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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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### **Citation**

Halfwerk, W. (2012, March 1). *Tango to traffic : a field study into consequences of noisy urban conditions for acoustic courtship interactions in birds*. Retrieved from <https://hdl.handle.net/1887/18535>

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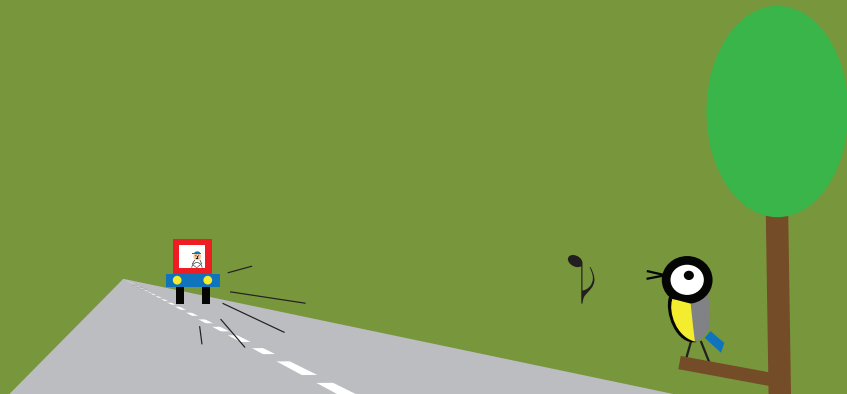
**Title:** Tango to traffic : a field study into consequences of noisy urban conditions for acoustic courtship interactions in birds

**Issue Date:** 2012-03-01

# Chapter 2

A behavioral mechanism explaining noise-dependent frequency use in urban birdsong

Published in *Animal Behaviour* as Halfwerk & Slabbekoorn 2009 (78):1301-1307



## ABSTRACT

Acoustic signals are usually very effective in long-distance communication. However, in many habitats animals suffer more and more from signal interference caused by traffic-generated low-frequency noise. Recent observations suggest that birds are able to change the pitch of their song to reduce masking interference, but we still lack experimental evidence. Theoretically, some bird species, when confronted with increased noise levels, may be able to switch to song types in their repertoire with higher frequencies. We tested this hypothesis in the great tit, *Parus major*, by exposing singing males to low-frequency 'city' noise in their natural territories and comparing frequency characteristics of songs before and after song type switching. We also exposed birds to high-frequency, 'inverse' city noise, as well as to white noise as a control. Great tits adjusted temporal switching behavior in response to noise exposure. Song types that were less masked by the noise treatment were sung for longer durations. As a result, all five birds that switched during the low-frequency noise treatment switched to song types with a higher minimum frequency. Similarly, seven of nine birds that switched while exposed to high-frequency noise switched to song types with lower maximum frequencies. These results provide experimental evidence for a short-term behavioral mechanism explaining noise-dependent frequency use in birdsong.

## INTRODUCTION

Many animals use acoustic signals to transmit biologically relevant information. However, their habitats can be noisy because of biotic and abiotic sounds, which can interfere with signal detection and limit the range over which mates can be attracted or territories defended<sup>1,2</sup>. As a consequence, noise-dependent selection on effective signal transfer may have had an evolutionary impact on the acoustic design of animal vocalizations<sup>3-5</sup>. Urban areas, but also many natural habitats, are increasingly dominated by the evolutionarily novel selection pressure of anthropogenic noise<sup>6</sup>. Traffic-generated low-frequency sounds in particular have become a likely selection pressure that many animals have to cope with to avoid signal interference<sup>7,8</sup>.

In general, animals can use different strategies to deal with unfavorable noise conditions reviewed in<sup>9</sup>. Information transfer from sender to receiver depends ultimately on the signal-to-noise ratio at the receiver's end<sup>1,2</sup>. A common strategy by which senders may cope with unfavorable noise conditions concerns an upregulation of signal amplitude in response to elevated noise levels as reported for birds and mammals<sup>10,11</sup>. Senders may also respond to noisier conditions by increasing signal duration or signaling rate, as reported for birds, frogs and

mammals<sup>12-14</sup>, or by timing their signals to avoid temporal overlap<sup>9</sup>. Another more recently discovered strategy is a change of frequency structure of an animal's vocalizations to reduce spectral overlap between signal and noise, which has been repeatedly shown in singing birds<sup>8,9,15</sup> and possibly in marine mammals<sup>16</sup>.

