

Effects of habitat and urbanization on the active space of brown-headed cowbird song

Megan D. Gall^{a)}

Neuroscience Institute, Georgia State University, Atlanta, Georgia 30303

Kelly L. Ronald, Eric S. Bestrom, and Jeffrey R. Lucas

Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907

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The ability of a receiver to detect a signal is a product of the signal characteristics at the sender, habitat-specific degradation of the signal, and properties of the receiver's sensory system. Active space describes the maximum distance at which a receiver with a given sensory system can detect a signal in a given habitat. Here the effect of habitat structure and urbanization on brown-headed cowbird (*Molothrus ater*) perched song active space was explored. The active space of the cowbird song was affected by both habitat type and level of urbanization. High frequency (4 to 6 kHz) portions of song resulted in the maximum active space. Surprisingly, the active space was the largest in open urban environments. The hard surfaces found in open urban areas (e.g., sidewalks, buildings) may provide a sound channel that enhances song propagation. When the introductory phrase and final phrase were analyzed separately, the active space of the introductory phrase was found to decrease in open urban environments but the active space of the final phrase increased in open urban environments. This suggests that different portions of the vocalization may be differentially influenced by habitat and level of urbanization.

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I. INTRODUCTION

At its most basic, animal communication involves a sender producing a signal which travels through an environment and is detected by a receiver (Bradbury and Vehrencamp, 1998). The quality of this signal when it is detected is determined by the intrinsic properties of the signal and habitat-specific signal degradation. Signal degradation differs among habitats because different environments impose different constraints on the propagation of acoustic signals. For instance, acoustic signals in forests are subject to reverberation and scattering during propagation, which tends to favor lower-frequency tonal sounds (Morton, 1975; Marten and Marler, 1977; Wiley and Richards, 1978). In open habitats wind masks low-frequency sounds and adds slow-modulations to acoustic signals during propagation, which tends to favor higher frequency and more rapidly modulated signals (Morton, 1975; Marten and Marler, 1977; Wiley and Richards, 1978). These habitat-specific propagation constraints are thought to result in a close match between signal and habitat both within and across species [acoustic adaptation hypothesis (Hunter and Krebs, 1979; Boncoraglio and Saino, 2007)].

While the habitat-specific attenuation and degradation of a signal plays a large role in the ability of a receiver to detect that signal, the detection of the signal is also a product of the receiver's sensory system. For an acoustic signal, the active space (the distance from the sender at which a signal can be detected) is determined by the propagating signal, the extent

to which that signal is masked by noise in the environment and the critical ratios of the receiver's sensory system (Marten and Marler, 1977; Brenowitz, 1982; Lohr *et al.*, 2003). The critical ratio is the lowest level of a signal (in dB) at which the signal is detectable in noise minus the spectrum level of the masking noise (dB/Hz). The critical-ratio varies across frequencies and across species. Therefore, determining the active space of a signal requires that we determine not only the level of the signal and the level of the masking noise at a given frequency but that we compare that ratio to the critical ratio of the species of interest at that frequency.

Anthropogenic disturbance can also play a role in the propagation and active space of signals. Anthropogenic structures (e.g., buildings, roads) in urban environments tend to reflect sound which causes reverberation. This reverberation can interfere with the phase or time domain of signals (Bradbury and Vehrencamp, 1998). Signals in urban environments are also subject to masking by low-frequency, high-amplitude anthropogenic noise, such as traffic noise (Slabbekoorn and Ripmeester, 2007). The active space of equivalent signals is therefore expected to be smaller in urban environments than in similar non-urban environments (Nemeth and Brumm, 2010). However, recent work suggests that urban habitats may actually degrade songs less than woodland habitats (Mockford *et al.*, 2011), suggesting that we need more information about how sound propagates through urban landscapes.

Here we explored the active space of brown-headed cowbird (*Molothrus ater*) perched song using song playbacks in four different sites: urban and non-urban habitats that were either open (e.g., fields) or closed (e.g., woodlands). Brown-headed cowbirds are a particularly interesting

^{a)}Author to whom correspondence should be addressed. Electronic mail: mgall1@gsu.edu

species in which to study sound propagation and active space for a number of reasons. Brown-headed cowbirds tend to prefer ecotonal (transitional or gradient) habitats (Lowther, 1993) and their signals are therefore subject to propagation constraints of both open and closed habitats. They also have a unique song with a very broad frequency range (West *et al.*, 1979). The perched song of the eastern brown-headed cowbirds consists of three parts: The first phrase (*P1* or the “glug-glug”), an interphrase unit (IPU) and the second phrase (*P2* or “glee”; see Fig. 1). *P1* consists of one to four introductory notes that are low-amplitude and low to mid-frequency (0.5 to 4 kHz). The IPU is usually between 8 and 12 kHz and consists of a short frequency sweep into a short tone. *P2* consists of rapid frequency sweeps between 3 and 12 kHz followed by a longer pure tone (West *et al.*, 1979; King *et al.*, 1981). West *et al.* (1979) show that the *P1* and IPU elements are important in the female choice, whereas the presence of the *P2* element is less salient in eliciting a female response. The *P2* element may be more important in male–male communication (West *et al.*, 1979), although this conjecture has yet to be tested explicitly.

The three parts of the brown-headed cowbird song are likely to be subject to different propagation constraints in open vs closed habitats and urban vs non-urban habitats. Therefore, we calculated the active space for (1) the entire brown-headed cowbird song, (2) the introductory phrase (*P1* or glug glug), and (3) the final phrase (*P2* or glee) in each of the four habitats. Reverberation in both urban and closed habitats should favor low-frequency and tonal elements, while frequency sweeps and high frequency elements would be subject to greater attenuation. On the other hand, open environments should favor higher frequency elements and frequency sweeps, while low-frequency and tonal sounds would suffer from wind-added modulations. In open habitats low-frequency wind-generated noise tends to be

higher in amplitude than wind-generated noise in closed habitats. Therefore, low frequency elements are more likely to be masked in open habitats than in closed habitats. In contrast, high-frequency insect-generated noise is usually higher in amplitude in closed (forest) habitats (Slabbekoorn, 2004). Therefore, in closed habitats high frequency elements are more likely to be masked and the active space of a brown-headed cowbird song is likely to be driven by lower frequency elements. Finally, anthropogenic noise in urban habitats tends to be low-frequency and higher in amplitude compared to non-urban habitats (Slabbekoorn and Ripmeester, 2007). Therefore, in urban habitats we expected that low frequency elements would be subject to greater masking than higher frequency elements, and that detection of high frequency elements would drive the active space of the signal in urban habitats.

