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REPLY

# Effect Sizes and the Integrative Understanding of Urban Bird Song

(A Reply to Slabbekoorn et al.)

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## Introduction

In a recent article, we presented a model to estimate communication distances of bird songs in forests and cities (Nemeth and Brumm 2010). Our aim was to compare higher-pitched songs, such as those observed in urban songbird populations, to songs with higher amplitude. The main result showed that in the two model species, an increase in amplitude had an overwhelmingly stronger influence on communication distances than did the increase in frequency that has been documented in these species. Therefore, we concluded that a rise in amplitude would be a more efficient response to the masking effect of urban noise than a rise in pitch.

Slabbekoorn et al. (2012) question the validity of our methods and results on several levels. We show that their criticism is based partly on a disregard of the importance of effect sizes and partly on a misconception of the relationship between amplitude and frequency in avian sound production. In our response, we first address the issue of urban bird song characteristics and then reply to the specific criticisms of our study.

## Adaptation and Urban Songs

It is often observed that birds in cities sing at a higher pitch, compared to their conspecifics in rural or forest areas (reviewed in Brumm and Zollinger 2011). The first to report such urban song divergence were Slabbekoorn

and his coworkers, with their pioneering work on great tits (*Parus major*; Slabbekoorn and Peet 2003; Slabbekoorn and den Boer-Visser 2006). They found that the minimum frequency of great tit song was higher in urban than in forest territories and also that within cities, minimum frequency correlated with background noise levels. On the basis of these correlations between song frequency and environmental parameters, Slabbekoorn and den Boer-Visser (2006, p. 2327) concluded that “environmental selection may have driven divergence in minimum frequency.” In later papers, Halfwerk and Slabbekoorn (2009) asserted that high-pitched city songs are a behavioral strategy to reduce acoustic masking, and Slabbekoorn and Ripmeester (2008) invoked the possibility of urban speciation if divergence in song pitch should persist. The notion that high-pitched city songs are the outcome of environmental selection was quickly adopted by other authors without questioning whether a behavior is necessarily adaptive just because it varies with the environment.

One of the primary criticisms Slabbekoorn et al. (2012) raise against our study concerns our conclusion that, on the basis of our comparison of transmission distances, adaptive claims about frequency shifts should be made with caution. In raising this criticism, they cite selectively from our study and omit important passages. In fact, we explicitly acknowledge that “even the very small benefits of increased song pitch could be adaptive” (Nemeth and Brumm 2010, p. 471). Nevertheless, our results show that this potential adaptation or phenotypic-plasticity effect could yield only very minor benefits in terms of signal transmission. As we emphasize in our original study, we believe that it is critical to determine whether these lesser increases in communication distance are ultimately powerful enough to lead to fitness benefits. Slabbekoorn et al. criticize our study for putting a “speculative” emphasis on the possibility that a rise in pitch is not very effective in counteracting anthropogenic noise. We do not think that it is too speculative to draw conclusions from quan-

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titative comparisons. We do, however, think that it is speculative to suggest that urban songs are adapted to masking noise without actually measuring the release from masking.

Adaptation is an important but slippery concept in biology (Reeve and Sherman 1993), and to describe every trait of an organism as the outcome of selection is a well-recognized pitfall (Gould and Lewontin 1979). One day, evidence may be found that high-pitched bird songs in cities provide higher fitness than lower-pitched songs or that there is direct selection on song pitch in urban habitats, but at the moment no published research shows this link unequivocally. Therefore, we still believe it prudent to caution against a simple adaptationist approach that draws conclusions about selection based solely on the presence of a character.

#### Frequency May Matter, but It Depends on the Effect Size

Our study quantified possible effect sizes in signal efficiency. Slabbekoorn et al. (2012) insist that we must also incorporate costs into our model in order to translate “transmission benefits to signal efficiency and fitness consequences.” We agree that it would be desirable to know more about relative costs, especially if louder songs are more costly to produce than higher ones. While a recent study in zebra finches (*Taeniopygia guttata*; Zollinger et al. 2011) demonstrated that increasing vocal amplitude did not significantly increase metabolic costs, we still must consider the possibility of other, nonmetabolic costs (McGregor and Dabelsteen 1996; Brumm and Ritschard 2011). Nevertheless, we think that large differences in signal transmission distance are likely to matter even after potential costs are considered. When we stress these effect sizes, we do not assume that singing higher is not important. However, if a factor shows as small an effect as pitch shift does in our model, we cannot help but question its value for communication. As an example, in high-noise conditions great tits can enlarge their communication distance from 61 to 67 m by using higher-pitched songs, but they can enlarge it from 61 to 91 m by singing louder songs (see fig. 2 in Nemeth and Brumm 2010). These differences in communication distances in great tits (and in common blackbirds [*Turdus merula*]) led us to wonder whether higher-pitched songs actually provide meaningful benefits in these species. Slabbekoorn et al. (2012) miss this point of effect sizes again in their figure 1 by selectively removing the effect of higher-amplitude songs from our original figure (fig. 2 in Nemeth and Brumm 2010).