Noise-dependent frequency use in birdsong can be a short-term or long-term adjustment. It may concern genetic or ontogenetic change, immediate signaling flexibility, or a combination of these<sup>17</sup>. An exclusively genetic explanation seems unlikely for noise-associated acoustic variation within populations<sup>8,15</sup>. An ontogenetic explanation may account for some of the variation in bird species that develop adult song through experience and learning. For instance, a young bird arriving in a noisy territory may copy those songs from its neighbor(s) that are least affected by masking, and retain those songs in its repertoire that are effective under the local noise conditions<sup>18</sup>. However, another explanation for noise-dependent acoustic variation could be a short-term flexibility through an immediate feedback mechanism. This explanation does not necessarily exclude the previous two, but could potentially be responsible for noise-associated patterns found both within<sup>8,15</sup> and between populations<sup>18</sup>.



To understand the behavioral mechanism underlying noise-dependent frequency use, we need to know how a spectral change in song comes about. Spectral shift of the whole song in response to noise has not been reported, but a shift in spectral energy distribution towards higher frequencies was, for example, found for song sparrows (*Melospiza melodia*)<sup>15</sup> and European blackbirds (*Turdus merula*)<sup>19</sup>. The latter species also revealed temporal variation in the proportion of high and low song components, such that the overall spectral distribution was shifted upwards for birds from noisy urban areas compared to those of more quiet forests<sup>19</sup>. Birds could also change the acoustic design of their songs by incorporating more narrow-banded elements which have lower detection thresholds in the presence of a noise masker<sup>7</sup>. However, the most obvious candidate for a mechanism of short-term flexibility seems song type selection<sup>18</sup>. Birds may respond to rising levels of low-frequency noise by singing higher-pitched song types.

Great tits, *Parus major*, provide a suitable model system to investigate whether and how song type selection may be underlying noise-dependent frequency use<sup>8,18</sup>. Individual great tit males have a small repertoire of up to nine song types and the frequency characteristics of song types within an individual's repertoire can vary considerably<sup>20</sup>. Furthermore, great tits sing with eventual variety, repeating the same song type for several minutes

before switching to a new song type. Such singing style may provide an individual with ample signal feedback to decide when and to what song type to switch. Great tits adjust switching behavior during social interactions by selecting song types to match songs of neighbors<sup>21</sup>, and are known to use song types not recently sung in response to unfamiliar songs<sup>20</sup>. It is currently unknown whether they are also able to adjust their song type use under varying noise conditions based on frequency-dependent masking. We tested whether masking by experimental noise affected song type switching behavior in great tits.

We exposed singing males to artificial city-like low-frequency noise in their natural territories and compared frequency characteristics of songs before and after switching. We also exposed birds to high-frequency noise, which had an inverse energy distribution relative to the 'city' noise, and to white noise as a control exposure stimulus. This allowed explicit testing for upward and downward shifts related to masking avoidance. We predicted that birds would switch to songs with a higher minimum frequency in response to 'city' noise, whereas they would switch to songs with a lower maximum frequency in response to the high-frequency 'inverse' noise. In terms of temporal adjustments, we had no a priori expectations about treatment-dependent variation.

## METHODS

### Study species and area

Great tit songs typically consist of one to four different notes (defined as a continuous sound trace on a spectrogram) grouped together in a stereotypical pattern called a phrase. The same phrase is delivered in series called strophes of about 3 s followed by a 2 s break. Strophes are sung in bouts of several minutes after which birds can stop singing or switch to singing strophes of a different phrase. Great tits have a small repertoire of two to nine distinct phrase patterns which are also referred to as song types and these song types can be identified readily on a spectrogram<sup>22,23</sup>. Song frequency use in great tits ranges from around 2.5 to 8.0 kHz and song types can differ by about 1 kHz in frequency characteristics both within and between subjects (see e.g. [Figure 2.1](#)). In a population-wide survey by Slabbekoorn & Peet (2003) individuals showed differences in average minimum song frequency use of as much as 0.9 kHz, while habitat-dependent differences in song frequency use can be over 0.3 kHz at the population level<sup>18</sup>.

