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SONG FREQUENCY SHIFTS IN AN URBAN BIRD SPECIES OPTIMIZE ACOUSTIC TRANSMISSION INSIDE NOISY URBAN AREAS

Mauricio Villarreal[1] · Gilbert Barrantes[1] · Luis Sandoval[1]

[1]Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica, CP-2090
E-mail: Luis Sandoval (biosandoval@hotmail.com)

Abstract · In animal acoustic communication, it is necessary that signals arrive to the receiver with reduced degradation and attenuation for a better transmission of the message. The noise pollution resulting from anthropogenic activities in cities reduces the efficiency and efficacy of acoustic communication. Some species respond to high levels of noise increasing the minimum frequency of their vocalizations to avoid noise masking, but this may affect how sounds transmit in the environment because sounds with higher frequencies experience greater levels of attenuation and degradation. Using a transmission experiment, we analyzed how minimum frequency shifts affect the sound transmission properties of the song of the Southern House Wren *Troglodytes musculus* in urban areas that differ in the level of anthropogenic noise. We broadcasted songs with minimum frequencies between 1.2–1.8 kHz, and the same songs with minimum frequencies artificially incremented one semitone, at 2.1–2.6 kHz, in high and low noise level territories at four distances. We quantified signal-to-noise ratio, tail-to-signal ratio, blur ratio, and excess attenuation. Our results showed that songs with lower minimum frequencies in low noise territories transmit with higher signal-to-noise ratio, lower blur ratio, and excess attenuation at longer distances. Songs with increased minimum frequencies only showed higher signal-to-noise ratio in noisier territories at longer distances. These results support the hypothesis of producing frequency shift to increase the communication distance in noisier environments. This is the first experimental study that tests the effect of shifting frequency on acoustic communication transmission on bird territories with different noise levels.

Resumen · Los cambios en la frecuencia del canto en una especie de ave urbana optimizan la transmisión acústica en áreas urbanas ruidosas.
En la comunicación acústica es necesario que las señales lleguen al receptor con una degradación y atenuación reducidas para mejorar la transmisión del mensaje. La contaminación acústica resultante de las actividades antropogénicas en las ciudades reduce la eficiencia y la eficacia de la comunicación acústica. Algunas especies responden a altos niveles de ruido aumentando la frecuencia mínima de sus vocalizaciones para evitar el enmascaramiento del ruido, pero esto puede afectar la forma en que los sonidos se transmiten en el entorno, porque los sonidos con frecuencias más altas experimentan mayores niveles de atenuación y degradación. Usando un experimento de transmisión de sonidos, analizamos cómo los cambios de frecuencia mínima afectan las propiedades de transmisión de sonido del canto de *Troglodytes musculus* en áreas urbanas que difieren en el nivel de ruido antropogénico. Transmitimos cantos con frecuencias mínimas entre 1,2–1,8 kHz, y los mismos cantos con un incremento artificial de frecuencias mínimas de un semitono, con frecuencias mínimas a 2,1–2,6 kHz, en territorios con niveles de ruido alto y bajo a cuatro distancias. Cuantificamos la relación señal-ruido, la relación cola-señal, la reverberación y el exceso de atenuación. Nuestros resultados mostraron que los cantos con frecuencias mínimas inferiores en territorios de bajo nivel de ruido transmiten con una relación señal-ruido más alta, reverberaciones y un exceso de atenuación más bajos a distancias mayores. Los cantos con frecuencias mínimas aumentadas solo mostraron una mayor relación señal-ruido en territorios ruidosos a distancias mayores. Estos resultados respaldan la hipótesis de producir un cambio de frecuencia para aumentar la distancia de comunicación en entornos ruidosos. Este es el primer estudio experimental que prueba el efecto del cambio de frecuencia en la transmisión de comunicación acústica en territorios de aves con diferentes niveles de ruido.

Key words: *anthropogenic noise · blur ratio · excess attenuation · signal-to-noise ratio · sound transmission*

INTRODUCTION

Birds vocalize to communicate with conspecific and heterospecific individuals (Bradbury & Vehrencamp 2011). Vocalizations are used for territory defense, mate attraction, social interactions, and antipredator behaviors (Langmore 1998, Marler 2004, Catchpole & Slater 2008, Bradbury & Vehrencamp 2011). Therefore, it is important that acoustic signals reach the intended receiver with minimal sound degradation or attenuation (Boncoraglio & Saino 2007, Ey & Fisher 2009). To minimize attenuation and degradation animals may employ several strategies, including perches with greater exposure (surrounded by less obstacles; Barker et al. 2009), singing at time periods in which other sounds are infrequent (e.g., cicadas sound or anthropogenic noise; Hart et al. 2015), or when weather conditions are favorable (e.g., less wind or no rain; Lohr et al. 2003, Krams 2001, Mathevon et al. 2005, Fuller et al. 2007).

