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Tango to Traffic

A field study into consequences of noisy urban conditions for acoustic courtship interactions in birds

Wouter Halfwerk

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Voor Assia en Hidde

Contents

Chapter 1

General Introduction

Living on a noisy planet

Animals rely on sensory systems, such as vision, hearing or smell, to survive and reproduce[1], but this is becoming more and more difficult due to human activities[2-5]. Humans disturb the sensory environment with artificial lighting, noise production or chemical emission, thereby affecting biological processes at various spatial scales[6-9]. The anthropogenic disturbance of natural areas is expected to increase exponentially[2] and will affect biodiversity worldwide[6,10].

Anthropogenic noise is a well-known feature associated with human activities, which is especially prominent at urban habitats, such as in cities or in the proximity of highways. Anthropogenic noise affects animals through the disturbance and deterrence of individuals, or by masking of important acoustic signals and cues[2,5,11]. Acoustics play an important role in predator avoidance as well as prey detection and many species rely on acoustic signals to find mates or to fight their rivals[1]. Signal interference through masking noise may therefore have important fitness consequences and may determine whether species will remain in or near the urban habitat[12,13].

Studies on animal communication and anthropogenic noise have reported patterns at the level of the individual as well as the population, without paying much attention to the underlying mechanisms nor to the associated consequences[12]. Individual animals have for instance been found to adjust their signaling behavior in response to anthropogenic noise[14]. However, whether such response is sufficient to avoid a negative impact of noise, or whether there are associated fitness consequences, has, so far, been largely ignored[12,15]. Likewise, most studies focusing on an impact of noise on animal populations[e.g.16,17,18] lack the integration with studies on underlying mechanisms at the individual level[2]. Furthermore, most experimental data come from lab studies[14,19], whereas understanding how noise affects individuals, populations and ultimately communities requires field studies, taking natural behavior and ecological conditions into account.

Animal communication in noise

Acoustic communication involves signal exchange between senders and receivers. A sender produces a sound that will be transmitted through a particular environment before it is detected by a receiver[1]. The production, transmission as well as perception of sound all have their own specific limitations that warrant attention when trying to understand signal evolution under changing acoustic conditions. The production of acoustic characteristics can be constrained by morphological structures, or physiological demands. Very low-frequency or fast signals, for example, can be difficult to produce, whereas very loud signals may require a lot of energy[20]. The transmission properties of the habitat influence the distance over which individuals can communicate and may affect signal evolution[21,22]. For instance, in most habitats high-frequency sounds are more attenuated compared to low-frequency sounds, favoring selection of low-frequency long-range signals. Finally, the cognitive machinery of receivers is tuned to specific acoustic features that typically match signal characteristics while sounds outside the perceptual tuning range are less well perceived[23].

Communication ultimately requires extraction of the relevant signal components from the background noise by a receiver[14,24]. This ability depends on the signal-to-noise ratio at the position of the receiver and his *masked* auditory threshold. Acoustic energy is processed in particular frequency ranges and when the neuronal response evoked by a signal can not be discriminated from the response evoked by irrelevant sounds, such as noise, that share the same frequency range, the signal is said to be *masked*. A sender can anticipate a rise in noise level and the associated increase in masking thresholds of the receiver by increasing the amplitude of his signal[14]. When confronted with urban noise, with most acoustic energy typically biased towards lower frequencies, senders can also respond by raising the frequency of their vocalizations, thereby reducing the spectral overlap with noise, and hence the masking impact[14].

The increased noise levels associated with the urban habitat can mask particular signals at the side of the receiver, consequently forcing senders to vocalize louder or at higher frequencies[11,15]. However, the benefits of such signal adjustment may come at the costs of reduced transmission or production efficacy, or negative fitness consequences, such as increased predation risk or reduced attractiveness to females. Therefore, understanding the impact of communication in noise requires an integrative approach, looking at processes found at the level of senders, receivers and transmission properties of the habitat, and both on a short- and a long-term.

THESIS FOCUS

In this thesis, I concentrate on the question how anthropogenic noise affects communication and reproduction in the great tit (*Parus major*). The effects of typical anthropogenic noise profiles associated with urban habitats will be addressed and the term ‘urban noise’ will be used in case the source is not specified. Urban noise profiles show a bias in spectral energy towards the lower frequencies and can refer to the common ‘soundscape’ found in cities, as well as more specifically to sounds coming from heavy machinery, or busy highways. I will focus on song behavior of male great tits and relate noise-dependent changes of individuals to fitness consequences, which may ultimately affect interactions at the population and community level (Figure 1.1).

The study system

The great tit is an ideal species to study acoustic communication in anthropogenic noise for several reasons. Great tits can be found in high numbers in relatively quiet forests as well as in anthropogenic noise impacted areas, such as cities and along highways[25-27], and can therefore be used as a model species to study the mechanisms related to communication and fitness that may have caused other species to disappear. The great tit also functions as key species in many studies regarding behavior, ecology and breeding performance, because of its preference for artificial nest boxes over natural cavities[28]. Song of the great tit has been related to the acoustic properties of the habitat[26,29] as well as to fitness[30,31], which allows us to translate an impact of noise on communication to an impact on lifetime reproductive success.

Great tit song variation has been related to variation in urban noise. Great tits produce higher songs in cities compared to nearby forests[32,33] and use higher frequency song types in noisy territories[26,34]. However, causes of this noise-dependent song frequency use were unknown prior to the studies reported in this thesis. Furthermore, we lack knowledge on consequences in terms of morphological or energy constraints. Sound propagation cannot be directly affected by urban noise, but other acoustic properties associated with urban environments, such as increased reverberation and attenuation may limit the use of high frequency songs in response to low-frequency noise[12,35,36]. The consequences of noise-dependent frequency use are likely to play their biggest role at the perceptual side. We know from lab studies that the auditory sensitivity of tits does not vary much over a large frequency range, which indicates that signal detection depends primarily on the amount of spectral overlap with the background noise[37]. However, we do not know how noise affects discrimination of songs by great tits and whether noise affects female assessment of signal attractiveness, as found for example for frogs[38]. Furthermore, although we expect the use of high-frequency songs to be favored through increased signal detection under urban noise conditions, we do not know how a noise-dependent signal change will affect female behavior.

Aim of the thesis

I will address how urban noise affects the sender's side through an impact on song production mechanisms. How do great tits change their song frequencies in response to noise? And how does this affect signal transmission? Next, I will focus on noise affecting females, one of the main receivers of male bird song. Do females provide feedback on acoustic performance to males? And how do noise-dependent signal strategies affect song attractiveness to females, or other types of receivers? A trade-off between signal detection and signal efficacy may translate into an impact of noise on reproductive success, which will be studied in the final part of the thesis. How does noise affect individual reproductive success? And can individual response to anthropogenic noise affect interactions within ecological communities?

Outline of the thesis

The thesis consists of eight chapters. This introduction chapter is followed by four data papers, two commentaries supplemented with extra discussion, or data, and concluded by a general discussion chapter.

Chapter 2: describes a noise exposure experiment with singing male great tits during the dawn chorus to test their ability to avoid masking by altering their singing behavior (Figure 1.1A).

Chapter 3: is a commentary paper on the mechanisms related to noise-dependent frequency use and the associated benefits in terms of signal transmission.

Chapter 4: examines the importance of song frequency in male-female communication and tests the consequences of noise-dependent frequency change in a noise exposure experiment with female great tits (Figure 1.1B).

Chapter 5: looks at noise-dependent female feedback and its role in affecting male song behavior, by exposing females inside their nest box to artificial urban noise, while leaving the singing male unaffected (Figure 1.1C).

Chapter 6: is a descriptive study in which fluctuations in traffic noise levels are related to long-term breeding data on great tits and discusses the mechanism underlying noise-dependent reproductive success (Figure 1.1D).

Chapter 7: discusses the impact of anthropogenic noise on bird breeding communities, with an additional case-study on a noise-dependent nest-site choice experiment (Figure 1.1E).

Chapter 8: summarizes results from previous chapters and suggests future directions.

REFERENCES

[1] Bradbury, J.W. & Vehrencamp, S.L., *Principles of Animal Communication*. (Sinauer Associates, Sunderland, MA, 1998).

[2] Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

[3] Seehausen, O. *et al.*, *Science* 277 (5333), 1808-1811 (1997).

[4] van der Sluijs, I. *et al.*, *Evol. Ecol.* 25 (3), 623-640 (2011).

[5] Slabbekoorn, H. *et al.*, *TREE* 25 (7), 419-427 (2010).

[6] Vitousek, P.M. *et al.*, *Science* 277 (5325), 494-499 (1997).

[7] Kempenaers, B. *et al.*, *Current Biology* 20 (19), 1735-1739 (2010).

[8] Forman, R.T.T., *Conservation Biology* 14 (1), 31-35 (2000).

[9] Walther, G.R. *et al.*, *Nature* 416 (6879), 389-395 (2002).

[10] Clergeau, P. *et al.*, *Biological Conservation* 127 (3), 336-344 (2006).

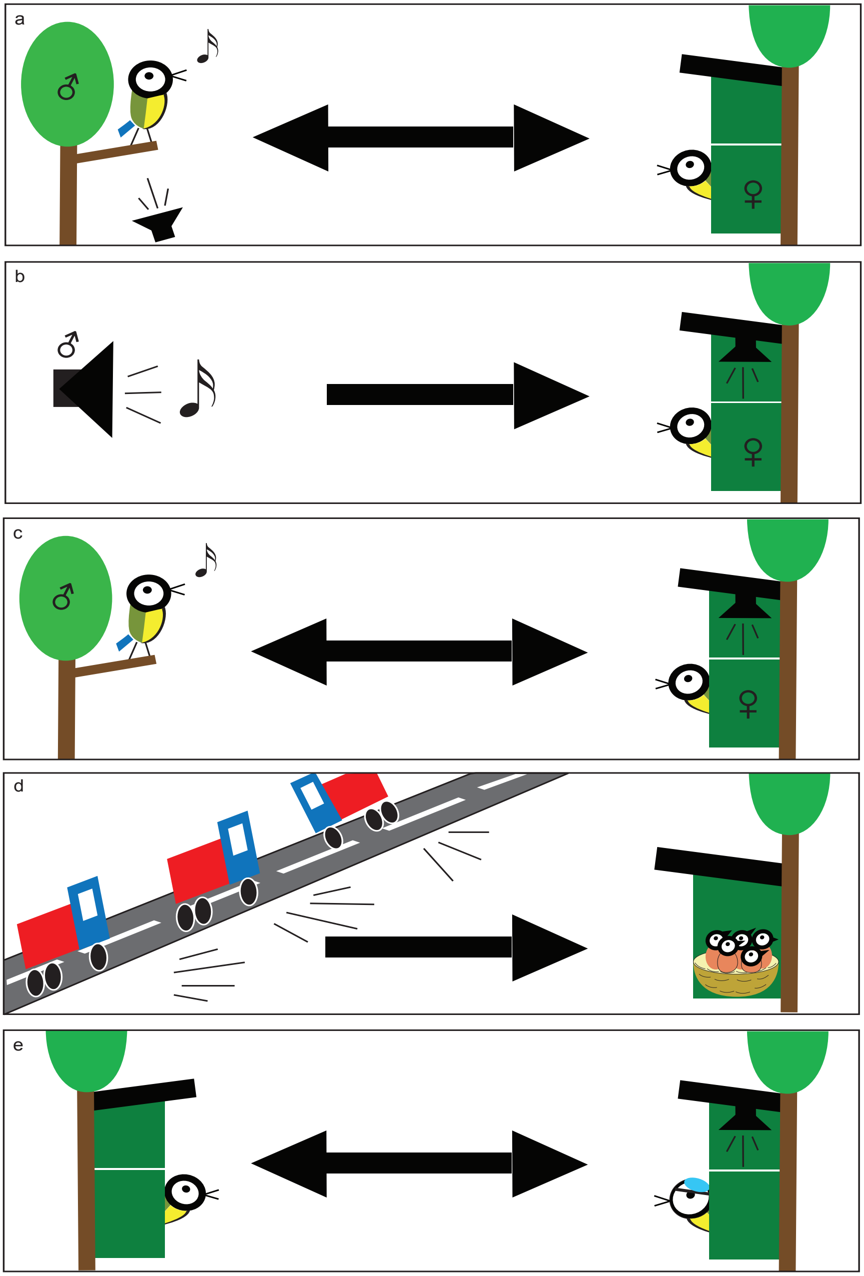

Figure 1.1. Schematic representation of the impact of traffic noise on avian communication as studied in the current thesis. An impact has been investigated **A**) at the sender side by experimental exposure of the natural dawn chorus song behaviour (chapter 2), **B**) at the receiver side by testing female responsiveness to playback with and without experimental noise exposure inside the nest boxes (chapter 4), and **C**) for effects on the interaction between senders and receivers (chapter 5). We also studied **D**) the impact on reproductive success by correlating spatial patterns of noise variation to a long-term data-set on breeding performance (chapter 6), and **E**) the impact at the community level by investigating noise-dependent competition between great tits and blue tits again with experimental noise exposure inside nest boxes and control boxes prior to settlement and occupation of nest boxes (chapter 7).