Experiments were carried out before sunrise (0400–0600 hours) from the end of March to early May 2008 in the suburban area of Utrecht Overvecht, The Netherlands (52°07N, 5°06E). Great tits in our study area started singing relatively early, 2 h before

sunrise, possibly as a result of artificial light levels<sup>24</sup>. Singing activity remained high until sunrise, providing a convenient time window to perform our experiments. We mapped the distribution of territories in March and we recorded several singing male great tits before sunrise to determine normal switching rate. These birds switched on average every 4 min to a new song type.

### Noise exposure experiments

We exposed singing great tits to a noise treatment using one of three different stimuli: low-frequency city-like noise ('City' noise), an inverse version of 'City' noise ('Inverse' noise) and white noise ('White' noise). The experiment started when the focal bird switched to a new song type (ST1, see [Figure 2.2](#)). A speaker was placed as close as possible to the bird (8 - 16 m) and a predetermined noise treatment started after  $\pm 1$  min ([Figure 2.2](#)), irrespective of the song types involved in the switch. Noise files had a 20 s amplitude ramp at on- and offset and lasted for 4 min. We used an Intertechnik M 130 KX4 speaker and a Monacor IPA-10 amplifier connected to a Sansa Express player for playing noise (WAV-format, 44.1 kHz sampling rate). The speaker was placed 25 cm from the ground and was directed towards the singing bird to keep noise exposure conditions as constant as possible between experiments. We measured the amplitude of







the noise stimuli (using a Cesva SC-30 sound analyser, A-weighted, 1 m from the speaker) and aimed to get an overall noise exposure of 60 - 66 dB at the position of the bird for all experiments. When a bird changed his song-post out of the direction of the noise we redirected the speaker once. When the bird moved away for a second time or flew away during noise exposure we discarded the experiment and did not use the same noise stimulus for this particular individual again.

All birds sang continuously during the noise exposure (except for six birds treated with 'White' noise) and we continued recording until 2 min after noise exposure had stopped, or until birds switched to a song type when this did not happen during the noise. We aimed at exposing at least 15 individuals to each of the three treatments. Neighbors were never treated on the same day and for subjects exposed to multiple noise stimuli we separated the experiments by at least 4 days.

### Noise stimuli and recordings

We created 'City' noise by applying a low-pass filter to random noise, with cutoff frequency set at 100 Hz and spectral energy decrease set at 6.5 dB/kHz towards the higher frequencies (Matlab 7.5, Mathworks, Inc., Natick, MA, U.S.A.). The spectral characteristics of this stimulus are similar to noise profiles found in cities<sup>25</sup>. We reversed the filter settings to get 'Inverse' noise

using a high-pass filter set at 10 kHz with a decrease in spectral energy of  $\pm 6.5$  dB/kHz towards the lower frequencies. 'White' noise was used as a control stimulus and all stimuli were band-pass filtered in the range of 1 - 10 kHz and normalized to the same overall amplitude levels.

Experiments were recorded 8 - 16 m away from the bird on a Marantz PMD670 recorder (sampled at 44.1 kHz) using a Sennheiser ME67 directional microphone pointed towards the bird and perpendicular to the speaker to ensure good recording conditions. After each experiment we measured the normal and experimental background noise levels at the position of the bird using the sound analyser and a Sennheiser ME62 omnidirectional microphone on an extendable pole.

Background noise recordings were band-pass filtered from 1 to 10 kHz and we selected a few seconds of recording prior to noise onset ('normal noise') and a few seconds of experimental noise to calculate overall root-mean-square (RMS) values in Matlab. RMS values were calibrated using measurements from the sound analyser and values were transformed to decibel scale to get overall amplitude levels of normal and experimental noise levels for each experiment. We used the critical bandwidth of great tits (after <sup>26</sup>) to assess spectral distribution of normal and experimental noise in



26 adjacent bands of 339 Hz ranging from 1 to 10 kHz.

### **Song measurements**

Songs recorded during experiments were analyzed in four categories: last song type before noise exposure (ST1b, [Figure 2.2](#)), same song type during noise exposure (ST1d), new song type switched to during noise exposure (ST2d) and, if no switch occurred during the exposure, new song type switched to after noise exposure (ST2a). We randomly selected six strophes, containing on average 4.6 phrases, from each category for spectral measurements. We measured peak frequency (frequency containing most of the acoustic energy) of the highest note within a phrase ('high-note') and of the lowest note within a phrase ('low-note') using LUSCINIA 1.0 (FFT = 1024; <sup>27</sup>). Additionally we assessed changes in spectral energy distribution using Matlab by determining the peak frequency ('peak frequency') and the frequency point below which 50% of total spectral energy is present ('spectral energy') for the whole strophe at a resolution of 2 Hz.

