Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use?

Eira Bermúdez-Cuamatzin¹⁾, Alejandro Ariel Ríos-Chelén^{1,3)}, Diego Gil²⁾ & Constantino Macías Garcia¹⁾

(¹ Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, A.P. 70-275, C.P. 04510, México D.F., México; ² Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutierrez Abascal 2, E-28006 Madrid, Spain, Madrid)

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Summary

The influence of ambient noise in shaping birdsong attributes has received much attention lately. Recent work shows that some birds sing higher-pitched songs in noisy areas, which may allow them to avoid acoustic interference; yet it is not clear how this is achieved. Higher-pitched songs may be produced either by using the same syllable types in quiet and noisy areas, but singing them at a higher frequency in the latter (syllable pitch plasticity), or by using different syllable types in silent and in noisy circumstances (differential syllable use). Here we explored both strategies in the Mexico City population of house finch (*Carpodacus mexicanus*), a species known to possess a repertoire of several hundreds of syllable types. Birds produced songs with higher minimum frequencies in noisy than in quiet areas. This was mostly due to the minimum frequency of some syllable types being higher in noisy areas than in quiet locations. Also, males modulated the minimum frequency of the same syllable type during momentary increases of noise. Our results can help explain the high success of house finches at colonizing urban areas, while providing evidence of syllable pitch plasticity.

Keywords: house finch, Carpodacus mexicanus, urban noise, birdsong, pitch plasticity.

³⁾ Corresponding author's e-mail address: aarios@miranda.ecologia.unam.mx

Introduction

The influence of ambient noise in shaping birdsong attributes has received much attention recently (e.g., Brumm & Todt, 2002; Slabbekoorn & Peet, 2003; Brumm, 2004, 2006; Leader et al., 2005; Brumm & Slater, 2006; Patricelli & Blickley, 2006; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006; Fuller et al., 2007). Some of these studies have shown that the song of birds in situations of high levels of noise show particular adaptations to favour signal transmission, such as increase in sound amplitude (Brumm, 2004), number of same song types within a bout before changing to another song type (Brumm & Slater, 2006), and increased minimum song frequency (Slabbekoorn & Peet, 2003; Fernández-Juricic et al., 2005; Wood & Yezerinac, 2006). With respect to the latter, singing high-pitched songs in noisy areas may lead birds to reduce noise interference. This is because ambient noise, whether naturally produced (e.g., wind) or anthropogenic (e.g., automobile traffic), is commonly composed of low frequencies, with its energy diminishing towards higher frequencies, and certain types of anthropogenic noise like car traffic can easily reach frequencies that overlap with the frequencies of birdsong (e.g., 2 kHz). Therefore, producing songs above these frequencies could prevent noise masking. As birdsong is known to play an important role in sexual selection processes (reviews in Searcy & Anderson, 1986; Catchpole & Slater, 1995; Gil & Gahr, 2002), avoiding noise masking may have important fitness consequences.

Indeed, some studies suggest that noise has negative effects on bird populations. For instance, several studies have found a reduction in density of breeding birds in the proximities of noisy roads and highways (e.g., Reijnen & Foppen, 1994; Reijnen et al., 1996), and a negative association between noise level and bird density (Reijnen et al., 1995). While it is not clear how high noise level may be related to population decline, some data suggest that the latter may be a consequence of noise masking birdsong (Rheindt, 2003), which in turn may impair processes of sexual selection, erode pair preferences (Reijnen & Foppen, 1994; Swaddle & Page, 2007), or disrupt bird vocal communication in general.

Since anthropogenic noise is a widespread phenomenon, particularly strong in or around cities, airports and highways, often reaching levels beyond those allowed by current legislation on public health (especially in big cities), it is important to study whether birds are able to deal with this kind of pollution. A positive correlation between anthropogenic noise level and frequency of birdsong was first reported in the great tit (*Parus major*, Slabbekoorn & Peet, 2003). This study was subsequently followed by additional work by Fernández-Juricic et al. (2005) in the house finch (*Carpodacus mexicanus*) and Wood & Yezerinac (2006) in the song sparrow (*Melospiza melodia*), who reported similar correlations. The consensus of these studies is that the typically low-pitched urban noise would favour higher-pitched songs since these would be more readily detected by conspecifics.