In cities, anthropogenic noise (e.g., motors, traffic, or industrial machinery) makes bird acoustic communication inefficient (Slabbekoorn & Pett 2003, Slabbekoorn & den Boer-Visser 2006). This noise pollution occurs at frequencies below 3 kHz; therefore, birds that vocalize within this frequency range will have to modify their behavior or sound characteristics to increase the probability of communicating when high levels of noise pollution occur (Slabbekoorn & Pett 2003, Slabbekoorn & den Boer-Visser 2006, Redondo et al. 2013). For example, some species vocalize at night (Fuller et al. 2007), other species shift sounds to higher frequencies (Slabbekoorn

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& Pett 2003, Slabbekoorn & den Boer-Visser 2006, Redondo et al. 2013), and other species increase sound energy (Lombard effect; Brumm & Todt 2002, Brumm et al. 2004, Brumm et al. 2009). However, it is under debate if increasing the frequencies of an acoustic signal is a response to noise pollution or a by-product of the Lombard effect (increase in the vocalization energy when vocalizing in loud environments; Nemeth & Brumm 2010, Cardoso & Atwell 2011, 2012, Nemeth et al. 2012, 2013, Slabbekoorn et al. 2012, Zollinger et al. 2012, Potvin & Mulder 2011).

Using a sound transmission experiment, we analyzed how minimum frequency shifts affect the sound transmission of Southern House Wren *Troglodytes musculus* songs in urban areas with high and low anthropogenic noise level. The Southern House Wren is a widely distributed species that inhabits open (e.g., urban area gardens, parks, or farms) and semi-open areas (e.g., secondary forest edges, coffee plantations, or wood plantations) in the Costa Rican Central Valley (Stiles & Skutch 1989, Juárez et al. 2020), the most urbanized area in the country. Many of these areas are located close to or between sources of high anthropogenic noise, including highways, factories, or airports (Redondo et al. 2013, Juárez et al. 2020). Previous studies in this species showed that wrens increased the minimum frequency of songs in noisy conditions (Redondo et al. 2013) and a have smaller song element repertoire (Juárez et al. 2021) suggesting that those changes play an important role for communicating in noisy environments, as occurs with several other bird species in urban areas (Slabbekoorn & Pett 2003, Slabbekoorn & den Boer-Visser 2006, Slabbekoorn et al. 2012, Mendez et al. 2021). Specifically, we analyze how anthropogenic noise affects the sound transmission of songs produced at different minimum frequencies but same amplitude. If minimum frequency shifts improve sound transmission distance under low-frequency noise conditions (i.e., urban noise), we predict that songs with increased minimum frequency will transmit with less attenuation and degradation at territories with more noise and at longer distances.

METHODS

Study sites. We conducted this study in two sites: Campus of the Universidad de Costa Rica, San Jose province (09°56'N, 84°05'W; altitude: 1200 m a.s.l.), and Jardín Botánico Lankester, Cartago province (09°50'N, 83°53'W; altitude: 1400 m a.s.l), where Southern House Wrens are common inhabitants in gardens and natural thickets (Juárez et al. 2020). Both study sites are located inside an urban matrix in which the anthropogenic noise level varies across it. Vegetation is similar in both sites; both areas are characterized by open gardens where isolated trees and bushes are abundant, with a mixture of small areas of young secondary forest and natural thickets.

Selection of test song for experiment playbacks. We used ten different songs from ten males (one per individual) living in territories with low noise levels (far from roads, sidewalks, or motors) recorded in 2016 as our testing songs (Table 1). We chose only those songs with the highest signal-to-noise ratio and no overlapping background sounds (Figure 1). We recorded testing songs using a solid-state recording Marantz PMD-661 (WAVE format, 44.1 kHz sampling rate, and 16-bit accuracy) attached to a directional microphone Sennheiser ME66/K6 (Sennheiser Electronic, Germany). We did not choose songs recorded from males living in territories with high levels of noise because the structure of these songs varies in other features besides minimum frequency (Redondo et al. 2013, Juárez et al. 2021). For example, males from noisy territories include different elements to produce songs with longer thrills (Redondo et al. 2013, Juárez et al. 2021), a characteristic that can influence song transmission. Therefore, using only the songs from low-noise territories allowed us to control for the effect of song structure in our sound transmission experiment.

We isolated and filtered the ten songs using the passive option of the Fast Fourier Transformed filter in Audition 1.0 (Adobe Systems, San Jose, CA). For each song we used a different filter because each song had a different bandwidth (Table 1). All testing songs were standardized to –1 dB using the Normalize feature in Audition 1.0. Then, we increased minimum frequency of the ten selected and filtered songs by one semitone, using the Pitch Shift with high precision feature included in the Constant Stretch Effects of Audition 1.0. We did not use a higher increase in the minimum frequency because songs do not sound natural.

We created a single song file composed of all 20 prepared songs using Audition 1.0. Each song was separated by 1 second of silence, and each low minimum-frequency song was followed by its high minimum-frequency-adjusted song (separated by 1 s of silence), creating a sequence of 20 songs. The sequence of 20 songs was played five times in each trial with 1 s of silence between the last song of one sequence and the first song of the next sequence.

We stored the test songs in an iPod Touch Nano (Apple, Cupertino, CA) for playing back in the field using an AN-Mini loudspeaker, frequency response 0.1–15 kHz (Anchor Audio, Carlsbad, CA). We re-recorded the playback testing songs using a

Table 1. Filters used to create the twenty stimulus of Southern House Wren songs used in the transmission experiment. Song code include one letter from song type and Low in songs with low-minimum frequency, and High in songs with increased minimum frequency.