II. METHODS

A. Song exemplars

We recorded song exemplars of ten male cowbirds for our playback experiment. Brown-headed cowbirds were acquired from USDA APHIS and housed in the Purdue University small animal building. The birds were housed in a communal aviary and kept on a 14:10 L:D light cycle. Birds were provided with mixed seed, grit, and vitamin-treated water *ad libitum* and supplemented with mealworms. All animal use was approved by the Purdue Animal Care and Use Committee (protocol # 11-066).

All exemplars were recorded in a 3 × 3 × 4 m room lined with acoustic tiles and acoustic foam (Foam Factory, Clinton Twp., MI). The background noise level in the recording chamber was <40 dB during the recordings with most of this energy below 200 Hz. Three male cowbirds were placed in a 0.5 × 0.5 × 0.5 m wire mesh cage with a single perch. A Sennheiser ME66 short directional microphone powered by a K6 powering unit was placed outside of the cage and 0.6 m from the perch. We recorded songs from a total of 10 groups over 2 days, with each trial lasting approximately 30 min. From each group we selected a single song exemplar. If songs were shared among males, any given song type was only selected once and as a result each song was a unique exemplar (see Fig. 1). All recordings were sampled at a rate of 44.1 kHz on a Marantz PDM-690 professional solid-state recorder and saved as .wav files. In two additional trials we replaced the microphone with a sound level meter (A-weighting, Radio Shack model 33-2055) to determine the peak amplitude of the cowbird song (generally 80 dB at 0.6 m).

B. Field methods

We conducted our propagation study at a number of private, public, and Purdue University properties in Lafayette and West Lafayette, Indiana, where brown-headed cowbirds had previously been seen vocalizing. We selected three sites for each of four categories: Urban closed, urban open, non-urban closed, and non-urban open. Urban sites were primarily located in Lafayette, IN (population density range: 400 to

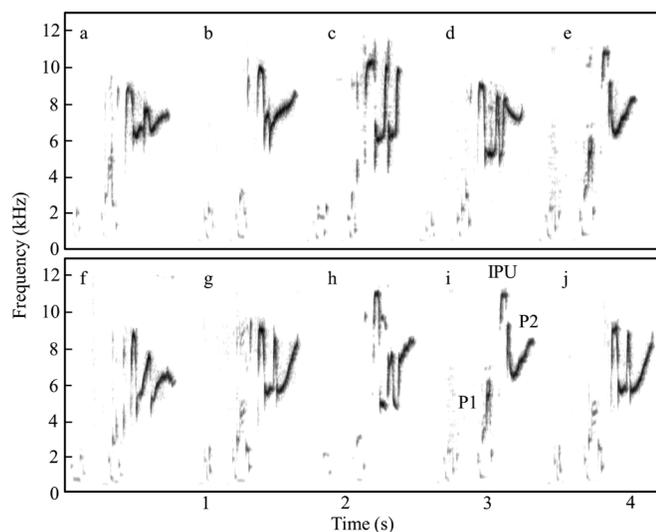


FIG. 1. Spectrograms of the ten exemplars used for the playbacks (a–j). Each exemplar came from a different male and we attempted to select unique exemplars, although some song types were shared among males. Each exemplar consists of a sequence of introductory notes (*P1*), an IPU, and a concluding phrase (*P2*; labeled on exemplar i). The spectrograms were created in PRAAT with a Gaussian Window (window length = 0.1 ms) and a dynamic range of 70 dB.

4000 people/km²; US Census Bureau, 2010) and on the Purdue University Campus in West Lafayette, IN (population density range: 4000 to 8000 people/km²; US Census Bureau, 2010). These areas were subject to heavy pedestrian and automotive traffic and were nearby to many man-made structures such as buildings, roads, and bridges. Non-urban sites were located in the Lafayette/West Lafayette metropolitan area, at least 200 m from roadways and buildings and subject to limited pedestrian and automotive traffic (population density range: 20 to 35 people/km²; US Census Bureau, 2010). For both rural and urban sites we defined open areas as having less than 25% tree cover and/or shrub cover and an open understory. Closed sites had greater than 75% tree and/or shrub cover. Cover was determined by trained observers at ground level by comparison to a standardized percent cover chart. The distance between sites was at least 1 km, but no more than 40 km.

All field playbacks were conducted between the hours of 07:00 and 09:00 EDT from June 15 to August 15, 2011. At the start location an amplified field speaker (Saul Mineroff Electronics, Elmont, NY, model: SME-AFS, frequency response: 0.1 to 12 kHz) was placed on a platform 1.9 m above and parallel to the ground. The speaker was connected to an Olympus DS-30 digital voice recorder which held the exemplar .wav files. We then placed a second platform at the same height at a distance of 0.6 m from the speaker. We placed a sound level meter on the platform and adjusted the playback level so that the songs had the same peak amplitude (80 dB) as that measured during an exemplar recording (see above). We then replaced the sound level meter with a Sennheiser ME67 long directional microphone powered by a Sennheiser K6 powering unit. The microphone was connected to a Marantz PDM-690 professional solid-state recorder. The recording level of the Marantz was set so that the voltage of the .wav file recorded at a distance of 0.6 m produced an intensity measurement of 80 db in PRAAT (ver. 5.1.32; Boersma and Weenink, 2009). Prior to our field playbacks we tested this setup in the same room in which we recorded our exemplars from the live birds (see above). We then cross-correlated these recordings with the original exemplar recordings and found that this setup reproduced our recordings faithfully (all normalized cross-correlation values >0.95).