Yet the strategy by which birds achieve higher frequency songs in noisy areas is far from clear, and at least two non-mutually exclusive hypotheses can be envisaged. First, birds may use different syllable types according to the level of noise, that is, they may include in their song more highfrequency syllable types in noisy areas than in quiet areas (differential syllable use). Such a strategy may be reinforced through differential learning by young birds, since by definition those syllables better suited to noisy environments would have a higher chance of being heard and learnt, by young birds (Hansen, 1979). Second, birds may use the same syllable types in noisy and in quiet areas, yet produce this syllable type with a higher minimum frequency in noisy environments (syllable pitch plasticity). A change in frequency could in fact be a side effect of an increase in song amplitude (the Lombard effect, Quedas et al., 2007), which is a well-known strategy that organisms use when facing noise (e.g., Cynx et al., 1998; Brumm & Todt, 2002; Brumm, 2004; Brumm et al., 2004). It is also unknown whether the positive correlation between noise intensity and minimum song frequency is the relatively slow, and long-term, result of selection favouring males whose song is less masked by environmental noise, or whether it results from the individuals being able to modulate the minimum frequency of their songs, thus being a short-term change due to behavioural plasticity (Brumm & Slabbekoorn, 2005). If the former is true we would expect individuals to sing high-pitched songs in noisy areas irrespective of current noise levels. A long-term change process has probably occurred in great tits (Parus ma*jor*) from noisy environments, which even during some particularly quiet periods continue to sing high-pitched songs (Slabbekoorn & Peet, 2003). Indeed, recent data show that in this species the song adaptation to urban conditions is based on song-type selection and not on spectral shifts or note deletion (Slabbekoorn & den Boer-Visser, 2006).

However, Slabbekoorn & den Boer-Visser (2006) study focused on between-population differences (city vs. forest) and, thus, individual adaptation could be masked by population differentiation and drift. In the present study we have taken a more direct approach and have analysed differences in syllable use and pitch plasticity within the same population with respect to different urban noise levels. In addition, by comparing minimum song frequencies in relation to changing levels of noise in particular moments, we tested whether individuals are capable of modulating their songs when facing sudden increases of background noise.

We studied a Southern population of house finches in Mexico City, one of the biggest and presumably noisiest cities in the World. Our objectives were three-fold: (1) to establish whether previous results reporting higher minimum frequencies in noisy areas in this species (Fernández-Juricic et al., 2005) also apply to our population; (2) to determine whether higher-pitched songs are produced in noisy areas through either differential syllable use or syllable pitch plasticity; and (3) to investigate whether house finches are capable of real-time modulation of the minimum frequency of their songs in response to changes in background noise levels.

Methods

Study site and song recordings

From May 17 to July 7, 2006, between 0800 and 1400 h, songs of 35 male house finches were recorded in 26 different locations in southern Mexico City. Spontaneously (not enticed by playback) singing males were recorded while perched from a distance of 5–10 m. We did not register whether recorded birds were interacting with other (male or female) individuals. To avoid recording each male more than once, the distances between recorded subjects were at least 1 km apart, which is larger than the maximum expected home range size of house finches (Manley & Schlesinger, 2000). Only one male was recorded on each location, except when several individuals could be recognized by differences in plumage colouration. This was the case at seven locations where two individuals were recorded and in one location in which three males were recorded. Following the study by Pytte (1997), who showed that five songs per individual are sufficient to establish a representative individual's syllable repertoire, we recorded at least five songs for each

male. We analysed (see below) an average of 21 songs per male (SE = 2.38, range = 6–71). Songs were recorded on audio cassettes (TDK SA60), using a directional microphone (Sennheiser ME66) connected to a Marantz PMD221 cassette recorder. Recordings were digitized on a PC computer using an Intel $^{\$}$ 5.10 Sound card with 16 bits accuracy, and sampled at a rate of 22 kHz using the Avisoft SASLab Pro software.

