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# House Wrens *Troglodytes aedon* reduce repertoire size and change song element frequencies in response to anthropogenic noise

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Anthropogenic noise (≤ 3 kHz) can affect key features of birds' acoustic communication via two different processes: (1) song-learning, because songbirds need to hear themselves and other birds to crystallize their song, and (2) avoidance of song elements that overlap with anthropogenic noise. In this study we tested whether anthropogenic noise reduces the number of song elements in the repertoire of House Wren *Troglodytes aedon*, an urban species. Additionally, we tested whether the proportion of high-frequency elements (i.e. elements where the minimum frequency is above 3 kHz) is related to anthropogenic noise levels, and how the frequencies and duration of shared elements between males change with different levels of anthropogenic noise. We recorded 29 House Wren males exposed to different anthropogenic noise levels (36.50–79.50 dB) during two consecutive breeding seasons from four locations. We recorded each male on 2 days during each season continuously for 50 min (we collected 104 h of recordings) and measured anthropogenic noise levels every 10 min inside each male territory during the recording period. In general, individuals inhabiting noisier territories had smaller repertoires. However, only in two locations with anthropogenic noise levels between 38.60 and 79.50 dB did males inhabiting noisier territories have smaller repertoires. In the other two locations with lower anthropogenic noise (36.50–66.50 dB), the anthropogenic noise inside each territory was not related to the repertoire size. Individuals inhabiting the noisiest location showed a tendency to include more high-frequency elements in their songs. In 26% of the elements, the anthropogenic noise affected their frequency features. Our results showed that not all House Wrens inhabiting urban environments modify their songs at the highest level of organization (i.e. repertoire) to reduce the masking effect of anthropogenic noise on acoustic communication.

**Keywords:** acoustic communication, songbird, urban species, urban environment, urban gradient.

Acoustic signalling is one of the most important means of communication in birds (Catchpole & Slater 2008). Acoustic communication of urban-dwelling birds could be compromised by anthropogenic noise (≤ 3 kHz), which often masks low-frequency vocalizations (Wood & Yezerinac 2006, Lowry *et al.* 2013, Slabbekoorn 2013). However, some species inhabiting urban environments have the flexibility to adjust spectro-temporal characteristics of vocalizations to avoid being masked by anthropogenic noise (Halfwerk & Slabbekoorn 2009, Redondo *et al.* 2013, Gough *et al.* 2014). For example, Common Blackbirds *Turdus merula*, Great Tits *Parus major* and Rufous-collared Sparrows *Zonotrichia capensis* sing at higher minimum frequencies in urban than in rural environments (Slabbekoorn & den Boer-Visser 2006, Hu & Cardoso 2010, Laiolo 2011). Furthermore,

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songs of Common Blackbirds have higher maximum frequencies in urban environments than in rural environments (Mendes *et al.* 2011).

In other species, anthropogenic noise affects the size of the vocal repertoire because low-frequency sounds may not reach potential receivers and therefore may be excluded from the repertoire (Hansen 1979, Lehtonen 1983, Lowry *et al.* 2013). To communicate effectively in noisy urban environments, some birds may: (1) switch to song types with higher frequencies, as occurs in the Great Tit (Halfwerk & Slabbekoorn 2009); (2) omit low-frequency elements that may not be well transmitted through noisy environments, as occurs in the House Finch *Haemorhous mexicanus* (Fernández-Juricic *et al.* 2005); or (3) introduce new elements, better suited for noisy environments, as occurs in Great Tits (Slabbekoorn & den Boer-Visser 2006). The last two strategies may lead to changes in the composition of the repertoire by increasing the proportion of high-frequency elements in order to communicate effectively.

An approach to understanding the role of anthropogenic noise in repertoire size is to conduct comparative studies between individuals that inhabit territories with different anthropogenic noise levels, both within and between populations (Slabbekoorn & den Boer-Visser 2006, Catchpole & Slater 2008). These studies are aimed at understanding the relative contributions of phenotypic plasticity and adaptation to urban environments. If noise influences repertoire size and spectral characteristics of bird vocalizations, it is expected that under similar noise conditions, individuals will show similar repertoire size and frequency characteristics in shared songs (Lehtonen 1983, Slabbekoorn & den Boer-Visser 2006, Luther & Baptista 2009). It is important to understand how anthropogenic noise affects acoustic signals, because changes in repertoire size and in spectro-temporal characteristics of songs may reduce the singer's ability to find a mate and defend a territory, as a modified song is less recognizable, less attractive or less threatening to conspecifics (Patricelli & Blickley 2006, Catchpole & Slater 2008, Luther *et al.* 2015).

Our main goals in this study were to evaluate whether anthropogenic noise levels change the element repertoire size of House Wren *Troglodytes aedon* songs, and to evaluate the effect of noise on the frequency and duration of shared elements of individuals that inhabit territories with different noise levels. We selected House Wren as our model species because male songs play an important role in mate choice, pair communication and male–male competition (Platt & Ficken 1987, Rendall & Kaluthota 2013, dos Santos *et al.* 2016). In addition, most House Wren song elements occur at frequencies between 0.80 and 5 kHz, thus potentially overlapping with anthropogenic noise (Platt & Ficken 1987, Lowry *et al.* 2013, Redondo *et al.* 2013, Rendall & Kaluthota 2013, dos Santos *et al.* 2016). Additionally, the House Wren is an open-ended learning species whose members develop songs by hearing other individuals nearby (Skutch 1953, Sawhney *et al.* 2006, Sosa-López & Mennill 2014a) and expand their repertoire after the first breeding season by including new elements in their songs from tutors (Catchpole & Slater 2008, Sosa-López & Mennill 2014a). A typical song in this species consists of $11.5 \pm 12.1$ sd elements on average (Platt & Ficken 1987). In Costa Rica, House Wrens sing throughout most of the year, but mainly during the prolonged breeding season, and inhabit open or semi-open habitats in rural and urban areas where anthropogenic noise levels vary considerably (Skutch 1953, Redondo *et al.* 2013). They are therefore an ideal model species for analysing the effect of noise on song repertoire.