Our stimuli set consisted of each of ten exemplars played in triplicate. The arrangement of the exemplar replicates on the recording was randomized, but fixed across trials. A 0.1 ms click preceded the exemplars and allowed us to accurately determine the beginning of the stimulus train in each recording. We recorded the stimulus train at a distance of 0.6, 1, and 5 m and from 10 to 100 m in 10 m increments. We moved the speaker and its platform rather than the microphone in order to minimize fluctuation in background noise at the recording location, taking care to level the platform and align the speaker and microphone. We repeated this recording procedure twice at each site. We also recorded 1-min of background noise before each of the trials and after the final trial (3 samples).

In the lab we transferred the field recording of the propagated cowbird song to a computer as .wav files. We then used PRAAT to isolate (1) the entire song, (2) the first

phrase, and (3) the final phrase for each exemplar replicate. We used two techniques to estimate active space: A masked threshold technique and a cross-correlation technique.

C. Active space—masked thresholds

In the masked threshold technique the signal-to-noise ratio (SNR) for the stimulus at each propagated distance is compared to the critical ratios of the brown headed-cowbird auditory system. In cowbirds, critical ratios are available for pure tones but not for cowbird songs. Therefore, this technique requires us to analyze the song in separate frequency bands.

To determine active space for a species-specific signal using the masked threshold technique we need three pieces of information: The critical ratios of the organism, the spectrum level of the masking noise, and the sound level of the signal. We obtained critical ratios for blackbirds (red-wing blackbirds and cowbirds combined) from the literature (Hienz and Sachs, 1987). We extrapolated critical ratios for our frequencies of interest. Blackbird critical ratios are published for frequencies ranging from 0.25 to 8 kHz. Therefore for frequencies from 8 to 12 kHz we use the critical ratio at 8 kHz. This likely results in an overestimate of the active space for signal elements above 8 kHz, as frequency sensitivity drops off above 8 kHz in most songbirds (Dooling *et al.*, 2000) and in brown-headed cowbirds, specifically (Hienz *et al.*, 1977).

We concatenated the three recordings of background noise for each site using a PRAAT script. We then created a power spectrum and extracted the spectrum level of the noise (dB/Hz) from 0.2 to 12 kHz in 200 Hz intervals. We then created a power spectrum for each of the cowbird song exemplars at each distance and extracted the amplitude of the propagated stimulus from 0.2 to 12 kHz in 200 Hz intervals. We then subtracted the noise spectrum level from the signal level to create a SNR. The signal should be detectable in a given frequency band if the SNR value is greater than the critical ratio. We then regressed the SNR on propagation distance and determined the propagation distance at which the SNR intercepted the critical ratio (i.e., SNR-CR = 0) for each frequency using PROC REG in SAS 9.2 (see Fig. 2, for example). The resulting value provides an estimate for the active space of the signal at that frequency band. For each song exemplar we found the frequency band with maximum active space. We used this value as the active space for the entire song.

D. Active space—cross-correlation

Cross-correlation is a way to measure the similarity between two waveforms as a function of a time-lag applied to one waveform. We used normalized cross-correlation values where identical waveforms will have a score of 1, while a waveform cross-correlated with white noise will have an average cross-correlation value of 0. Here active space is defined as the distance at which the cross-correlation value of propagated signal with the reference signal (signal at 0.6 m) intercepts the noise floor. This method takes into account many types of degradation and its effect on the entire

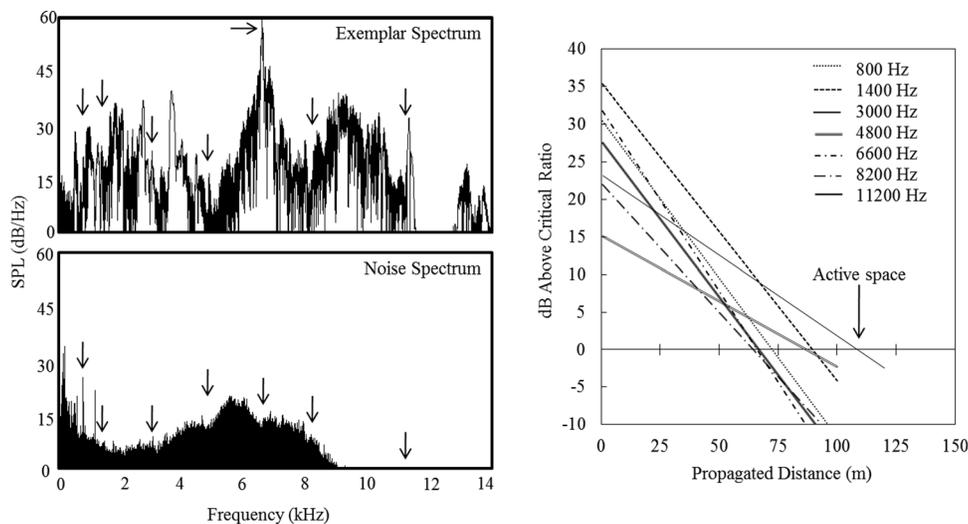


FIG. 2. Example of active space construction for song exemplar *c* in a non-urban closed habitat. Pictured top left is the power spectrum for the first replicate of song *c* recorded at 1 m and the bottom left is the spectrum of the noise. The noise was subtracted from the signal to get a SNR. Pictured right is an example of the regression technique used to determine the active space of the signal for several frequencies (indicated by arrows in power spectrums). The active space at each frequency is the distance at which SNR was equal to the critical ratio. The active space for the signal was defined by the frequency with the largest active space.

waveform but does not incorporate the receiver's sensory processing. We calculated active space for the entire song, the introductory phrase, and the final phrase using this method.

First we cross-correlated the stimulus that was recorded at 0.6 m with the stimulus recorded at each subsequent distance. This gave us a normalized cross-correlation value for each propagation distance. We also cross-correlated the stimulus recorded at 0.6 m with the background noise. Cross-correlation with background noise resulted in a distribution of cross-correlation values that had a normal distribution and a mean of 0. We determined the standard deviation of the cross-correlation value and calculated a 95% confidence interval for the background noise. We then regressed the cross-correlation values for each stimulus on distance using PROC REG in SAS 9.2 and determined the intercept of this function with the 95% confidence interval of background noise. This intercept represents the distance at which the signal cannot be statistically distinguished from background noise and therefore provides a second estimate for the active space of the signal.