Songs	Low filter (kHz)	High filter (kHz)
High A	2.1	7.9
Low A	1.5	7.3
High B	2.3	8.3
Low B	1.7	7.7
High C	2.4	10.8
Low C	1.8	10.2
High D	2.6	10.8
Low D	1.2	9
High E	2.1	9
Low E	1.2	7.5
High F	2.2	11.6
Low F	1.7	9.3
High G	2.4	10.2
Low G	1.6	9.3
High H	2.4	10.3
Low H	1.6	8.1
High I	2.1	12.3
Low I	1.3	9.6
High J	2.6	10.6
Low J	1.7	8.1

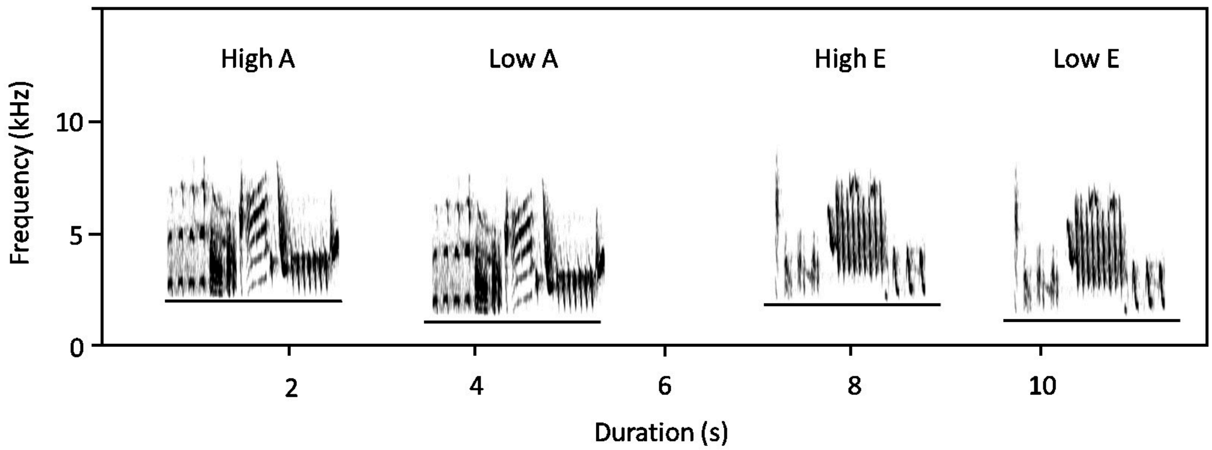

Figure 1. Sonograms of two of the Southern House Wren songs used for the transmission experiment. *High* represent the songs in which the minimum frequency was artificially increased and *Low* represent the songs with the minimum frequency as it was recorded in the field. The letters represent the song code.

solid-state recording Marantz PMD-661 (WAVE format, 44.1 kHz sampling rate, and 16-bit accuracy) attached to an omnidirectional microphone Sennheiser ME62/K6 (Sennheiser Electronic, Germany), via a microphone preamplifier (Sound Device MP-1; frequency response: 0.02–22 kHz). We set up the preamplifier at 0 dB gains from transmission experiment conducted between 5 to 20 m of distance between the loudspeaker and microphone, but at –18 dB for experiments at 40 m of distance. Playbacks were reproduced at 80 dB sound pressure level measured at 1.25 m from the speaker using a Sper Scientific Digital Sound Meter (NIB-850014, Scottsdale, AZ) with A weighting and fast response.

Transmission experiment set-up. We conducted the study from 16 to 19 May 2016, during the breeding season of Southern House Wrens in Costa Rica (Stiles & Skutch, 1989), within eight territories with similar vegetation structure (isolate trees, sparse bushes, and grassland areas). Four territories were allocated in areas with high levels of noise (next to roads and sidewalks) and four territories in areas with low levels of noise (far from roads, motors, or sidewalks). All transmission experiments were conducted between 6:00 and 10:00 h, when Southern House Wrens are active vocally.

In each territory, we played the songs across four horizontal distances (5, 10, 20, and 40 m between loudspeaker and microphone). The speaker and microphone were placed at a height of 1.5 m, which represents a common height of singing Southern House Wren males in both study sites. The 20 m distance represents the average distance between members of the pair in this species in the study area, the maximum distance was selected by doubling the 20 m distance, while 5 and 10 m represent one quarter and half of the average distance respectively. Within each territory, we distributed the four distances at different axes, following the new approach for this experiments that allows for a more representative sampling of territory characteristics (Sandoval et al. 2015, Piza & Sandoval 2016, Graham et al. 2017).

Sound analyses. We used SigPro 3.25 software (Pedersen 1998) to analyze the first three re-recorded songs of each of the 20 songs included in a sequence, that were not overlapped for other sounds. We compared our re-recorded songs with songs re-recorded at a distance of 1.25 m, with the speaker oriented upwards and the microphone hanging directly overtop in the center of a vegetation gap of 30 x 25 m. This approach allows us to control for changes in songs that may be produced for the playback equipment, and avoid recording songs with reverberations produced by the vegetation and the ground.

We measured four degradation and attenuation variables, after eliminating the background noise beyond the range of the signal of interest, using the filter setting for each song: (1) signal-to-noise ratio, (2) tail-to-signal ratio, (3) blur ratio, and (4) excess attenuation (for details of this measurements see Dabelsteen et al. 1993, Holland et al. 1998, Lampe et al. 2007). We excluded 60 of the 480 measurements of the 40 m playbacks sessions from the analysis, because noise levels in the frequency range of the playback song were too high to properly recognize songs in SigPro.