We predicted smaller repertoires in individuals and locations exposed to higher anthropogenic noise levels, because the noise level prevents the effective transmission of low-frequency elements (Slabbekoorn & Peet 2003, reviewed in Patricelli & Blickley 2006). We also predicted a higher proportion of high-frequency elements (elements where the minimum frequency is above 3 kHz) in the repertoire of individuals at locations exposed to higher anthropogenic noise, because high-frequency elements will be less masked by anthropogenic noise (Slabbekoorn & Peet 2003, Patricelli & Blickley 2006). Finally, we predicted that higher anthropogenic noise levels will correlate with the highest minimum frequency of low-frequency elements. In contrast, we expected that anthropogenic noise would not affect high-frequency elements, as has been reported for White-crowned Sparrow *Zonotrichia leucophrys* and House Finch (Bermúdez-Cuamatzin *et al.* 2009, Luther *et al.* 2015), because elements with higher minimum frequencies will not be masked by anthropogenic noise (Gil & Brumm 2014).

# METHODS

## Study area

We conducted this study in four locations in the Costa Rican Central Valley (Fig. 1):

*Sede Rodrigo Facio* (09°56'12.8''N, 84°03' 09.7''W; 1203 m asl): The habitat at this location is a mix of a small secondary forest, gardens, isolated trees and buildings surrounded by secondary roads with reduced traffic, and primary roads with a high volume of traffic. The maximum number of individuals observed per day was 22.

*Ciudad de la Investigación* (09°56'17.1''N, 84°02'40.2"W; 1223 m asl): The habitat at this location is a mix of a riparian strip, gardens, isolated trees and buildings surrounded by secondary roads with reduced traffic, and primary roads with a high volume of traffic. The maximum number of individuals observed per day was 16.

*Instalaciones Deportivas* (09°56'46.3"N, 84°02'46.3"W; 1222 m asl): The habitat at this location is a mix of a medium size secondary forest, gardens and some buildings surrounded by secondary roads with reduced traffic, and primary roads with a high volume of traffic. The maximum number of individuals observed per day was 16.

*Jardín Botánico Lankester* (09°50'20.7"N, 83°53'25.1"W; 1370 m asl): The habitat at this location is a mix of a medium size secondary forest, gardens and a few buildings surrounded by trails and secondary roads with reduced traffic. The maximum number of individuals observed per day was 14.

We considered these locations as independent populations because House Wrens are year-round territorial birds and, once settled, they maintain the territory for several years (Skutch 1953, Johnson 2014). We named these four locations based on the average anthropogenic noise level recorded, although only the noisiest site was statistically different from the others (see RESULTS). We therefore refer to these locations as 'high noise level' (Sede Rodrigo Facio = 56.62 ± 5.62 dB; mean ± sd), 'medium–high noise level' (Ciudad de la Investigación = 51.09 ± 4.65 dB), 'medium–low noise level' (Instalaciones Deportivas = 49.50 ± 5.38 dB) and 'low noise level' locations (Jardín Botánico Lankester = 48.83 ± 5.92 dB). Rather than dividing our locations into low noise vs. high noise, or rural vs. urban (Gross *et al.* 2010, Hu & Cardoso 2010, Redondo *et al.* 2013), we are interested in understanding how differences in noise along an urban gradient (i.e. from noisy territories to quiet territories) affect House Wren songs.

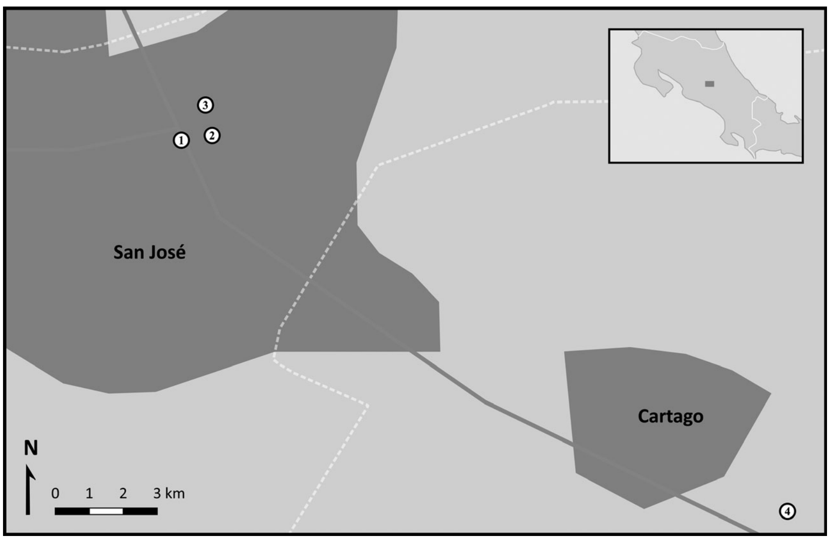


**Figure 1.** Map of the Costa Rican Central Valley. The circles show the study locations: (1) Sede Rodrigo Facio, (2) Ciudad de la Investigación, (3) Instalaciones Deportivas and (4) Jardín Botánico Lankester. The dark grey shading indicates the most densely urbanized areas in the Central Valley. The inset at upper right shows the location of Central Valley within Costa Rica.

## Song recordings and noise measurements

We recorded House Wrens from April to June of 2015 and 2016, at the onset of each breeding season, when all individuals are expected to be equally stimulated to sing (Skutch 1953, Young 1994, Rendall & Kaluthota 2013, dos Santos *et al.* 2016). The recordings were conducted between 05:30 and 07:30 h, when this species is most vocally active (dos Santos *et al.* 2016). We used the focal recording method to record each male from 2 to 4 days per year; this method consists of recording directly and continuously the focal bird for a session of approximately 1 h (Sosa-López & Mennill 2014a). House Wrens are typically confiding, which allowed us to record them at close distances and to obtain high-quality recordings (average of 10 m, range = 8–12 m). Each male was banded with a unique colour combination as part of a long-term study. Thus we were confident that we recorded the same individuals on different days and in both years. We recorded House Wren songs using a directional microphone (Sennheiser ME66/K6) and a digital recorder (Marantz PMD661). All recordings were collected in WAVE format, with 24-bit accuracy and a 44.1-kHz sampling rate.

