

## Short communication

# Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*

PRISCILLA REDONDO,<sup>1</sup> GILBERT BARRANTES<sup>1</sup> & LUIS SANDOVAL<sup>2\*</sup>

<sup>1</sup>*Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica*

<sup>2</sup>*Department of Biological Sciences, University of Windsor, Windsor, ON, Canada*

Urban habitats are noisy and constrain acoustic communication in birds. We analysed the effect of anthropogenic noise on the vocalization characteristics of House Wrens *Troglodytes aedon* at two sites with different noise levels (rural and urban). We measured in each song and song trill the frequency bandwidth, maximum amplitude, highest and minimum frequency, and trill rate. In noisy urban environments, there was a reduction in bandwidth and an increase in trill rate relative to quieter, rural environments. The whole song of birds from both populations increased in minimum frequency as noise increased, improving song transmission.

**Keywords:** individual response, noise, song, trills, Troglodytidae, urban habitats.

In urban habitats, noise often affects communication between birds by masking songs (Slabbekoorn & den Boer-Visser 2006, Warren *et al.* 2006). In response, birds may sing more loudly (Brumm 2004), at night (Fuller *et al.* 2007) or with higher minimum frequencies (Slabbekoorn & Peet 2003, Bermúdez-Cuamatzin *et al.* 2011, Halfwerk *et al.* 2011). These changes often increase the energetic costs of song production (Lambrechts 1996). Noise and turbulence are thought to have favoured evolution of vocalizations that consist of short elements that are produced at a fast rate (e.g. trills), which transmit more efficiently (Slabbekoorn & den Boer-Visser 2006).

House Wrens *Troglodytes aedon* inhabit open and semi-open habitats ranging from forest edges to vege-

tated urban areas (Skutch 1953). These habitats vary in noise level, especially anthropogenic noise, which is higher in urban than in rural habitats (Slabbekoorn & den Boer-Visser 2006). Anthropogenic noise often overlaps with the minimum frequencies of House Wren songs (1.5 kHz) (e.g. Platt & Ficken 1986), possibly reducing the effectiveness of communication.

Considering noise constraints on song features (Slabbekoorn & den Boer-Visser 2006) and the importance of vocalizations in social interactions of House Wrens (Johnson & Kermott 1991, Johnson & Searcy 1996, Muller *et al.* 1997), we tested the effect of anthropogenic noise on temporal and frequency characteristics of House Wren songs. We first assessed whether trill features, a song element well adapted for acoustical transmission in open areas, differed between urban and rural habitats. We then tested the effect of changes in noise levels on the whole song of House Wrens at a population level. We predicted that a faster trill rate and songs with a higher minimum frequency in noisier environments would reduce song masking, as has been reported for other bird species (Wood & Yezerinac 2006, Mockford & Marshall 2009).

## METHODS

### Study sites

We sampled birds in two sites in the Costa Rican Central Valley that vary in urban development, traffic density and anthropogenic noise. The rural site is in the Heredia province (10°01'N, 84°05'W, between 1200 and 1500 m asl) and the urban site is on the Campus of the Universidad de Costa Rica (09°56'N, 84°05'W, 1200 m asl), 17 km away (see Biamonte *et al.* 2011 for site descriptions).

### Song recordings and noise measurements

We recorded House Wren songs from 29 March to 14 June 2010, using a Marantz PMD 661 digital recorder and a Sennheiser ME66 directional microphone, at a 44.1-kHz sample rate on WAVE format. All songs were recorded between 06:00 h and 10:00 h, 5–10 m from the focal bird, and at the same recording level. Birds were recorded during partially cloudy or clear days, and low wind conditions. All recordings were deposited in the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica.

We recorded only birds that were alone in their territories so as to avoid effects of social interactions on song characteristics (Searcy & Beecher 2009). A bird recording was stopped if the bird did not sing for 2 min or when it flew away. We used only recordings of at least 1 min in our analyses. Birds were not individually

\*Corresponding author.  
Email: biosandoval@hotmail.com

marked, so one person maintained contact with the bird just recorded while another located a new bird at a distance of at least 50 m. The minimum distance between two individuals recorded on different days was 100 m. This reduces the likelihood of re-recording the same individuals, because House Wren territories are smaller than 1 ha (Johnson 1998).

During a recording session, we registered the noise level every minute using a Sper Scientific 840014 mini sound meter (measuring range 32–130 dB, at fast response on A weight). We calculated the mean of the lowest and the highest noise value measured each minute.