[11] Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

[12] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[13] Rabin, L.A. & Greene, C.M., *J of Comparative Psychology* 116 (2), 137-141 (2002).

[14] Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

[15] Patricelli, G.L. & Blickley, J.L., *Auk* 123 (3), 639-649 (2006).

[16] Reijnen, R. & Foppen, R., *J of Applied Ecology* 32 (3), 481-491 (1995).

[17] Bayne, E.M. *et al.*, *Conservation Biology* 22 (5), 1186-1193 (2008).

[18] Forman, R.T.T. *et al.*, *Environmental Management* 29 (6), 782-800 (2002).

[19] Kight, C.R. & Swaddle, J.P., *Ecology Letters* (2011).

[20] Gil, D. & Gahr, M., *TREE* 17 (3), 133-141 (2002).

[21] Morton, E.S., *Am. Nat.* 109, 17-34 (1975).

[22] Wiley, R.H. & Richards, D.G., *Beh Eco and Soc* 3 (1), 69-94 (1978).

[23] Dooling, R.J. *et al.*, in *Comparative hearing in birds and reptiles* (Springer, Berlin, 2000).

[24] Brumm, H. & Naguib, M., *Adv in the Study of Behavior, Vol 40* 40, 1-33 (2009).

[25] Tratalos, J. *et al.*, *Global Change Biology* 13 (8), 1685-1695 (2007).

[26] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[27] Reijnen, R. *et al.*, *J of Applied Ecology* 32 (1), 187-202 (1995).

[28] Kluyver, H.N., *Ardea* 39 (1), 1 - 135 (1951).

[29] Hunter, M.L. & Krebs, J.R., *J of Animal Ecology* 48, 759-785 (1979).

[30] McGregor, P.K. *et al.*, *Am. Nat.* 118 (2), 149-159 (1981).

[31] Lambrechts, M. & Dhondt, A.A., *Beh Eco and Soc* 19 (1), 57-63 (1986).

[32] Slabbekoorn, H. & den Boer-Visser, A., *Current Biology* 16 (23), 2326-2331 (2006).

[33] Mockford, E.J. & Marshall, R.C., *Proc R Soc B* 276 (1669), 2979-2985 (2009).

[34] Hamao, S. *et al.*, *Ethol. Ecol. Evol.* 23 (2), 111-119 (2011).

[35] Slabbekoorn, H. *et al.*, *Condor* 109 (1), 67-78 (2007).

[36] Nemeth, E. & Brumm, H., *Am. Nat.* 176 (4), 465-475 (2010).

[37] Langemann, U. *et al.*, *Animal Behaviour* 56, 763-769 (1998).

[38] Wollerman, L. & Wiley, R.H., *Animal Behaviour* 63, 15-22 (2002).

Chapter 2

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

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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[1,2]. As a consequence, noise-dependent selection on effective signal transfer may have had an evolutionary impact on the acoustic design of animal vocalizations[3-5]. Urban areas, but also many natural habitats, are increasingly dominated by the evolutionarily novel selection pressure of anthropogenic noise[6]. Traffic-generated low-frequency sounds in particular have become a likely selection pressure that many animals have to cope with to avoid signal interference[7,8].

In general, animals can use different strategies to deal with unfavorable noise conditionsreviewed in [9]. Information transfer from sender to receiver depends ultimately on the signal-to-noise ratio at the receiver's end[1,2]. 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[10,11]. Senders may also respond to noisier conditions by increasing signal duration or signaling rate, as reported for birds, frogs and mammals[12-14], or by timing their signals to avoid temporal overlap[9]. 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[8,9,15] and possibly in marine mammals[16].

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[17]. An exclusively genetic explanation seems unlikely for noise-associated acoustic variation within populations[8,15]. 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[18]. 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[8,15] and between populations[18].

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)*[15] and European blackbirds (*Turdus merula)*[19]. 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[19]. 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[7]. However, the most obvious candidate for a mechanism of short-term flexibility seems song type selection[18]. 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[8,18]. 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[20]. 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[21], and are known to use song types not recently sung in response to unfamiliar songs[20]. 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[22,23]. 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[18].

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[24]. 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 ± 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

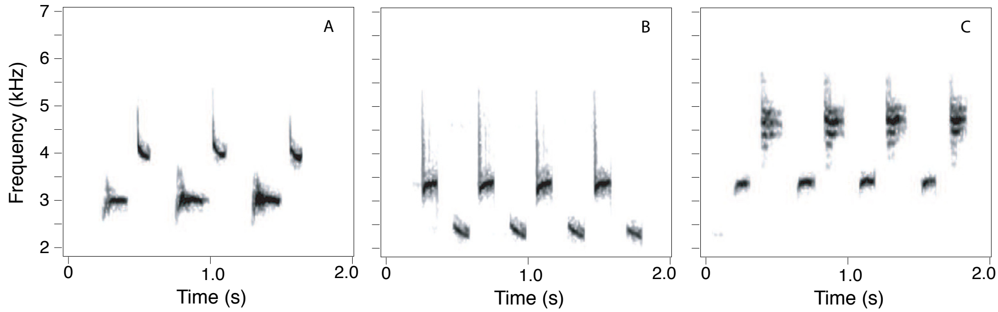


Figure 2.1. Three great tit song type examples from our study population showing variation in peak frequency of the low-notes and high-notes. The song types in these examples consist of two notes and are delivered in series called 'strophes'. Song type frequency characteristics can vary discretely both within and between individuals. Song types B and C are recorded from the same individual and switching between these song types results in a low-note frequency change of 1.2 kHz.

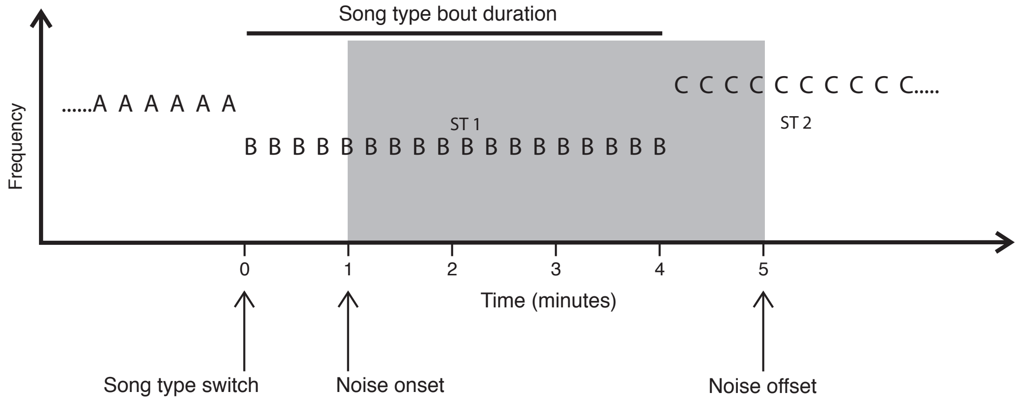


Figure 2.2. Experimental noise exposure. Great tit singing behaviour is indicated schematically: A = 'strophe of the same song type'; A A A A … = bout of the same song type. The playback of noise stimuli started 1 min after the first switch to a new song type, from A to B and lasted 4 min. Birds either switched during (this example) or after noise exposure to a new song type, from B (ST1) to C (ST2). We assessed the song type bout duration of ST1 from the first to the last B, which may be within or beyond the noise exposure period.

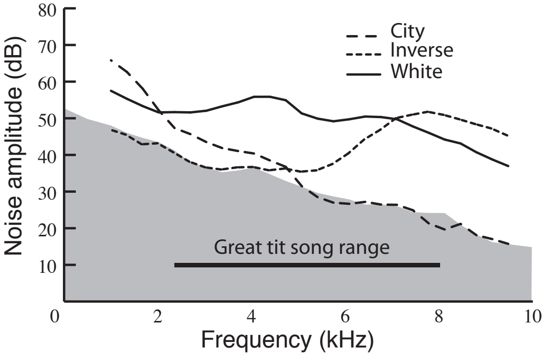


Figure 2.3. Energy distribution of noise stimuli. Power spectrograms illustrate the three noise treatments, averaged over experiments. Noise recordings made at the position of the focal bird were analysed in 26 adjacent frequency bands in the range of 1 – 10 kHz. The shaded area illustrates the spectrum of average background noise in our study area. Note that the normal background noise is added to the experimental noise which especially affects the 'Inverse' stimuli. Great tit song range is indicated by the black bar for comparison.

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 songpost 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., Natck, MA, U.S.A.). The spectral characteristics of this stimulus are similar to noise profiles found in cities[25]. 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 ± 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 [26]) 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; [27]). 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.

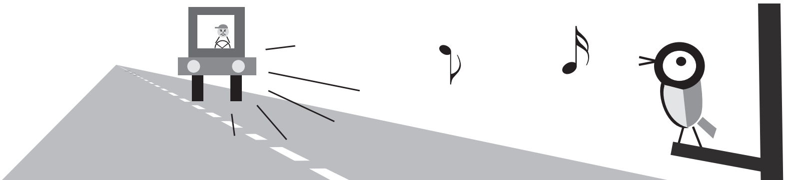
We quantified temporal switching behavior by measuring song type bout duration, which was defined as the time from the first phrase of a song type until the end of the last phrase of that same song type (Figure 2.2), irrespective of whether birds paused momentarily or changed singing positions. We assessed 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.



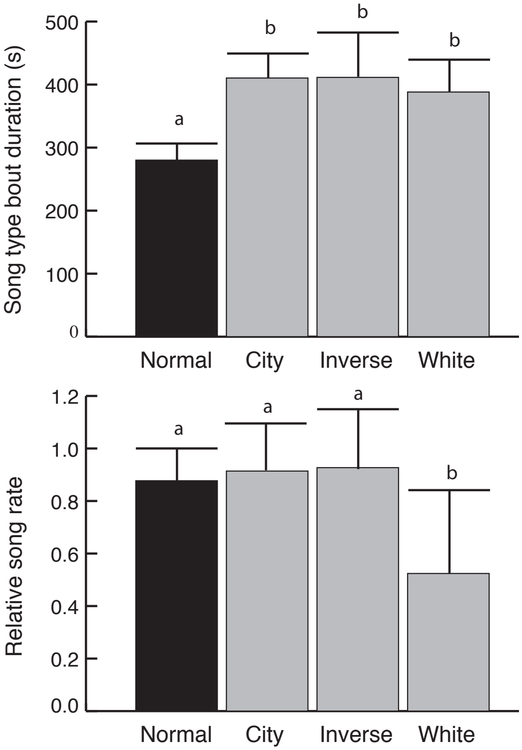


Figure 2.4. Singing behaviour of great tits in response to noise exposure. Mean and SDs are shown for normal song and during 'City', 'Inverse' and 'White' noise treatment. (**A**) Song type bout duration. (**B**) Change in song rate after the first minute of a song type bout. Bars with different letters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

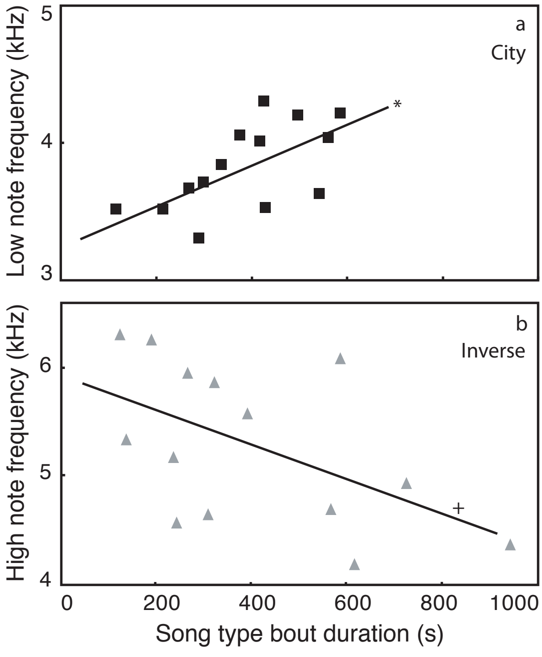


Figure 2.5. Masking-dependent switching. Song types that were less masked by the noise treatment were sung for longer durations by great tits. (**A**) Low-note frequency use during exposure to 'City' noise (*P = 0.01) and (**B**) high-note frequency use during exposure to 'Inverse' noise (+P < 0.08).

