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Tango to traffic : a field study into consequences of noisy urban conditions for acoustic courtship interactions in birds

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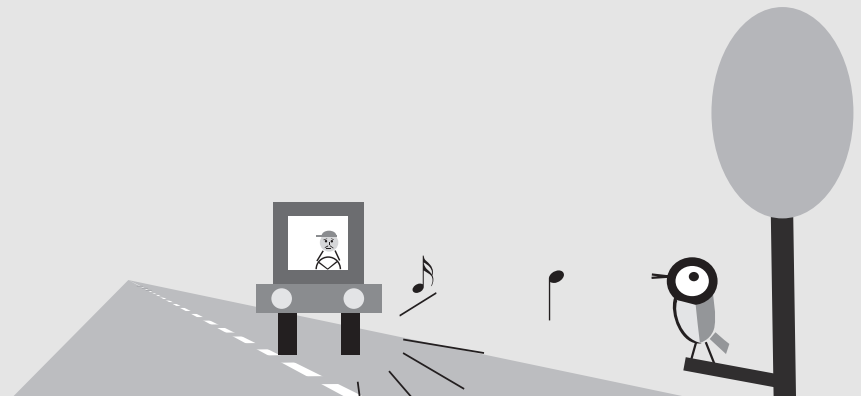
Chapter 3

Causes and consequences of singing high songs in urban noise



ABSTRACT

A recent theoretical paper by Nemeth & Brumm (2010) addressed the impact of both amplitude and frequency variation on signal transmission and discussed whether or not high-frequency songs are an adaptation to low-frequency urban noise conditions. We agree with the authors of this paper that it is important to quantify signal transmission under different scenarios, but we argue that studying adaptations requires the incorporation of benefits, as well as costs. Furthermore, the authors stress that the obtained data about increases in frequency and amplitude show that an increase in amplitude has a significantly larger effect on transmission distances compared to an increase in frequency, but they do not report that high-frequency songs transmit better in urban noise conditions compared to low-frequency songs in their model. Nemeth & Brumm also argue that noise-dependent frequency use is not an adaptation, but a physiological side effect of singing louder. We believe that it is interesting to explore the mechanisms underlying noise-dependent signal production, and therefore come up with a model that links amplitude, performance constraints and masking-dependent song type switching to explain noise-dependent frequency use by urban great tits. However, we want to stress that consequences of noise-dependent vocal variation in frequency (and other parameters) are interesting in their own right and to some extent independent of the causal mechanisms.

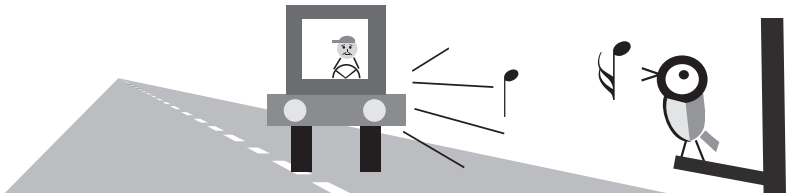
INTRODUCTION

In a recent theoretical paper entitled 'Birds and Anthropogenic Noise: Are Urban Songs Adaptive?'[1], Nemeth & Brumm explored the impact of signal plasticity in song amplitude and song frequency on signal transmission in forested and noisy urban environments. They used empirical data on signal amplitude, song frequency ranges, discrimination thresholds, habitat-dependent attenuation rates and typical noise level and spectra, to calculate maximum transmission distances for birdsongs under typical forest and typical city conditions. They selected two bird species for which there was enough data available: the relatively high-pitched singing great tit (*Parus major*) and the relatively low-pitched singing European blackbird (*Turdus merula*). Based on the calculations derived from their model, they argue that 1) amplitude adjustments have a larger effect than an increase in vocal pitch in increasing transmission distance for singing birds under noisy urban conditions and, that 2) *"increased song pitch might not be an adaptation"* but *"a side effect"* or *"an epiphenomenon"* related to urbanization.

We can follow the first argument, which is in line with their calculations and statistical test, but we disagree with the second. We believe that data or a proper rationale for this second argument are lacking from an functional point of view and that if a factor A has a larger impact than a factor B, one can not conclude that factor B is not important. Furthermore, translating transmission benefits to signal efficiency and fitness consequences would also require the incorporation of costs[see 2,3,4]. So, we argue that the amplitude versus frequency comparison, which is the only aspect of the data statistically tested in the paper, provides relevant insight with respect to transmission benefits, but does not address whether upward frequency shifts are adaptive under noisy urban conditions, as suggested by the title.