Statistical analysis. We conducted four Linear Mixed-effect Models (LMM) to compare how songs with different minimum frequencies attenuate and degrade. Each LMM included as independent variables: (1) song type (low vs high minimum frequency), (2) distance between the speaker and microphone (5, 10, 20, and 40 m); (3) territory noise level (low and high levels of noise); and (4) second order interactions. We included (1) songs used in playback and (2) the territory where the experiment was conducted as random factors, to control for the intrinsic variation of each one. Finally, we used (1) signal-to-noise ratio, (2) tail-to-signal ratio, (3) blur ratio, and (4) excess attenuation as our response variables, each per LMMs. For all LMM we conducted all pairwise comparisons as post-hoc tests to determine which variables were significant. All values reported as mean ± SE. Statistical analyses were conducted in JMP (version 10.0; SAS Institute, Cary, NC, USA).

RESULTS

We found that tail-to-signal ratio ($F_{3.1765}$ = 200.28, P < 0.001) and blur ratio ($F_{3.1762}$ = 1004.07, P < 0.001) increased with distance (Figure 2). Signal-to-noise ratio decreased with distance though difference was not significant between 20 and 40 m ($F_{3.1762}$ = 1249.00, P < 0.001; Figure 2). Excess of attenuation was significantly higher at 40 m than at the other distances ($F_{3.1761}$ = 56.53, P < 0.001; Figure 2). The noise level (low vs. high) had no effect on signal-to-noise ratio ($F_{1.6}$ = 0.10, P = 0.76), tail-to-signal ratio ($F_{1.6}$ = 0.44, P = 0.53), blur ratio ($F_{1.6}$ = 0.59, P = 0.47), nor excess attenuation ($F_{1.6}$ = 0.78, P = 0.41; Fig. 2). We found that blur ratio was higher in the song with high minimum frequency than in songs with low minimum frequency ($F_{1.18}$ = 7.99, P = 0.01; Figure 2). However, we found no differences for signal-to-noise ratio ($F_{1.18}$ = 0.56, P = 0.46), tail-to-signal ratio ($F_{1.18}$ = 0.30, P = 0.59), and excess attenuation ($F_{1.18}$ = 1.70, P = 0.21) on both song types (Figure 2).

Second order interactions between independent variables varied among the four measurements of attenuation and degradation (response variables). Signal-to-noise ratio was high in territories with low noise for distance between 5 and 20 m, but higher in territories with high levels of noise at 40 m ($F_{3.1762}$ = 50.35, P < 0.001; Figure 3). Tail-to-signal ratio increased in ter-