During each focal recording session, we measured environmental noise using a Sper Scientific 840014 mini sound meter (measuring range 32–130 dB, at the fast response on A weight). We recorded the highest and lowest noise level every 10 min throughout each recording session. We then calculated the mean value of environmental noise for each territory and recording session.

## Acoustic analysis

We analysed song recordings using a combination of the sound spectrogram, power spectrum and waveform windows in RAVEN PRO 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA). The spectrogram window was used to identify each element (i.e. a continuous trace on the spectrogram) in a song, and the wave and power spectrum windows were used to measure time and frequency limits, respectively. This approach reduces the human effect on time and frequency limits measurements because neither measurement is affected by contrast or brightness change in the spectrogram. We used the following RAVEN PRO 1.4 settings: a temporal resolution of 0.5 s and a frequency resolution of 2 kHz (settings: Hann window; 256 kHz sampling, and 50% overlap) for the spectrogram window.

We focused on the repertoire of elements because House Wrens use a limited number of elements to produce an unlimited repertoire of song types (Rendall & Kaluthota 2013, Sosa-López & Mennill 2014b). To classify elements, we created a library based on their appearance in the spectrograms, following similar approaches used in other House Wren studies (Sosa-López & Mennill 2014a). We also used frequency characteristics to further classify the elements as ‘low-frequency’ (minimum frequency $\leq 3$ kHz) or ‘high-frequency’ (minimum frequency $> 3$ kHz), with this threshold chosen because most anthropogenic noise has frequencies below 3 kHz (Slabbekoorn & Peet 2003). We therefore expected that elements with minimum frequencies below 3 kHz would be most affected by anthropogenic noise (Hu & Cardoso 2009, Lowry *et al.* 2013). We then estimated ‘element repertoire size’, hereafter simply called repertoire size, as the total number of unique element types recorded for each bird in each year (Fig. 2). Then, for all elements not overlapped by any other sound we measured the minimum frequency, in Hz; the maximum frequency, in Hz; the frequency of maximum amplitude, in Hz; and the duration, in seconds.

## Statistical analysis

We used the R language and environment 3.3.3 for all statistical analyses (R Core Team 2017). We conducted a set of models that increased in complexity to answer the different questions in our study. We first conducted a linear mixed-effects model with a Gaussian error sructure to test if noise levels in House Wren territories differ between locations. This model had noise level as a response variable, location as fixed effect and territory identity as random factor.

### *Modelling repertoire size*

We first used a general linear mixed model (GLMM) with a Poisson error distribution to test whether there is an overall effect of noise on repertoire size. In this analysis, we used noise as the independent variable and repertoire size per

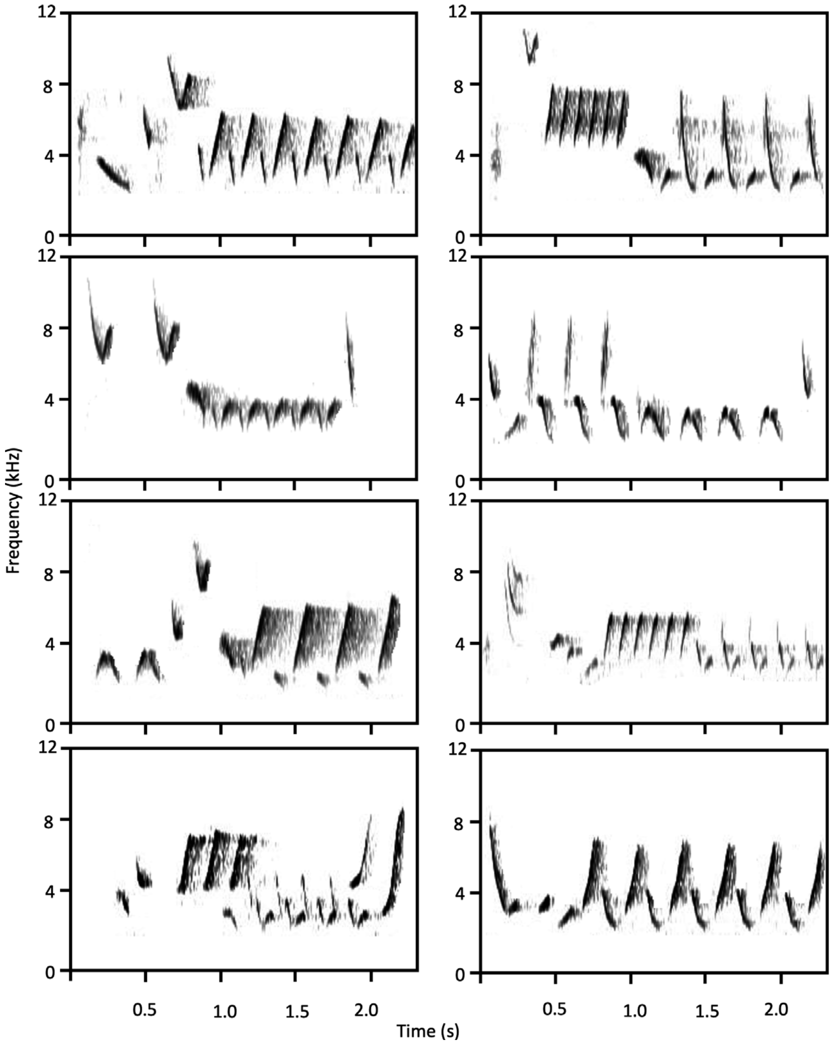


**Figure 2.** Sound spectrograms showing examples of songs recorded from two House Wrens at each of our four study locations in the Costa Rican Central Valley, ordered from low-noise environment individuals (top) to high-noise environment individuals (bottom).

individual, per year, as the dependent variable. We then extended this model to test if the noise effect differs among locations by fitting an interaction term between noise and location. Finally, we further extended this model to test if the effect of noise on the repertoire size differs within individuals. In this analysis, we partitioned the variation of noise between and within individual territories, using a within-subject centering approach in which we fitted the mean noise level in a territory and deviations from that mean for each recording season (van de Pol & Wright 2009). All three models included male identity as a random factor to account for the non-independence of the measurements.