Measuring the songs and constructing a syllable catalogue

For each song we measured minimum frequency of each syllable (kHz), maximum frequency of song (kHz) and song length (s). Spectrograms were obtained using the Avisoft SASLab Pro software (FFT length, 256; frame size, 100%; window, Hamming; frequency resolution, 86 Hz; temporal resolution, 8 ms). Frequency and temporal measures of songs were conducted manually on the spectrograms, always by the same person, with the onscreen free moveable reticule cursor available in Avisoft SASLab Pro software. Only those songs whose minimum frequencies were discernible from the background noise were measured and subject of analyses. Figure 1 shows an example of a song recorded in a very noisy site and one song recorded in a quieter site.

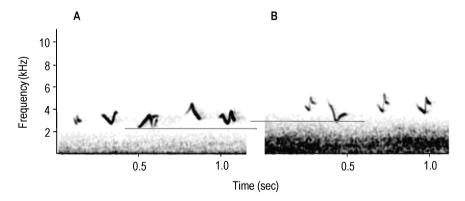


Figure 1. Two examples of house finches song recorded at two locations with low (A) and high (B) levels of noise. (A) A song recorded in Instituto de Biología, UNAM. (B) A song recorded in Gabriel Mancera Avenue. This figure exemplifies that even in noisy locations, the minimum frequency of songs could reliable be measured. The spectrogram of the song at the quiet location shows a lower minimum frequency than the song recorded at the noisy location. The line in A and B shows the minimum frequency of the song in A and B, respectively.

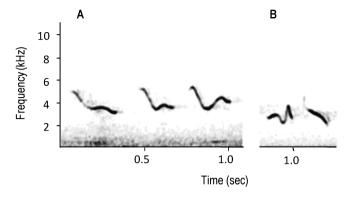


Figure 2. Examples of discrete and continuous variation in syllable types. (A) An example of three syllables with continuous variation; that is, with variation resulting in intermediate forms. These three syllables are considered as the same syllable type. (B) An example of two syllables that show discrete variation. These two syllables always showed these two discrete forms and, thus, were considered as different types.

In order to establish whether house finches increase syllable pitch or differentially use high-pitched syllable types in noisy areas, a catalogue of syllables was compiled. Syllables were classified into several types according to their shape. Variation between syllables was either discrete (i.e., a syllable type was clearly differentiated by its shape from other types) or continuous (i.e., there was a smooth transition in the shape of similar syllables). Following Pytte (1997), syllables with discrete variability were grouped in the same type if they shared the same general shape, whereas syllables that showed continuous variability and were similar in shape were grouped as the same type (Pytte, 1997). Thus, under these criteria, if the syllable decreased in bandwidth but kept its basic shape we considered it as the same syllable type. Figure 2A shows an example of a syllable showing continuous variability. Following these criteria, a total of 261 different syllable types were recognized in our sample.

Measuring noise

Noise level (dB SPL re 20 μ Pa) was measured at the same locations where songs were recorded, using a SEW® 2310 SL digital sound level meter (range, 30–130 dB; weight, A, fast response, ANSI S1.4 Type II) between September 1 and October 25, 2006. Since, because of logistic reasons, this work could not be done at the same time of the song recordings, we choose

to measure noise in September, thus avoiding the Mexican holiday period during which noise levels are typically reduced. To have a representative measure of noise, we measured it at the same time-span during which songs were recorded (there were six intervals: 8–9, 9–10, 10–11, 11–12, 12–13 and 13–14 h). We measured noise at each interval following a modified version of Brumm's (2004) protocol. Briefly, Brumm's protocol consisted of registering the highest value of ambient sound level, measured during 10 s at repeated times, at each of four directions of the compass. We measured noise at 2 m above the ground during 5 min; 1 min was used for each of five different directions in a clockwise direction (North, East, South, West and Upwards (i.e., towards the sky)). Each minute, noise was measured every 10 s (6 measurements/min). We flipped a coin to randomize the direction in which we started to register noise (North or South). West was always followed by Upwards. For each recorded male, noise level was registered at the same location where the bird was recorded. This means that even for those males that were recorded in the same location we registered independent noise levels for each one of them. Sound levels were averaged for each site, and these values used in further analyses.

Because we measured ambient noise levels in different months than when songs were recorded, we decided to test the repeatability of noise measures. For this purpose, we obtained new noise measures in a sub-sample (N=10) of the 26 sites where songs were recorded in October 2008 and compared it with the first measurements. This sub-sample encompassed places of low, moderate and high noise levels.