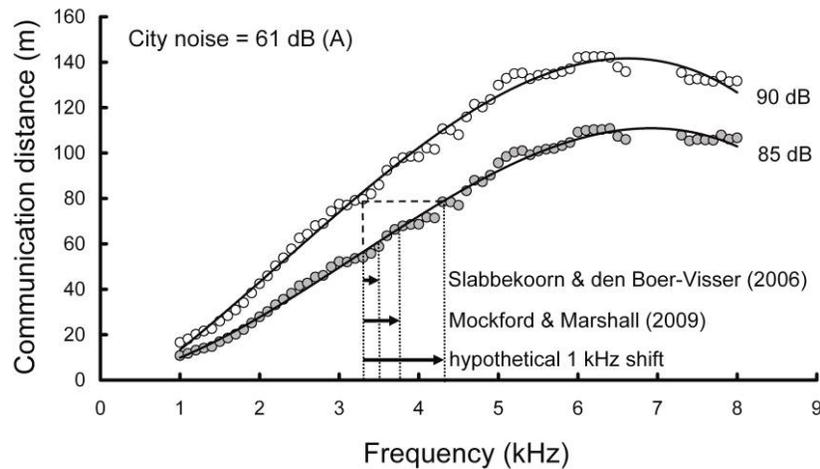
Slabbekoorn et al. (2012) also argue that we underestimate the potential benefits of frequency shifts in great

tits because they were based on population averages “that are likely to be an underestimate of the potential for frequency shifts, as they typically are not based on recordings from the most noisy periods of the day and also include recordings from less noisy areas.” If the pitch shift in urban birds is much higher than the 205 Hz we used in our model, then the results of our model indeed change considerably. If these frequency shifts are the outcome of noise-dependent behavioral plasticity and reach 1 kHz or more, then we predict that singing higher would be an effective way to avoid masking. In our model, an increase in pitch of 1 kHz would be approximately equivalent to a rise in sound pressure level of 5 dB (fig. 1). Slabbekoorn et al. (2012) think that a shift of 478 Hz, as found by Mockford and Marshall (2009), is a more realistic effect size than the 205 Hz reported in Slabbekoorn and den Boer-Visser (2006), but as already discussed in Nemeth and Brumm (2010), even a frequency shift of this magnitude is much less effective than a 5-dB change in amplitude (see also fig. 1). If future studies provide data showing that published averages of pitch shifts in urban birds are not representative, we would be happy to reconsider the interpretation of our model, but at the moment we know of no convincing evidence for higher effect sizes.

It again comes to a question of effect sizes when Slabbekoorn et al. (2012) refer to Halfwerk et al. (2011) and Pohl et al. (2012) as confirming the perceptual advantages of higher-frequency songs. Both of the cited studies demonstrate enhanced detection by females of higher-pitched songs in noise, but both used test stimuli with differences in frequency considerably greater than the previously reported average differences between rural and urban songs. Halfwerk et al. (2011) compare the reactions of female great tits to songs that differ in frequency by nearly 600 Hz on average, with a range between ~300 and 900 Hz, so even the smallest differences were larger than the previously reported averages used in our model. Pohl et al. (2012) tested discrimination by female great tits in different noise conditions of male songs that were digitally shifted to higher frequencies. However, the low- and high-frequency song stimuli they used differed by more than 1 kHz. As both studies used effect sizes much larger than those previously reported in the field, their results confirm the results of our model, which predicts greater differences in transmissibility (and therefore, presumably, greater detection and discrimination by listening birds) with larger shifts in frequency (fig. 1).