*Modelling effects on the element composition*

We used a linear mixed-effect model with a Gaussian error distribution to test if anthropogenic noise influences the composition of elements in the repertoire of House Wrens. Specifically, we evaluated the effect of anthropogenic noise on the proportion of high-frequency elements, because we predicted that more high-frequency elements would be found in the repertoire of individuals exposed to higher anthropogenic noise and because the number of high-frequency and low-frequency elements was positively correlated (Pearson correlation analysis: $n = 53$, $r = 0.83$, $P < 0.001$). In these analyses we included noise and location as independent variables. We used male identity as a random factor to account for the fact that each male was sampled repeatedly.

*Evaluating the effect on the frequencies and duration of shared elements*

First, we defined shared elements as those elements found in two or more locations, present in the repertoire of 10 or more individuals, and measured at least 10 times per individual during the 2 years of recording. We conducted a linear regression analysis to evaluate the effect of noise on the four fine acoustic characteristics (minimum and maximum frequencies, frequency of maximum amplitude and duration) of shared elements between individuals and locations. For this analysis the independent variable was the average of noise per territory and the dependent variable was the average of each of the four acoustic characteristics measured per individual.

## RESULTS

We recorded 104 h (mean = 3.59 h per individual) for a total of 14 826 songs (mean = 511 ± 311 sd songs per individual) from 29 House Wren males: seven at the high noise level location, seven at the medium–high noise level location, six at the medium–low noise level location and nine at the low noise level location. We recorded 48 906 song elements and measured the frequency and duration of 27 822 of these with a high signal-to-noise ratio and not overlapped by any other sound. We identified 130 different song elements for all individuals combined from the four locations (mean = 58 elements per individual).

### Noise

Noise level varied along the urban gradient (range = 36.50–79.50 dB, $n$ = 548); anthropogenic noise was higher at the location we classified as high noise level than at the medium–high, medium–low and low noise level locations (LMM: $F_{3,25} = 13.52$, $P < 0.001$, Fig. S1). Anthropogenic noise at the high noise location was on average 6 dB louder than at the medium–high noise location, 7 dB louder than at the medium–low location and 8 dB louder than at the low noise location. However, anthropogenic noise was not significantly different between the other locations ($P > 0.05$).

### Effect of noise on repertoire size

In general, anthropogenic noise reduced the repertoire size of House Wren males (GLMM: $F_{24,48} = -2.93$, $P = 0.003$). When the variable location was included in the model, we found that males from medium–low noise level (GLMM: $F_{1,5} = -4.45$, $P < 0.001$) and high noise level (GLMM: $F_{1,6} = -2.11$, $P = 0.03$) locations showed smaller repertoires as anthropogenic noise level increased (Fig. 3). The repertoire size of males from medium–high noise level (GLMM: $F_{1,6} = 0.87$, $P = 0.\ 39$) and low noise level (GLMM: $F_{1,8} = 0.87$, $P = 0.38$) locations was not affected by anthropogenic noise (Fig. 3). Additionally, we fitted a model to study how variation in anthropogenic noise between territories and within territories affected repertoire size using a within-subject centering approach (van de Pol & Wright 2009). We found that males reduced their repertoire size in situations where the anthropogenic noise was above the noise levels they experience on average (GLMM: $F_{3,48} = -3.14$, $P = 0.001$).

### Noise does not influence high-frequency elements

Anthropogenic noise did not affect the proportion of high-frequency elements in House Wren songs (LMM: $F_{1,23} = -1.15$, $P = 0.87$). We did not detect differences in the proportion of high-frequency elements between any pair of locations ($P > 0.10$ for all pairwise comparisons, Fig. 4).

### Effect of noise on frequency and duration of elements

We found 112 elements shared between two or more locations in the recordings of the 29 males. Nevertheless, only 31 elements (seven of low-frequency, 13 of high-frequency, nine trills of low-frequency and two trills of high-frequency) were measured at least in 10 individuals and on 10 or more occasions per individual (Table 1; Figs 5 and 6). These 31 elements were part of the repertoire of 28 males, 61% of these elements ($n$ = 19) were found at least at three locations, and all the other elements ($n$ = 12) were found at all four locations. Below we summarize the changes in frequencies in response to anthropogenic noise observed in those 31 elements. The minimum frequency of some elements increased when

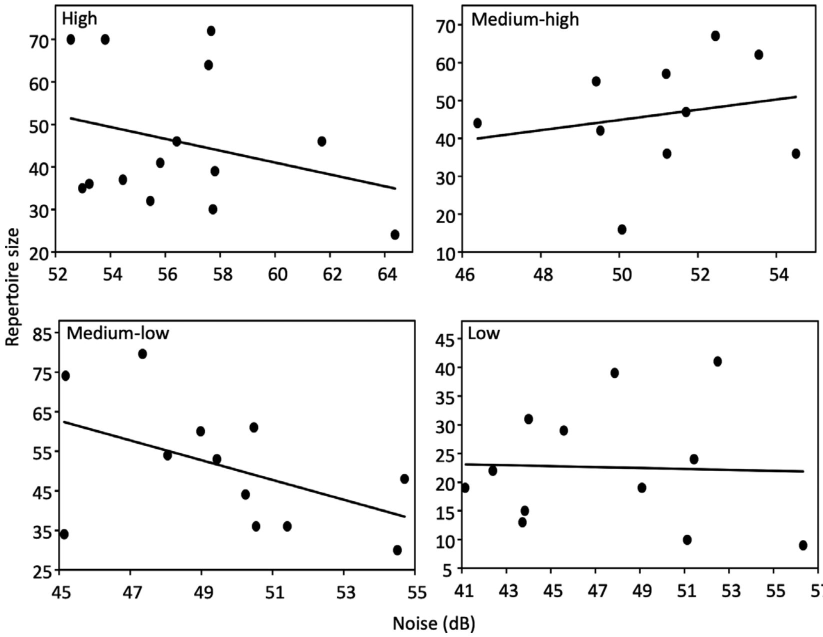


**Figure 3.** Relationship between noise and repertoire size in the songs of House Wren in four locations that vary in noise levels from high, medium–high, medium–low, to low. The lines depicted were estimated using a simple linear regression for each location.