Data analyses

Parametric tests were used when data conformed to normal distributions. Otherwise, non-parametric statistics were used. Whenever the same data set was analysed more than once, a sequential Bonferroni correction was performed to correct the level of significance (Rice, 1989).

Differential syllable use

To determine whether house finches sing different syllable types in relation to noise level (i.e., differential syllable use), we first catalogued all syllables as 'high frequency syllable (HFS)' or 'low frequency syllable (LFS)' depending on whether their average frequency was, respectively, above or

below the overall mean syllable frequency. The mean frequency of each syllable type was calculated by obtaining the mean frequency of each syllable type per male, and then averaging the mean frequencies of each syllable type across all males. From these mean frequencies of syllable types we obtained the overall mean syllable frequency. If birds use different syllables types depending on background noise, we expected a positive correlation between the proportion of HFS and noise level.

Syllable pitch plasticity

To determine whether house finches use the same syllable types, but sing them at a higher frequency in noisy areas (i.e., syllable pitch plasticity), we compared the minimum frequency of the same syllable types between locations that differed in noise level. This comparison was designed to maximise the variance in the independent variable (differences in noise levels), and each bird was used only once in order to avoid pseudoreplication. We proceeded by first ranking the different birds according to the measured noise levels, then we paired male 1 (from the noisiest location) with male 35 (from the less noisy place), male 2 with male 34, and so on until 17 pairs were formed (leaving one male out of the analysis). We then calculated pair-wise differences in noise level (always subtracting quiet from noisy) as well as the average difference in minimum frequency of shared syllables types. Under the syllable pitch plasticity hypothesis we predicted a positive correlation between the difference in noise level and the difference in minimum frequency of shared syllables types.

Since the above procedure is open to the possibility that whatever result it yields is only valid for that particular set of pairs, we performed, in addition, a Mantel test in which all possible pairs (N=595) were included. Again, we calculated for each pair both the difference in ambient noise and the average difference in the minimum frequency of shared syllables. Inevitably this procedure generates a much more scattered association but has the advantage of a greater external power than the previous one.

Real-time modulation of song pitch in response to current changes in noise level

A further criterion required under the syllable pitch plasticity hypothesis is to demonstrate that house finches are able to modulate the minimum frequency of their songs according to different noise levels (i.e., short-term change, Brumm & Slabbekoorn, 2005). We took advantage of the fact that, while we were recording, there were sudden bursts of noise due to cars passing close by. This gave us the opportunity to investigate whether males are able to increase the minimum frequency of their songs during these moments of increased noise level with respect to quieter moments. We searched our song files for cases in which, at the same time when the focal male was singing, a sudden and evident increase of noise occurred (as determined by an increase in the density of the spectrogram's trace between 0 and 2 kHz). Provided that we had also a recorded song for this focal male (in the same sound file) in a moment of lower noise level, we could compare both songs. We had 13 such cases. We compared the minimum frequency of a song in the low noise level condition with the minimum frequency of another song from the same individual in the high noise level condition. To test whether there were significant differences in minimum frequencies between both conditions, we used a paired t test. An additional criterion was to choose the first song that precisely matched the same type of song (i.e., same sequence of syllables, same number of syllables, etc.) as the song in the noisy condition. This is because we wanted to compare the same syllable types to see if house finches modulate their frequency, and the same syllable type is easier to find in a song of the same type. This meant that we compared the minimum frequencies of the same syllable type in both conditions. This criterion was chosen after knowing the results of the previous analyses and was conducted in order to confirm the use of syllable pitch plasticity by male house finch. Unless specified otherwise, values are reported as mean \pm SE.