### Song measurements

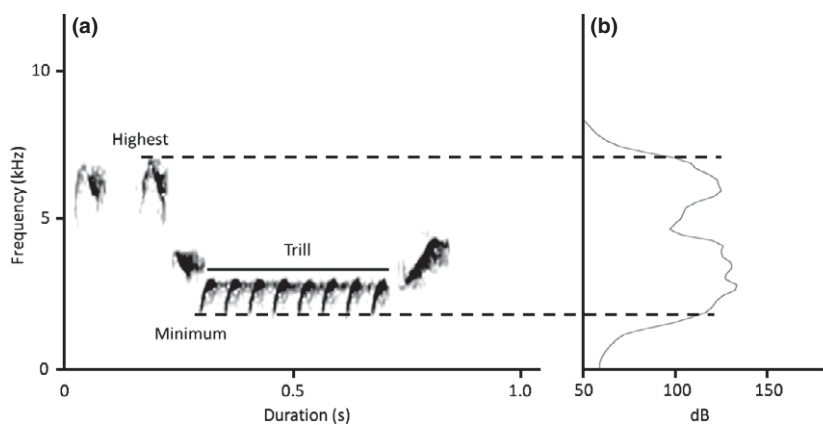
We divided recordings into 1-min intervals to match with noise measurements. To analyse the effect of noise on the whole song, we measured the maximum amplitude frequency (frequency with more energy), frequency bandwidth and minimum and highest frequencies, using a combination of spectrogram screen with the power spectrum in RAVEN PRO 1.4 (Fig. 1) (Charif *et al.* 2004). Frequency values in the power spectrum are not affected by the greyscale settings on the spectrogram screen or by background noise (Charif *et al.* 2004). For each trill, we obtained the same frequency measurements as for the whole song, trill duration (Fig. 1) and trill rate (number of trill elements per second). For statistical analyses of the whole song, we used the minimum value for the minimum frequency and the highest value for maximum amplitude frequency, highest frequency and frequency range in each minute. All acoustical analyses were conducted using RAVEN PRO 1.4 on the original recordings. The

spectrograms were digitized at 44 100 Hz and 16-bit and measurements were obtained using the following parameters: a frequency resolution of 256 samples, a grid spacing of 188 Hz and a time grid with 50% overlap using the window Hann function.

### Statistical analyses

To test the effects of noise on acoustic characteristics of the trill and song, we used general linear mixed models (GLMM) following Hanna *et al.* (2011). The normality assumption (Jiang 2007) for each response variable was verified using Kolmogorov–Smirnov tests ( $P > 0.07$  all comparisons), so no correction for overdispersion was needed (Zuur *et al.* 2009). Trill and song measurements in 1-min blocks were treated as replicates, with bird identity as a random effect. The two study sites (urban and rural) and their interaction with noise level were included in the model as fixed explanatory variables.

We conducted an additional analysis of the effect of noise on the trill. Trill performance is defined by the interaction between bandwidth and trill rate, and these variables are inversely correlated. Because noise affects the frequency of vocalizations in birds, we tested explicitly the effect of noise on trill performance. In this analysis, modelled noise is a function of the residuals of the regression between trill rate and trill bandwidth. Trills with high performance are those that have either a slower rate and larger bandwidth (trills with positive residuals at the left side of the regression) or trills with faster rate and smaller bandwidth (trills with negative residuals at the right side of the regression). Values reported are mean  $\pm$  1 se.



**Figure 1.** (a) House Wren song spectrogram showing the trill and the minimum and highest frequency measurements used for analysis. (b) Power spectrum used to define the highest and the minimum frequency in the song. Broken lines show the highest and minimum frequency limit in the spectrogram and the power spectrum. Maximum amplitude frequency and bandwidth are not represented in the figure because the maximum amplitude occurs when the bird allocates the maximum energy in the song and this is not visible in the spectrogram. Bandwidth is the difference between the highest and minimum frequency (the two broken lines).

## RESULTS

### Effect of noise on song between populations

In total, we recorded 1371 song-minutes from 20 individuals (14 at the rural and six at the urban site). The mean noise level was lower in the rural site ( $47.26 \pm 3.54$  dB) than in the urban site ( $55.12 \pm 4.39$  dB) ( $t_{136} = -10.22$ ,  $P < 0.001$ ).