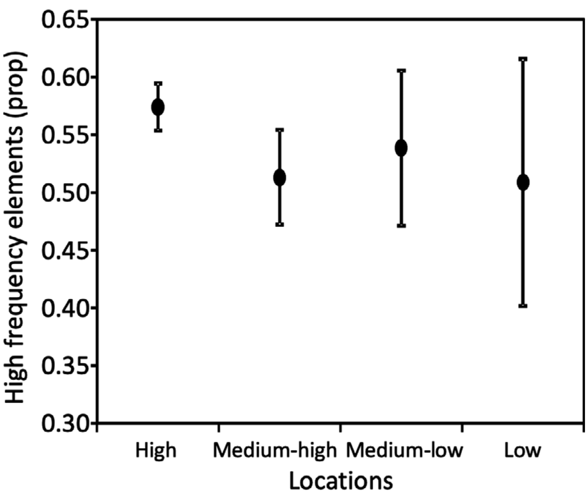


**Figure 4.** Comparison of the proportion of high-frequency elements in the House Wren songs at four locations that vary in noise levels from high, medium–high, medium–low, to low. Error bars are standard deviations around the mean.

anthropogenic noise increased (Table 1; $r^2 \geq 0.26$, $P < 0.05$). This pattern was observed for one low-frequency element (7LF), one low-frequency trill (T5LF) and two high-frequency elements (15HF, 20HF). The minimum frequency of one high-frequency element (10HF) decreased as anthropogenic noise increased (Table 1; $r^2 = 0.30$, $P = 0.05$). The maximum frequency of one low-frequency trill (T11LF) increased as anthropogenic noise increased (Table 1; $r^2 = 0.40$, $P = 0.03$). The maximum frequency of two elements, one high-frequency (10HF) and one low-frequency (5LF), decreased as anthropogenic noise increased (Table 1; $r^2 \geq 0.23$, $P < 0.05$ for both elements). The frequency of maximum amplitude of one high-frequency element (5HF) increased as anthropogenic noise increased (Table 1; $r^2 = 0.37$, $P = 0.02$). The frequency of maximum amplitude of one high-frequency element (10HF) decreased as anthropogenic noise increased (Table 1; $r^2 = 0.41$, $P = 0.02$). We did not find changes in frequency or duration in the other 23 elements, which include high-frequency elements, low-frequency elements and trills, when anthropogenic noise increased ($P > 0.05$).

## DISCUSSION

Our findings support the prediction that anthropogenic noise affects the characteristics of House Wren songs. Repertoire size decreased as anthropogenic noise increased. Individuals exposed to high anthropogenic noise tended to produce more high-frequency elements in their songs, and

**Table 1.** Relationships between noise and frequency measurements, and between noise and duration of elements in the song of House Wrens inhabiting the Central Valley, Costa Rica.