#### Habitat Acoustics and Environmental Noise Both Matter When Comparing Different Habitats

Slabbekoorn et al. (2012) argue that our model already supports high-frequency benefits because the “relatively



**Figure 1:** Estimated communication distances of great tit songs in typical city noise. Polynomial regression lines are fitted to frequency values at two different vocal sound pressure levels (90 and 85 dB), calculated by our model (Nemeth and Brumm 2010). The chart allows the estimation of the release from auditory masking by frequency shifts. For example, a shift of 1 kHz, from 3.3 to 4.3 kHz, yields almost the same effect as an increase in sound pressure level by 5 dB at 3.3 kHz (dashed lines). Pitch shifts observed in natural great tit populations (Slabbekoorn and den Boer-Visser 2006; Mockford and Marshall 2009) and a hypothetical frequency shift are indicated by arrows (see text for details). The auditory threshold for discrimination of songs in noise was set to 28 dB. It is assumed that the discrimination threshold in great tits is the same across the whole frequency range modeled here (Langemann et al. 1998). For details on the model assumptions for sound transmission, masking properties, and spectral characteristics of noise, see Nemeth and Brumm (2010).

high-pitched great tit songs reach over a larger distance than the relatively low-pitched blackbird songs in urban conditions and ... the situation is reversed in forested conditions.” The purpose of our study was to compare within rather than between species, but it is certainly true that the lower-frequency blackbird song is more strongly affected by urban noise than are great tit songs, because of the proportionally higher noise levels at low frequencies in urban environments. We never questioned the idea that urban noise would mask low-frequency songs more. Thus, we are not certain what additional information Slabbekoorn et al. (2012) are trying to illustrate by the replication of our original graph (fig. 2 in Nemeth and Brumm 2010) in their figure 1. However, when comparing communication distances of songs of blackbirds and great tits between habitats, we must consider the influence not only of noise but also of habitat structure (e.g., vegetation) on sound. Sound attenuation in forests increases with higher frequencies (Marten and Marler 1977), and blackbird song specifically has been found to transmit better in forest habitats than great tit song does because of this frequency-dependent attenuation (Dabelsteen et al. 1993; Nemeth and Brumm 2010). In addition, a recent study found that higher-pitched great tit songs transmit better in urban environments than lower-pitched songs regardless of background noise levels, suggesting that habitat structure may

be as strong a driving force for frequency shifts in cities as increased noise levels (Mockford et al. 2011).

As we discuss above, it is important to consider effect sizes when comparing the relative benefits of frequency and amplitude shifts, and this is true for both within- and between-species comparisons. Blackbird songs are considerably lower-pitched (peak frequencies between ~1.5 and 4.5 kHz; Nemeth and Brumm 2009) than great tit songs (peak frequencies between ~3 and 7 kHz; Roselaar 1993), yet the average shift in frequency in urban blackbirds is only 198 Hz (Nemeth and Brumm 2009; Ripmeester et al. 2010). Still, despite the presumed disadvantage of such low-frequency songs, blackbirds are one of the most successful songbirds in noisy urban centers across Europe (Evans et al. 2010). We submit that, if anything, the success of blackbirds in cities despite a “maladaptive” song points to a lack of adaptive value (or at least a lack of selective pressure) for higher-pitched song types in cities.

#### Levels of Explanation and the Relationships between Amplitude and Frequency in Bird Song

Slabbekoorn et al. (2012) stress the differences between causation and function and suggest that we are confused about these two levels of research. They point out that “whether or not the Lombard effect is responsible for a

spectral shift, it does not affect the functional implications of masking avoidance” (by frequency shifts). We are surprised by the assertion that we confuse proximate and ultimate levels of behavior, as we set out only to compare the relative benefits of frequency and amplitude for improving signal effectiveness. We absolutely agree that the mechanism or cause of a spectral shift does not affect its functional implications or potential adaptive benefits. However, as we address above, it is important to take effect sizes and relative benefits into account when considering the functional relevance of different traits, and we simply caution against adaptive storytelling. If small increases in frequency are linked causally to increases in amplitude via the Lombard effect, then one must consider the relative benefit of these two concurrent changes and question which trait might be more strongly selected on.