We quantified temporal switching behavior by measuring song type bout duration, which was defined as the time from the first phrase of a song type until the end of the last phrase of that same song type ([Figure 2.2](#)), irrespective of whether birds paused momentarily or changed singing positions. We assessed song rate decrease by counting the phrases in the first minute and dividing this value by the

average number of phrases per min in the second to the fifth minute interval (or until a song type switch occurred if a song type bout was less than 5 min long). We recorded normal dawn chorus singing on the days around an experiment using several automatic Song Meters (Wildlife Acoustics, Inc., Concord, MA, U.S.A.) and compared song types on the automatic recording with the experimental recording to make sure we recorded the same individual. For each individual we selected three bouts of different song types and assessed average song type bout duration and average song rate decrease as a reference to singing performance during experimental conditions. Additionally, we used the recordings of normal dawn singing to get the repertoire of songs that a bird was using on the days around the noise exposure experiment.

### **Statistical analysis**

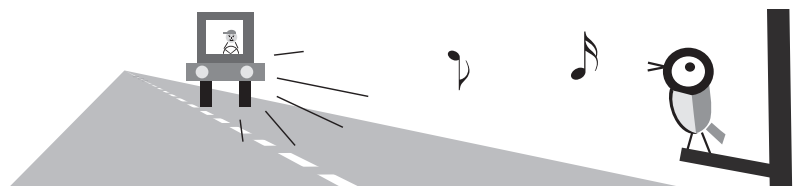
We tested whether experimental noise levels differed when compared to the normal background levels using a repeated measures ANOVA in Statistica 7 (Statsoft, Tulsa, OK, U.S.A), with treatment as a fixed factor. We used exact Wilcoxon signed-ranks tests to examine whether song type switching during noise exposure led to an increase in low-note frequency and to a decrease in frequency for high-notes in inverse noise. We also checked whether there were any similar changes in the nontarget spectral measurements for all three treatments. Additionally, we compared spectral characteristics of the first song

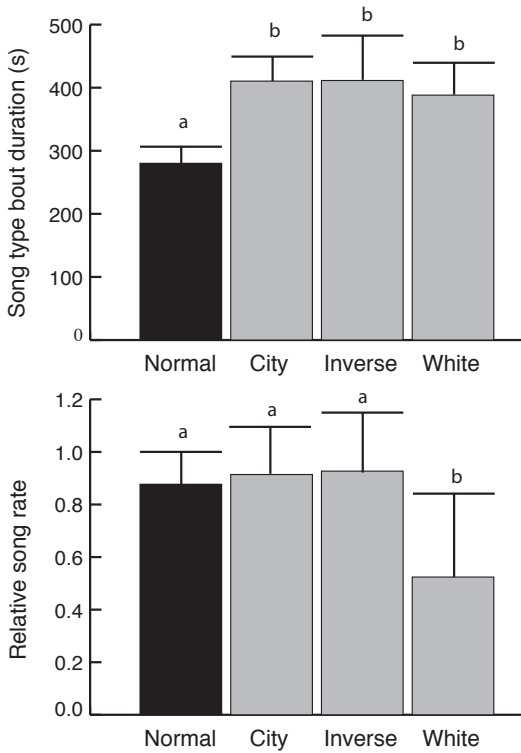
type before (ST1b) and this same song type during noise exposure (ST1d) using a repeated measures ANOVA, with noise treatment as a fixed factor. Song type bout duration and song rate decrease during experiments were compared with measurements taken from normal dawn chorus singing in a repeated measures ANOVA, with noise treatment and subject as fixed factors.