Results

Urban noise

Urban noise was mostly represented by cars and vehicles that passed far away (i.e., around 1 km away, in quite areas) or near (i.e., as close as 1 m to the place where noise was registered, in noisy sites). Mean urban noise levels significantly differed among sites (Kruskal–Wallis test: $\chi^2 = 146$, df = 25, p < 0.001), and ranged between sites from 40 dB(A) SPL to 74 dB(A) SPL. Mean noise level in our study sites was 58 ± 2 dB(A) SPL. Noise level was not correlated with number of recorded songs (Pearson correlation: r = 0.15,

 $N=35,\ p=0.367)$ nor with number of syllables (Pearson correlation: $r=-0.04,\ N=35,\ p=0.782)$, showing that our data were comparable between locations differing in noise level. Additionally, we found a highly significant correlation ($r=0.94,\ N=10,\ p<0.001$) between our measures of noise level obtained in September–October 2006, and our measures of noise levels obtained in October–November 2008. The repeatability value for this sub-sample of 10 sites was 0.94.

House finch songs

In exploratory analyses, we found that longer songs had lower minimum frequencies (Pearson correlation: r = -0.45, N = 35, p = 0.006), and higher maximum frequencies (Pearson correlation: r = 0.49, N = 35, p = 0.002). Maximum and minimum song frequencies were not correlated (r = -0.28, N = 35, p = 0.104).

We found an average of 27 ± 1.6 different types of syllables per male in our sample. When comparing places of high and low noise levels, we found that only an average of 7.5 ± 0.8 syllable types were shared among males. The mean house finch song duration in our sample (N=35) was 2.02 ± 0.10 s, range 0.99-3.93 s. The mean minimum frequency of songs was 2221 ± 31.30 Hz (range 1916-2697 Hz), and the mean maximum frequency was 5873 ± 103.42 (range 4630-7032 Hz).

House finch songs and urban noise

We found a positive correlation between noise level and minimum frequency of song (r=0.42, N=35, p=0.012), which remained significant after Bonferroni correction. This result supports previous findings with this species (Fernández-Juricic, 1985), in which a positive correlation between noise level and minimum frequency of song was also found. We failed to find a significant correlation between noise level and maximum frequency (r=0.23, N=35, p=0.176), and between noise level and song length (r=-0.27, N=35, p=0.11). In other words, as noise levels increases, the minimum frequency of songs increases as well, but not their maximum frequencies or their lengths. This results in syllables being 'compressed' in the frequency axis (Figure 5).

The relative use of high-pitch over low-pitch syllable types was not significantly related to noise levels, although there was a non-significant trend

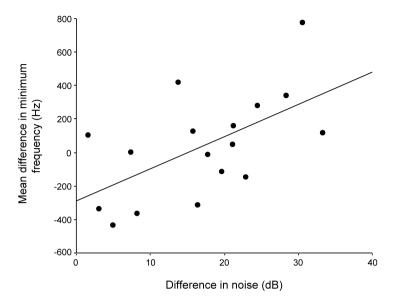


Figure 3. Relation between difference in noise intensity and difference in minimum frequency of syllables shared between songs. As the difference in noise level between two locations increases, the difference in minimum frequency of shared syllable types between two males in these locations also increases. For this analysis the difference in minimum frequency of syllable types shared between two locations was averaged across syllables types. See text for statistics.

for a higher use of high-pitched syllables in noisier environments (Pearson correlation: r=0.30, N=35, p=0.07), suggesting that differential use of syllable types may be a subsidiary strategy in song adaptation to noise. However, we found stronger evidence for the alternative hypothesis, syllable pitch plasticity, as shown by a significant positive correlation between difference in noise intensity and mean difference in minimum frequency averaged for same syllable types (Pearson correlation: r=0.58, N=17, p=0.014, Figure 3). This pattern obtained with our set of pairs was also supported by the results of the Mantel test using all possible (N=595) pairs (r=0.19, p=0.001).

Males facing a sudden increase in noise (high noise condition) increased the minimum frequency of the song emitted during that moment in comparison with the same type of song produced during a quieter moment (paired t-test: t = -3.80, df = 12, p = 0.002, Figure 4). This was achieved by increasing the minimum frequency of the same syllable type. During these bursts of noise, the background noise was increased from a mean of

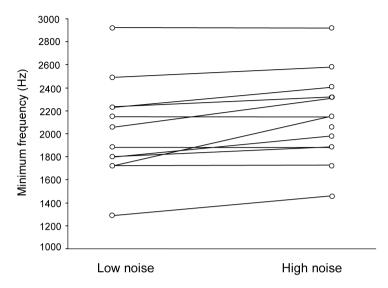


Figure 4. Minimum frequency of songs emitted during a moment of relative low noise level (Low noise) and during a sudden increase of noise level (High noise). Nine out of 13 males increased the minimum frequency of their songs during a moment of noise increment in comparison to another moment of lower noise. See text for statistics.