Wrens at the urban site had songs with a lower highest frequency ( $F_{1,135} = 7.15$ ,  $P = 0.008$ , Table 1) and narrower bandwidth ( $F_{1,117} = 8.33$ ,  $P = 0.005$ , Table 1) but noise had no additional effect on these characteristics (highest frequency:  $F_{1,135} = 0.09$ ,  $P = 0.76$ ,  $\beta = -38.49 \pm 20.31$ ; bandwidth:  $F_{1,135} = 3.01$ ,  $P = 0.08$ ,  $\beta = -92.77 \pm 19.70$ ). Songs had a similar minimum frequency in both sites ( $F_{1,135} = 0.13$ ,  $P = 0.72$ ; Table 1), but increased with noise across sites ( $F_{1,135} = 39.18$ ,  $P < 0.001$ ,  $\beta = 54.28 \pm 6.26$ ). Songs had a similar maximum amplitude frequency in both sites ( $F_{1,135} = 0.11$ ,  $P = 0.75$ ; Table 1), with no within-site effect of noise ( $F_{1,135} = 0.41$ ,  $P = 0.52$ ,  $\beta = 8.16 \pm 14.32$ ).

### Effect of noise on trills

We analysed 792 trills from 20 individuals:  $39.6 \pm 6.6$  trills per individual. Wrens at the rural site sang trills with a lower minimum frequency, and the minimum frequency increased with noise across sites (site effect:  $F_{1,117} = 11.67$ ,  $P = 0.001$ ; Table 1; noise effect:  $F_{1,117} = 14.10$ ,  $P < 0.001$ ,  $\beta = 85.62 \pm 12.47$ ). At the

rural site, Wrens produced trills with a higher frequency bandwidth, and the bandwidth decreased with increasing noise across sites (site effect:  $F_{1,117} = 53.42$ ,  $P < 0.001$ ; Table 1; noise effect:  $F_{1,117} = 7.43$ ,  $P = 0.007$ ,  $\beta = -175.32 \pm 24.07$ ). At the urban site, Wrens sang shorter trills (site effect:  $F_{1,117} = 6.93$ ,  $P = 0.01$ , Table 1), with a lower highest frequency (site effect:  $F_{1,117} = 25.60$ ,  $P < 0.001$ ; Table 1) but within sites these features were not affected by noise level (duration:  $F_{1,117} = 0.07$ ,  $P = 0.80$ ,  $\beta = -0.007 \pm 0.003$ ; highest frequency:  $F_{1,117} = 0.22$ ,  $P = 0.64$ ,  $\beta = -89.68 \pm 22.95$ ). Wrens at both sites sang trills with similar maximum amplitude frequency (site effect:  $F_{1,117} = 0.50$ ,  $P = 0.48$ ; Table 1), and this feature increased with noise within sites ( $F_{1,117} = 6.46$ ,  $P = 0.01$ ,  $\beta = 27.84 \pm 10.55$ ).

House Wrens showed a negative relationship between frequency bandwidth and trill rate (linear regression:  $F_{1,97} = 18.67$ ,  $P < 0.001$ ; Fig. 2a). Wrens varied the trill structure to maintain a high performance in response to the noise levels. At low noise levels, Wrens sang trills at a slow rate and larger bandwidth, but when the noise level increased, the trill bandwidth decreased and the rate increased (linear regression:  $F_{1,97} = 11.94$ ,  $P < 0.001$ ; Fig. 2b).

## DISCUSSION

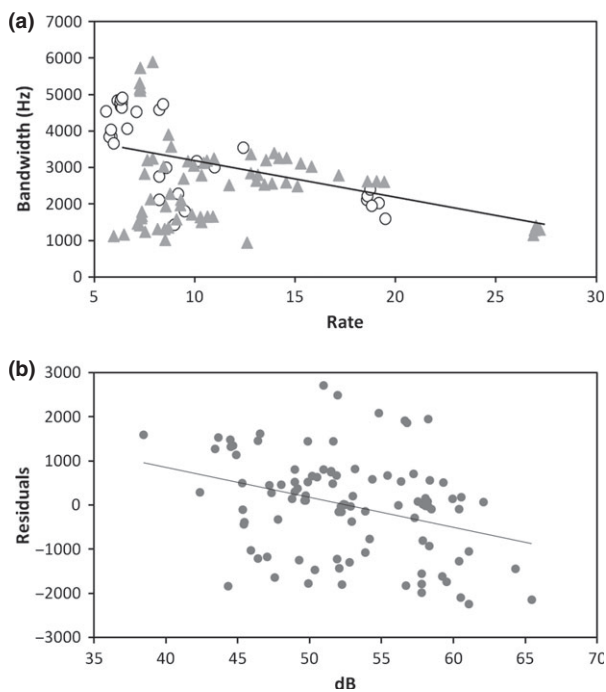
The characteristics of House Wren trills (rate and frequency range) were influenced by noise levels. Wrens sang trills with a wider frequency range and slower rate at the less noisy site (rural) than the noisy site (urban). Wrens also increased trill rate and reduced frequency bandwidth within sites when noise levels increased. Increasing trill rate often produces more reverberations, which enhance vocal signal transmission in noisy environments (Slabbekoorn *et al.* 2002, Naguib 2003). Likewise, reducing trill bandwidth increases signal tonality, and this transmits better through noisy environments than do broadband signals (Lohr *et al.* 2003, Hanna *et al.* 2011). These results suggest that House Wrens modify trill structure to reduce noise masking and improve signal transmission.

