitats, we carried out separate logistic regressions with attack as the dependent variable (attack or non-attack) and the following as the predictor variables: habitat and signal (soft songs, wing waves or loud songs), and the interaction between habitat and the signal. The main effects and interaction effects were entered sequentially, representing two 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? We also compared the proportion of soft songs among all songs to wing waves in urban areas. Soft songs and wing waves are highly correlated with each other (Akçay et al. 2014). Thus, we need to control for the level of overall signaling effort to determine whether wing waves were more common in urban areas. In order to do that, we first added together all aggressive signals (counts of wing waves and soft songs) and then took the proportion of wing waves among the total number of aggressive signals for subjects who gave at least one soft song or wing wave. We then compared the proportion of wing waves between the habitats with a Mann-Whitney $U$ test.

Finally, we asked whether there was a multimodal shift from soft songs to wing waves in urban areas. Soft songs and wing waves are highly correlated with each other (Akçay et al. 2014). Thus, we need to control for the level of overall signaling effort to determine whether wing waves were more common in urban areas. In order to do that, we first added together all aggressive signals (counts of wing waves and soft songs) and then took the proportion of wing waves among the total number of aggressive signals for subjects who gave at least one soft song or wing wave. We then compared the proportion of wing waves between the habitats with a Mann-Whitney $U$ test.

RESULTS

Ambient noise levels were significantly higher by approximately 8 decibels in the urban territories ($\bar{M} \pm SD$: 71.22 ± 3.11 dB; $n = 12$) than the rural territories ($\bar{M} \pm SD$: 64.37 ± 5.54 dB; $n = 16$; independent samples $t$-test: $t_{15} = 3.84, P = 0.0007$). 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 (Wood and Yezersinac 2006). Urban birds were significantly more aggressive than rural birds in all of the aggressive behaviors except rate of flights during the mount period (Tables 1 and 2, Figure 1d). More urban birds (14 out of 36, 38.9%) attacked the mount than rural birds (4 out of 42, 9.5%; $\chi^2 = 9.42; P = 0.002$).

Table 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>$W$</th>
<th>$P$-value</th>
<th>Hedges’ $g$</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight rate</td>
<td>500</td>
<td>0.0099</td>
<td>0.59</td>
<td>0.13 to 1.06</td>
</tr>
<tr>
<td>Closest approach</td>
<td>1129</td>
<td>0.000002</td>
<td>−0.56</td>
<td>−0.10 to 1.02</td>
</tr>
<tr>
<td>Proportion of time within 1 m</td>
<td>376.5</td>
<td>0.00013</td>
<td>0.95</td>
<td>0.47 to 1.42</td>
</tr>
<tr>
<td>Soft song rate</td>
<td>397</td>
<td>0.00028</td>
<td>0.69</td>
<td>0.23 to 1.16</td>
</tr>
<tr>
<td>Loud song rate</td>
<td>645</td>
<td>0.27</td>
<td>0.19</td>
<td>−0.26 to 0.65</td>
</tr>
<tr>
<td>Wing wave rate</td>
<td>385</td>
<td>0.000008</td>
<td>0.78</td>
<td>0.31 to 1.25</td>
</tr>
</tbody>
</table>

Positive effect sizes mean higher values for urban birds.

Table 2

<table>
<thead>
<tr>
<th>Variable</th>
<th>$W$</th>
<th>$P$-value</th>
<th>Hedges’ $g$</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight rate</td>
<td>624</td>
<td>0.19</td>
<td>0.39</td>
<td>0.06 to 0.86</td>
</tr>
<tr>
<td>Proportion of time within 1 m</td>
<td>538.5</td>
<td>0.000007</td>
<td>0.93</td>
<td>0.45 to 1.40</td>
</tr>
<tr>
<td>Loud song rate</td>
<td>538</td>
<td>0.046</td>
<td>0.50</td>
<td>0.04 to 0.96</td>
</tr>
<tr>
<td>Wing wave rate</td>
<td>524</td>
<td>0.015</td>
<td>0.38</td>
<td>−0.07 to 0.83</td>
</tr>
</tbody>
</table>

Positive effect sizes mean higher values for urban birds.