We tested whether song type bout duration was related to frequency of low-notes or high-notes of the song type before switching (ST1b) using a Pearson correlation or Spearman rank correlation for cases of non-normality. We examined masking-dependent relationships, that is, whether birds exposed to city noise were singing relatively low-note song types for relatively short durations (and the same for high-note song types when exposed to inverse noise). Again, we checked for nontarget relationships of the other measurements and treatments to test whether the predicted changes were masking specific. Experiments were discarded if birds flew away, or could not be relocated. Three individuals contributed to all three treatment groups, 11 individuals contributed to two treatment groups, and 16 individuals were only tested once, resulting in a mixed set of dependent and independent data points. All individuals that were used in multiple treatment groups sang a different song type at the start of the noise onset and we

therefore assumed no effect of subject on switching behavior. Nevertheless, to control for potential dependency effects we reanalyzed the predicted relationship using an independent data set by randomly choosing only one experiment per individual.

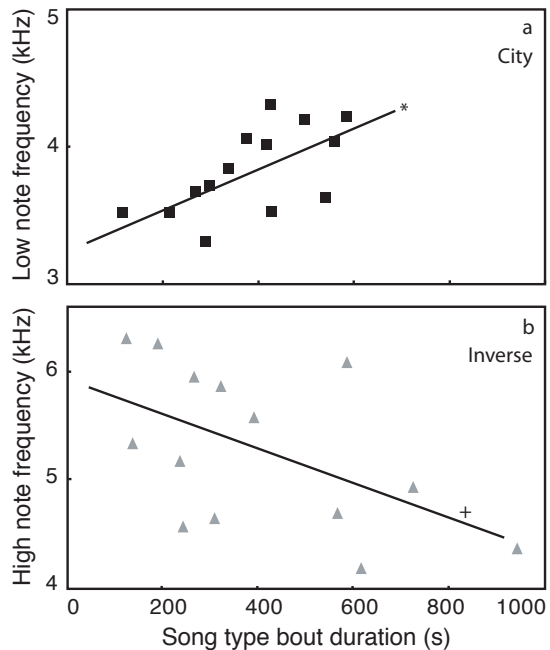
We designed a randomization test to assess whether the subset of birds that switched during noise exposure selected song types based on their frequency characteristics, so that, given the alternatives available in the repertoire, this song type would be the least masked by the experimental noise. We ranked all song types that a bird was known to sing according to note frequency. For the 'City' experiments we used rank numbers based on 'low-note' and for the 'Inverse' experiments we used 'high-note' rank numbers. We randomly selected a rank number for the starting song type (ST1) and the song type after switching (ST2) and determined the differences in rank number for 1000 simulated trials per experiment. Rank differences were divided by individual repertoire sizes before we calculated the random normal distribution. We applied the same method to song types actually sung during the experiments and determined whether observed differences in rank number fell in the 0.05 range of the normal distribution of random song type switching.





**Figure 2.4.** Singing behaviour of great tits in response to noise exposure. Mean and SDs are shown for normal song and during 'City', 'Inverse' and 'White' noise treatment. **(A)** Song type bout duration. **(B)** Change in song rate after the first minute of a song type bout. Bars with different letters (a, b) differ significantly (see text).

**Figure 2.5.** Masking-dependent switching. Song types that were less masked by the noise treatment were sung for longer durations by great tits. **(A)** Low-note frequency use during exposure to 'City' noise (\* $P = 0.01$ ) and **(B)** high-note frequency use during exposure to 'Inverse' noise (+ $P < 0.08$ ).



## RESULTS

Overall experimental noise levels were higher compared to normal background noise irrespective of noise treatment (repeated measures ANOVA:  $F_{2,43} = 7.54$ ,  $P = 0.002$ ; RMS values between 6.0 and 20.1 dB SPL louder). All individuals except one individual in the 'City' group experienced higher noise levels during the experimental exposure compared to normal background noise. The single exception was removed from the analysis. Overall RMS levels differed between treatment groups (ANOVA:  $F_{2,43} = 6.19$ ;  $P < 0.005$ ) with slightly lower levels for 'Inverse' noise. Spectral analysis of noise recordings using great tit critical bandwidths showed that during exposure to 'City' noise most of the spectral energy was below 5 kHz, masking the lower part of great tit song, whereas for 'Inverse' there was a clear bias in experimentally added noise energy towards frequencies above 5 kHz. During exposure to 'White' noise there was no clear bias in spectral energy towards higher or lower frequencies (Figure 2.3).