| | Minimum frequency | | | Maximum frequency | | | Frequency of maximum amplitude | | | Duration | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Element code | $r^2$ | $P$ | $B_1$ | $r^2$ | $P$ | $B_1$ | $r^2$ | $P$ | $B_1$ | $r^2$ | $P$ | $B_1$ |
| High-frequency elements (minimum frequency > 3 kHz) | | | | | | | | | | | | |
| 1HF | 0.25 | 0.12 | 26.24 | 0.10 | 0.34 | 41.32 | 0.18 | 0.19 | 29.87 | 0.04 | 0.55 | 0.00 |
| 3HF | 0.01 | 0.66 | −6.57 | 0.17 | 0.10 | 53.14 | 0.00 | 0.98 | 0.58 | 0.00 | 0.98 | 0.00 |
| 5HF | 0.03 | 0.57 | 6.31 | 0.10 | 0.26 | 25.62 | **0.37** | **0.02** | **62.23** | 0.01 | 0.76 | 0.00 |
| 6HF | 0.07 | 0.35 | 22.30 | 0.02 | 0.58 | 13.06 | 0.02 | 0.64 | 19.97 | 0.01 | 0.71 | 0.00 |
| 7HF | 0.22 | 0.08 | 44.07 | 0.17 | 0.13 | 41.83 | 0.11 | 0.24 | 33.71 | 0.05 | 0.43 | 0.00 |
| 10HF | ***0.30*** | ***0.05*** | ***−24.31*** | ***0.58*** | ***0.00*** | ***−73.04*** | ***0.41*** | ***0.02*** | **−29.86** | 0.05 | 0.47 | 0.00 |
| 13HF | 0.04 | 0.42 | 13.22 | 0.22 | 0.06 | 13.10 | 0.01 | 0.72 | −7.98 | 0.01 | 0.76 | 0.00 |
| 14HF | 0.02 | 0.66 | 21.84 | 0.00 | 0.83 | −6.14 | 0.00 | 0.87 | 4.30 | 0.00 | 0.96 | 0.00 |
| 15HF | **0.26** | **0.02** | **27.50** | 0.03 | 0.50 | −10.84 | 0.07 | 0.25 | 21.63 | 0.09 | 0.20 | 0.00 |
| 19HF | 0.01 | 0.74 | −21.36 | 0.01 | 0.77 | −24.02 | 0.02 | 0.65 | −29.68 | 0.02 | 0.67 | 0.00 |
| 20HF | **0.33** | **0.01** | **21.97** | 0.10 | 0.18 | −30.48 | 0.00 | 0.99 | 0.05 | 0.09 | 0.20 | 0.00 |
| 22HF | 0.01 | 0.75 | 8.38 | 0.08 | 0.42 | 17.86 | 0.18 | 0.22 | −22.04 | 0.07 | 0.46 | 0.00 |
| 30HF | 0.04 | 0.53 | 24.55 | 0.04 | 0.52 | 37.57 | 0.10 | 0.30 | 49.24 | 0.27 | 0.08 | 0.00 |
| T1HF | 0.27 | 0.08 | −24.10 | 0.06 | 0.43 | −9.51 | 0.05 | 0.47 | −21.71 | 0.06 | 0.44 | 0.01 |
| T6HF | 0.02 | 0.65 | −11.99 | 0.26 | 0.11 | −80.97 | 0.09 | 0.38 | −38.24 | 0.08 | 0.39 | 0.00 |
| Low-frequency elements (minimum frequency ≤ 3 kHz) | | | | | | | | | | | | |
| 3LF | 0.01 | 0.74 | 8.82 | 0.11 | 0.34 | 25.72 | 0.03 | 0.62 | 12.62 | 0.03 | 0.63 | 0.00 |
| 5LF | 0.00 | 0.92 | −1.49 | ***0.23*** | ***0.04*** | ***−44.77*** | 0.00 | 0.93 | 2.77 | 0.12 | 0.16 | 0.00 |
| 7LF | **0.44** | **0.03** | **29.66** | 0.04 | 0.57 | 7.12 | 0.04 | 0.56 | 6.18 | 0.00 | 0.98 | 0.00 |
| 10LF | 0.16 | 0.25 | −28.46 | 0.18 | 0.22 | −70.52 | 0.22 | 0.17 | −40.20 | 0.17 | 0.23 | 0.00 |
| 12LF | 0.02 | 0.55 | 10.61 | 0.01 | 0.65 | 13.58 | 0.05 | 0.41 | 19.24 | 0.08 | 0.26 | 0.00 |
| 13LF | 0.22 | 0.06 | −32.55 | 0.01 | 0.67 | 24.84 | 0.00 | 0.98 | −0.70 | 0.02 | 0.64 | 0.00 |
| 15LF | 0.00 | 0.82 | −3.68 | 0.05 | 0.43 | −13.45 | 0.07 | 0.34 | −15.36 | 0.02 | 0.62 | 0.00 |
| T1LF | 0.20 | 0.19 | 7.13 | 0.28 | 0.11 | 36.51 | 0.35 | 0.07 | 102.73 | 0.07 | 0.45 | 0.01 |
| T3LF | 0.01 | 0.81 | 3.27 | 0.27 | 0.11 | −65.55 | 0.08 | 0.40 | −18.78 | 0.01 | 0.82 | 0.00 |
| T4LF | 0.02 | 0.64 | −4.12 | 0.02 | 0.62 | 17.06 | 0.02 | 0.63 | −12.84 | 0.02 | 0.58 | 0.00 |
| T5LF | **0.42** | **0.02** | **19.07** | 0.04 | 0.56 | 9.90 | 0.01 | 0.71 | 8.39 | 0.06 | 0.44 | 0.01 |
| T7LF | 0.00 | 0.97 | −0.34 | 0.09 | 0.33 | −32.79 | 0.28 | 0.06 | −29.90 | 0.00 | 0.98 | 0.00 |
| T8LF | 0.04 | 0.44 | −7.63 | 0.15 | 0.10 | −21.22 | 0.11 | 0.17 | −16.40 | 0.02 | 0.58 | 0.00 |
| T9LF | 0.27 | 0.10 | 20.07 | 0.06 | 0.48 | 17.39 | 0.12 | 0.29 | 18.08 | 0.13 | 0.28 | -0.01 |
| T10LF | 0.24 | 0.11 | 13.49 | 0.03 | 0.56 | 13.17 | 0.00 | 0.86 | −2.91 | 0.27 | 0.08 | 0.02 |
| T11LF | 0.11 | 0.29 | 15.36 | **0.40** | **0.03** | **29.99** | 0.15 | 0.22 | 18.19 | 0.03 | 0.56 | 0.00 |

We organized the list, from top to bottom, starting with elements classified as 'high-frequency' or 'low-frequency' elements. Element code descriptions: HF after the number indicates a high-frequency element, LF after the number indicates a low-frequency element, and capital T before the number indicates that element is a trill. Bold values indicate a positive relationship, bold and italicisized values indicate a negative relationship.

increased the minimum frequency of two low-frequency elements. However, contrary to our predictions, the minimum frequency of two high-frequency elements increased with anthropogenic noise.

Generally, repertoire size decreased as anthropogenic noise increased. The same pattern was also observed at the individual level: individuals showed smaller repertoires on noisier days, suggesting the occurrence of individual plasticity in repertoire size. Noisy environments could become a selecting factor that might result in a reduction in the repertoire size of House Wrens, as has presumably occurred in Great Tits, in which the number of song syllables decreased from three to two over a 34-year period of gradual noise increase (Lehtonen 1983). Likewise, White-crowned Sparrows replaced songs in three dialects over a 30-year period, presumably in response to an increase in anthropogenic noise, as the songs omitted by this species had a lower minimum frequency and probably more acoustic interference from