E. Statistics

We used mixed models (PROC MIXED, SAS 9.2) to address factors affecting active space calculated using both the masked threshold and cross-correlation methods. For the masked threshold we first determined whether different frequency bands had different active spaces and whether this pattern was affected by habitat and urbanization. Here the dependent variable was active space and the independent variables were frequency band (0.2 to 12 kHz), habitat (open or closed), urbanization level (urban or non-urban), song exemplar (songs a–j), and their interactions. We then determined whether the active space for the song (dependent variable) was affected by the independent variables habitat type, urbanization, song exemplar, and their interactions. Finally, we determined whether the frequency driving the maximum active space (dependent variable) was affected by habitat type and urbanization (independent variables).

We ran separate models using data derived from the cross-correlation method to investigate the active space of the (1) entire song, (2) the introductory phrase, and (3) the

final phrase. In each cross-correlation model active space was the dependent variable and the independent variables were habitat, urbanization, song exemplar, and their interactions. Non-significant interaction effects ($P > 0.05$) were removed from each model in order of P -value and are not reported in the results. Therefore, final models differ in the interaction terms that were included. Significant interaction effects were investigated *post hoc* with the diff option in the LSMEANS statement. The P -values were adjusted with the Tukey method. We used between-within degrees of freedom for all models. Residuals for all models were checked for normality in PROC UNIVARIATE (SAS 9.2).

III. RESULTS

A. Noise profiles

The noise profiles of the closed and open habitats were relatively similar in non-urban areas. There was little wind during our recording sessions (wind speed < 0.5 m/s), which likely contributed to the similarity of the noise profiles (Fig. 3). Noise in non-urban habitats was primarily generated by light winds and distant traffic (< 2 kHz) and by insects (~ 5 to 8 kHz). The noise levels were significantly higher in urban habitats than in non-urban habitats ($F_{1,9} = 12.11$, $P = 0.007$), with urban habitats having a mean noise level of 50.88 ± 2.57 dB sound pressure level (SPL) and rural habitats having a mean noise level of 38.25 ± 2.57 dB SPL. This difference was primarily due to increases in low frequency noise generated by traffic in urban areas. There were no significant differences in the overall noise levels between open and closed habitats ($F_{1,9} = 0.29$, $P = 0.6$). Low frequency noise strongly masked the low frequency components of the brown-headed cowbird song in all habitats (Fig. 3). Also, vehicular traffic and airplanes made noise in the urban sites more episodic (Fig. 3).

B. Active space—masked thresholds

The active spaces calculated using the masked threshold technique varied across frequency bands ($F_{59,44000} = 323$, $P < 0.001$) and habitat ($F_{1,44000} = 1804$, $P < 0.001$) but there was no significant main effect of urbanization