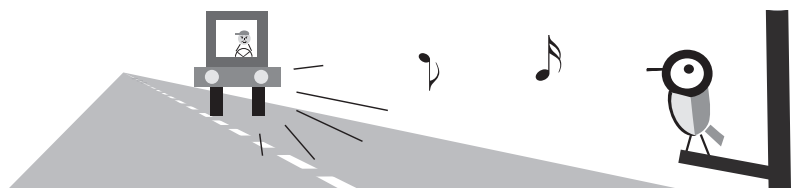
### Noise-dependent song type switching

Great tit males switched to another song type during noise exposure in only 19 of 46 experiments. All five switching birds treated with 'City' noise switched to song types with increased low-note frequencies (Wilcoxon signed-ranks test:  $N = 5$ ,

$P = 0.063$ ), whereas there was no trend in low-note frequency change in the other treatment groups (Inverse:  $N = 9$ ,  $P = 0.25$ ; White:  $N = 5$ ,  $P = 0.13$ ). Seven of nine switching birds treated with 'Inverse' noise showed a switch to song types with decreased high-note frequencies ( $N = 9$ ,  $P = 0.027$ ), whereas the other treatment groups did not show such a bias in switch direction (City:  $N = 5$ ,  $P = 0.81$ ; White:  $N = 5$ ,  $P = 0.81$ ). Peak frequency and spectral energy did not consistently increase or decrease with song type switching for any of the treatments (all  $P > 0.4$ ).

### Noise-dependent bout duration

Song type bout duration increased during all three treatments compared to normal dawn singing (repeated measures ANOVA:  $F_{1,43} = 13.41$ ,  $P < 0.0001$ ; Figure 2.4A) and the response was independent of noise treatment ( $F_{2,43} = 0.66$ ,  $P = 0.52$ ) or subject ( $F_{29,16} = 1.18$ ,  $P = 0.37$ ). This explains the unexpected low number of birds that switched to a song type during noise exposure. Birds that did not switch during exposure could have adjusted the same song type up- or downward instead of selecting new song types. However, we did not find an effect of song type adjustment in any of the four spectral measurements (repeated measures ANOVA: low-note:  $F_{2,43} = 0.53$ ,  $P = 0.59$ ; high-note:  $F_{2,43} = 0.13$ ,  $P = 0.69$ ; peak frequency:  $F_{2,43} = 0.37$ ,  $P = 0.69$ ; spectral energy:  $F_{2,43} = 0.80$ ,  $P = 0.46$ ).



Increasing song type bout duration instead of switching song types may theoretically result in more exhaustion and therefore be related to decreasing song rates. Great tit song rates slightly decreased after the first minute of a song type bout during normal dawn singing (Figure 2.4B). Song rate decrease was the same during noise exposure, but there was an effect of treatment (repeated measures ANOVA:  $F_{2,43} = 11.8, P < 0.001$ ). Birds exposed to 'White' noise significantly slowed down song rates (Tukey's post hoc:  $P < 0.001$ ; Figure 2.4B). This song rate decrease can be explained by a significant number of six birds that paused singing during 'White' noise exposure (chi-square test:  $\chi^2_2 = 7.97, P = 0.02$ ). These birds continued with the same song type after noise exposure had stopped.

### Masking-dependent song type use

Song type bout duration increased during noise exposure and we assessed whether this increase was related to frequency-dependent masking. Birds that were singing a song type with relatively low notes sang this song type for shorter durations when masked by 'City' noise (Pearson correlation:  $R^2_{13} = 0.41, F_{1,14} = 8.90, P = 0.01$ ; Figure 2.5A), but not during other types of noise (Inverse:  $R^2_{13} = 0.0003, F_{1,14} = 0.01, P = 0.91$ , White:  $R^2_{14} = 0.03, F_{1,15} = 0.44, P = 0.52$ ). Birds that were singing relatively high songs showed a trend to switch song types earlier when exposed to 'Inverse' noise (Spearman rank correlation:  $r_s = -0.49, N = 15, P = 0.08$ ;

Figure 2.5B) and not during other noise treatments (City:  $r_s = 0.23, N = 15, P = 0.2$ , White:  $r_s = 0.01, N = 16, P = 0.2$ ).

Five individuals were treated with 'City' as well as 'Inverse' noise, which may effect testing through nonindependence. Although none of these individuals switched to a new song type during noise exposure in either treatment, we repeated the analysis with a completely independent data set. Despite lower sample size, the relationship between low-note frequency and song type bout duration remained for the 'City' treatment ( $R^2_9 = 0.76, P = 0.007$ ), but disappeared for the 'Inverse' treatment ( $r_s = -0.31, N = 10, P = 0.39$ ).