RESULTS

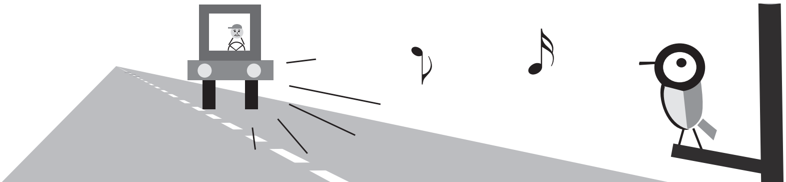
Overall experimental noise levels were higher compared to normal background noise irrespective of noise treatment (repeated measures ANOVA: $F_{2, 43} = 7.54$, $P = 0.002$; RMS values between 6.0 and 20.1 dB SPL louder). All individuals except one individual in the 'City' group experienced higher noise 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 ± SD 4.7 ± 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

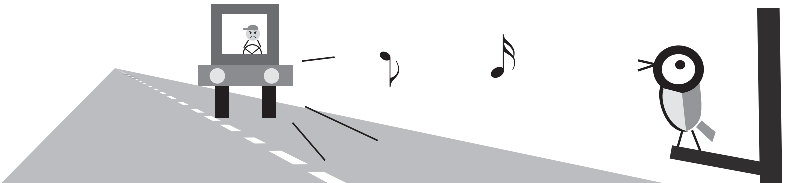
Our results concern experimental evidence for noise-dependent adjustment of singing behavior in a common urban songbird species. Singing great tit males stopped or paused singing because of either masking disturbance or a general startle response related to the experimental set-up, but a subset of birds 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[18], as well as European blackbirds[28]. Furthermore, a correlation of minimum song frequency use and background noise levels at the individual level has been reported for urban great tits[8,29], urban house finches (*Cardopocus mexicanus*)[30] and urban song sparrows[15], as well as for chaffinches, (*Fringilla coelebs*), in the context of variation in a natural noise source[31]. 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[9]. 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[32] 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[33]. 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.

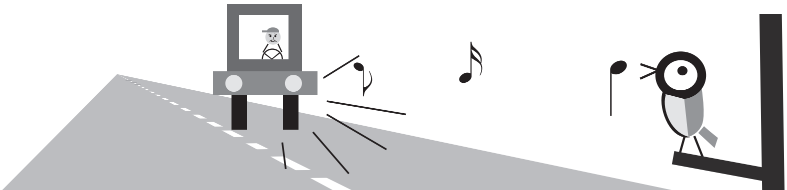
Noise-dependent song changes

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[18,34]. An impact of noise-dependent song divergence on relative response strength to playback has been reported for great tits[29], as well as blackbirds[19].

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[6]. Noise may also restrict switching rate (current study) or song rate[11,31], which can negatively affect male-male interactions[35,36]. Furthermore, although great tits are able to adjust their repertoire without reducing its size[20], 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'[37]. 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[37]. Such performance constraints are assumed to be especially important during intense singing, which great tits do during the dawn chorus[37]. 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[38,39] and they also seem to use this ability to increase bout durations in noisier territories[31,39,40]. 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.

REFERENCES

[1] Klump, G.M., in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma & E. H. Miller (Cornell University Press, Ithaca, 1996), pp. 321–338.

[2] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[3] Wiley, R.H. & Richards, D.G., *Beh Eco and Soc* 3 (1), 69-94 (1978).

[4] Morton, E.S., *Am. Nat.* 109, 17-34 (1975).

[5] Ryan, M.J. & Brenowitz, E.A., *The American Naturalist* 126 (1), 87-100 (1985).

[6] Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

[7] Pohl, N.U. *et al.*, *Animal Behaviour* 78 (6), 1293-1300 (2009).

[8] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[9] Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

[10] Manabe, K. *et al.*, *J. Acoust Soc Am* 103 (2), 1190-1198 (1998).

[11] Potash, L.M., *Psychonomic Science* 26 (5), 252-254 (1972).

[12] Penna, M. *et al.*, *Animal Behaviour* 70, 639-651 (2005).

[13] Brumm, H. *et al.*, *J of Experimental Biology* 207 (3), 443-448 (2004).

[14] Leonard, M.L. & Horn, A.G., *Behavioral Ecology* 19 (3), 502-507 (2008).

[15] Wood, W.E. & Yezerinac, S.M., *Auk* 123 (3), 650-659 (2006).

[16] Rendell, L.E. *et al.*, *J of Zoology* 249, 403-410 (1999).

[17] Patricelli, G.L. & Blickley, J.L., *Auk* 123 (3), 639-649 (2006).

[18] Slabbekoorn, H. & den Boer-Visser, A.,

Current Biology 16 (23), 2326-2331 (2006).

[19] Ripmeester, E.A.P. *et al.*, *Behavioral Ecology* 21 (4), 876-883 (2010).

[20] Franco, P. & Slabbekoorn, H., *Animal Behaviour* 77 (1), 261-269 (2009).

[21] McGregor, P.K. & Krebs, J.R., *Behaviour* 108, 139-159 (1989).

[22] McGregor, P.K. & Krebs, J.R., *Nature* 297 (5861), 60-61 (1982).

[23] Lambrechts, M. & Dhondt, A.A., *Beh Eco and Soc* 19 (1), 57-63 (1986).

[24] Bergen, F. & Abs, M., *J Fur Ornithologie* 138 (4), 451-467 (1997).

[25] Lohr, B. *et al.*, *Animal Behaviour* 65, 763-777 (2003).

[26] Langemann, U. *et al.*, *Animal Behaviour* 56, 763-769 (1998).

[27] Lachlan, R.F., Luscinia: a bioacoustics analysis computer program (2007).

[28] Ripmeester, E.A.P. *et al.*, *Beh Eco and Soc* 64 (3), 409-418 (2010).

[29] Mockford, E.J. & Marshall, R.C., *Proc R Soc B* 276 (1669), 2979-2985 (2009).

[30] Fernández-Juricic, E., R. *et al.*, *Urban Habitats* 3 (1), 49-69 (2005).

[31] Brumm, H. & Slater, P.J.B., *Beh Eco and Soc* 60 (4), 475-481 (2006).

[32] Peake, T.M. *et al.*, *Animal Behaviour* 69, 1063-1068 (2005).

[33] Brumm, H. & Slater, P.J.B., *Animal Behaviour* 72, 699-705 (2006).

[34] Slabbekoorn, H. & Smith, T.B., *Phil Trans R Soc B* 357 (1420), 493-503 (2002).

[35] Stoddard, P.K. *et al.*, *Beh Eco and Soc* 22 (2), 125-130 (1988).

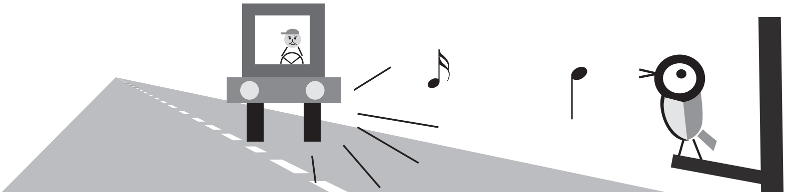
[36] Weary, D.M. *et al.*, *Animal Behaviour* 36, 1242-1244 (1988).

[37] Lambrechts, M. & Dhondt, A.A., *Animal Behaviour* 36, 327-334 (1988).

[38] Riebel, K. & Slater, P.J.B., *Animal Behaviour* 57, 655-661 (1999).

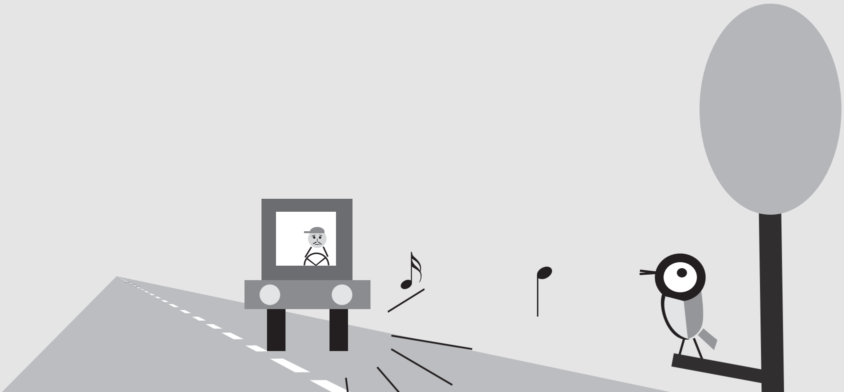
[39] Riebel, K. & Slater, P.J.B., *Animal Behaviour* 59, 1135-1142 (2000).

[40] Brumm, H. *et al.*, *Animal Behaviour* 77 (1), 37-42 (2009).



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.

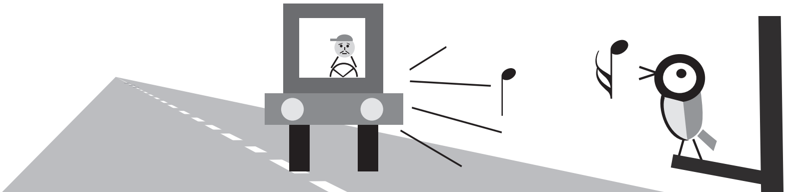
INTRODUCTION

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

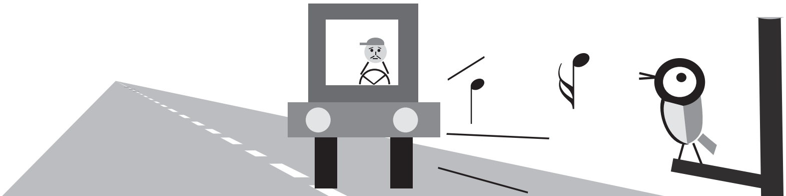
The complexity of noise-dependent patterns of song frequency use may be better reflected by an integration of three different theories about song production mechanisms explaining acoustic variation. The Lombard effect, performance constraints, and masking-dependent song type switching (chapter 2) may 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



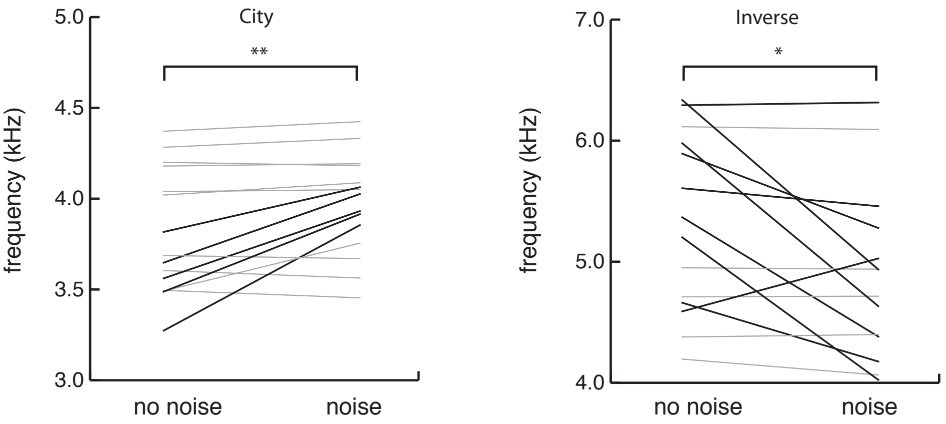


Figure 3.1. Masking avoidance by great tits in response to experimental noise exposure. Song frequency changed after four minutes of noise exposure depending on the type of noise played (GLMM: low-note frequency; χ2 = 13.8; p = 0.003; high-note frequency; χ2 = 9.5; p = 0.023). Low-note frequency only 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.

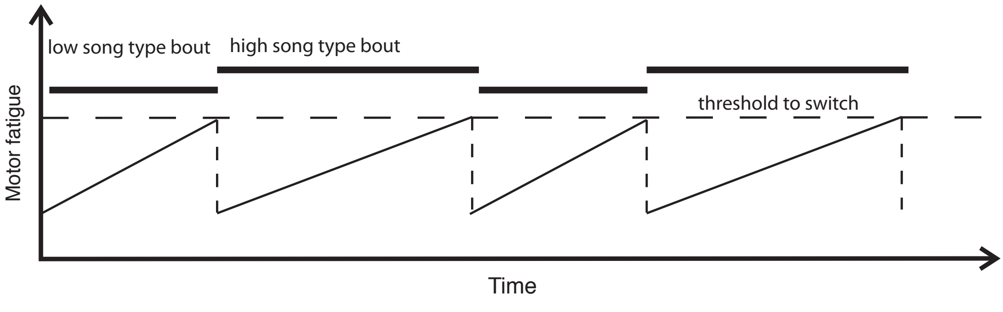


Figure 3.2. Model of performance constrained song type switching in urban noise. The model assumes that birds increase the amplitude level of their songs depending on the amount of spectral overlap with background noise and that singing louder is energetically demanding or physically exhausting. Singing 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).

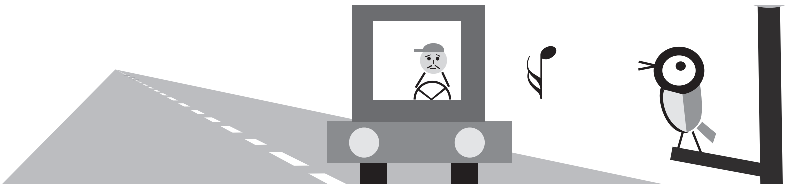
A mechanism of masking-dependent performance constraints might be a general explanation of noise-dependent frequency use. It may lead to selective song type use in some bird species, or to element adjustment in those species that do not possess a repertoire of different songs. However, all species, including 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.

REFERENCES

1 Nemeth, E. & Brumm, H., *Am. Nat.* 176 (4), 465-475 (2010).

2 Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

3 Halfwerk, W. *et al.*, *PNAS* 108 (35), 14549-14554 (2011).

4 Gross, K. *et al.*, *Am. Nat.* 176 (4), 456-464 (2010).

5 Halfwerk, W. & Slabbekoorn, H., *Animal Behaviour* 78 (6), 1301-1307 (2009).

6 Mockford, E.J. & Marshall, R.C., *Proc R*

Soc B 276 (1669), 2979-2985 (2009).