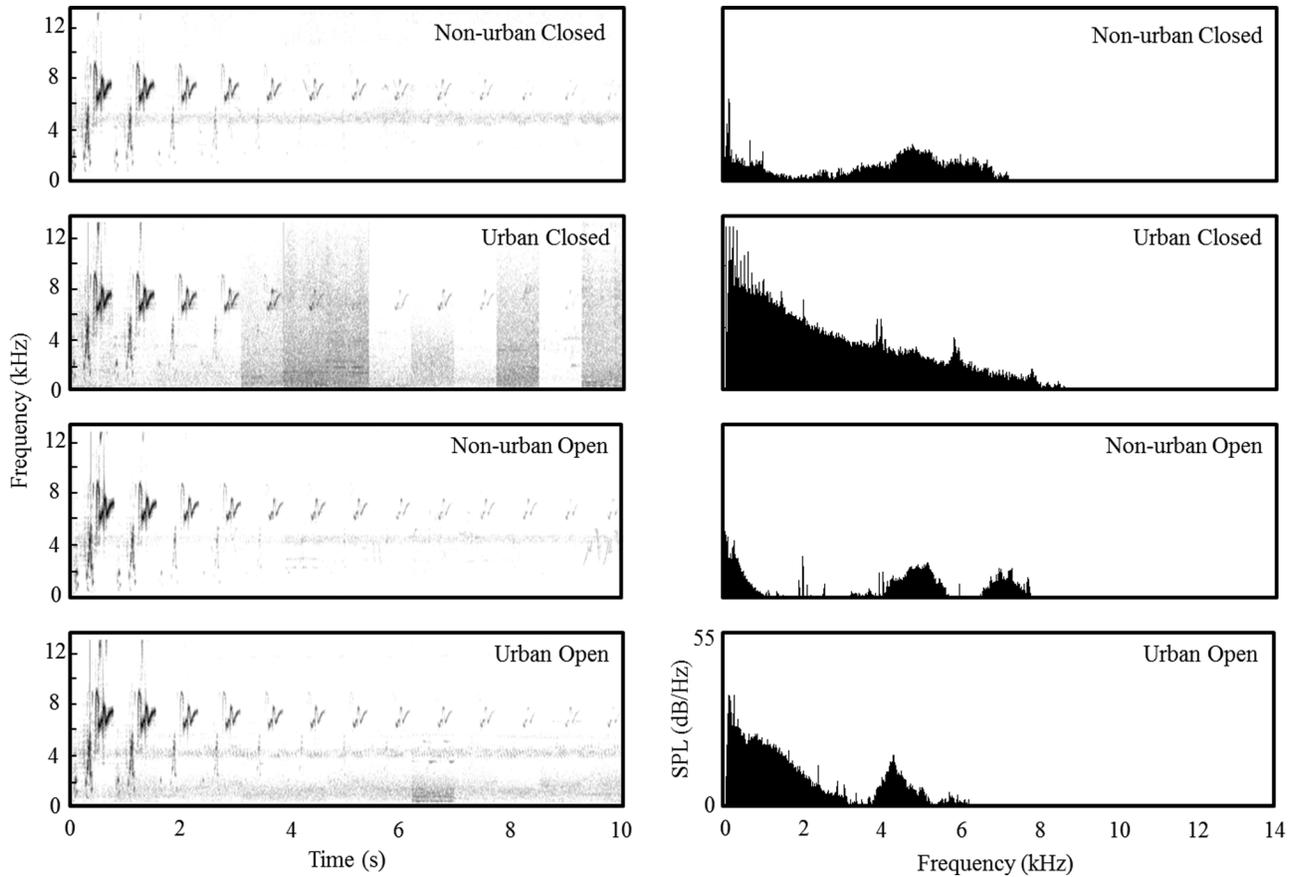


FIG. 3. Spectrograms of a song that were recorded after propagating in each of the four habitats are shown on the left. Exemplars are in order of propagation distance and include recordings at 0.6, 1, and 5 m and from 10 to 100 m in 10 m increments. The spectrograms were created in PRAAT with a Gaussian Window (window length = 0.1 ms) and a dynamic range of 70 dB. Power spectra for noise in each of the four habitats are shown on the right. Low frequency noise had more power in the urban than non-urban habitats. In most habitats there was a second peak of noise from 5 to 8 kHz that was generated by insects. In non-urban closed habitats there was also a third spectral peak that was generated by insects and the song of other bird species. The power spectra were created in PRAAT from a concatenation of all the recordings of noise in a given habitat.

($F_{59,44000} < 0.01$, $P = 0.99$). These main effect patterns were complicated by a significant three-way interaction whereby the active space in different frequency bands varied in different ways with habitat and urbanization [habitat \times urbanization \times frequency: $F_{118,44000} = 33.6$, $P < 0.001$ (significant two-way effects: Habitat \times urbanization $F_{1,44000} = 1071$, $P < 0.001$; urbanization \times frequency $F_{59,44000} = 55.27$, $P < 0.001$)]. The most striking feature in this three-way interaction was that the active space for frequencies at 6 kHz (± 1 kHz) were substantially larger in open urban areas than they were in any other habitat-urbanization combination (Fig. 4). Additionally, the active space for lower frequencies (< 2 kHz) was much smaller in urban areas, suggesting that masking noise at low frequencies is reducing the active space for these elements. Above 8 kHz there was little difference between the habitats and levels of urbanization (Fig. 4).

The maximum active space (i.e., active space for the entire brown-headed cowbird song) varied with exemplar ($F_{9,710} = 5.5$, $P < 0.001$), habitat ($F_{1,710} = 233$, $P < 0.001$) and urbanization ($F_{1,710} = 10.8$, $P = 0.001$). The active space for different exemplars ranged from an average of 88 ± 1.7 to 101 ± 1.7 m [Fig. 5(a)] and differed with urbanization (exemplar \times urbanization: $F_{9,710} = 2.1$, $P = 0.03$) but not across habitats (exemplar \times habitat: $F_{9,710} = 1.5$, $P = 0.2$).

As we predicted, the active space tended to be greater in open habitats than in closed habitats [Fig. 5(b)]. Contrary to our predictions, however, we found that active space was actually greater in urban areas than in non-urban areas

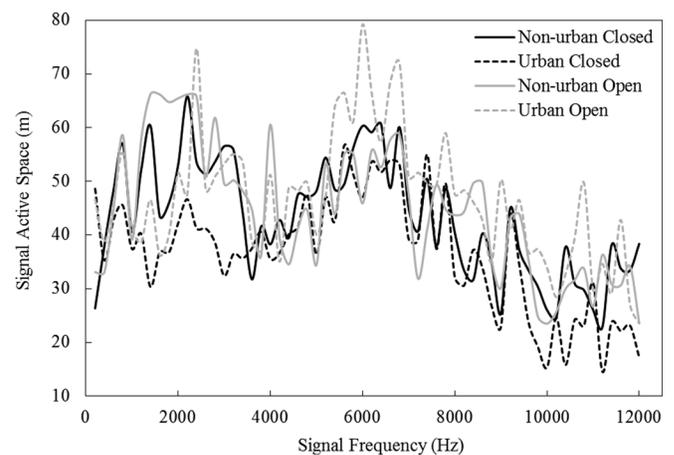


FIG. 4. Active space as a function of frequency for each of the four habitat types averaged across exemplars using the masked threshold method. There are two main peaks in active space—one at lower frequencies representing active space of the introductory phrase (P1) and one at a higher frequency representing the final phrase (P2). Standard errors ranged from 1.01 to 1.67 m.