During the pre-mount period, urban birds sang more soft songs and gave more wing waves than rural birds. Loud song rates did not differ significantly between urban and rural birds during the pre-mount period (Table 1). During the mount period, urban birds sang more soft songs and gave more wing waves than rural birds (Figure 1a and 1c). Loud song rates did not differ significantly between urban and rural birds during the mount period (Table 2, Figure 1b).

Logistic regression models on attacks as the response variable showed that the main effect of habitat and each of soft song (Figure 2a), wing wave (Figure 2b) and loud song (Figure 2c) was significant (Table 3). Birds that sang high rates of soft songs and gave high rates of wing waves were more likely to attack. Interestingly, birds that sang fewer loud songs were also more likely to attack. Consequently, the proportion of soft songs was also a highly significant predictor of attack: birds that sang a higher proportion of their songs as soft songs were more likely to attack (Figure 2d, Table 3). The two-way interaction between the signal and habitat was not significant in any of the models, suggesting the honesty of signaling did not differ between urban and rural habitats.

In general, soft songs were sung closer to the speaker than loud songs for both urban and rural birds. Furthermore, urban birds sang both soft and loud songs closer to the speaker than rural birds (Table 4, Figure 3). The linear mixed model on song distances for loud and soft songs showed a significant effect of habitat and song category (soft songs were sung in closer proximity to the speaker) but no interaction effect between habitat and song category (Table 5).

During the pre-mount period, there was a non-significant trend for urban birds to give proportionally more wing waves than rural birds (0.43 vs. 0.30 for urban vs. rural subjects) ($U = 348.5, P = 0.074, n = 62$, Hedges’ $g = 0.39; 95% CI: −0.12 to 0.91$). During the mount period, urban birds also gave proportionally more wing waves than rural birds (0.32 vs. 0.19), and the difference
DISCUSSION

We aimed to test the hypothesis that low amplitude songs in urban song sparrows may be a less honest signal of aggression than loud songs due to anthropogenic noise in urban habitats. Contrary to this prediction, soft songs were predictive of a physical attack in urban and rural habitats alike and song sparrows in urban habitats sang more soft songs than rural birds, consistent with the fact that they were also more aggressive than rural birds. Wing waves also showed the same pattern: urban birds gave more wing waves, again consistent with the fact they were more aggressive than rural birds. Wing waves also reliably predicted attack in both habitats. Interestingly, the most honest signal of attack in both habitats was low rates of loud songs: attackers sang fewer loud songs per minute than non-attackers. We found that urban birds generally sang at a
shorter distance from the speaker for both loud and soft songs, and soft songs were given at a closer distance than loud songs in both habitat types. Finally, we found that during the mount period urban birds gave proportionally more wing waves as part of their total signaling effort. To our knowledge, this is the first study to examine honest multimodal signaling in aggressive interactions in relation to urbanization and adds to the growing literature on behavioral effects of urbanization on animal social behavior. Below we discuss these results in the context of previous research on signal honesty in this and other songbirds.

### Table 3

<table>
<thead>
<tr>
<th>Model</th>
<th>Soft song model</th>
<th>Wing wave model</th>
<th>Loud song model</th>
<th>Proportion of soft songs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>9.74 (0.002)</td>
<td>9.74 (0.002)</td>
<td>9.74 (0.002)</td>
<td>5.18 (0.022)</td>
</tr>
<tr>
<td>Signal</td>
<td>5.13 (0.023)</td>
<td>5.36 (0.020)</td>
<td>17.28 (0.000003)</td>
<td>13.21 (0.0003)</td>
</tr>
<tr>
<td>Habitat*Signal</td>
<td>0.32 (0.57)</td>
<td>2.43 (0.12)</td>
<td>1.14 (0.28)</td>
<td>0.65 (0.42)</td>
</tr>
</tbody>
</table>

A separate model for each signal was run. The cells report χ² values (P-values, alpha <0.05 indicated with bold text) from a forward sequential logistic regression. Note that in all models, we entered habitat first, followed by the signal and the interaction term. We excluded six subjects that did not sing any songs (soft or loud) from the model with proportion of soft songs (rightmost column).