Consequences of high-frequency songs: benefits in urban noise

The data in Nemeth & Brumm (2010) actually provide strong theoretical support for high-frequency benefits in urban noise. The inter-specific comparison shows that the relatively high-pitched great tit songs reach over a larger distance than the relatively low-pitched blackbird songs in urban conditions and that the situation is reversed in forested conditions. As amplitude does not vary much between the species, the difference can be explained by the fact that high-frequency singers have an advantage over low-frequency singers in noisy urban habitat. The impact on transmission distance of intra-specific frequency shifts was also addressed and high-frequency variants do again



better than low-frequency variants in urban habitat.

Nemeth & Brumm (2010) based the spectral values for transmission range calculations on population averages which are likely to be an underestimate of the potential for frequency shifts as they are typically not based on recordings from the noisiest periods of the day and also include recordings from less noisy areas. Therefore, it may be useful to look at noise-dependent variation within individuals, for which experimental data are available for great tits in natural urban territories[5]. Experimentally exposed birds that switched to another song type exhibited upward shifts in their minimum frequency of on average 436 Hz (Figure 3.1), whereas the maximum change available to individuals from the lowest to the highest song type in their repertoire was on average 771 Hz. A spectral shift of 478 Hz (based on [6]) appears, therefore, reasonable to look at and yielded a 20 % increase in transmission distance according to the calculations of Nemeth & Brumm (2010). Such an effect size seems very much in line with the interpretation of masking avoidance driving noise-related patterns of frequency use in empirical studies[7-11].

Causes of noise-dependent song frequency use

Nemeth & Brumm (2010) address the mechanisms that potentially may underlie noise-dependent frequency use and repeat the suggestion postulated by two earlier papers that song amplitude and frequency are physically linked[10,12]. An increase in signal amplitude in response to rising noise levels (also known as the Lombard effect) is thought to be taxonomically widespread[13] and a linkage between amplitude and frequency would explain the use of higher frequency songs in noisy urban environments. The available data, however, is contradicting, and suggests that the underlying mechanism of such physical linkage is either complex or species-specific. For instance, in Eastern towhee song, amplitude and frequency are positively correlated[14] , whereas in dark-eyed junco song they are negatively correlated[15]. Furthermore, the linkage has been experimentally shown to exist in budgerigars[16], but is reported to be absent in zebrafinches[17] Finally, amplitude and frequency have been found to correlate in the latter species, both negatively, and positively, depending on morphological filter settings of the vocal tract, such as beak gape and vocal sac inflation[18].

Nemeth & Brumm (2010) cite the paper by Halfwerk & Slabbekoorn (chapter 2) in their discussion on the underlying mechanisms of noise-dependent frequency use, but ignore alternative explanations that are addressed by the paper. The experimental exposure of that study revealed that territorial great tits do not alter the frequency use when they persist in singing the same song type during a rise in noise level[5], but rely on selective use of the song type repertoire to change their singing frequencies (see

Figure 3.1; chapter 2). These findings provide further evidence that song amplitude and frequency are not directly linked, or at least not in all species, and that noise-dependent frequency use is certainly not just possible in combination with singing louder.

A mechanistic explanation of noise-dependent song frequency

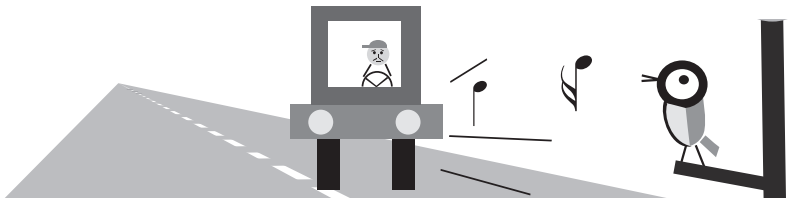
The complexity of noise-dependent patterns of song frequency use may be better reflected by an integration of three different theories about song production mechanisms explaining acoustic variation. The Lombard effect, performance constraints, and masking-dependent song type switching (chapter 2) may each come into play when bird species singing like great tits shift up in frequency under noisy conditions. The explanation relies on two important assumptions: 1) the Lombard effect depends on the spectral overlap between signal and noise, and 2), singing is energetically or physically demanding and leads to amplitude dependent costs. Both assumptions are in need of thorough verification, but we do know that spectral overlap of noise and song is most effective in eliciting the Lombard effect in nightingales[19]. Furthermore, we have some evidence that an increase in song amplitude is physically limited[19] or energetically demanding (but see[17,20]).