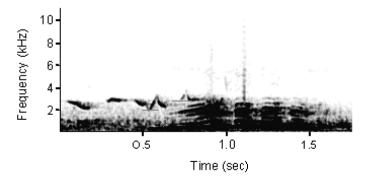


Figure 5. A house finch song when the male producing it faces a sudden burst of noise. The minimum frequency of the same syllable type was increased, within the song, from 1890 to 2750 Hz when a motor vehicle passed nearby, momentary increasing the background noise level. Also note that this syllable type was 'compressed' as a result of its minimum frequency being increased to a much grater extent than its maximum frequency. Lines show minimum frequencies of the same syllable type.

 64 ± 10 dB to 71 ± 10 dB, as measured in the song files. This increase in noise was significant (paired *t*-test: t = -6.24, df = 12, p < 0.001). Figure 5 shows an example in which a house finch increases the minimum

frequency of the same syllable type (in this case within a single song) during a sudden rise in noise.

Discussion

Our results confirm previous studies that show that house finches and other songbirds sing higher-pitched songs in noisy areas (e.g., Slabbekoorn & Peet, 2003; Fernández-Juricic, 2005; Wood & Yezerinac, 2006), a pattern that may be an adaptation for living in noisy environments (but see Leader et al., 2005). By increasing the minimum frequency of their songs, house finches in Mexico City appear to be producing songs that are less likely to be masked by urban noise.

Besides ambient noise, habitat structure is another potential factor that may influence the structure of bird song. For instance, Slabbekoorn et al. (2007) found a relationship between habitat structure and minimum frequency in dark-eyed juncos (Junco hyemalis). They showed that males sing higher-pitched songs in an urban habitat than their counterparts in natural forest. Thus, it can be argued that the relationship between ambient noise and minimum frequency that we found may be confounded by differences in habitat structure. We believe, however, that habitat structure is not as important a factor as ambient noise in shaping song properties in our study. First, we limited our sample to an urban population and, thus, possible effects of different habitat structure on song frequency are expected to be minimized. Second, we avoided recording birds in parks, where habitat structure (i.e., close habitat) is typically different from other parts of the city (i.e., open habitat). Finally, the study by Fernández-Juricic et al. (2005), with house finches in urban parks, unmasked the relationship between several ambient factors, including ambient noise and micro-habitat structure, and different song attributes. While they showed a significant correlation between ambient noise and song minimum frequency, they failed to report any relation between habitat structure and song attributes (e.g., minimum frequency, frequency range, number of notes), suggesting that ambient noise is a more important factor in shaping the structure of house finches song than microhabitat structure.

Producing high-pitched vocalizations in the presence of high levels of noise can lead to the production of unexpectedly high frequencies for an oscine bird. Perhaps the most extreme example of an oscine bird producing high frequency vocalizations in places with high levels of noise is the one reported by Narins et al. (2004). They showed that both a frog (*Amolops tormutus*) and a songbird (*Abroscopus albogularis*) living near streams emit acoustic signals containing ultrasonic harmonics. These harmonics reached maximum frequencies of up to 54 kHz in the case of the passerine. Although we did not look for ultrasonic sounds in our study, a different phenomenon appears to emerge with the house finch: as opposed to the minimum frequency of songs, the maximum frequency was not higher with increasing levels of ambient noise. This resulted in some syllables being 'compressed' (Figure 5). Wood & Yezerinac (2006) report a similar relation between noise amplitude and the minimum frequency of song sparrows (*Melospiza melodia*) songs, but a lack of relationship with 'high frequency of song'.

The fact that we found a highly significant correlation between the measures of noise levels obtained in September–October 2006 and October–November 2008, and a high repeatability value for these measures, demonstrates that noise intensities were consistent between different months and years. That is, a place with a high or low noise level remains a place with a high or low noise level, respectively, regardless of the month or year when the measure is taken.