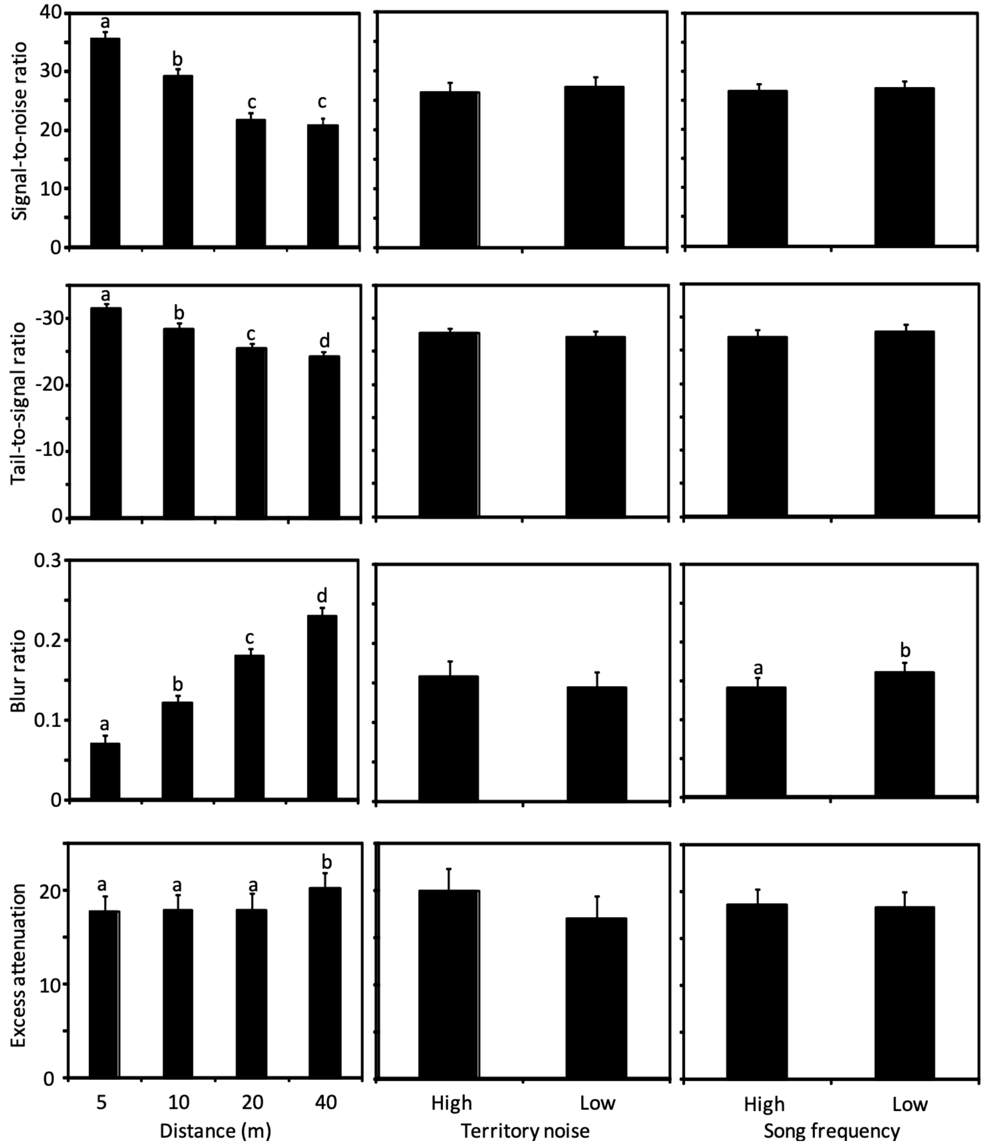

Figure 2. Differences in four degradation or attenuation measurements relative to the distance to the sound source, noise levels inside territories, and values of song minimum frequency. Error bars are standard errors of the mean. Different lowercase letters above the bars indicate significant differences of post-hoc tests; bars with the same letters are not statistically different.

ritories with high noise at 10 and 20 m, and in territories with low noise at distances of 10 and 20 m ($F_{3.1765}$ = 38.25, P < 0.001; Figure 3). Blur ratio increased in territories with high noise at 5, 20 and 40 m, and in territories with low noise at 10 m ($F_{3.1762}$ = 54.89, P < 0.001; Figure 3). Excess attenuation increased in territories with high noise at 5 and 20 m, and in territories with low noise at 40 m ($F_{3.1761}$ = 85.95, P < 0.001; Figure 3).

We found that both blur ratio and excess attenuation measurements varied with the interaction of distance and frequency level of song types. Blur ratio was significantly lower in song types with low minimum frequency only at 40 m, but not at 5, 10, and 20 m ($F_{3.1762}$ = 54.89, P < 0.001; Figure 3). Frequency level did not affect excess attenuation at distances between 5 and 20 m, but excess attenuation significantly decreased in songs with low minimum frequency at 40 m ($F_{3.1761}$ = 7.56, P < 0.001; Figure 3). For signal-to-noise ratio ($F_{1.1761}$ = 1.08, P = 0.36) and tail-to-signal ratio ($F_{1.1761}$ = 0.97, P = 0.40) we found no significant effect of the interaction between minimum frequency level (song types) and distance (Figure 3).

We found a significant effect of the interaction of noise level × minimum frequency level for signal-to-noise ratio. Signal-to-noise ratio increased in territories with low level of noise and songs with low minimum frequency; and in territories with high level of noise and songs with higher minimum frequency ($F_{1.1761}$ = 18.47, P < 0.001; Figure 3). For tail-to-signal ratio ($F_{1.1761}$ = 3.20, P = 0.07), blur ratio ($F_{1.1761}$ = 1.25, P = 0.26), and excess attenuation ($F_{1.1761}$ = 1.46, P = 0.22) we found no significant effect of the interaction between frequency level (song types) and levels of noise (Figure 3).

DISCUSSION

Our study directly compared how transmission properties of songs (attenuation and degradation) varied with different minimum frequencies (low and high) on territories with different anthropogenic noise levels. This study demonstrated that shifting minimum frequency in noisy environments improved the acoustic communication of Southern House Wrens since their songs are less masked and attenuated. We also found that the frequency shift does not negatively affect song transmission up to 20 m, but it does at 40 m, where the transmission properties of the songs decrease. These results indicate that vocalizations used to communicate at longer distances were more affected when the minimum frequency is shifted upward in response to noise pollution, the response more commonly reported in studies of noise effect on bird vocalizations (Martens and Geduldig 1990, Slabbekoorn & Pett 2003, Slabbekoorn & den Boer-Visser 2006, Redondo et al. 2013, Slabbekoorn 2019, Duquette et al. 2021).

As we predicted, when we broadcasted songs with minimum frequency shifts inside noisier territories, these songs experienced less degradation and attenuation (Figure 3), improving song transmission. On the contrary, songs with lower minimum frequency transmitted in territories with lower noise level experienced less degradation (i.e. higher signal-to-noise ratios) than songs with minimum frequency shifts (Figure 3). But, when we broadcasted songs with minimum frequency shifts inside territories with lower noise, and songs with lower minimum frequency inside noisier territories, both degraded and attenuated more (Figure 3). Consequently, our results support previous correlative studies, which reported that minimum frequency shifts in noisy environments, such as cities, increase the sound communication efficiency (e.g., Martens and Geduldig 1990, Slabbekoorn & Pett 2003, Slabbekoorn & den Boer-Visser 2006, Slabbekoorn et al. 2012, Redondo et al. 2013, Slabbekoorn 2019, Duquette et al. 2021).

Contrary to our expectations, distance did not affect the transmission properties of songs broadcasted at two minimum frequencies (low or high), when noise level was not considered (Figure 3). Songs with different minimum frequency showed comparable levels of degradation and attenuation from 5 to 20 m. The social interactions performed by Southern House Wren pair members often occurred within short distances (pers. obs.), so shifting minimum frequency of songs in noisy sites may improve sound communication, as has been previously argued (Hu & Cardoso 2009, Slabbekoorn et al. 2012, Slabbekoorn 2013). However, at the furthest distance tested (40 m), frequency shifts begin to affect the transmission of the song; as expected for high-frequency sounds according to the acoustic adaptation hypothesis, songs with high-minimum frequencies experience more attenuations and scattering (Boncoraglio & Saino 2007, Ey & Fisher 2009), compared to songs with low-minimum frequencies (Figure 3). These results indicate that the benefit of frequency shifts is distance dependent: at short distances they avoid the frequency masking by noise, but those frequency shifts at further distances increase degradation and attenuation, reducing the sound communication efficiency.