[7] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[8] Hu, Y. & Cardoso, G.C., *Animal Behaviour* 79 (4), 863-867 (2009).

[9] Potvin, D.A. *et al.*, *Proc R Soc B*(2011).

[10] Verzijden, M.N. *et al.*, *J of Experimental Biology* 213 (15), 2575-2581 (2010).

[11] Ripmeester, E.A.P. *et al.*, *Behavioral Ecology* 21 (4), 876-883 (2010).

[12] Brumm, H. & Naguib, M., *Adv in the Study of Behavior, Vol 40* 40, 1-33 (2009).

[13] Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

[14] Nelson, B.S., *Animal Behaviour* 59, 57-67 (2000).

[15] Cardoso, G.C. & Atwell, J.W., *Animal Behaviour* (2011).

[16] Osmanski, M.S. & Dooling, R.J., *J. Acoust Soc Am* 126 (2), 911-919 (2009).

[17] Zollinger, S.A. *et al.*, *PLoS ONE* 6 (9) (2011).

[18] Ohms, V.R. *et al.*, *PLoS ONE* 5 (7) (2010).

[19] Brumm, H. & Todt, D., *Animal Behaviour* 63, 891-897 (2002).

[20] Oberweger, K. & Goller, F., *J of Experimental Biology* 204 (19), 3379-3388 (2001).

[21] Lambrechts, M. & Dhondt, A.A., *Animal Behaviour* 36, 327-334 (1988).

[22] Weary, D.M. *et al.*, *Animal Behaviour* 41, 540-542 (1991).

[23] Podos, J. *et al.*, in *Adv in the Study of Behavior, Vol 40*, edited by M. Zuberbuhler K. Clayton N. S. Janik V. M. Naguib (2009), Vol. 40, pp. 159-195.

[24] Rivera-Gutierrez, H.F. *et al.*, *Biology Letters* 7 (3), 339-342 (2011).

[25] Botero, C.A. *et al.*, *Animal Behaviour* 77 (3), 701-706 (2009).

[26] de Kort, S.R. *et al.*, *Proc R Soc B* 276 (1665), 2315-2321 (2009).

[27] Lambrechts, M.M., *Ardea* 85 (1), 99-109 (1997).

[28] Mayr, E., *American Naturalist* 121 (3), 324-334 (1983).

[29] Gould, S.J. & Lewontin, R.C., *Proc R Soc B* 205 (1161), 581-598 (1979).

[30] Patricelli, G.L. & Blickley, J.L., *Auk* 123 (3), 639-649 (2006).

[31] Ripmeester, E.A.P. *et al.*, *Beh Eco and Soc* 64 (3), 409-418 (2010).

[32] Slabbekoorn, H. & Smith, T.B., *Phil Trans R Soc B* 357 (1420), 493-503 (2002).

[33] Dingle, C. *et al.*, *Evolution* 64 (12), 3537-3548 (2010).

[34] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[35] Dingle, C. *et al.*, *J of Evolutionary Biology* 21 (4), 1079-1089 (2008).

[36] Kirschel, A.N.G. *et al.*, *Behavioral Ecology* 20 (5), 1089-1095 (2009).

[37] Slabbekoorn, H. & Smith, T.B., *Evolution* 56 (9), 1849-1858 (2002).

[38] Brumm, H. & Slater, P.J.B., *Beh Eco and Soc* 60 (4), 475-481 (2006).

[39] Pohl, N.U. *et al.*, *Animal Behaviour* (2012).

Chapter 4

Low-frequency songs lose their potency in noisy urban conditions

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ABSTRACT

Many animal species communicate with their mates through acoustic signals, but this seems to become a struggle in urbanized areas due to increasing anthropogenic noise levels. Several bird species have been reported to increase song frequency by which they reduce the masking impact of spectrally overlapping noise. However it remains unclear whether such behavioral flexibility provides a sufficient solution to noisy urban conditions or whether there are hidden costs. Species may rely on low frequencies to attract and impress females and the use of high frequencies may therefore come at the cost of reduced attractiveness. We studied the potential trade-off between signal strength and signal detection in a successful urban bird species, the great tits (*Parus major*). We demonstrate that the use of low-frequency songs by males is related to female fertility as well as sexual fidelity. We experimentally show that urban noise conditions impair male-female communication and that signal efficiency depends on song frequency in the presence of noise. Our data reveal a response advantage for high-frequency songs during sexual signaling in noisy conditions, while low – frequency songs are likely to be preferred. These data are critical for our understanding of the impact of anthropogenic noise on wild-ranging birds as they provide evidence for low-frequency songs to be linked to reproductive success and to be specifically affected by noise-dependent signal efficiency.

INTRODUCTION

The use of acoustic signals to attract and stimulate sexual partners is a widespread phenomenon in the animal kingdom and many species rely to some extent on auditory contact for reproductive success[1]. However, rapid worldwide urbanization[2] and the associated rise in noise pollution makes efficient acoustic communication increasingly difficult in areas in and around cities, and in proximity of highways, airports, and industrial areas[3-5]. Most anthropogenic noise is related to traffic or industrial machinery and is typically biased towards low frequencies[3,6]. Interestingly, several urban bird species have been found to reduce the impact of spectrally overlapping anthropogenic noise by shifting songs up to higher frequencies[7-9], which is presumed to aid communication and thereby increase reproductive performances[6,7].

The ability to adjust song frequency on a short evolutionary timescale may be an important factor determining avian breeding success in noisy urban environments[5,10]. Anthropogenic noise has been reported to have a detrimental impact on bird breeding density and reproductive output (chapter 6)[11-13] with particularly negative effects for species vocalizing at low frequencies[14]. The effect can be partly explained by a lack of song frequency flexibility in those species that do not learn their vocalizations (e.g. pigeons & cuckoos[11,14]). However, even species that have been shown to immediately adjust song frequency in the presence of experimental noise (chapter 2)[15-18] may suffer reduced breeding success, when potential benefits of a spectral adjustment are not sufficient[19] or come at a considerable cost[5].

Low frequencies can be crucial to stimulate females as they have the potential to convey a message of male quality[20,21] and they transmit relatively well through vegetation and probably into nest cavities[22,23]. However, the rising noise levels of our modern society may turn these concordant advantages into a trade-off between frequencies that are optimal for *signal strength* or optimal for *signal range*. Noisy human activities may interfere with what may have been a stable factor in signal efficiency over long periods of evolutionary time.

Two major gaps in assessing the impact of urban noise on fitness and the advantage of song frequency flexibility are: 1) a lack of insight into whether singing low matters in avian mate attraction and 2) a lack of evidence from the field that signal efficiency depends on song frequency in the presence of anthropogenic noise.

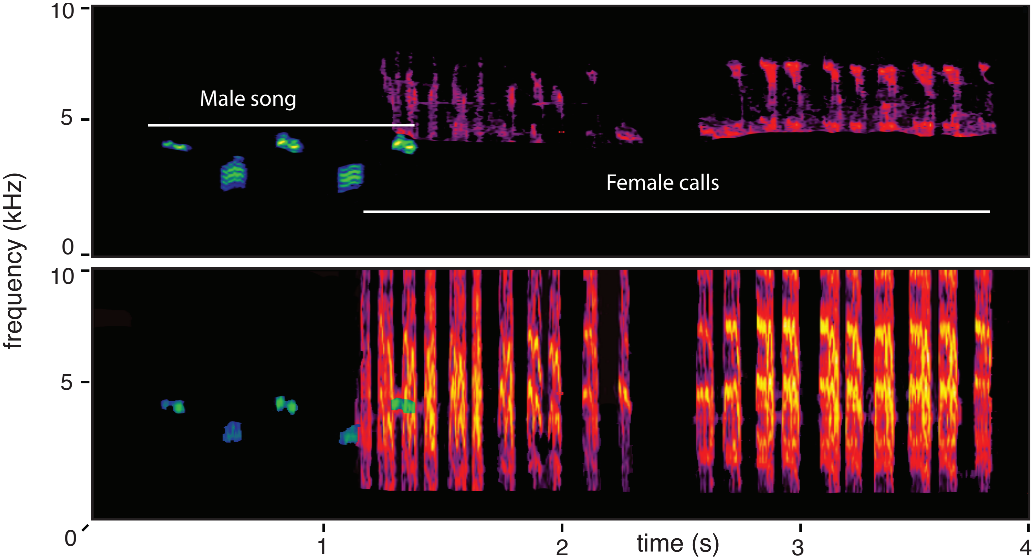


Figure 4.1. The dawn chorus ritual of great tits (*Parus major*). Sonogram of a stereo recording shows the acoustic interaction between a male (song in blue) and a female (calls in red). Males continuously sing or call close to the nest box during dawn and females can call in response. Females call most at the start of male dawn singing, during song type switches and shortly before emergence from the nest box. Upper and lower panels show recordings made with the out- and inside microphone respectively.

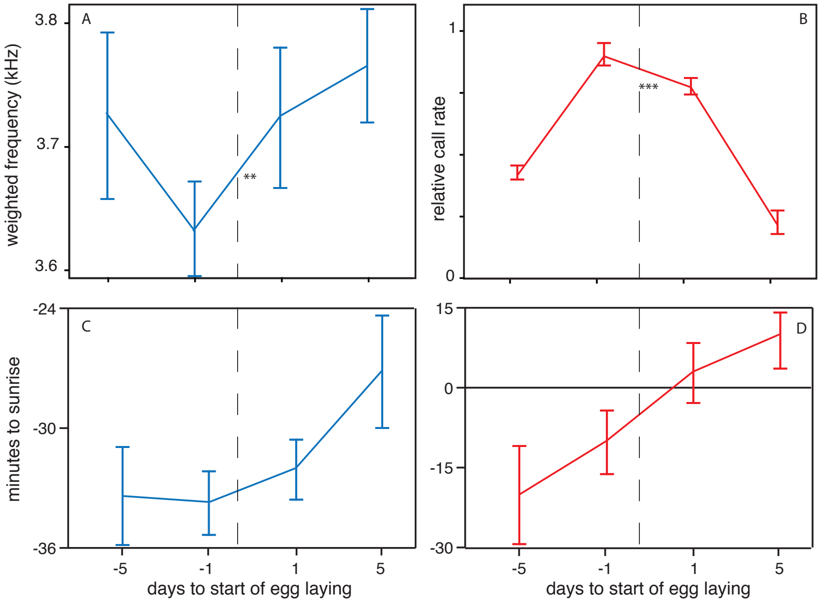


Figure 4.2. Within-individual variation of male and female behavior during the dawn chorus. (**A**) Male song performance peaks with female fertility (GLMM; ***$P < 0.001$) and males sing lowest when fertility is highest (egg-day -1). (**B**) Female calling changes with egg-laying (GLMM; ***$P < 0.001$) and females call most on days around the start of laying. (**C,D**) start of the dawn chorus and female emergence progresses with laying. The graphs show means ± one standard error. The x-axes show days related to start of laying (= egg-day 0, indicated by barred line), y-axes show male average weighted frequency of low notes, female calling (number of calls produced during dawn chorus, normalized per female) and minutes to sunrise.

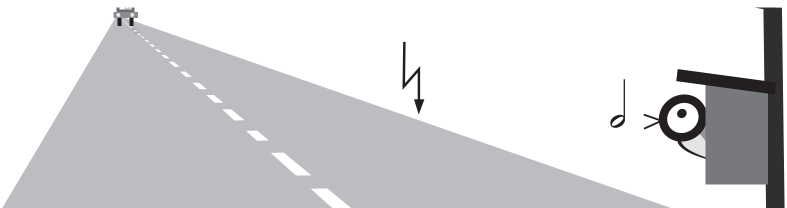
Although spectral characteristics have been correlated to male qualities that could affect female choice[20,24] and song-related sexual infidelity has been reported for female birds[25-27], we lack data that indicate a reproductive advantage for singing low-frequency songs. Assuming higher quality to be related to potentially costly low-frequency songs we may expect male performance to peak when it counts most: during the few days a year when eggs are fertilized[28,29]. Similarly, although within- and between population patterns can show consistently higher frequency use at noisy sites, such as in great tits[7,30,31], and although we recently revealed the underlying mechanism of active spectral avoidance in this species experimentally[17], we lack data on communicative consequences in the field. Any evidence showing a noise impact on the perception of communicative sounds in birds has, so far, only come from studies under laboratory conditions[32-34], outside a context meaningful to signal efficacy and reproductive success.

Here we studied acoustic courtship interactions in a natural woodland area among male and female great tits during the courtship ritual at dawn. We studied breeding great tit pairs at their nest box, which allowed us to document close-range male-female interactions. We used pairs of microphones, one inside and one outside the nest box, simultaneously to record male song behavior and female response behavior (Figure 4.1;[35]), starting when nests were near completion. We explored the role of singing low-frequency song types in male – female communication during the dawn chorus. We analyzed male song behavior in relation to the laying sequence and tested whether male song frequencies were related to female fertility as well as female sexual fidelity. Subsequently, we conducted a field experiment in which we played songs from a male's repertoire to his female inside the nest box. Females are known to discriminate accurately under these acoustically difficult conditions[23,36], which allows us to test for an effect of experimental noise exposure on the efficiency in triggering a female response, specifically for low- versus high-frequency songs.