Our data allow us to draw conclusions about the strategies that are used by birds to achieve song adaptation. We failed to find convincing evidence that singing higher-pitched songs in noisy areas is due to increasing the proportion of high frequency syllables types in these locations, as predicted by the differential syllable use hypothesis. However, a marginally significant tendency in that direction implies that we cannot completely rule-out the hypothesis that male house finches sing different syllable types according to local noise levels. On the other hand, we provide robust evidence that higherpitched songs in noisy areas are the result of uttering the same shared syllable types in quiet and in noisy circumstances, but with a higher minimum frequency when there is more noise (i.e., they show syllable pitch plasticity). This, however, does not annul the possibility that other syllables (i.e., nonshared syllables) may have also increased their minimum frequency. Additionally, our results indicate that house finches are able to adjust in real time the minimum frequency of their songs to changes in noise level and, thus, the observed pattern of minimum frequency in relation to noise can be explained in terms of plasticity and may be viewed as a short-term adaptation.

This result does not discard the possibility that a long-term adaptation is, as well, in process (Brumm & Slabbekoorn, 2005). Since this modulation was achieved by increasing the frequency of the same syllable type, this latter result provides further support for the syllable pitch plasticity hypothesis. This plasticity may well be related to the great success with which house finches have colonized different cities. Our results do not mean that house finches are unable to individually select different syllable types when sudden bursts of noise occur. To our knowledge, there is only another study that has proved vocal plasticity in a bird in relation to frequency song parameters and noise (Tumer & Brainard, 2007). This laboratory study used white noise in a reinforcement contingency procedure, whereby Bengalese finches (Lonchura striata var. domestica) were conditioned to change the fundamental frequency of a particular syllable in their songs. By applying bursts of white noise to a specific targeted syllable, Tumer & Brainard (2007) demonstrated that Bengalese finches are able to increase or decrease the fundamental frequency of this specific syllable, without changing the fundamental frequency of other syllables types within the same song. This proves that, like the house finch (this study), Bengalese finches display syllable pitch plasticity when noise result in auditory disruption or compromise acoustic communication.

Nolan & Hill (2004) provide experimental evidence that female house finches prefer longer over sorter songs in laboratory conditions. On the other hand, Mennill et al. (2006) found that male house finches singing longer songs (i.e., with more syllables) had an earlier nest initiation date, which is a good predictor of reproductive success. We found that higher-pitched songs were also shorter, but, on the other hand, we failed to find a negative correlation between noise level and song length, casting doubts on the idea that house finches sing shorter songs in noisy places. If this is true, house finches in our studied population may not be facing a trade-off between singing to attract a female and making their signals heard in a noisy place, as was suggested for another studied population in California (Fernández-Juricic et al., 2005). With respect to song length, our results on syllable pitch plasticity, coupled with the fact that only an average of 7 syllable types were shared between compared males, support the idea that males do not need a large repertoire of syllables to deal with noise. Since males adjust the frequency of the same syllable types that are produced in noisy and in quiet conditions, a few learnt syllables may be enough to produce a song adapted to noise.

To conclude, besides corroborating the results of Fernández-Juricic et al. (2005) we show that the observed pattern of noise amplitude and minimum frequency of house finch songs is a result of singing the same syllable types that are found in quiet and noisy conditions, but with a higher frequency in the latter case. We also show that individuals are able to instantaneously adjust the minimum frequency of their songs to deal with contemporary changes in noise levels. More studies (e.g., on female choice) are needed to assess whether, and how, noise pollution has an effect on house finches populations, a bird species that appears to settle particularly well in cities. Finally, it is worth studying whether this plasticity is shared by species that use less variable and complex songs and are perhaps less capable of song plasticity, since this might limit the capacity to cope with the acoustic challenges posed by human activities.