Frequency shifting, as we tested experimentally, likely improves sound communication in noise-polluted habitats as it reduces the probability of sounds being masked by low-frequency noise (Hu & Cardoso 2009, Luther & Derryberry 2012), reducing attenuation of the emitted songs when arriving at the potential receiver. However, frequency shifts may be limited by at least

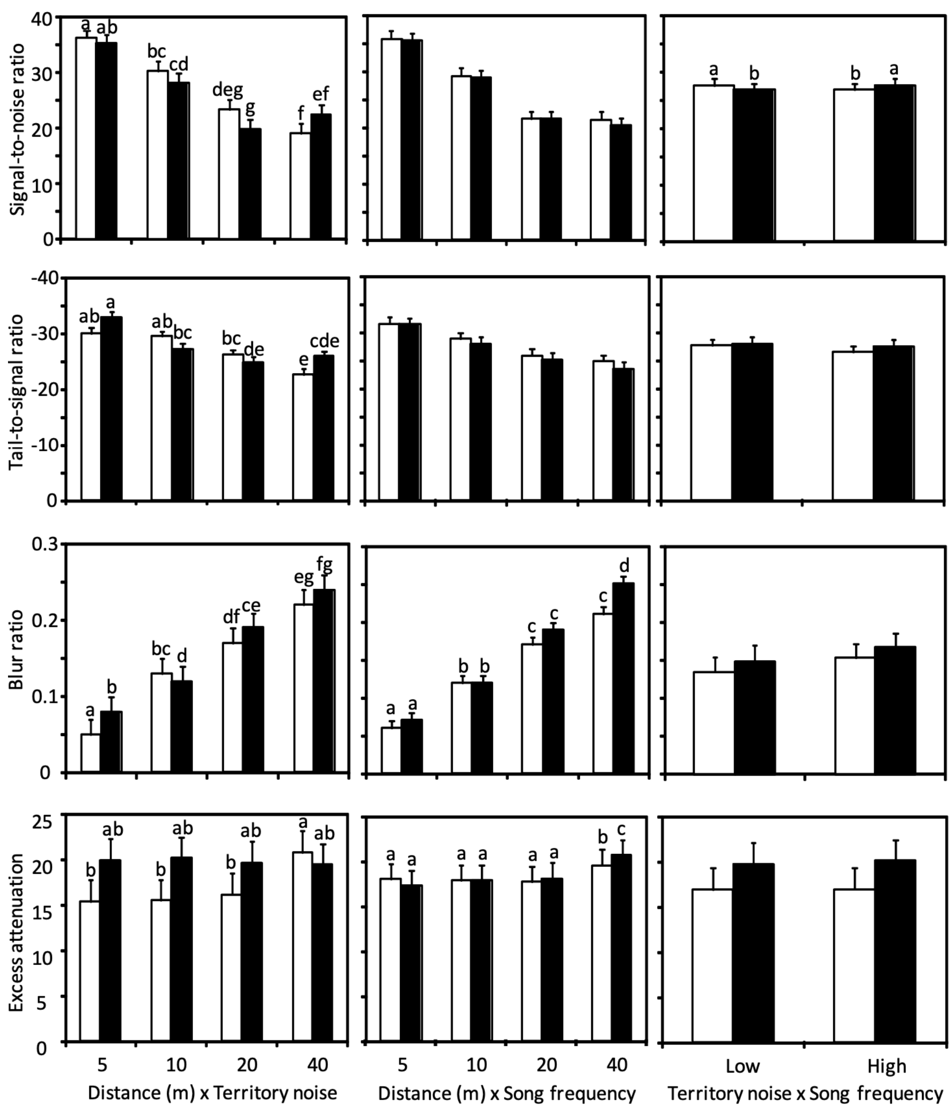

Figure 3. Interactions between distance and territory noise level (black = high; white =low), between distance and song minimum frequency (black = high; white = low), and between territory noise level and song minimum frequency (black = high; white = low). Error bars are standard errors of the mean. Different lowercase letters above the bars indicate significant differences of post-hoc tests; bars with different letters are statistically different. Graphics without letters represent cases in which no differences were detected between categories in the LMM.

two aspects: 1) it is energetically expensive because it requires greater syrinx contractions (Lambrechts 1996, Suthers et al. 1999, Hu & Cardoso 2009, Sandoval 2011) and 2) has more attenuation and scattering because trees, leaves, or branches increase the interference with their higher frequencies (Wiley 1991, Bradbury & Verhencamp 2011). It is then intuitive to expect that frequency shift occurs, despite its cost, only if sound transmission is improved, as has previously been suggested (Hu & Cardoso 2009, Slabbekoorn et al. 2012, Slabbekoorn 2013). In our case, minimum frequency shift of songs is worthy for closer communication interactions, such as pair members' communication or territory interactions at the territory border.