RESULTS

Singing low peaks with female fertility

Males vary in how low the different song types in their repertoire are as well as how often they use the relatively low song types (accumulating into spectral performance). Song spectral performance varied over time within individuals and peaked with the moment of highest fertility (GLMM: egg-day^2; $\chi^2 = 18.76$; d.f. = 3; $P < 0.001$), as individual males sang lowest just before the start of egg-laying (Figure 4.2A). In contrast, males



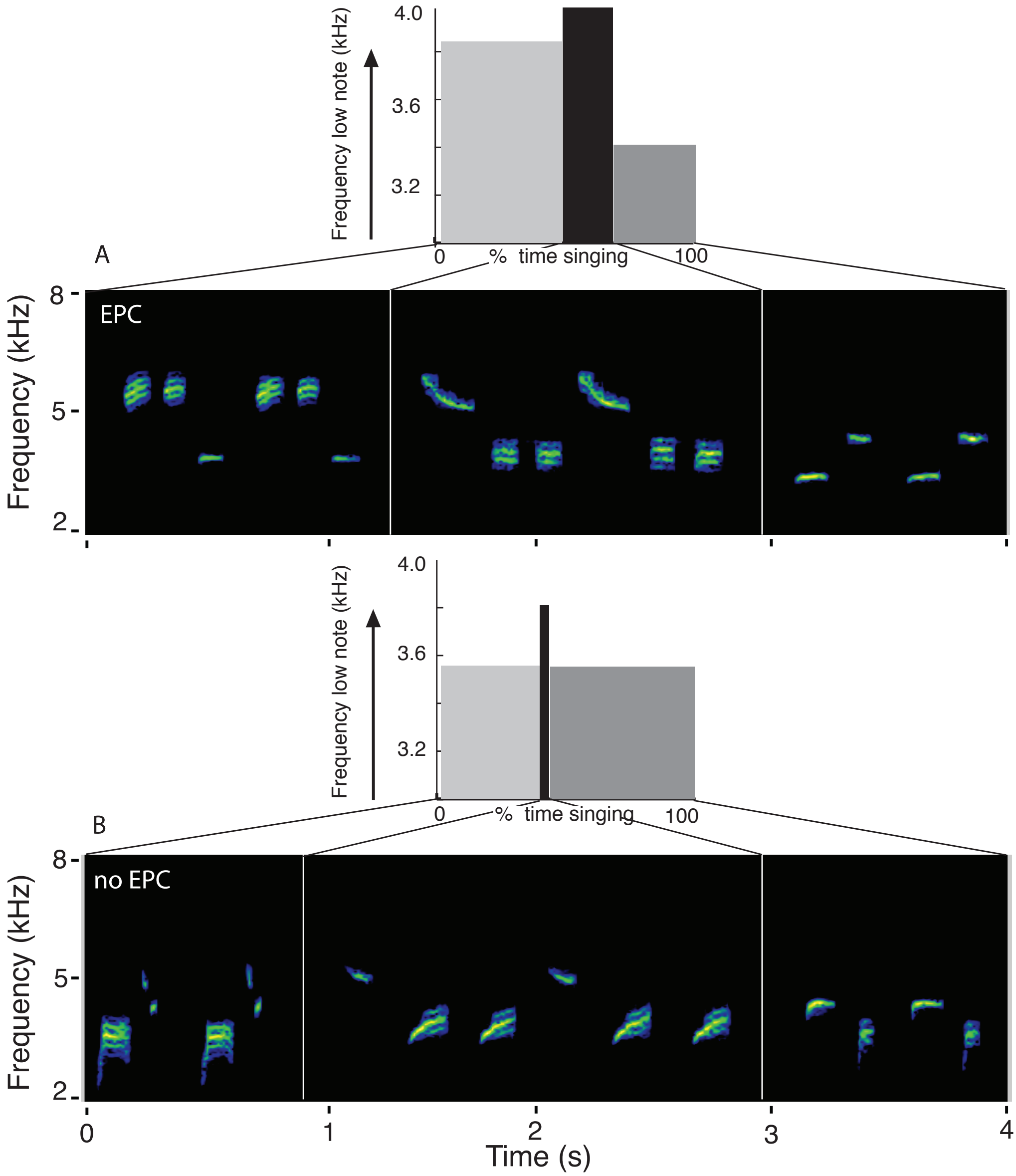


Figure 4.3. Males singing low frequency songs suffer less paternity loss. (**A,B**) Examples of song type repertoires and song type use for two neighboring males in relation to paternity loss. The cuckolded male (**A**, EPC) has similar song types compared to the non-cuckolded male (**B**, No EPC) and the neighbors mainly differ in the percentage of time during which they use their low and high-frequency song types. Sonograms show their repertoires consisting of three song types and the graphs show the peak frequency of the lowest note in relation to the percentage of time the individual is using a particular song type.

did not change the spectral frequency of their song types in relation to laying (GLMM; egg-day^2: χ^2 = 1.43; d.f. = 3; P = 0.70), which implies that great tit males selectively used low-frequency song types especially when interacting with their fertile mates. Other song features did not peak with fertility (song type duration: P = 0.27; repertoire size: P = 0.31), though start of dawn singing increased with progress in the laying stage (χ^2 = 8,75; d.f. = 3; P = 0.033; Figure 4.2.C). Female calling activity level peaked synchronously with male song performance at the start of egg-laying (χ^2 = 18.34; d.f. = 3; P < 0.001) and rapidly dropped after the first few eggs had been laid (Figure 4.2B). Females generally left the nest box earlier before than after egg-laying (GLMM: egg-day; χ^2 = 19.71; d.f. = 1; P<0.001; Figure 4.2D).

Low-singing males get cuckolded less

We tested whether performing with low-frequency songs at the peak in fertility was related to female sexual fidelity, and found that non-cuckolded males sang lower songs compared to cuckolded males (LMM; $F_{1,21}$ = 6.84; P = 0.018; Figure 4.3&4.4). Non-cuckolded males did not have lower frequency song types (Figure 4.4B), but used the low-frequency song types from their repertoire for a larger proportion of time (Figure 4.4C). Interestingly, female fidelity was also related to nest box emergence (GLM; χ^2 = 7.14; d.f. = 1; P = 0.008). Unfaithful females, at the peak of fertility, left their nest box earlier (17.5 ± 4.8 minutes prior to sunrise; mean ± SD) compared to females who did not engage in extra-pair copulations (0.04 ± 5.71 minutes after sunrise).

Low songs lose signal efficiency in anthropogenic noise

We measured female response (emerging or calling from the nest box) to playback of high- and low-frequency song types from the repertoire of their own mate under noisy and control conditions (see Figure 4.5 for an example of signal-to-noise ratio's of both song types under both noise conditions). Both song types (high and low) were played on two consecutive days, with and without noise exposure inside the nest box. Female emergence from the nest box differed across tests (GLMM; χ^2 = 8.63; d.f. = 3; P = 0.035; Figure 4.6), depending on noise and the song type played. Females responded less to low-frequency song types with noise than without noise (pairwise-comparison; low noise-low control: P < 0.001), whereas female emergence response to high-frequency song types was unaffected by our noise exposure (high noise-high control: P = 0.39). Females did not respond stronger to low-frequency song types under control conditions (low control-high control: P = 0.20), but emerged during noise exposure more often in response to playback of high-frequency song types (high

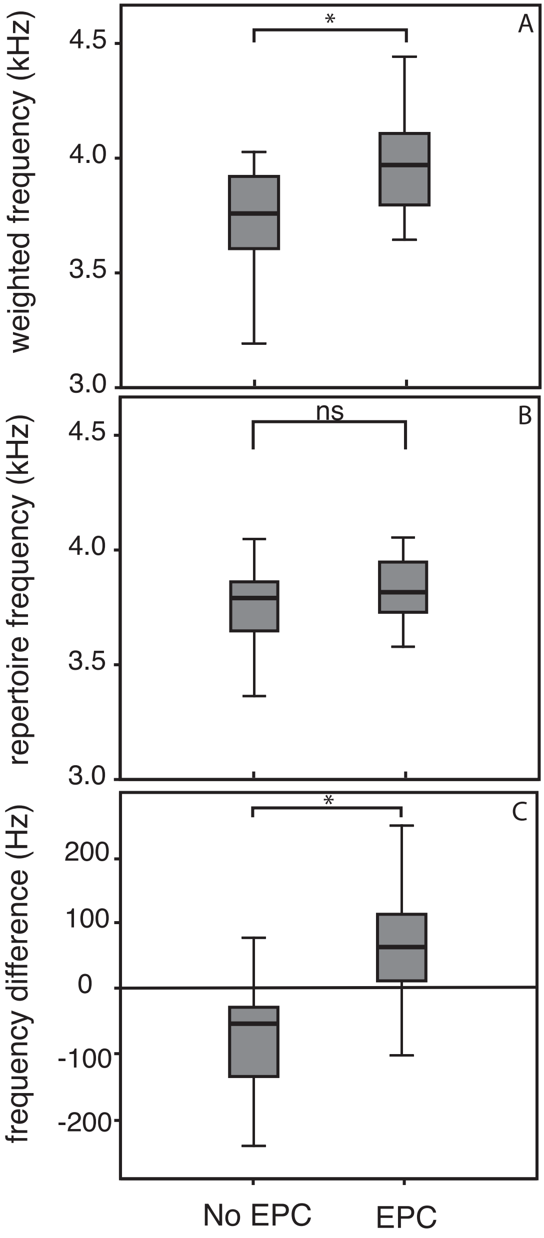


Figure 4.4. Males singing low frequency songs suffer less paternity loss. (**A**) Non-cuckolded males sing on average lower than cuckolded males during the dawn chorus at the peak of female fertility (LMM; $F_{1,21} = 6.84$; *$P = 0.018$). (**B**) Differences cannot be ascribed to non-cuckolded males having lower song types in their repertoire (LMM; $F_{1,21} = 1.64$; $P = 0.22$; peak frequencies of low notes averaged over song types of an individual's repertoire). (**C**) Differences are the result of using the lower song types more often (LMM; $F_{1,21} = 7.39$; *$P = 0.014$; difference between average weighted song frequency (**A**) and frequency averaged over repertoire (**B**) per individual).

noise-low noise: $P = 0.044$), Only 9 of the 16 females called prior to nest box emergence, but calling nonetheless showed a similar trend in response pattern: less response to low-frequency song types under noisy than under control conditions ($P = 0.08$) and noise-independent response levels to high song types ($P = 0.78$).

DISCUSSION

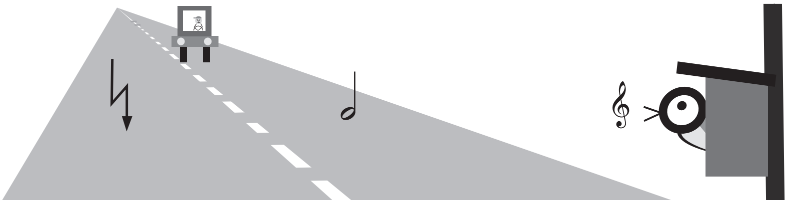
Our findings show that male great tits sing their lowest songs at the peak of female fertility with a reward of sexual fidelity, This suggests that low-frequency song types play an important role in male – female communication and that low song types are sexually selected through the reduced risk of cuckoldry. We also demonstrate that signal efficiency depends on song frequency in the presence of anthropogenic noise. Low-frequency songs show reduced effectiveness in triggering female responses in noise and are thereby less effective than high-frequency songs, showing that it pays urban birds to increase song frequencies when confronted with noisy conditions.

Sexual selection for low-frequency songs is in line with the fact that acoustic variation among singing birds concerns the most reliable information on male qualities under poor light conditions The females in our study seem to actively sneak away before sunrise when searching for extra-pair copulations (cf. [37]). Female songbirds have been shown to make such song-based reproductive decisions during the dawn chorus[26,27] and the female great tits in our study could have relied on spectral variation for male quality assessment when the production of low frequencies is, for example, physically constrained or bears retaliation costs[20,38].

Alternatively, low-frequency songs may be under indirect sexual selection as low frequencies can covary with more complex spectral features[38]. For instance, females could prefer broad-banded song types that can be physically demanding to produce[38].

Low-frequency songs could also be favored by natural selection pressures such as the transmission properties of the acoustic environment[22], including the complex acoustic structure of a nest box[23]. Lower frequencies may experience transmission-dependent increase in signal-to-noise ratio's under normal circumstances and whether high- or low- frequency songs are favored under anthropogenic noise will then depend on the relative strengths of these two environmental selection pressures.

Finally, low songs could be used specifically in male-female communication, whereas high songs could be used in male-male communication.