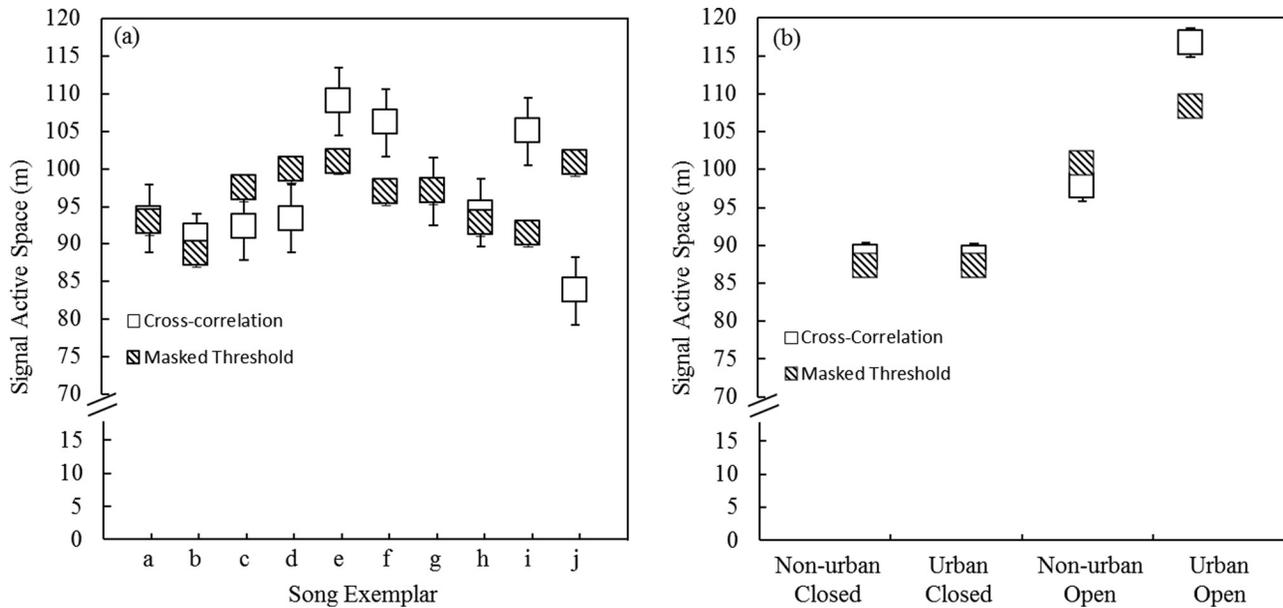


FIG. 5. (a) Active space of each of the ten song exemplars (entire song) averaged across all recording sites using both the cross-correlation method and the masked threshold method. (b) Active space of the entire brown-headed cowbird song in each of the four habitat types averaged across all exemplars. Data shown are lsmeans \pm S.E. which were generated by the LSMEANS statement in PROC MIXED for SAS 9.2.

despite the higher overall noise levels in urban areas. This pattern was complicated by a significant interaction of habitat and urbanization (habitat \times urbanization: $F_{1,710} = 11.3$, $P < 0.001$). In closed habitats there was no significant difference in active space between urban and non-urban areas; however, in open habitats active space was greater in urban areas than it was in non-urban areas [Fig. 5(b)].

The maximum active space of the brown-headed cowbirds song was primarily determined by the final pure tone whistle (P_2) and the frequency driving the active space differed with exemplar ($F_{9,710} = 4.4$, $P < 0.001$) because of differences in the frequency of the whistle (Fig. 6). Generally, exemplars with lower frequency whistles tended to have larger active spaces than exemplars with higher frequency whistles. The frequencies which primarily contributed to

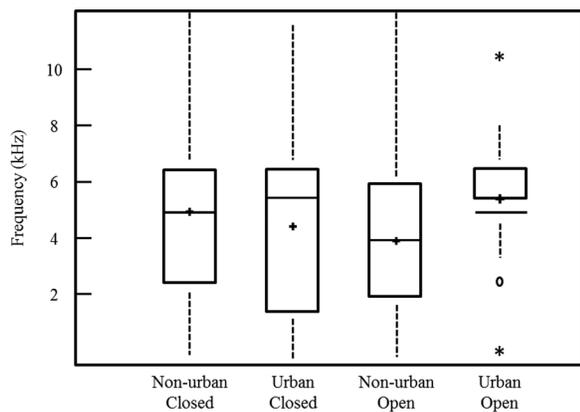


FIG. 6. Box and whisker plot of the frequency band that had the maximum active space (highest SNR at threshold) in each of the four habitats. This active space in this frequency band was then used as the active space for the entire song. The plot shows the mean (+), median (—), interquartile range, and potential outliers (o,*). The dotted lines indicate the entire range of frequencies driving active space in each of the four habitats (excluding outliers).

active space varied with urbanization ($F_{1,710} = 7.4$, $P = 0.007$). There was no significant main effect of habitat type ($F_{1,710} = 0.4$, $P = 0.84$) but this pattern was complicated by a significant interaction of urbanization and habitat (habitat \times urbanization: $F_{1,710} = 22.9$, $P < 0.001$; Fig. 5). In open habitats the frequencies driving active space were higher in urban areas (mean \pm S.E. = 5440 ± 145 Hz) than in non-urban areas (mean \pm S.E. = 4141 ± 205 Hz). However, in closed habitats the frequencies driving active space were slightly lower in urban areas (mean \pm S.E. = 4576 ± 195 Hz) than in non-urban areas (mean \pm S.E. = 4934 ± 181 Hz) but the difference was not as great as in open habitats.

C. Active space—cross-correlation

The active space of the entire song based on the cross-correlation method varied with exemplar ($F_{9,749} = 3.06$, $P = 0.001$) and ranged from 83.7 ± 4.3 to 109 ± 4.5 m [Fig. 4(a)]. There were no significant interaction effects that included exemplar. Active space also differed across habitat ($F_{1,749} = 43.37$, $P < 0.001$) and urbanization level ($F_{1,749} = 10.6$, $P = 0.001$). This relationship was complicated by a significant habitat \times urbanization interaction ($F_{1,749} = 11.06$, $P < 0.001$), whereby active space was larger in urban open areas than non-urban open areas ($t_{749} = 4.6$, $P < 0.001$), while in closed habitats active space did not differ between non-urban and urban areas [$t_{749} = 0.05$, $P = 0.96$; Fig. 4(b)].

Active space of the introductory element varied with habitat type ($F_{1,740} = 38.9$, $P < 0.001$) and urbanization ($F_{1,740} = 71.1$, $P < 0.001$). There was also a significant interaction between habitat and urbanization ($F_{1,740} = 81.7$, $P < 0.001$; Fig. 7). The active space of the introductory element was larger in closed non-urban habitats than in closed urban habitats ($t_{740} = 12.5$, $P < 0.001$), while in open habitats there was no significant difference between levels of