Differences in trill features between sites probably reflect birds adjusting to different noise environments, rather than there being different dialects in urban and rural populations, because the study sites are demographically connected. However, the presence of micro-dialects without geographical barriers in this species is a possibility that should be investigated.

Trill characteristics (rate and bandwidth) have been related to female preference, diet and, primarily, bill morphology (Podos 2001, Ballentine *et al.* 2004, Ballentine 2006). There is a mechanical limitation that prevents larger bills from producing faster trills (Podos & Nowicki 2004), or trills at higher performance levels (Podos 2001). We did not measure bills to exclude their

**Table 1.** Variation in the structure of House Wren songs and trills in two sites that differ in intensity of ambient noise. The values reported are the mean  $\pm$  1 se.

	Rural	Urban
Songs		
Minimum frequency (Hz)	1604.22 $\pm$ 65.87	2050.86 $\pm$ 48.07
Highest frequency (Hz)	8848.49 $\pm$ 172.88	8069.93 $\pm$ 136.44
Maximum amplitude (Hz)	7244.28 $\pm$ 183.28	6019.06 $\pm$ 129.51
Bandwidth (Hz)	3861.61 $\pm$ 179.53	3883.78 $\pm$ 81.51
Trill		
Minimum frequency (Hz)	1249.23 $\pm$ 31.30	2221.46 $\pm$ 100.28
Highest frequency (Hz)	7667.78 $\pm$ 158.80	6059.50 $\pm$ 149.44
Maximum amplitude (Hz)	3461.77 $\pm$ 78.80	3583.47 $\pm$ 78.52
Bandwidth (Hz)	6418.55 $\pm$ 165.57	3838.58 $\pm$ 145.50
Duration (s)	0.71 $\pm$ 0.03	0.58 $\pm$ 0.02



**Figure 2.** (a) Relationship between trill rate and trill frequency in the songs of House Wren, in an urban (triangles) and rural site (circles), depicted by a simple linear regression for all data points (black solid line,  $y = -98.51x + 3950$ ,  $R^2 = 0.16$ ). (b) Linear regression between the residuals of the trill rate and trill frequency and the mean noise during the recording period ( $y = -68.04x + 3580$ ,  $R^2 = 0.11$ ).

effect on the trill characteristics, but this effect is unlikely, as the same individuals produce trills with different characteristics in response to changes in noise level (L. Sandoval, P. Redondo, & G. Barrantes, unpubl. data).

House Wren songs had similar minimum frequencies at both sites, but there was an increased frequency as noise levels increased. Vocalizations in this species play an important role in territoriality, mate attraction and pair communication (Johnson & Searcy 1996, Muller *et al.* 1997). Thus, singing songs with a higher minimum frequency in noisy conditions reduces the masking effect of the noise, making communication more efficient (Brumm 2004, Slabbekoorn & Ripmeester 2007). The maximum amplitude frequency in House Wren song and trills is at frequencies higher than ambient noise (Table 1). This suggests that the Wrens are allocating more energy at higher frequencies to avoid the noise-masking effect of signal transmissions, and therefore do not need to change the maximum amplitude frequency when noise levels change.

The House Wren also adjusts song frequency (by increasing minimum frequency) and reverberations (by reducing highest frequency and bandwidth frequency) simultaneously to improve communication.

These results contrast with those of Dowling *et al.* (2012) who proposed that birds cannot increase the minimum frequency and reduce the highest frequency at the same time. Hence, it is possible that species differ in their response to noise environments as a consequence of differences in the functioning of their vocal apparatus. In conclusion, House Wrens reduce the noise-masking effect of signal transmission by adjusting the acoustical and temporal characteristics of the song and trill in response to changes in noise level.

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