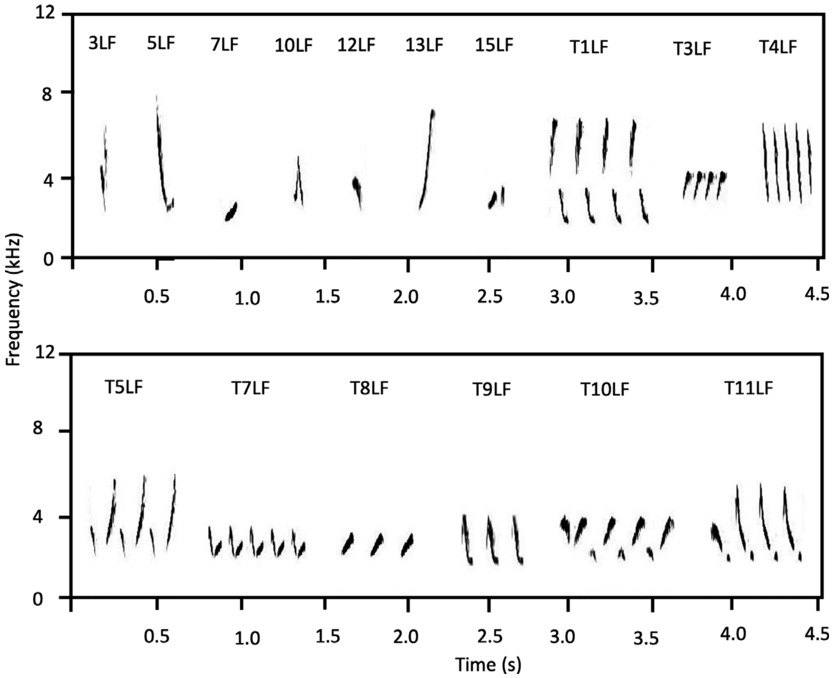


**Figure 5.** Low-frequency elements found in House Wren songs. These elements are shared between individuals and locations in the Central Valley, Costa Rica (2015–2016). The elements are organized following the list presented in Table 1.

anthropogenic noise (Luther & Baptista 2009). Changes in the repertoire size of House Wrens inhabiting noisy environments could affect the vocal learning process because birds need to hear their own vocalizations as well as those of conspecifics to incorporate elements in their repertoire (Hansen 1979, Slabbekoorn & den Boer-Visser 2006, Catchpole & Slater 2008). These changes in repertoire size in urban House Wrens may reduce their mating probability and success at defending territories, affecting their reproduction and survival (Patricelli & Blickley 2006, Catchpole & Slater 2008, Gil & Brumm 2014). In species whose females prefer males with large repertoires, such as Song Sparrow *Melospiza melodia* and Great Reed Warbler *Acrocephalus arundinaceus*, males that drop lower-frequency elements from their repertoire to avoid masking may decrease their attractiveness to females (Catchpole 1986, Reid *et al.* 2004).

Against our prediction, repertoire size was twice as large at the high noise level location than at the low noise level location. This result may arise due to the high abundance of House Wrens in noisy urban environments (Skutch 1953, Johnson 2014). Regardless of the intensity of noise, House Wrens living in high densities probably need to communicate with more conspecifics, so they incorporate more elements from their neighbours into the repertoire, which consequently expands the individual repertoire (Kroodsma & Canady 1985, Catchpole & Slater 2008). Another possible explanation for the difference in repertoire size between locations may be the time that this species has been exposed to anthropogenic noise in the Central Valley. House Wrens occurring at our high noise level location have been exposed to urbanization for a longer period of time compared with those at other locations (Pujol & Pérez 2012). Thus, those individuals have had more time to adapt their repertoire to anthropogenic noise.

Low-frequency elements of House Wren song may be completely or partially masked by anthropogenic noise because frequency ranges of songs overlap with anthropogenic noise (Platt & Ficken 1987, Slabbekoorn & Peet 2003, Sosa-López & Mennill 2014a). Such overlapped elements may therefore be less suitable for communication in urban environments (Hansen 1979, Slabbekoorn & Peet 2003), and birds may increase the minimum frequency with increasing noise (Patricelli & Blickley 2006, Wood & Yezerinac 2006). However, in

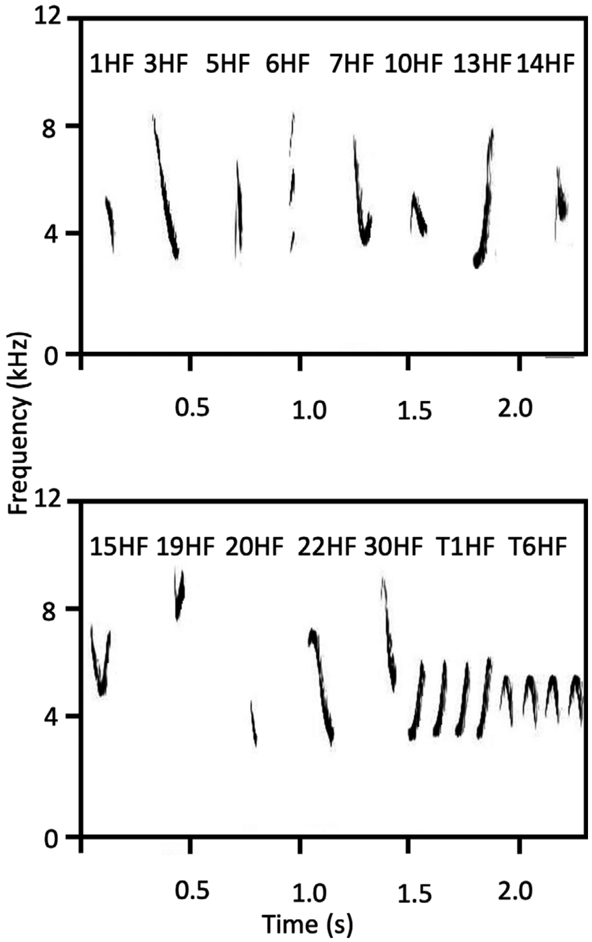


**Figure 6.** High-frequency elements found in House Wren song. These elements are shared between individuals and locations in the Central Valley, Costa Rica (2015–2016). The elements are organized following the list of elements presented in Table 1.

this study only 13% of the 16 shared low-frequency elements between locations and individuals showed an increase in minimum frequency with an increase in noise (Table 1). Four elements (two low-frequency and two high-frequency), of a total of 31 low- and high-frequency elements shared between males and locations, increased their minimum frequency when anthropogenic noise increased. These elements were all frequency modulated (i.e. an element whose frequency varies temporally, either beginning or ending with higher frequency, and appears on the sonogram as a slope), three had short duration (i.e. lasting at most 0.15 s; codes: 7LF, 15HF, 20HF; Table 1; Figs 5 and 6), and one had long duration (i.e. lasting at least 0.40 s; code: T5LF; Table 1; Fig. 5). All 16 low-frequency shared elements had modulated frequency, so if modulation is one of the factors driving the adjustment of the minimum frequency, we expect to find an increase in the minimum frequency of all elements; however, we only found changes in the minimum frequency of two of these elements. This suggests that not all low-frequency elements are equally affected by noise.