Performance constraints of song

Great tits deliver their songs at a high rate and for long durations, especially during the dawn chorus, and it is very likely that their acoustic performance is energetically or physically demanding[21-23]. Most great tit males have a repertoire of song types that differ in many temporal, spectral and structural characteristics. It is important that these song types are delivered with high stereotypy, as song consistency can signal an individual's quality during male-male interactions[24] and possibly male-female interactions[24-26]. However, great tits occasionally make mistakes in terms of song consistency, which can be attributed to motor control or performance constraints[27]. These performance constraints depend on acoustic characteristics of the song types, which can be avoided by switching to other song types[21,27].

Performance-dependent great tit song type switching in urban noise

Great tits do not immediately change the frequency of their songs in response to urban noise exposure, but switch to a song type with a different frequency after some time (chapter 2). This song type switching is masking-dependent, and males singing a low-frequency song type in urban noise switch quicker to another song type, that is by chance higher in frequency (chapter 2). I hypothesize, that when a great tit male, or some other eventual variety singer, sings a low-frequency



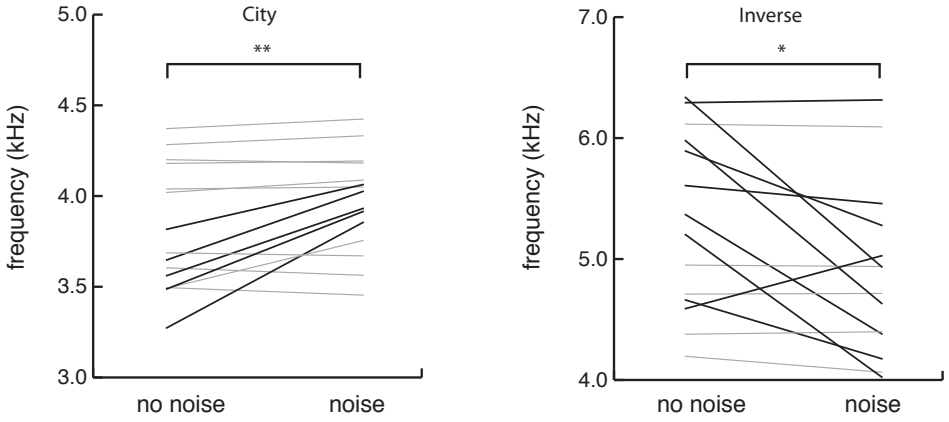


Figure 3.1. Masking avoidance by great tits in response to experimental noise exposure. Song frequency changed after four minutes of noise exposure depending on the type of noise played (GLMM: low-note frequency; $\chi 2 = 13.8$; $p = 0.003$; high-note frequency; $\chi 2 = 9.5$; $p = 0.023$). Low-note frequency only increased during exposure with low-frequency 'city' noise (**$p = 0.002$) as a result of song type switching (black lines). High-note frequency only increased during the 'inverse' noise treatment (*$p = 0.03$), again as a result of song type switching. The switching of song types during 'city' noise resulted in an increase in low-note frequency of 436±178 s.d. Hz whereas the maximum change in low-note frequency that each individual could gain by switching from its lowest to its highest song type was 771±412 (range 390 – 1719) Hz. Song type switching in the 'inverse' noise treatment led to a decrease of 631±645 Hz in high-note frequency, whereas the maximum difference based on an individuals known repertoire was 1211±648 (range 444 – 2086) Hz.

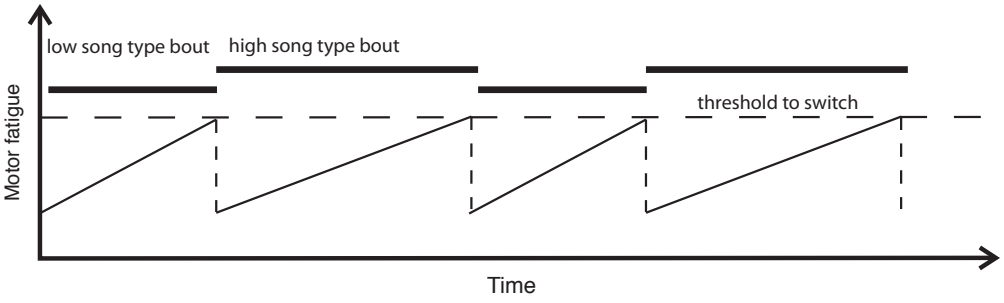


Figure 3.2. Model of performance constrained song type switching in urban noise. The model assumes that birds increase the amplitude level of their songs depending on the amount of spectral overlap with background noise and that singing louder is energetically demanding or physically exhausting. Singing a low-frequency song type suffers more masking in urban noise conditions and will therefore sung at higher amplitudes and increase performance demand faster compared to singing a high-frequency song type. At a particular threshold a song type switch occurs that restores energy or physical demands to baseline levels. The model integrates the Lombard effect with masking-dependent song type switching and the anti-exhaustion hypothesis to explain why great tits sing low-frequency song types for shorter durations compared to high-frequency song types in urban noise.