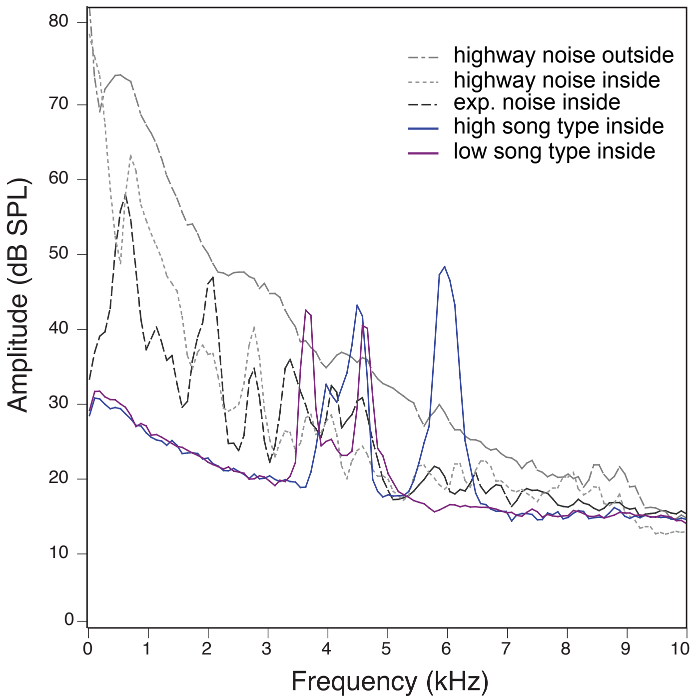


Figure 4.5. Noise profiles of anthropogenic noise and great tit song types. Shown are power spectrographic examples of a recording made inside and outside a nestbox situated ~70m from a major highway, as well as a recording of the experimental noise and a high and low song type inside the nestbox. Traffic noise is typically louder towards the lower frequencies and noise levels are reduced inside the nestbox compared to outside. Sound is resonated inside the nestbox causing the rugged noise profile. Note that the high song type has a higher signal-to-noise ratio overall compared to the low song type.

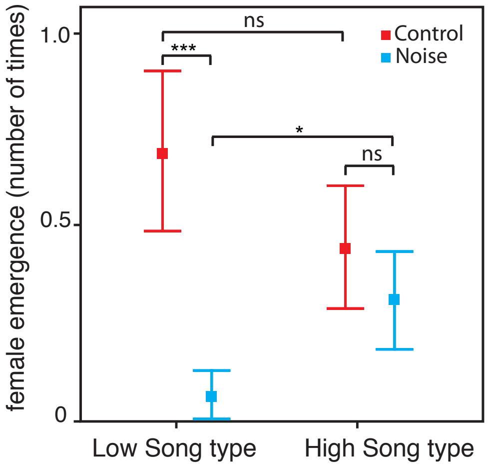


Figure 4.6. Reduced female response to low male songs in noise. Females were played the lowest and highest song type from their mate's repertoire on days with and without experimental noise exposure. Shown is the number of trials during which females emerged from their nest box as the response measure. Under noisy conditions female response to song changed for the low-frequency song types (GLMM; low noise vs low control: ***P < 0.001) but not for the high-frequency song types (P = 0.39). This resulted in high-frequency songs being more effective compared to low-frequency songs in noise (P = 0.044). Females had no prior experience with noise and were adjusted to noise conditions for ~24 hr before the start of the playback.

Several bird species are known to have different song types for intra- and intersexual signaling[39] and song frequency of great tits has been shown to be positively related to male density[40]. During the dawn chorus great tit males also interact with neighboring males, flying back and forward between territory boundaries and matching song types. If males selectively use low songs towards females and high songs towards males and if the amount of interaction time spent with females varies with laying stage and mate guarding, this would explain the observed patterns in frequency use in relation to female fertility and sexual fidelity.

Our playback experiment revealed two important findings: 1) song frequency dependent impact of noise on signal efficiency and 2) no benefit of using low-frequency songs over high-frequency songs under control conditions. This latter finding is in contrast to previous results that low songs are likely to be preferred by females. One explanation could be that low songs are under indirect selection driven by a link with a preferred song characteristic as we did not pay specific attention to other acoustic parameters in our song type selection procedure. The playback results show for the first time a noise-dependent advantage of high-frequency songs. Low-frequency songs suffer reduced effectiveness in male-female communication under noisy conditions, favoring the use of high-frequency songs. This is in line with experimental data showing that great tits actively avoid spectral overlap with background noise (chapter 2)[17]. In these earlier experiments, male great tits were not only shown to switch to high-frequency song types during exposure with low-frequency ‘city’ noise, but they were also shown to do the reverse during exposure to high-frequency ‘inverse-city’ noise. Many species have now been observed to raise song frequencies upwards in urban noise in both natural and experimental setting[7,8,15] and, although the benefits in terms of masking release have been debated recently[19], our results show that in great tits such a change will substantially improve male-female communication. Such a strategy of reducing spectral overlap with background noise can act concomitant with other signaling strategies, such as raising song amplitude[41], or can be used as an alternative for those species for which raising amplitude above a certain level is too energetically demanding.

The evolutionary novel urban conditions may affect both natural and sexual selection pressures acting on bird song. If low-frequency songs are under sexual selection through female preference and if high-frequency songs are under natural selection through noise-dependent signal efficacy we may expect a modern trade-off with

crucial fitness consequences: use low-frequency songs to stimulate females or use high-frequency songs to avoid masking noise. If a signal is not detected it can also not be discriminated from other signals and so for species in which females make sound-based reproductive decisions we would expect signal detection to prevail over signal strength in high noise conditions. A focus on detection, rather than discrimination can result in a preference shift from the low to the high frequencies[42]. Consequently, the trade-off will limit high-quality males in urban areas to distinguish themselves spectrally from competitors. An interesting follow-up study could be to find out whether there are alternative vocal parameters in which high-quality males can excel and which may explain urban divergence through sensory drive towards for example higher-and-faster songs[30,38]. Great tits living in noisy territories in cities have already been found to respond stronger to songs recorded in similar territories[31] and although familiarity remains to be excluded as a factor[43] these findings suggest that urban noise conditions have the potential to alter sexual selection pressures.

Our findings contribute to the extensive field of research that links the presence of roads, traffic and traffic noise to reduced bird breeding densities[44-47]. Noise can mask acoustic signals and is known for example to cause a decline in the number of breeding bird territories[6,11]. Individuals that have to settle for noisy locations may suffer from reduced pairing and thus reproductive success[12,44] or may end up with low-quality, or at least less productive mates, laying smaller clutches and raising fewer offspring close to noisy highways (chapter 6)[13]. The masking impact by traffic noise will be highest for those species that use low frequencies to attract females, as demonstrated by our field playback experiment, and can explain why species vocalizing at lower frequencies suffer most from anthropogenic noise pollution[11,14,48].

In conclusion, we have shown that evolutionarily novel urban conditions can undermine the selective advantage of using low-frequency song types. Furthermore, we found the use of low song types to be related to reproductive success, which suggests that low-frequency songs are under direct or indirect sexual selection. These findings also show that benefits of masking release are not constrained by a potential loss in signal strength and point to the existence of a modern trade-off. It would be interesting to examine how anthropogenic noise can alter the strength, direction or target of selection pressures acting on bird song. Studies on urban acoustics will continue to provide both scientific opportunity and conservation concern as they stimulate novel views on environmental causes underlying evolutionary change, but should also raise awareness of the consequences of noisy human behavior.

MATERIALS AND METHODS

The study was conducted in four different nest box-sites situated at 'Nationaal Park Dwingelderveld', the Netherlands, between April and May, in 2009 and 2010. Territories were mapped and nest boxes were checked for nest building every other day. Behavioral recording and nest box extension began when nests were near completion to minimize nest desertion due to our activities. Playbacks began when females started incubating to minimize interference with males. All males and females were included only once in this study.

Acoustic measurements

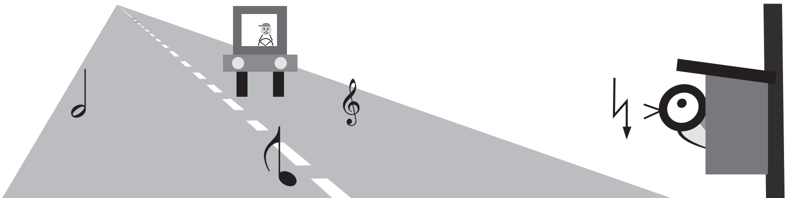
We used SongMeters (16 bit, 24 kHz sample rate; Wildlife Acoustics Inc.) to automatically record male and female acoustic behavior. A microphone placed inside the nest-box was used to record female calls while the other microphone outside recorded the male's dawn song. Both microphones were used to assess time of female emergence by the sounds of her claws on the nest box and movement of the wings when taking off. We recorded the dawn ritual (one hour prior to until one hour after sunrise) across the laying phase. We identified song types of the social male and determined start of dawn singing, song type repertoire size, time of female emergence and total number of calls produced by females with the program Audacity 1.3. Bout duration and low-note frequency were measured for each song type independently[17] and were used to calculate a weighted song frequency per day (adjusting frequency with percentage used before averaging over song type).

Paternity analysis

Chicks were sampled for blood on the 2nd day and parents on the 7th day post hatching for DNA extraction. To assign paternity we used the six microsatellite loci (described in [49]). Loci were PCR amplified using a QIAGEN Multiplex PCR Kit and manufacturers protocol. Allele lengths were determined (as described in [50]). Cervus 3.0[51] calculated the mean exclusion power of the six markers to be 0.99 for the first (female) parent and 0.99 for the second (male) parent (given the genotype of the first parent). We assessed for each chick whether or not it was sired by the social mate. Paternity of the social mate was excluded, and the offspring assigned as extra-pair (EPC), if there were at least 2 mismatches between the social father's and offspring's genotype.

Experimental noise exposure

We extended the normal nest box by removing the roof and adding a second box on top (made of the same material), inaccessible by the birds, but with a hole in the bottom. We inserted a speaker at a height of 15 cm within this second box to allow play-



back of noise mimicking conditions as if the nest box was situated 50-100m from a major highway[13] and to avoid near field effects at the position of the female. See Figure 4.5 for an example of experimental and natural noise profiles.

Noise playback of artificially generated low-frequency traffic noise (described in [17]) was carried out using full-range speakers (Peerless, 2.5 inch) connected to an mp3-player and battery-pack hidden under the leaf litter. Noise level was gradually increased to ~68.0 dB (SPL, A-weighted) at the position of the nest and females were familiarized with the noise in their nest box for 24h.

Stimuli preparation and playback

We determined the highest and lowest song type from a male's repertoire based on peak frequency of the low note (average difference of 591.1 ± 285.7 Hz; mean ± SD). We selected a high-quality recording of a strophe of a single song type for each female tested with songs from the repertoire of her own social mate and created a stimulus-file 30s in length (as described in [36]). Both high- and low-frequency song type stimuli were band-passed filtered from 2 – 10 kHz, normalized for amplitude and played from a speaker (Visaton SC 4ND) on a pole positioned at ~1.5m and an angle of 45° from the nest entrance. Great tits typically sing at a distance of 8 – 16m from the nest box which results in a song amplitude of ~60 dB(A) at the position of the female. We played the songs that had been recorded at the position of the nest box at an amplitude of ~62 dB (A-weighted, measured 1m away from the speaker) to get similar song amplitudes at the position of the female and to avoid detection by the focal male (see Figure 4.5 for an example of song type signal-to-noise ratio's inside the nest box under noisy and control conditions). The song amplitude at the position of the female always exceeded the detection thresholds for great tits in noise[52] to allow discrimination among song types. Playback experiments were carried out during incubation and during daytime to avoid male interference. We carried out four experiments per female using both high- and low-frequency song types on two different days (with and without noise). Females received four consecutive 30s trials of either high- or low-frequency song types during an experiment. The order of song type or noise presentation was balanced across females. Nest boxes were observed from a hide and an experiment started when females had been inside the nest box for at least 15 minutes and a trial only started when males were away from the nest box and not singing (see [36]). All but one female received the playbacks on two consecutive days and the time between the high- and low-frequency song type playback experiment was ~30 min. We scored whether females emerged or called during a trial.

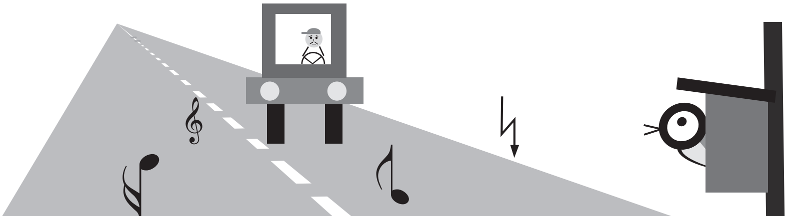
Data analyses

All multivariate analyses were carried out in SPSS 17.0 and data were transformed when necessary to meet model assumptions. We used different subsets of males and females for the observational analyses depending on the availability of suitable recordings and paternity data.