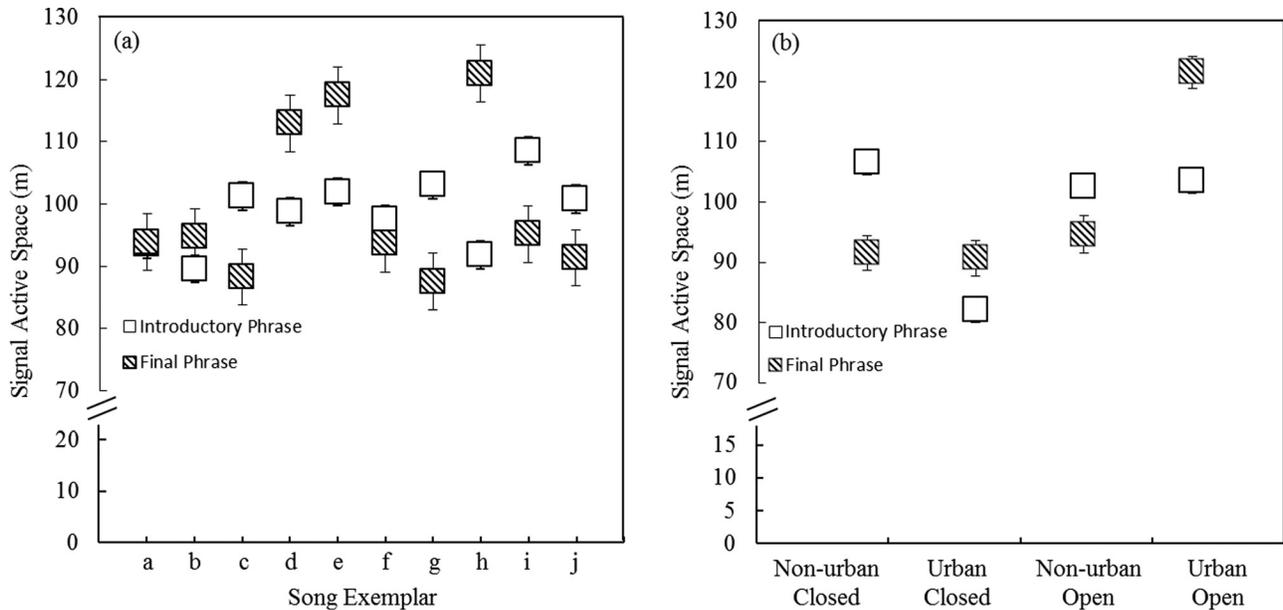


FIG. 7. (a) Active space for the introductory phrase (P1) of a brown-headed cowbird song and the final phrase (P2) for each of the exemplars. (b) Active space for the introductory phrase (P1) of a brown-headed cowbird song and the final phrase (P2) in each of the four habitat types averaged across all exemplars estimated using the cross-correlation method. Data shown are lsmeans \pm S.E. which were generated by the LSMEANS statement in PROC MIXED for SAS 9.2.

urbanization in active space ($t_{740} = 0.42$, $P < 0.67$). The active space of the introductory element also varied among exemplars ($F_{9,740} = 6.7$, $P < 0.001$; Fig. 7) and differences in active space between the exemplars varied with level of urbanization (exemplar \times urbanization: $F_{9,740} = 2.8$, $P = 0.002$).

The active space of the final element varied from $87 \text{ m} \pm 4.7 \text{ m}$ to $121 \text{ m} \pm 4.6 \text{ m}$ [Fig. 7(a)]. Exemplar ($F_{9,722} = 7.3$, $P < 0.001$), habitat ($F_{1,722} = 34.2$, $P < 0.001$), and urbanization ($F_{1,722} = 20.1$, $P < 0.001$) all had a significant impact on active space. A significant three way interaction complicates the main effects: Active space of the exemplars varied in different ways with habitat type and urbanization [habitat \times urbanization \times exemplar $F_{9,722} = 5.3$, $P < 0.001$ (two-way interactions: habitat \times exemplar $F_{1,722} = 3.1$, $P = 0.001$; habitat \times urbanization $F_{1,722} = 22.7$, $P < 0.001$; urbanization \times exemplar $F_{9,722} = 1.3$, $P = 0.23$)]. Generally, urbanization increased active space in open areas; however, the size of this effect differed across exemplars. For some of the exemplars (e.g., a, b, and i) the degree of change among the habitats and levels of urbanization was moderate (10 to 15 m). However, for other exemplars there were dramatic changes in the active space across habitats and urbanization levels ($>30 \text{ m}$). For all but one exemplar, open urban areas produced the largest active space. The smallest active space was found in closed urban habitats for four exemplars, closed non-urban habitats for five exemplars, and open non-urban for one exemplar.

IV. DISCUSSION

A. Urbanization and communication

As predicted, the active space of the brown-headed cowbird song varied with both the type of habitat (open vs closed) and the level of urbanization. Moreover, the effects of urbanization on the active space of the brown-headed

cowbird song differed among the habitat types. In closed habitats we found that the active space of the song did not differ across levels of urbanization. Interestingly, in open areas we found that the active space of the cowbird song was larger when the habitat was urban despite overall higher noise levels in urban compared to non-urban areas. This was true of active spaces calculated using both the cross-correlation and masked threshold technique.

Our finding that the active space of the brown-headed cowbird perched song was larger in open urban areas may be due to spectral release of the cowbird song from anthropogenic masking noise (Klump and Nieder, 2001). The brown-headed cowbird song spans a large frequency range, while anthropogenic noise tends to be low in frequency. Therefore, higher frequency elements of the brown-headed cowbird song are unlikely to be masked by anthropogenic noise. Indeed, we found that in open areas it was these higher frequencies which were primarily responsible for the maximum active space of the brown-headed cowbird song. Many species have been found to increase the minimum frequency of their songs in urban areas, possibly to avoid masking by anthropogenic noise (Cardoso and Atwell, 2011; Francis *et al.*, 2011a,b; Hanna *et al.*, 2011).

Our work was conducted when leaves were out, which should contribute to the decreased active space in wooded areas as leaves accentuate attenuation (Blumenrath and Dabelsteen, 2004). The larger active space in open urban areas could also be the result of a “sound window” for higher frequency elements. The coordinated reflection of high frequencies by hard surfaces (roads, buildings) can enhance the propagation of these signals, ultimately resulting in higher SNRs at the receiver (Slabbekoorn *et al.*, 2002; Nemeth *et al.*, 2006).

For example, Mockford *et al.* (2011) found that urban areas degraded songs less than rural areas when leaves were not out, suggesting some persistent feature of urban

environments that alters signal propagation. Future work should focus on seasonal changes in signal propagation in rural and urban areas.

We found that the active space of the introductory phrase, *P1*, and final phrase, *P2*, of the brown-headed cowbird song were differentially affected by the interaction of habitat and urbanization. The final phrase had a similar pattern to that of the entire song, with the active space being greatest in open urban areas, and approximately equivalent in all other habitat-urbanization combinations. For both the final phrase and the entire song, this is likely due to a release from low-frequency masking and a sound window for higher frequencies.