In conclusion, although our results appear to be contradictory because some of them showed a significant effect of shifting minimum frequency upward in noisy places, others fail to support it. These results just showed how the transmission properties of the minimum frequency of sounds are affected by different noise levels in the territories. First, the frequency shift does not affect sound transmission at close distances but it reduces it at further distances, as predicted by the acoustic adaptation hypothesis, therefore affecting communication. Second, frequency shifts improve sound transmission inside noisy territories though reducing attenuation and degradation, as suggested in previous studies which found higher minimum frequencies in places with high-noise level (e.g., cities and next to roads, rivers or oceans) than in places with low-noise level (Lohr et al. 2003, Bermúdez-Cuamatzin et al. 2009, Redondo et al. 2013, Luther & Derryberry 2012). This is the first detailed study that compares the frequency shift effect on song transmission on territories with different noise levels. We encourage more investigators to conduct these transmission experiments to directly test the effects of minimum frequency shifts on sound transmission under noisier conditions.

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REFERENCES

Barker, NKS, T Dabelsteen & DJ Mennill (2009) Degradation of male and female rufous–and–white wren songs in a tropical forest: effects of sex, perch height, and habitat. *Behaviour* 146: 1093–1122. https://doi.org/10.1163/156853909X406446

Bermúdez-Cuamatzin, E, AA Ríos-Chelén, D Gil & C Macías (2009) Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? *Behaviour* 146: 1269–1286. https://doi.org/10.1163/156853909X423104

Boncoraglio, G & N Saino (2007) Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology* 21: 134–142. https://doi.org/10.1111/j.1365-2435.2006.01207.x

Bradbury, JW & SL Vehrencamp (2011) *Principles of Animal Communication 2nd Edition*. Sinauer Press, Sunderland, Massachuset, USA.

Brumm, H (2004) The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* 73: 434–440. https://doi.org/10.1111/j.0021-8790.2004.00814.x

Brumm, H & D Todt (2002) Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour* 63: 891–897. https://doi.org/10.1006/anbe.2001.1968

Brumm, H, R Schmidt & L Schrader (2009) Noise-dependent vocal plasticity in domestic fowl. *Animal Behaviour* 78: 741–746. https://doi.org/10.1016/j.anbehav.2009.07.004

Brumm, H, K Voss, I Köllmer & D Todt (2004) Acoustic communication in noise: regulation of call characteristics in a New World monkey. *Journal of Experimental Biology* 207: 443–448. https://doi.org/10.1242/jeb.00768

Cardoso, GC & JW Atwell (2011) On the relation between loudness and the increased song frequency of urban birds. *Animal Behaviour* 82: 831–836. https://doi.org/10.1016/j.anbehav.2011.07.018

Cardoso, GC & JW Atwell (2012) On amplitude and frequency in birdsong: a reply to Zollinger et al. *Animal Behaviour* 84: e10–e15. https://doi.org/10.1016/j.anbehav.2012.08.012

Catchpole, CK & PJB Slater (2008) *Bird song biological themes and variations*. Cambridge University Press, New York, New York, USA. https://doi.org/10.1017/CBO9780511754791

Dabelsteen, T, ON Larsen & SB Pedersen (1993) Habitat-induced degradation of sound signals: Quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *Journal of Acoustic Society of America* 93: 2206–2220. https://doi.org/10.1121/1.406682

Duquette, CA, SR Loss & TJ Hovick (2021) A meta-analysis of the influence of anthropogenic noise on terrestrial wildlife communication strategies. *Journal of Applied Ecology* 58: 1112–1121. https://doi.org/10.1111/1365-2664.13880

Ey, E & J Fisher (2009) The "acoustic adaptation hypothesis" a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19: 21–48. https://doi.org/10.1080/09524622.2009.9753613

Fuller, RA, PH Warren & KJ Gaston (2007) Daytime noise predicts nocturnal singing in urban robins. Biology Letters 3: 368–370. https://doi.org/10.1098/rsbl.2007.0134

Graham, B, L Sandoval, T Dabelsteen & DJ Mennill (2017) A test of the Acoustic Adaptation Hypothesis in three types of tropical forest: degradation of male and female Rufous–and–white Wren songs. *Bioacustics* 26: 37–61. https://doi.org/10.1080/09524622.2016.1181574

Hart, PJ, R Hall, W Ray, A Beck & J Zook (2015) Cicadas impact bird communication in a noisy tropical rainforest. *Behavioral Ecology* 26: 839–842. https://doi.org/10.1093/beheco/arv018

Holland, JO, T Dabelsteen, SB Pedersen & ON Larsen (1998) Degradation of wren *Troglodytes troglodytes* song: Implications for information transfer and ranging. *Journal of Acoustic Society of America* 103: 2154–2166. https://doi.org/10.1121/1.421361

Hu, Y & GC Cardoso (2009) Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioral Ecology* 20: 1268–1273. https://doi.org/10.1093/beheco/arp131

Juárez, R, YG Araya-Ajoy, G Barrantes & L Sandoval (2021) House Wrens reduce repertoire size and change song element frequencies in response to anthropogenic noise. *Ibis* 163: 52–64. https://doi.org/10.1111/ibi.12844

Juárez, R, E Chacón-Madrigal & L Sandoval (2020) Urbanization has opposite effects on the territory size of two Passerine birds. *Avian Research* 11: 1–9. https://doi.org/10.1186/s40657-020-00198-6

Krams, I (2001) Perch selection by singing chaffinches: a better view of surroundings and the risk of predation. *Behavioral Ecology* 12: 295–300. https://doi.org/10.1093/beheco/12.3.295