### Random song type switching

Thirty great tits had on average  $\pm$  SD  $4.7 \pm 0.9$  (absolute range 3 - 6) known song types that they used before dawn. Birds switched to song types with an average rank difference of 1.18 in the expected direction of less masked songs, but this was not different from a random distribution ( $P > 0.39$ ). In other words, the song type switch was masking dependent, but birds did not select the least masked song types from their repertoire.

## DISCUSSION

Our results concern experimental evidence for noise-dependent adjustment of singing behavior in a common urban songbird species. Singing great tit males stopped or paused singing



because of either masking disturbance or a general startle response related to the experimental set-up, but a subset of birds remained singing and provided insight into song type and noise treatment-dependent effects. There was a congruent masking-dependent impact on temporal switching behavior: relatively high song types were sung for longer in response to low-frequency noise, whereas relatively low song types were sung for longer in response to high-frequency noise. As a consequence, the subset of birds that did switch during noise exposure switched to spectrally more favourable song types, resulting in higher low-notes with low-frequency noise and lower high-notes with high-frequency noise. These results demonstrate that a short-term behavioral flexibility is involved in the response of great tits to changing noise conditions and can explain noise-dependent frequency use in urban birdsong.

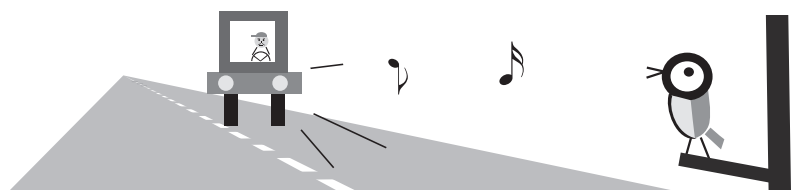
### Causal relationship confirmed

Evidence is accumulating that noise-dependent frequency variation is a geographically and taxonomically widespread phenomenon in birds. A link between song frequency use and ambient noise at the population level has so far been found for great tits<sup>18</sup>, as well as European blackbirds<sup>28</sup>. Furthermore, a correlation of minimum song frequency use and background noise levels at the individual level has been reported

for urban great tits<sup>8,29</sup>, urban house finches (*Cardopocus mexicanus*)<sup>30</sup> and urban song sparrows<sup>15</sup>, as well as for chaffinches, (*Fringilla coelebs*), in the context of variation in a natural noise source<sup>31</sup>. However, none of the previous studies explicitly tested for a causal relationship between noise and song frequency use. The present study is therefore the first to go beyond correlative data to show that what a bird sings depends on the ambient noise conditions.

### Species constraints on mechanisms

Although our results can provide insight into causal mechanism(s) underlying noise-dependent frequency use in great tits, we need to be cautious in extrapolation to other species. Flexible song type switching for example cannot be used by bird species that only sing one song repeatedly. Flexibility in repertoire use may furthermore depend on typical repertoire size and singing style. Small-repertoire singers such as great tits and song sparrows typically sing with eventual variety, repeating the same song type several times before switching to a new song type. Such a singing style could allow for the use of current signal-to-noise ratios to make a reliable prediction about the masking conditions of the subsequent song if birds continue with the same song type. However, such a prediction may become less reliable if a switch is made, as this requires internal evalu-



ation of spectral overlap for possible song types in an individual's repertoire under the current noise conditions.

Optimal song type selection is even more challenging for large-repertoire singers that need to process internal comparisons for multiple song types. Many large-repertoire singers also sing with immediate variety, singing a song type only once, and thus do not decide whether but only how to switch with each subsequent song. European blackbirds and house finches, for example, may have to compare over 100 song types for optimal avoidance of spectral masking, which seems an unlikely feedback mechanism. Even for great tits we found no evidence for an optimal pick from the available repertoire as song type selection appeared to be random. Nevertheless, we have shown that great tits use current noise conditions in their switching decision, either based on just current signal-to-noise ratios, or by making use of some sort of internal comparison of the current song type with potentially available song types.