We related male and female behavior to start of laying (egg-day = 0) when fertility is presumed to be high. We selected a subset of pairs (n = 15) for which we had suitable recordings prior to (egg-day -5 and -1) and during laying (egg-day 1 and 5). We tested whether within-individual vocal performance peaked at fertility using generalized linear mixed model (GLMM) with a power-link function, a normal error distribution (or Poisson for number of calls), individual as subject and nest box-site and egg-day as fixed factors. We assigned a unique code to each song type of an individual male and tested whether the frequency averaged over song type changed across egg-laying in a GLMM with individual song type as subject and site and egg-day as fixed factors.

We used a subset of individuals (n = 22) for which we had control recordings at the peak of fertility (egg-day -1) to test whether cuckolded males (EPC: males with extra-pair chicks in their nest) differed in male song frequency using linear mixed models (LMM), with date as random factor and site and EPC as fixed factors. We compared weighted song frequency with frequency averaged over song type to assess whether singing by EPC-males differed in repertoire composition, repertoire use or both. We used the same subset to compare female nest box emergence among EPC-groups on egg-day -1 in a GLM with site and EPC as fixed factors.

We used a balanced playback design (n = 16) to test for a differential impact of noise on female response to high- and low-frequency song types, controlling for order of stimulus presentation and day of noise exposure. Female response (number of trials emerged or called) to male playback of high- and low-frequency song types was tested in a GLMM with a Poisson error distribution, loglink-function and noise treatment, song type (high or low), stimulus order and day as fixed factors.



REFERENCES

[1] Bradbury, J.W. & Vehrencamp, S.L., *Principles of Animal Communication*. (Sinauer Associates, Sunderland, MA, 1998).

[2] Grimm, N.B. *et al.*, *Science* 319 (5864), 756-760 (2008).

[3] Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

[4] Slabbekoorn, H. *et al.*, *TREE* 25 (7), 419-427 (2010).

[5] Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

[6] Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

[7] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[8] Hu, Y. & Cardoso, G.C., *Animal Behaviour* 79 (4), 863-867 (2009).

[9] Potvin, D.A. *et al.*, *Proc R Soc B*(2011).

[10] Patricelli, G.L. & Blickley, J.L., *Auk* 123 (3), 639-649 (2006).

[11] Francis, C.D. *et al.*, *Current Biology* 19 (16), 1415-1419 (2009).

[12] Bayne, E.M. *et al.*, *Conservation Biology* 22 (5), 1186-1193 (2008).

[13] Halfwerk, W. *et al.*, *J of Applied Ecology* 48 (1), 210-219 (2011).

[14] Goodwin, S.E. & Shriver, W.G., *Conservation Biology* 25 (2), 406-411 (2011).

[15] Gross, K. *et al.*, *Am. Nat.* 176 (4), 456-464 (2010).

[16] Verzijden, M.N. *et al.*, *J of Experimental Biology* 213 (15), 2575-2581 (2010).

[17] Halfwerk, W. & Slabbekoorn, H., *Animal Behaviour* 78 (6), 1301-1307 (2009).

[18] Bermudez-Cuamatzin, E. *et al.*, *Biology Letters* 7 (1), 36-38 (2010).

[19] Nemeth, E. & Brumm, H., *Am. Nat.* 176 (4), 465-475 (2010).

[20] Gil, D. & Gahr, M., *TREE* 17 (3), 133-141 (2002).

[21] Davies, N.B. & Halliday, T.R., *Nature* 274 (5672), 683-685 (1978).

[22] Wiley, R.H. & Richards, D.G., *Beh Eco and Soc* 3 (1), 69-94 (1978).

[23] Blumenrath, S.H. *et al.*, *Bioacoustics* 14 (3), 209-223 (2004).

[24] Kirschel, A.N.G. *et al.*, *Behavioral Ecology* 20 (5), 1089-1095 (2009).

[25] Hasselquist, D. *et al.*, *Nature* 381 (6579), 229-232 (1996).

[26] Mennill, D.J. *et al.*, *Science* 296 (5569), 873-873 (2002).

[27] Kempenaers, B. *et al.*, *Current Biology* 20 (19), 1735-1739 (2010).

[28] Mace, R., *Nature* 330 (6150), 745-746 (1987).

[29] Moller, A.P., *Am. Nat.* 138 (4), 994-1014 (1991).

[30] Slabbekoorn, H. & den Boer-Visser, A., *Current Biology* 16 (23), 2326-2331 (2006).

[31] Mockford, E.J. & Marshall, R.C., *Proc R Soc B* 276 (1669), 2979-2985 (2009).

[32] Lohr, B. *et al.*, *Animal Behaviour* 65, 763-777 (2003).

[33] Pohl, N.U. *et al.*, *Animal Behaviour* 78 (6), 1293-1300 (2009).

[34] Swaddle, J.P. & Page, L.C., *Animal Behaviour* 74, 363-368 (2007).

[35] Gorissen, L. & Eens, M., *Auk* 121 (1), 184-191 (2004).

[36] Blumenrath, S.H. *et al.*, *Animal Behaviour* 73, 789-796 (2007).

[37] Double, M. & Cockburn, A., *Proc R Soc B* 267 (1442), 465-470 (2000).

[38] Podos, J., *Nature* 409 (6817), 185-188 (2001).

[39] Kroodsma, D.E., in *Nature's Music:*

The Science of Bird Song, edited by P. Marler & H. Slabbekoorn (Elsevier Academic Press, London, 2004), pp. 108-130.

[40] Hamao, S. *et al.*, *Ethol. Ecol. Evol.* 23 (2), 111-119 (2011).

[41] Brumm, H. & Todt, D., *Animal Behaviour* 63, 891-897 (2002).

[42] Wollerman, L. & Wiley, R.H., *Animal Behaviour* 63, 15-22 (2002).

[43] Falls, J.B. *et al.*, *Animal Behaviour* 30 (NOV), 997-1009 (1982).

[44] Reijnen, R. & Foppen, R., *J Fur Ornithologie* 132 (3), 291-295 (1991).

[45] Reijnen, R. & Foppen, R., in *The Ecology of Transportation: Managing Mobility for the Environment*, edited by J. Davenport & J.L. Davenport (Springer-Verlag, Heidelberg, 2006), pp. 255–274.

[46] Kociolek, A.V. *et al.*, *Conservation Biology* 25 (2), 241-249 (2011).

[47] Forman, R.T.T., *Conservation Biology* 14 (1), 31-35 (2000).

[48] Rheindt, F.E., *J Fur Ornithologie* 144 (3), 295-306 (2003).

[49] Brommer, J.E. *et al.*, *Am. Nat.* 176 (2), 178-187 (2010).

[50] Magrath, M.J.L. *et al.*, *Current Biology* 19 (9), 792-797 (2009).

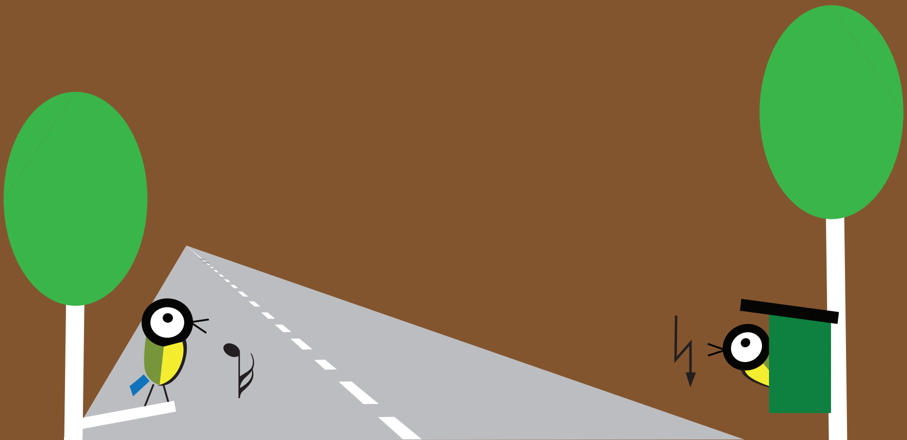
[51] Kalinowski, S.T. *et al.*, *Molecular Ecology* 16 (7), 1099-1106 (2007).

[52] Langemann, U. *et al.*, *Animal Behaviour* 56, 763-769 (1998).

Chapter 5

Female control over noise-dependent song perch adjustment

Submitted as Halfwerk, W. Bot, S. & Slabbekoorn H.



ABSTRACT

Anthropogenic noise can affect intra-pair communication and therefore interfere with reproductive success. However, many animals have various signal strategies to cope with noise, although it is unclear whether they rely on direct auditory feedback from their own perception of noise or signal-to-noise level or on indirect social feedback from receivers. We studied the role of social feedback on male great tit (*Parus major*) song adjustment by exclusively exposing females to artificial traffic noise inside their nest box. We found a delay in initial female response latencies to male song in the noisy condition. Males with females in noisy nest boxes, while being well outside the auditory exposure range themselves, sang closer to the nest box within a few days after the start of exposure. The spatial difference in song post selection led to higher song amplitudes at the noisy nest boxes compared to quiet control nest boxes, which restored the inside signal-to-noise ratios to equal levels between treatment and control nest boxes. The initial delay in female response latencies also disappeared accordingly. Our results strongly suggest an active role for female birds in steering male communicative behavior and reveal the critical role of ecology in shaping animal interactions.

INTRODUCTION

Communication between members of a breeding pair plays an important role in many different contexts[1,2]. Pair members that cooperate during territory defense or parental care can benefit from exchanging signals as this enables them to synchronize their behaviors and investments [3,4]. Optimal communication requires signal efficacy, which strongly depends on environmental conditions and signals are likely to match the properties of habitats to maximize transmission between individuals[3-5]. However, habitats can change rapidly, especially in areas occupied by humans, forcing strong selection on signaling behavior[8-10].

Many animals use sounds to communicate with their mates, but also using this medium becomes increasingly difficult in an urbanizing world[6-8]. Human-generated noise coming from heavy machinery, such as factories and traffic, is known to interfere with signal detection and may affect intra-pair communication and consequently reproductive success[6,9]. Anthropogenic noise has been reported to affect communication in frogs[10,11], mammals[12,13] and fish[14-16]. There are also several reports on masking of male-female communication by anthropogenic noise in birds and has been related to reduced mate attraction[17,18] and breeding performance (chapter 6)[19-21].

Noise-related selection pressures on communication have likely led to the evolution of a variety of strategies to cope with fluctuating noise levels, both on the side of the sender and the side of the receiver (reviewed in)[8]. Senders can raise amplitude or call rate[12,19], or avoid overlap between their signals and the noise[20-22]. Receivers have evolved various perceptual mechanisms that allow signal extraction from noisy environments, referred to with often partly overlapping terminology such as spatial release from masking, auditory stream segregation, and the 'cocktail party effect'[8,23]. Furthermore, both senders and receivers can affect signal transmission by choosing a particular location during intra-pair communication. Birds can improve detection and discrimination thresholds by moving closer[24], choosing higher song posts[25] or staying in- or outside their nest cavities[26], but we currently lack insight into whether such spatial strategies are exploited under fluctuating noise conditions.

Birds can use either an internal or external feedback mechanism to sing louder, higher, faster or closer to their intended receivers when confronted with low-frequency urban noise (chapter 2)[27]. Male changes in singing behavior can be based on direct auditory feedback from noise level or the signal-to-noise ratio of their own vocal output (internal feedback) or on indirect social feedback from conspecific

receivers, such as females or territorial neighbors (external feedback) to adjust their songs in response to changing noise conditions[27]. Distinguishing between these two types of mechanisms requires noise exposure to either the sender or the receiver during communication, which is challenging for field as well as laboratory conditions, given the physical properties of sound.

The great tit (*Parus major*) provides an excellent study system to expose only one side of the communication channel to increased noise levels. Females, at the start of the breeding season, interact with their mates from within their nest cavities during the dawn chorus ritual (chapter 4)[28,29]. Females have been found to call and emerge less in response to playback of their mate's song under noisy conditions[29], but they can also be exposed to noise inside an artificial nest box during natural dawn singing of their own male. Their response to playback was found to be masking-specific as females responded less to low song types compared to high song types when exposed to artificial traffic noise (chapter 4)[29]. Therefore, theoretically males could use female response as an external social feedback mechanism, for instance during masking-dependent song type switching[27], but which remains to be tested empirically.

In the present study, we exposed females at the peak of intra-pair interactions to artificial traffic noise inside their nest box, while leaving the singing male outside unaffected. We monitored male song signal-to-noise ratios inside the nest box and expected females in the noise treatment to reduce or delay calling response due to increased masking levels. We assessed male song behavior throughout the experimental period and expected males to sing higher, or louder songs, or to sing from closer distances, depending on noise-dependent female feedback.

METHODS

Study site and species

The study was conducted in a nest box-population of great tits at 'Nationaal Park Dwingelderveld', the Netherlands, between March and May, in 2009 and 2010. The nest boxes were divided over four different sites that either consisted of deciduous forest or mixed woodland. The great tit (*Parus major)* is a hole-nesting passerine that uses song in both male-male as well as male-female communication[30,31]. Females start to roost inside their nest cavity (or wooden nest box in our population) at this stage and are visited by their mates who will sing towards them from a nearby song perch. Males typically start to sing 30 - 45 minutes before sunrise and end their dawn chorus song when the female emerges from the nest box, after which the pair often copulates[31,32].