We also found that a low-frequency element (code T11LF; Fig. 5) increased its maximum frequency with an increase of anthropogenic noise; meanwhile, a high-frequency element (code 5HF; Fig. 6) increased its frequency of maximum amplitude when anthropogenic noise increased. A positive relationship between anthropogenic noise level and maximum frequency or between noise and frequency of maximum amplitude is seldom found because the maximum frequency and the frequency of maximum amplitude are mainly produced well above the anthropogenic noise spectrum (Patricelli & Blickley 2006, Bermúdez-Cuamatzin *et al.* 2009, Hu & Cardoso 2010). Birds may not be able to change the high frequencies of some elements because of the limitations imposed by their morphology and vocal production organs such as beak shape, trachea and syrinx that constrain the maximum frequencies that a bird can produce (Patricelli & Blickley 2006, Catchpole & Slater 2008). However, the Common Blackbird is one of the few species in which the maximum frequency of the whole song has presumably increased in response to anthropogenic noise, probably to avoid anthropogenic noise-masking (Mendes *et al.* 2011).

We also found that the frequency of maximum amplitude, and minimum and maximum frequencies in two elements correlated negatively with anthropogenic noise. These two elements were frequency modulated and of short duration (Table 1; Figs 5 and 6). Although the three measurements of frequencies in these two elements decreased with noise, they were still above 4 kHz. Hence, anthropogenic noise may not affect the transmission of those elements. Rather, the observed changes may be related to the chance of increasing the communication distance with the intended receivers, because low-frequency sounds travel further and are more easily distinguished from noise (Lohr *et al.* 2003, Catchpole & Slater 2008, Barber *et al.* 2010). Support for this hypothesis will be found if the changes in elements occur in birds whose territories are further apart, but precise data on the limits of neighbours' territories are still lacking. Birds may also decrease the frequency of some elements as they increase the frequency of others to produce songs that are more threatening or attractive, but further research is needed to evaluate the adaptive benefits for birds implementing those changes.

Although in densely vegetated areas a predominance of low-frequency elements and a narrow frequency range of bird vocalizations is expected (transmission hypothesis, cf. Catchpole & Slater 2008), our analysis of the proportion of high-frequency elements and fine acoustic characteristics of shared elements suggests the opposite is true in more open areas. Because in the Central Valley House Wrens consistently inhabit semi-open areas (Skutch 1953, Redondo *et al.* 2013), vegetation density may not play a role in observed vocal changes. Considering that development of complex songs (i.e. large repertoires) is energetically costly and that juveniles inhabiting noisier locations are generally in poor physical condition (Catchpole & Slater 2008, Meillère *et al.* 2015), a trade-off between communication efficiency and energy saving to maintain good physical condition is expected. Our analysis of the effect of anthropogenic noise on repertoire size suggests that this trade-off may be taking place in songbirds of urban environments. A negative correlation between House Wren repertoire size and body condition would support this hypothesis.

## CONCLUSIONS

Our results showed that in the House Wren not all individuals and populations respond equally to anthropogenic noise because only in two of four locations was anthropogenic noise negatively related to repertoire size. Therefore, to understand how noise affects vocal communication within a species it is important to include several locations with different noise levels, rather than just focus on comparing urban and non-urban populations, as in many studies (Slabbekoorn & den Boer-Visser 2006, Laiolo 2011, Redondo *et al.* 2013). Working along a noise gradient provides additional information on the factors affecting bird adaptation to noise increase. The increase of frequencies in some elements of House Wren songs may reduce the masking effect of anthropogenic noise and allow House Wrens to communicate more effectively at higher noise levels, as some song elements are produced at frequencies that overlap with the anthropogenic noise. A decrease in the high frequencies or the frequency of maximum amplitude of some elements may be implemented to achieve larger distances because low-frequency sounds are transmitted further than high-frequency sounds. House Wrens did not change the frequencies of all elements; instead, they seemed to be adjusting the frequencies of some particular elements that perhaps most affect their communication in noisy urban environments. As in Song Sparrow and Great Reed Warbler (Catchpole 1986, Reid *et al.* 2004), our results highlight the need to manage anthropogenic noise levels, especially during the breeding season, to prevent negative impacts on songbird populations. We consider that noise may have a negative impact in the communication and probable reproduction of House Wrens and other bird species sharing urban habitats, and that it is necessary to develop strategies to ameliorate its impact. For example, in urban environments, primary roads should be located away from the few tracts of natural habitats that still remain within urbanized areas, and natural habitats and bird territories should be surrounded by either man-made or natural (a wall of bushes or trees) barriers that reduce noise. These actions will reduce the impact of anthropogenic noise on birds and other animals that inhabit the few, often suboptimal, natural environments present in the urban jungle.

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## DATA AVAILABILITY STATEMENT

The datasets used for this publication are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Noise level in the four studied locations along an urban gradient. We classified locations according to the mean anthropogenic noise measured, from the high noise level to the low noise level location at the far right. Superscript letters indicate significant differences in anthropogenic noise between locations, based on an LMM that accounts for multiple sampling of each male's territory. Error bars are standard deviations around the mean.