We believe that the criticism may partially result from a misunderstanding on the part of Slabbekoorn et al. (2012), who seem to confuse two distinct phenomena related to amplitude and frequency relationships in vocal production. They cite a study by Nelson (2000) that demonstrates a link between call amplitude and frequency in eastern towhees (*Pipilo erythrophthalmus*), in which he shows that higher frequencies are produced at a higher sound pressure level in this species. They then suggest that “linking this mechanism to singing louder in noisier conditions (Lombard effect) concerns a speculation about causation.” We believe that these comments confound two aspects of sound production in birds; frequency shifts that may occur as a by-product of the Lombard effect are fundamentally different from the relationship between frequency and amplitude as described in the towhees. In the Lombard effect, an increase in the background noise results in increases in vocal amplitude (Zollinger and Brumm 2011). In human speech, this involuntary elevation in amplitude often leads to a corresponding elevation of fundamental frequency (Jessen et al. 2005; Cooke and Lu 2010). This is not the same as the coupling of frequency and amplitude, such as that described by Nelson (2000), in which higher-frequency syllables or portions of syllables are produced more loudly than lower-frequency sounds. With the Lombard effect, a particular sound produced in noise is higher in both amplitude and frequency than the same sound produced in quiet conditions. The two vocal phenomena occur independently and are not, as Slabbekoorn et al. (2012) seem to suggest, necessarily related in a mechanistic sense. To illustrate the point, if towhees respond to noise the same way humans do, then as background noise levels rise, even the loudest and highest-frequency parts of the towhee call will get louder and higher than when produced in the absence of noise.

### Higher Pitch in Urban Song Can Be Related to Higher Amplitude in Two Ways

We are glad to have the chance to clarify this distinction between the two possible ways in which amplitude and frequency could be linked. Both phenomena (an increase in pitch caused by the Lombard effect and the ability to sing louder at higher frequencies) provide hypotheses for mechanisms by which urban birds might sing at higher frequencies than rural ones. In our study (Nemeth and Brumm 2010), we discussed one of these two hypotheses, namely, that the high levels of noise in cities would induce the Lombard effect and that the higher pitch might be a passive by-product of the resulting elevation in song amplitude. Since amplitude has not been carefully measured in urban and forest great tits, we cannot as yet rule out the Lombard effect and a coupled rise in pitch. Indeed, the Lombard effect appears to be a basic vocal mechanism for communication in noise in birds and mammals (Brumm and Zollinger 2011). Although the link between amplitude and frequency shifts in Lombard speech in humans is clearly defined, the link in songbirds is less well understood. Songbirds also show the Lombard effect and increase vocal amplitude in noise under laboratory conditions (Cynx et al. 1998; Brumm and Todt 2002; Zollinger et al. 2011), but whether this is coupled with a rise in pitch in songbirds is not yet known.

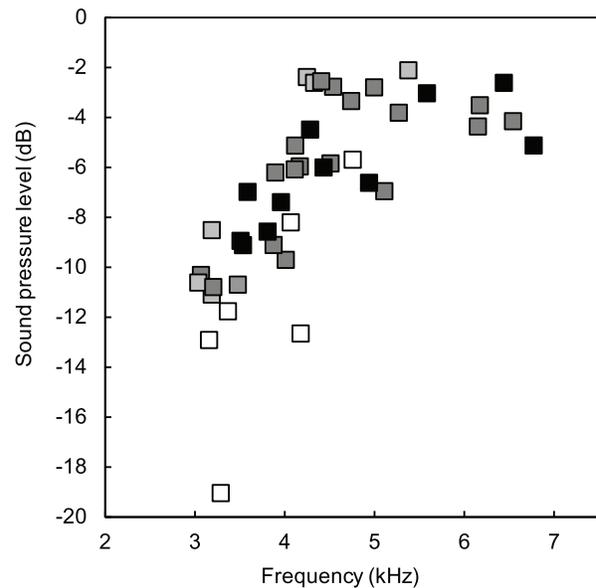
Slabbekoorn et al. (2012) cite a paper by Halfwerk and Slabbekoorn (2009) as evidence that the difference in minimum frequency in urban great tits cannot be explained by the Lombard effect, because great tits switch to different song types in different noise conditions rather than elevating the frequencies of the same song type. If the results presented in Halfwerk and Slabbekoorn (2009) were straightforward, these results would indeed cast doubt on the Lombard effect as a causal explanation for observed differences in urban and rural populations. However, we believe that this hypothesis cannot be ruled out on the basis of their published data. First and foremost, song amplitude was not measured in their study, and so a link between song amplitude and frequency shifts in great tits remains unknown. Second, their claim that great tits shift to different, higher song types in response to low-frequency (citylike) noise perhaps overstates their results. Most of the birds in their study did not switch song types during noise exposure (only 19 of 46 birds tested changed their songs during the experimental period). Of those birds that did switch, fewer than one-third did so during “city noise” exposure trials. So to suggest that an observation made in 6 birds out of 46 is representative of urban great tit behavior in general seems premature to us.