### Table 4

<table>
<thead>
<tr>
<th>Pre-mount</th>
<th>Mount</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rural</td>
<td>Urban</td>
</tr>
<tr>
<td>Loud songs</td>
<td>6.14 (4.16)</td>
</tr>
<tr>
<td>Soft songs</td>
<td>4.40 (3.71)</td>
</tr>
</tbody>
</table>

These results support the hypothesis that urban birds are more aggressive than rural birds. Another potential strategy that song sparrows might engage in to deal with urban noise is to close the distance to the receiver (Halfwerk et al. 2012) such that the signal-to-noise ratio of the acoustic signals would be improved at the receiver end of the transmission. Indeed, we found that urban birds sang at shorter distances to the speaker (the presumed receiver of the signals) for both loud songs and soft songs compared to rural birds. Approaching closer to the speaker would also mean that the playback songs, which were played at the same amplitude in urban and rural habitats, would also not suffer from decreased signal-to-noise ratios in urban habitats compared to rural habitats at the point of the reception.

Evidence that songbirds close the distance to receivers to overcome masking by noise comes from an elegant experiment by Halfwerk and colleagues (2012). In this experiment, male great tits (*Parus major*) singing to their mates adjusted their singing locations to be closer to the nest box when they experimentally presented noise inside the nest box when their mates were in the nest box. Remarkably, the males did not experience the noise themselves (as the noise was only presented in the nest box and was not audible...
outside) but evidently acquired the information about the noise socially from their mates. In another recent study, male white-crowned sparrows living in noisier territories approached the speaker closer than the males in the same population that lived in quieter territories. (Phillips and Derryberry 2018). One interpretation of this latter finding is that high levels of ambient noise might require birds to approach each other closer to evaluate and transmit signals efficiently. This interpretation would be consistent with our finding that urban song sparrows display closer proximity to simulated intruders. Unlike the Halfwerk et al. study, however, neither the current study nor Phillips and Derryberry (2018) experimentally manipulated noise levels to allow a causal inference about the role of noise in determining proximity in aggressive interactions. Therefore, the hypothesis that noise (or altered signal-to-noise ratios) has a causal role in aggression should still be viewed as tentative, especially given that other ecological factors, such as food availability also affect aggressive behaviors in urban and rural birds (Foltz et al. 2015).

Whether the urban-rural differences that we see in song sparrows and other species are due to developmental plasticity, ongoing flexibility in response to ecological conditions, or genetic variation is still poorly understood. Experimental studies manipulating ecological variables (e.g., noise or food availability, like Foltz et al. 2015) and developmental studies, particularly common garden or cross-fostering experiments of urban and rural birds, will be crucial to make causal inferences about the factors that drive behavioral and physiological changes in response to urbanization (Partecke et al. 2014; Ouyang et al. 2018).

### Multimodal signaling in urban habitats

Although urban noise did not decrease the use or honesty of soft songs, we found tentative evidence for a multimodal shift: urban birds tended to give more wing waves proportionally to their total aggressive signaling effort at least during the mount period although the effect size was moderate and the confidence intervals were large. This finding, if confirmed, is consistent with the hypothesis that acoustic noise found in urban habitats may lead to switching signaling effort to the visual modality (Partan et al. 2010; Partan 2017). It is also important to note that if a multimodal 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 an honest signal of aggressive intent in urban birds.

Whether wing waves are a more effective signal compared to soft songs in urban habitats (compared to rural habitats) is an open question. To determine the relative effectiveness of these signals an experiment displaying the visual (wing wave) and acoustic (soft song) signal separately and together with a robotic model would be required (Partan et al. 2009; Partan et al. 2010; Anderson et al. 2013). To the best of our knowledge, only one experiment compared responses to signals in different modalities in urban and rural habitats. In this study, Partan and her colleagues (2010) found that urban gray squirrels (*Sciurus carolinensis*) responded more to the visual alarm signal (tail flagging) displayed by a robotic squirrel compared to the rural squirrels. There was, however, no significant difference in response strength to the vocal