Lambrechts, MM (1996) Organization of birdsong and constraints on performance. Pp. 305–320 *in* Kroodsma, DE & EH Miller (eds.) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, New York, USA. https://doi.org/10.7591/9781501736957-025

Lampe, HM, ON Larsen, SB Pedersen & T Dabelsteen (2007) Song degradation in the hole-nesting pied flycatcher *Ficedula hypoleuca*: Implications for polyterritorial behaviour in contrasting habitat-types. *Behaviour* 144: 1161–1178. https://doi.org/10.1163/156853907781890887

Langmore, NE (1998) Functions of duets and solo songs of female birds. *Trends in Ecology and Evolution* 13: 136–140. https://doi.org/10.1016/S0169-5347(97)01241-X

Lohr, B, TF Wright & RJ Dooling (2003) Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour* 65: 763–777. https://doi.org/10.1006/anbe.2003.2093

Luther, DA & EP Derryberry (2012) Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. *Animal Behaviour* 83: 1059–1066. https://doi.org/10.1016/j.anbehav.2012.01.034

Marler, PA (2004) Bird calls: a cornucopia from communication. Pp. 132–177 *in* Marler, P & H Slabbekoorn (eds.) *Nature's music: the science of bird song*. Elsevier Academic Press, San Diego, California, USA. https://doi.org/10.1016/B978-012473070-0/50008-6

Martens, J & G Geduldig (1990) Acoustic adaptations of birds living close to Himalayan torrents. Pp. 123–133 *in* Garmisch P (ed.) *Proceedings of the 100th International Meeting of the Deutsche Ornithologische Gesellschaft; 1989.* Verlag der Deutschen Ornithologen-Gesellschaft, Germany.

Mathevon, N, T Dabelsteen & SH Blumenrath (2005) Are high perches in the blackcap *Sylvia atricapilla* song or listening posts? A sound transmission study. *Journal of Acoustic Society of America* 117: 442–449. https://doi.org/10.1121/1.1828805

Mendez, C, G Barrantes & L Sandoval (2021) The effect of noise over time and between populations on the acoustic characteristics of different vocalization types. *Behavioural Processes* 182: 104282. https://doi.org/10.1016/j.beproc.2020.104282

Nemeth, E & H Brumm (2010) Birds and anthropogenic noise: are urban songs adaptive? *American Naturalist* 176: 465–475. https://doi.org/10.1086/656275

Nemeth, E, N Pieretti, SA Zollinger, N Geberzahn, J Partecke, AC Miranda & H Brumm (2013) Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of Royal Society B* 280: 20122798. https://doi.org/10.1098/rspb.2012.2798

Nemeth, E, SA Zollinger & H Brumm (2012) Effect sizes and the integrative understanding of urban bird song. *American Naturalist* 180: 146–152. https://doi.org/10.1086/665994

Pedersen, SB (1998) *Preliminary operational manual for signal processor Sigpro*. Center of Sound Communication Odense University, Odense, Denmark.

Piza, P & L Sandoval (2016) The differences in transmission properties of two bird calls show relation to their specific functions. Journal of Acoustic Society of America 140: 4271–4275. https://doi.org/10.1121/1.4971418

Potvin, DA, KM Parris & RA Mulder (2011) Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). *Proceeding of Royal Society B* 278: 2464–2469. https://doi.org/10.1098/rspb.2010.2296

Redondo, P, G Barrantes & L Sandoval (2013) Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*. *Ibis* 155: 621–625. https://doi.org/10.1111/ibi.12053

Sandoval, L (2011) Male–male vocal interactions in a territorial neotropical quail: which song characteristics predict a territorial male's response? *Behaviour* 148: 1103–1120. https://doi.org/10.1163/000579511X596570

Sandoval, L, T Dabelsteen & DJ Mennill (2015) Transmission characteristics of solo songs and duets in a neotropical thicket habitat specialist bird. *Bioacoustics* 24: 289–306. https://doi.org/10.1080/09524622.2015.1076346

Slabbekoorn, H (2013) Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour* 85: 1089–1099. https://doi.org/10.1016/j.anbehav.2013.01.021

Slabbekoorn, H (2019) Noise pollution. *Current Biology*, 29: R957–R960. https://doi.org/10.1016/j.cub.2019.07.018

Slabbekoorn, H & A den Boer–Visser (2006) Cities change the songs of birds. *Current Biology* 16: 2326–2331. https://doi.org/10.1016/j.cub.2006.10.008

Slabbekoorn, H & M Peet (2003) Ecology: Birds sing at a higher pitch in urban noise. *Nature* 424: 267. https://doi.org/10.1038/424267a

Slabbekoorn, H, XJ Yang & W Halfwerk (2012) Birds and anthropogenic noise: singing higher may matter. *American Naturalist* 180: 142–145. https://doi.org/10.1086/665991

Stiles, FG & AF Skutch (1989) *A guide to the birds of Costa Rica*. Cornell University Press, Ithaca, New York, USA.

Suthers, RA, F Goller & C Pytte (1999) The neuromuscular control of birdsong. *Philosophical Transactions of Royal Society of London* 354: 927–939. https://doi.org/10.1098/rstb.1999.0444

Wiley, RH (1991) Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist* 138: 973–993. https://doi.org/10.1086/285263

Zollinger, SA, J Podos, E Nemeth, F Goller & H Brumm (2012) On the relationship between, and measurement of, amplitude and frequency in bird song. *Animal Behaviour* 84: e1–e9. https://doi.org/10.1016/j.anbehav.2012.04.026