Nevertheless, even if it is demonstrated that great tits do not increase pitch as a passive result of singing louder,

it does not mean that they do not rely on changes in amplitude to increase their signal-to-noise ratio in urban noise. An alternate hypothesis is that songs at lower frequencies cannot be produced as loudly (with the same efficiency) as those at higher frequencies. In birds with syrinx morphologies simpler than that of songbirds (e.g., doves), independent modulation of frequency and amplitude may not be possible, and so louder sounds also tend to have a higher fundamental frequency (Beckers et al. 2003; Elemans et al. 2008). In songbirds, sound production is a more complex system involving two independently controlled sound sources, vocal learning, rapid bilateral coordination of central song control nuclei, and respiratory and syringeal muscles as well as the dynamic movement of the upper vocal tract (Suthers and Zollinger 2008; Wang et al. 2008), which likely affords songbirds a greater degree of vocal control. But despite this increased complexity, a positive correlation between frequency and amplitude has been found in at least four songbird species in addition to eastern towhees (Dabelsteen 1984; Nelson 2000; Goller and Cooper 2008; Ritschard and Brumm 2011). One of these species is the common blackbird, in which vocal amplitude varies with sound frequency in the long-ranging whistle part of their songs (see figs. 1–3 in Dabelsteen 1984). Moreover, the same correlation also appears to be the case in great tit song (fig. 2). Thus, by switching to higher-pitched song elements, urban birds would automatically choose elements produced at higher amplitudes. Hence, urban birds may switch to higher-pitched syllable types because they are louder.

### Conclusions

Considering all the arguments set forth by Slabbekoorn et al. (2012), we see no reason to withdraw any conclusions in Nemeth and Brumm (2010). We agree with Slabbekoorn et al. (2012) that our model does not show whether higher-pitched songs are adaptive in urban environments. However, the model was designed not to answer this question but to compare the relative benefits of increasing song amplitude and increasing pitch in terms of communication distances. The results of our communication-distance model indicate only very small gains in sound transmission from typical frequency increases found in urban bird songs, and we believe that it is valid to question the widespread assumption that high-pitched urban songs are adaptive. We applaud Slabbekoorn and his coworkers for their important discovery that urban great tits sing with higher minimum frequencies in cities (Slabbekoorn and den Boer-Visser 2006) and in traffic noise in particular (Slabbekoorn and Peet 2003). Singing high may matter, but the observation that urban birds sing at a higher pitch



**Figure 2:** Relationship between sound frequency and amplitude of great tit song elements. Each data point gives the mean value from 10 renditions of one element type ( $N = 5$  males, depicted by different shading). Calibrated digital song recordings with a sampling rate of 44.1 kHz and 16-bit accuracy were made in a sound-shielded room with the microphone at a fixed position above the bird's head (for details of the recording procedure, see Ritschard et al. 2011). The sound analysis was conducted with Avisoft-SASLab Pro software (ver. 4.53, R. Specht, Berlin). Frequency values are mean frequencies measured in power spectra (Hamming window) with a resolution of 0.7 Hz. Sound pressure levels were normalized within each male to the highest measured value.

is not sufficient to conclude that environmental selection has driven divergence in song frequency.

In urban songbirds, the selected characteristic may be song amplitude: not only is it important in female choice (Searcy 1996; Ritschard et al. 2010) and male-male competition (Dabelsteen and Pedersen 1992; Brumm and Ritschard 2011; Ritschard et al. 2012), but an increase in song amplitude also leads to considerably higher transmission gains in urban environments (Nemeth and Brumm 2010). As we have hoped to make clear in our reply, a rise in song pitch can be the by-product of singing at higher amplitudes in at least two independent ways. Nevertheless, future studies might find that birds with higher-pitched songs have greater fitness in areas with low-frequency traffic noise, independent of amplitude or other correlated traits, which may mediate selection. Until then, however, one cannot dismiss the possibility that the high pitch of urban bird songs is just a correlational artifact.

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