### Table 5

<table>
<thead>
<tr>
<th>Model</th>
<th>Coefficient (SE)</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-Mount period</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>6.01 (0.59)</td>
<td>10.24</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Habitat (urban)</td>
<td>-2.14 (0.85)</td>
<td>-2.51</td>
<td>0.014</td>
</tr>
<tr>
<td>Song category (soft)</td>
<td>-1.41 (0.65)</td>
<td>-2.17</td>
<td>0.035</td>
</tr>
<tr>
<td>Habitat*Song category</td>
<td>-0.20 (0.90)</td>
<td>-0.23</td>
<td>0.82</td>
</tr>
<tr>
<td>Mount period</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>5.48 (0.54)</td>
<td>10.05</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Habitat (urban)</td>
<td>-1.88 (0.83)</td>
<td>-2.27</td>
<td>0.026</td>
</tr>
<tr>
<td>Song category (soft)</td>
<td>-3.13 (0.56)</td>
<td>-5.59</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Habitat*Song category</td>
<td>0.78 (0.82)</td>
<td>0.96</td>
<td>0.34</td>
</tr>
</tbody>
</table>

Significant values are indicated in bold.

### Figure 4

Proportion of wing waves among the sum of soft songs and wing waves for (a) pre-mount period and (b) mount period. The dots are individual data points; boxes indicate the interquartile range and medians. Whiskers are 95% confidence intervals.
signals between urban and rural squirrels. These results suggest that urban gray squirrels may rely more on the visual signals in urban habitats even if vocal signals are still as effective in urban habitats as in rural habitats.

In another relevant study, Ríos-Chelén and colleagues (2015) examined whether red-winged blackbirds changed their signaling effort from acoustic to visual signals (the “song-spread display,” in which singing males spread their wings to expose their red epaulets) in noisier habitats (Ríos-Chelén et al. 2015). They found no effect of the ambient noise on the intensity of visual displays although males in the noisier habitats did change some features of their vocalizations.

How animals deal with noise in multiple modalities has been examined in relatively few studies, although it is increasingly becoming a focus of attention (Brumm and Slabbekoorn 2005; Halfwer and Slabbekoorn 2015). We believe the aggressive signaling system of song sparrows (and related species like swamp sparrows; Ballentine et al. 2008; Anderson et al. 2013) provides an excellent model system to address how noise affects multimodal signaling. As noted, wing waves and soft songs are highly correlated with each other and are therefore likely to be redundant, although noisy conditions in one modality may change the perception of these signals (Halfwerk and Slabbekoorn 2015).

In summary, we confirmed earlier findings that urban song sparrows are more aggressive than rural song sparrows and also found that urban birds use soft songs as an honest signal, despite the expectation that urban noise may make it a less effective signal. Given the scarcity of studies on the honesty of acoustic signaling in urban habitats (despite a plethora of studies on how anthropogenic noise affects signal feature), it is still an open question whether urbanization, in general, alters honesty of communication systems found in less disturbed habitats. We also found that urbanization may affect multimodal 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 multimodal signaling evolves under anthropogenic habitat change.

**SUPPLEMENTARY DATA**

Supplementary data are available at Behavioral Ecology online.

**FUNDING**

This work was supported by funding from Virginia Tech Global Change Center and Fralin Life Sciences Institute. We would like to thank Ben Vernasco and John Gerwin for providing taxidermic mounts and Sam Lane for his help in the field.

**Ethics:** All procedures in the study reported here were conducted under the appropriate State (Virginia Department of Game and Inland Fisheries permit 80538685) 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 accessibility: Analyses reported in this article can be reproduced using the data provided by Akçay et al. (2019). R-script required to reproduce the results is included as a Supplementary Material.

**Handling editor:** Niels Dingemanse

**REFERENCES**


Akçay Ç, Beck ML, Sewall K. 2019. Data from: are signals of aggressive intent less honest in urban habitats? Behav Ecol. https://doi.org/10.5061/dryad.2fz7h


Davies S, Beck ML, Sewall KB. 2018. Territorial aggression in urban and rural Song Sparrows is correlated with corticosterone, but not testosterone. Horm Behav. 98:8–15.


Evans J, Boudreau K, Hyman J, Dabelsteen T, McGregor PK, Lampe HM, Langmore NE, Holland J. 1998. Amplitude regulation of vocalization may affect multimodal 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 multimodal signaling evolves under anthropogenic habitat change.


Davies S, Beck ML, Sewall KB. 2018. Territorial aggression in urban and rural Song Sparrows is correlated with corticosterone, but not testosterone. Horm Behav. 98:8–15.


Davies S, Beck ML, Sewall KB. 2018. Territorial aggression in urban and rural Song Sparrows is correlated with corticosterone, but not testosterone. Horm Behav. 98:8–15.