Although our results suggest that noise-dependent feedback does affect song type switching in great tits in some way, we point out that in addition to the uncertainties discussed above, such feedback can be internal or external. Birds that no longer perceive their own song appropriately may sing louder, switch song types to higher frequencies, or stop singing<sup>9</sup>. This is the internal explanation. Feedback can also be

provided through social interaction or lack thereof; the external explanation. Great tits are known to engage in matched counter-singing with their neighbors<sup>32</sup> and ambient noise could lead to a masking-dependent switching response. Birds may for instance continue with a high-pitched song type while their neighbor has already switched to a low-pitched song type. On a similar vein, zebra finches (*Taeniopygia guttata*), increase vocal amplitude when conspecifics are further away<sup>33</sup>. Also here the perceptual mechanism remains unclear: zebra finches may either in some way anticipate the signal-to-noise ratio at the receiver's side or just respond to the impact of their vocalizations on their listeners.

### **Noise-dependent song changes**

Our results show short-term flexibility in singing response to fluctuating noise conditions that may explain more long-term associations between song type frequencies and average levels of urban noise. Reduced singing, or dropping all together, of unfavorable song types may explain noise-dependent spectral sorting at the individual (i.e. comparing noisy and quiet territories) and population level (i.e. comparing urban and forest habitat). Habitat-dependent sorting of song types could potentially affect gene flow through an impact on territory establishment or mate attraction for individuals dispersing across areas with different noise profiles<sup>18,34</sup>. An impact of noise-dependent song divergence on relative response strength to playback has



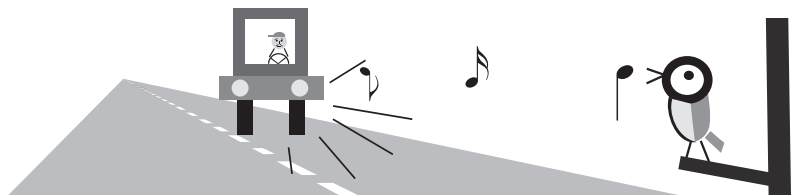
been reported for great tits<sup>29</sup>, as well as blackbirds<sup>19</sup>.

Singing flexibility, as exhibited by the great tits in this study, and assumed for several other urban bird species, may be one of many prerequisites to survive in an urbanizing world that is getting more and more noisy. However, although great tits are among the survivors, they may still suffer from elevated levels of anthropogenic noise found in and around cities. Low-frequency traffic noise interferes with the use of low-pitched song types that may be important for female choice<sup>6</sup>. Noise may also restrict switching rate (current study) or song rate<sup>11,31</sup>, which can negatively affect male-male interactions<sup>35,36</sup>. Furthermore, although great tits are able to adjust their repertoire without reducing its size<sup>20</sup>, noise may reduce the number of efficient song types in a male's repertoire and thereby limit his potential both to deter competitors and to attract mates. In conclusion, although great tits do relatively well in cities, urban noise pollution may still be detrimental to their welfare.

As a final remark, our finding of a general increase in song type bout duration related to experimental noise exposure may be valuable for the ongoing debate surrounding the 'anti-exhaustion hypothesis'<sup>37</sup>. According to this hypothesis, singing long bouts of the same song type will

lead to motor fatigue of the vocal apparatus and birds would therefore have to switch to a new song type to maintain high singing rates<sup>37</sup>. Such performance constraints are assumed to be especially important during intense singing, which great tits do during the dawn chorus<sup>37</sup>. We found, however, that great tits increased song type bout durations when exposed to noise, while the singing rates did not decrease more compared to singing rates under normal conditions. Only during treatment with white noise did birds decrease singing rates substantially. The ability to adjust song type bout length while keeping song output the same has been reported in chaffinches as well<sup>38,39</sup> and they also seem to use this ability to increase bout durations in noisier territories<sup>31,39,40</sup>. These results from great tits and chaffinches suggest that performance constraints may have less of an effect on switching behavior than previously presumed.

In conclusion, we have experimentally shown that great tits respond to elevated noise levels with relatively short-term singing flexibility. Singing males continue to sing those songs that do well under current noise conditions for longer, which can result in noise-dependent sorting of song types at both individual and population levels. Consequently, although we do not rule out the possibility of an ontogenetic or genetic impact, our results



can explain noise-dependent acoustic variation among urban individuals and among populations of different habitats. We have discussed the limitations and implications for what our results tell about causes and consequences of noise-dependent spectral adjustment of birdsong and we now await further studies that experimentally test for similar or alternative behavioral mechanisms in other bird species or other animals in general.

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