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References

- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. Anim. Ecol. 73: 434-440.
- Brumm, H. (2006). Animal communication: city birds have changed their tune. Curr. Biol. 16: R1003-R1004.
- Brumm, H. & Slabbekoorn, H. (2005). Acoustic communication in noise. Adv. Study Behav. 35: 151-209.
- Brumm, H. & Slater, P.J.B. (2006). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behav. Ecol. Sociobiol. 60: 475-481.
- Brumm, H. & Todt, D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. Anim. Behav. 63: 891-897.
- Brumm, H., Voss, K., Köllmer, I. & Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. Exp. Biol. 207: 443-448.
- Catchpole, C.K. & Slater, P.J.B. (1995). Bird song. Biological themes and variations. Cambridge University Press, Cambridge.

- Cynx, J., Lewis, R., Tavel, B. & Tse, H. (1998). Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. Anim. Behav. 56: 107-113.
- Fernández-Juricic, E., Poston, R., De Collibus, K., Morgan, T., Bastain, B., Martin, C., Jones, K. & Treminio, T. (2005). Microhabitat selection and singing behaviour patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. Urban Habitats 3: 49-69.
- Fuller, R.A., Warren, P.H. & Gaston, K.J. (2007). Daytime noise predicts nocturnal singing in urban robins. — Biol. Lett. 3: 368-370.
- Gil, D. & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. Tree 17: 133-141.
- Hansen, P. (1979). Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. Anim. Behav. 27: 1270-1271.
- Leader, N., Wright, J. & Yom-Tov, Y. (2005). Acoustic properties of two urban song dialects in the orange-tufted sunbird (*Nectarinia osea*). — Auk 122: 231-245.
- Manley, P.N. & Schlesinger, M.D. (2000). Designation of focal vertebrate species for the Lake Tahoe Basin. — In: Lake Tahoe watershed assessment, Vol. II, Appendix L. (Murphy, D.D. & Knopp, C.M., eds). United States Department of Agriculture, Washington, DC, p. L1-L6.
- Mennill, D.J., Badyaev, A.V., Jonart, L.M. & Hill, G.E. (2006). Male house finches with elaborate songs have higher reproductive performance. Ethology 112: 174-180.
- Narins, P.M., Feng, A.S., Lin, W., Schnitzler, H.-U., Denzinger, A., Suthers, R. & Xu, C. (2004). Old World frog and bird vocalizations contain prominent ultrasonic harmonics. J. Acoust. Soc. Am. 115: 910-913.
- Nolan, P.M. & Hill, G.E. (2004). Female choice for song characteristics in the house finch. Anim. Behav. 67: 403-410.
- Patricelli, G.L. & Blickley, J.L. (2006). Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123: 639-649.
- Pytte, C.L. (1997). Song organization of house finches at the edge of an expanding range. Condor 99: 942-954.
- Quedas, A., Duprat, A. & Gasparini, G. (2007). Lombard's effect's implication in intensity, fundamental frequency and stability on the voice of individuals with Parkinson's disease. Rev. Brasil. Otorrinolaringol. 73: 675-683.
- Reijnen, R. & Foppen, R. (1994). The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway. J. Appl. Ecol. 31: 85-94.
- Reijnen, R., Foppen, R., Ter Braak, C. & Thissen, J. (1995). The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. J. Appl. Ecol. 32: 187-202.
- Reijnen, R., Foppen, R. & Meeuwsen, H. (1996). The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. Biol. Conserv. 75: 225-260.
- Rheindt, F.E. (2003). The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? J. Ornithol. 114: 295-306.
- Rice, W.R. (1989). Analysing tables of statistical tests. Evolution 43: 223-225.
- Searcy, A.W. & Andersson, M. (1986). Sexual selection and the evolution of song. Annu. Rev. Ecol. Syst. 17: 507-533.
- Slabbekoorn, H. & den Boer-Visser, A. (2006). Cities change the songs of birds. Curr. Biol. 16: 2326-2331.

- Slabbekoorn, H. & Peet, M. (2003). Birds sing at a higher amplitude in urban noise. Nature 424: 267.
- Slabbekoorn, H., Yeh, P. & Hunt, K. (2007). Sound transmission and song divergence: a comparison of urban and forest acoustics. Condor 109: 67-78.
- Swaddle, J.P. & Page, L.C. (2007). High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. Anim. Behav. 74: 363-368.
- Tumer, E.C. & Brainard, M.S. (2007). Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. Nature 450: 1240-1244.
- Wood, W.E. & Yezerinac, S.M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123: 650-659.