song type under urban noise, these song types will suffer more masking and will consequently be sung at higher amplitudes, compared to high-frequency song types. The amplitude increase will increase song performance or energy demands and when particular energetic threshold or performance limit is reached, birds singing low song types are forced to switch song types, which will occur faster (in time, or at lower noise levels) compared to birds singing high song types (Figure 3.2).

A mechanism of masking-dependent performance constraints might be a general explanation of noise-dependent frequency use. It may lead to selective song type use in some bird species, or to element adjustment in those species that do not possess a repertoire of different songs. However, all species, including great tits, can rely on song performance monitoring to adjust their signals appropriately, either by using some sort of internal feedback mechanisms, or by using social feedback from conspecifics (chapter 2), and future studies should therefore be designed to distinguish between these two alternative explanations (chapter 5).

Are urban songs adaptive?

Nemeth & Brumm (2010) question in their title whether 'urban songs' are adaptive and, although not clearly defined, from the text one could derive that they consider increased frequency but not increased loudness as being a typical characteristic of these urban songs in their title. Their main conclusion paragraph focuses solely on frequency as '*perhaps not the outcome of an adaptation*', at which they arrive after discussing functional implications, as well as causal explanations of high songs being "a side effect" or "an epiphenomenon" of urban conditions. We like to point out that part of the answer to their question depends on 1) the definition of an adaptation, and 2) on the level of analysis.

Nemeth & Brumm do not clearly define 'adaptation' and it therefore remains unclear whether they refer to it as a trait that is the product of past, present, direct or indirect selection[28,29]. A trait may initially have arisen as a byproduct of something else, but once there, become subject of selection, modification and adaptation itself. Likewise, plasticity in frequency could have evolved as an additional component of the Lombard effect, which would be beneficial to signal transmission and production under particular acoustic conditions and may itself become a trait under selection.

The noise-dependent patterns of increased frequency characteristics in birdsongs recorded in urban environments have been attributed to potential processes at different time scales: evolutionary, ontogenetic, and imme-

diate shifts, which are not mutually exclusive processes and their contribution to the patterns likely varies among species[e.g. 5,30,31]. Immediate shifts may lead to high-frequency song types, which can subsequently increase in number in a population of songbirds through cultural transmission. Segregation of song types between urban and forest populations may lead to reproductive isolation and subsequent genetic divergence through drift or directional selection[11,32,33]. Consequently, we may end up with two distinct populations in which the acoustic phenotype (song frequency) matches with environmental conditions (noise). Such congruent pattern of phenotypic, genetic and environmental variation would by most of us be attributed to be the result of adaptations.

CONCLUSIONS

The theoretical explorations by Nemeth & Brumm (2010) clearly confirm that a rise in amplitude as well as a rise in frequency will benefit signal transmission under noisy urban conditions, a pattern that may be strengthened by the relative absence of dense vegetation in the urban habitat[34]. Singing louder may be the most widespread phenomenon that leads to a non-specific improvement of signal efficiency in any challenging condition[13]. Singing higher may concern a more specific adjustment, tailored to urban noise spectra, which is congruent with several examples of noise-spectra related song frequency use in natural habitats[35-38].

The ultimate question raised by Nemeth & Brumm (2010) in their title ("*are urban songs adaptive?*") requires more work on benefits as well as costs, but based on their data, we would have answered: "*there is certainly a lot of potential as louder songs as well as higher songs yield longer transmission distances under noisy urban conditions*". These longer transmission distances should translate to perceptual advantages in terms of detection and discrimination, which seems obvious for increased amplitude, but which has been confirmed now for increased frequency in the laboratory[39] as well as in the field (chapter 4). So, although more work on benefits as well as costs is needed, we believe that it is safe to conclude that a rise in amplitude can be an effective way to deal with anthropogenic noise, but for crying out loud: singing high does matter.

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