The active space of the introductory phrase was greater in closed non-urban environments than in closed urban environments. In open areas there was no effect of urbanization on the active space of the introductory elements. The frequency range of these introductory elements overlaps with the spectral range of anthropogenic noise. Therefore, in closed urban areas the lower frequency elements of song are likely to be masked. In open areas, wind (and its movement through vegetation) generates low frequency noise (Morton, 1975); therefore, the addition of anthropogenic noise may not substantially increase the degree to which these signals are masked in the environment. Together these results suggest that although the active space of the entire song may not suffer substantially from anthropogenic noise, the introductory elements may be masked. Therefore, songs in urban environments may not have the same functional relevance as unmasked songs.

B. Brown-headed cowbirds, signal structure, and active space

The brown-headed cowbird is a particularly interesting species in which to examine the effects of habitat and urbanization on communication. Brown-headed cowbirds have larger and more varied home ranges than other songbirds primarily due to their brood parasitic reproductive strategy (Smith *et al.*, 2000). As a result, brown-headed cowbird home ranges will often span multiple habitat types with varying levels of urbanization (Rothstein *et al.*, 1986; Smith *et al.*, 2000). During the course of a day an individual cowbird will use spatially distinct areas for different behaviors: Closed habitats (forest and shrublands) are generally preferred in the morning, during egg laying, because these habitats contain more host nests, while open areas are preferred for foraging in the afternoon (Dufty, 1982; Rothstein *et al.*, 1984, 1986; Thompson and Djak, 2000).

The introductory phrase and final phrase of the brown-headed cowbird song are thought to have distinct functional roles in communication, with *P1* primarily being important for male–female communication in a breeding context, while *P2* may play a role in long distance communication and individual recognition (West *et al.*, 1979). We would expect, therefore, that *P1* would be adapted to propagate with minimal attenuation in closed habitats, where breeding activities are concentrated, while *P2* may be adapted to propagate with minimal attenuation in open areas where foraging

activities are concentrated. Indeed, we found that the effects of habitat and the level of urbanization affected the active space of the introductory phrase and the final phrase of the brown-headed cowbird song differently. This suggests that the various elements of the brown-headed cowbird song may reflect acoustic adaptations to the different environments in which they are of primary importance (Boncoraglio and Saino, 2007; Brumm and Naguib, 2009).

It is important to note that the active space of the brown-headed cowbird song was substantially smaller than the active space of the closely related red-winged blackbird's song, calculated using similar methods (Brenowitz, 1982). This may be the result of conflicting selection pressures on brown-headed cowbird communication. On one hand, signals with minimal attenuation and large active spaces should enhance the ability of a male to attract or copulate with females. On the other hand, signals with very large active spaces may increase the chance of the signal being detected by either a conspecific or heterospecific eavesdropper. Cowbirds may therefore reduce the active space of their song to avoid cuckoldry by rival males (King *et al.*, 1981) or detection by potential hosts (Forsman and Martin, 2009). The selective pressure from eavesdroppers may be greater in brown-headed cowbirds than in other icterids because males do not defend a territory (Darley, 1982) and their reproductive success is dependent on their ability to locate and successfully parasitize host nests (Friedmann, 1929; Lowther, 1993). A sender could, in theory, produce a signal that is designed with structural features that minimize attenuation, and still vary the active space of the signal by manipulating the signal amplitude.

C. Habitat effects and auditory processing

In the animal communication literature, and indeed in this study, the signal processing abilities of a receiver are often treated as a fixed entity (reviewed in Dooling *et al.*, 2000). However, mounting evidence suggests that receivers may differ in their signal processing abilities according to their species identity (Dooling *et al.*, 2000; Henry and Lucas, 2008), sex (Henry and Lucas, 2010a; Gall *et al.*, 2011), or even breeding condition (Lucas *et al.*, 2007; Caras *et al.*, 2010). Therefore, the active space of a particular signal may differ among different classes of individuals. In the brown-headed cowbird, for instance, females have been shown to have lower auditory thresholds than males (Gall *et al.*, 2011). This suggests that the active space of a given signal may be larger when the intended receiver is a female than when the intended receiver is a male.

Receivers may also vary in the processing of auditory signals depending on the habitat they primarily occupy (Witte *et al.*, 2005). Species that occupy closed habitats have relatively narrow auditory filters that enhance the processing of pure tones, while open habitat species have wider auditory filters that enhance the processing of modulated elements (Henry and Lucas, 2010b). Narrower auditory filters are also expected to improve the detection of signals in noise because each “channel” in the auditory system admits a narrower noise bandwidth, while wider filters admit more noise into

each channel; therefore species with narrow filters tend to have lower critical ratios (Dooling *et al.*, 2000). This suggests that species occupying different habitats may differ in their sensitivity to anthropogenic masking noise and therefore in their ability to detect conspecific vocalizations in urban habitats.

Interestingly, male and female brown-headed cowbirds differ in the width of their auditory filters. Females have narrower filters than males and are more efficient at extracting signals from noise (Gall and Lucas, 2010). This suggests that females may be less sensitive than males to anthropogenic masking noise and, therefore, better able to detect and process vocalizations in urban areas. As researchers increase their use of psychoacoustic (Lohr *et al.*, 2003, Pohl *et al.*, 2009) and other behavioral experiments (Mockford and Marshall, 2009; Ripmeester *et al.*, 2010) to investigate the ability of receivers to detect or discriminate among songs in anthropogenic masking noise, it will be interesting to see if there is differential sensitivity among species or between sexes. Moreover, it would be valuable to determine whether traditional measures of auditory processing such as critical ratios (Hienz and Sachs, 1987; Langemann *et al.*, 1995; Wright *et al.*, 2003; Noiro *et al.*, 2011) or auditory filter bandwidths (Langemann and Klump, 2006; Gall and Lucas, 2010; Henry and Lucas, 2010b) are predictive of the ability of species to cope with anthropogenic disturbances to their acoustic communication.

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