Male-female interaction rapidly increases when the female begins with nest building[31]. Females are actively listening to their singing mates from inside their nest box and occasionally call back in response (Figure 5.1;[28]). Female calling starts a few days before beginning of egg-laying and rapidly decreases again when the first eggs have been laid[29]. Males have a small repertoire of song types (2 – 6 in our study population) that they display with eventual variety[33,34]: the same song type is repeated for several minutes before a switch is made to a different song type (Figure 5.1). The majority of song types consist of a low-frequency note and a high-frequency note, in the range of 2 - 9 kHz (Figure 5.2; [27,35]).

Experimental procedure

The behavioral data presented here are part of a larger study on the impact of noise on great tit breeding behavior. Territories were mapped in March and early April and nest boxes were checked for nest building every other day. Nest box treatment was randomly assigned and 67 great tit pairs started nest building in a control box whereas 68 pairs started building in noise box. A total of 29 pairs abandoned their nest box before the incubation phase, but the rates were equal among treatment groups (12 control; 17 noise).

Noise playback of artificially generated low-frequency traffic noise (filtered white noise in the range of 1 - 10 kHz with a decrease of 6.5 dB/kHz; {chapter 2}[27]) was carried out using full-range speakers (Peerless, 2.5 inch) connected to an mp3-player and battery-pack hidden under the leaf litter. We extended the normal nest box by removing the roof and adding a second box on top (made of the same material), inaccessible by the birds, but with a hole at the bottom, for both noise and control territories. In 2009, we added the second box and started the treatment during the final stage of nest building. In 2010, we added the second box to all nest boxes in a pair's territory and started the treatment at the beginning of nest building.

We inserted a speaker at a height of 15 cm within this second box to allow playback of noise mimicking conditions inside as if the nest box was situated at 50m from a major highway[36]. Noise level was increased in two steps to ~65 dB (SPL, A-weighted, measured at the position of the female with a Cesva SC-30 sound analyser) within two days to let the female gradually habituate. Noise was played day and night in 30 minute loops with a 10 second ramp on and off to avoid abrupt changes in noise level. Due to high spring temperatures in both years, females started quickly with egg-laying (on average 1.8±2.6 s.d. days after start of the experiment) which therefore coincided with the first day of full noise exposure.

Noise levels outside the nest box, recorded on a microphone positioned

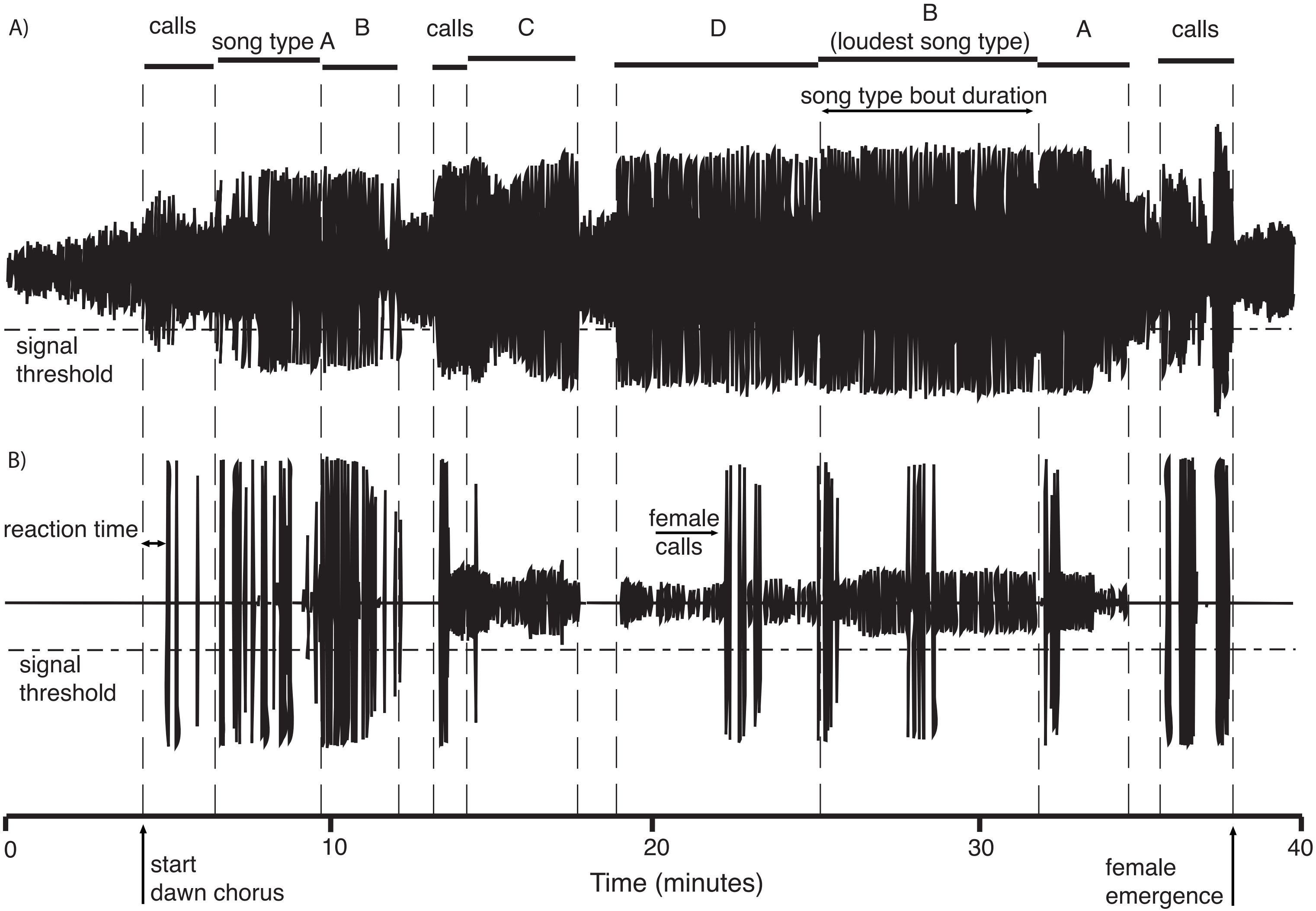

A)
calls
song type A
B
calls
C
D
B
(loudest song type)
A
calls
song type bout duration
signal
threshold
B)
reaction time
female
calls
signal
threshold
0
10
20
30
40
start
dawn chorus
Time (minutes)
female
emergence

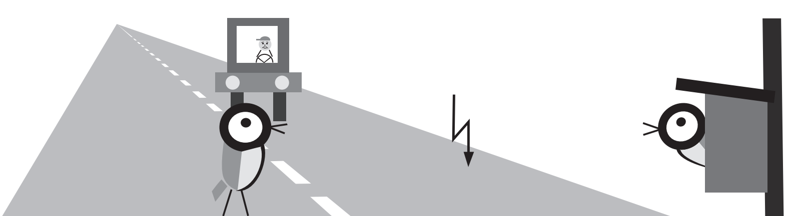
Figure 5.1. Male and female acoustic interactions during a complete dawn chorus bout. (**A**) an amplitude wave of a recording made outside the nest box, starting 40 minutes prior to sunrise. The male typically initiates the dawn chorus with a few calls towards the female after which he starts singing sequences of song types. Males have a small set of song types in their repertoire and repeat the same song type for several minutes before switching to an other vocalization bout (e.g. from song type A to B). Note that the same song type (e.g. B in this example) can vary in amplitude, likely due to the male getting closer to the nest box. Males continue to sing until the female has emerged from the nest box, which during the peak in female fertility is often followed by copulation. (**B**) a simultaneous recording made inside the nest box. Females call in response to male vocal behaviour, but reaction time to the start of a male vocalization bout can vary strongly.

on the tree at the same height as, and within 50 cm of the nest box entrance, did not differ in the great tit song range (Anova; n = 29; $F_{1,28} = 0.36$; p = 0.85) and the noise was not audible to a human observer at 10 m from the nest box, which corresponds to the average singing distance of great tits in our area.

Acoustic analyses

We used SongMeters (16 bit, 24 kHz sample rate; Wildlife Acoustics Inc.) to automatically record male and female behavior. In 2009 we recorded behavior at 20 nest boxes (11 control and 9 noise) and we complemented the set in 2010 to a total of 29 (16 control, 13 noise). A microphone placed inside the nest-box was used to record female calls and male song signal-to-noise ratio (with a fixed gain of +24 dB) while the other microphone outside recorded only the male's dawn song (fixed gain +42 dB). Recording microphones were also used to assess time of female emergence by the sounds of her claws on the nest box when taking off.

In 2009, two human observers made simultaneous focal observations at a different set of nest boxes without recorders (n = 22; 11 control, 11 noise) from both treatment groups to score the position of the male song post. Observations were carried out after three days of full noise exposure (which was five days after the start of



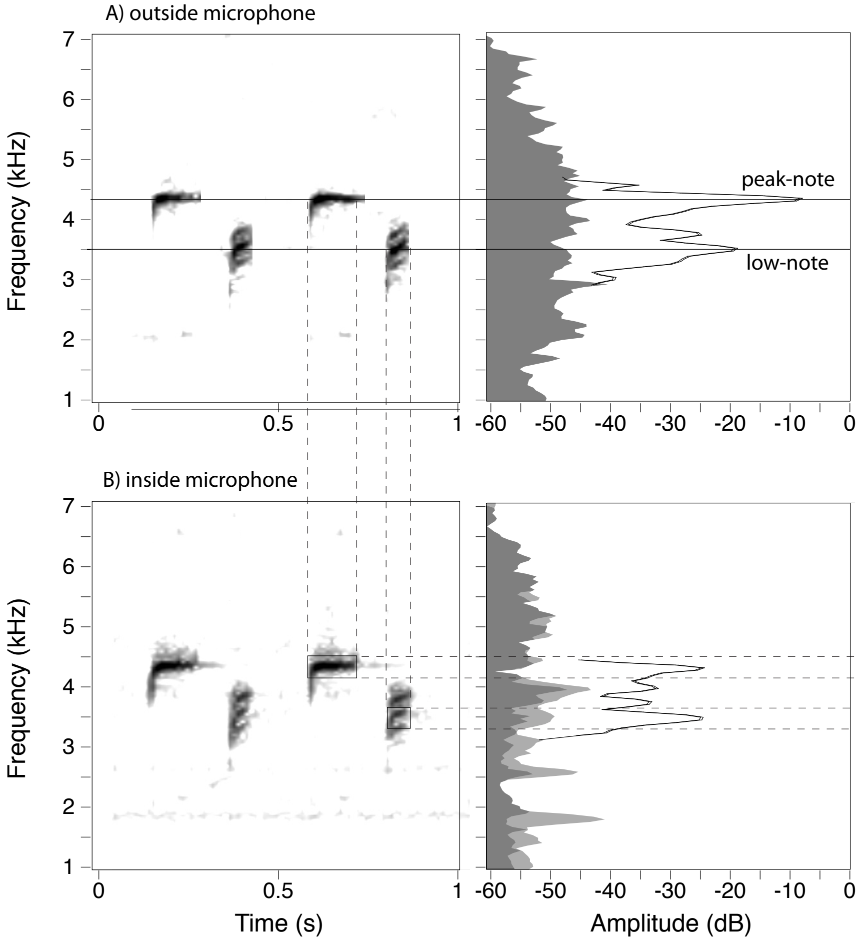


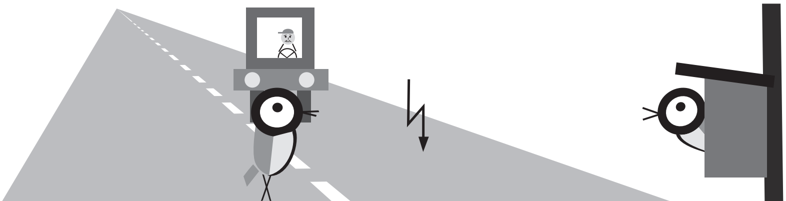
Figure 5.2. Examples of male song and noise profiles inside and outside the nest box (**A**) a sonogram of a recording made on the outside microphone of a two-note song type (left panel, time on the x-axes, frequency on the y-axes) and a powerspectrogram (right panel, relative amplitude level on the x-axis, frequency on the y-axis) of the same recording showing male song (black lines) as well as background noise (dark grey area). Both peak frequencies of the loudest (peak-note) and lowest note (low-note) are indicated. (**B**) sonogram of a simultaneous recording made inside the nest box (left panel) and powerspectrogram (right panel) showing male song (black lines) as well as noise profile under control (dark grey) and experimental noise exposure (light grey). The amplitude levels of both the song as well as the background noise decrease from outside to inside. The nest box resonance characteristics are quite complex, leading to attenuation of particular frequencies and amplification of other frequencies (note for instance the relative change in amplitude of the peak-note compared to the low-note and the peaks in experimental noise around 1.8 and 2.7 kHz). The on- and offset of the signal as well as the critical frequency band (based on Langemann *et al.* 1998) centered on the peak frequency of the notes are indicated (dotted lines). Both the low- and peak-note as well as a representative noise sample were band-pass filtered using critical bands to calculated signal-to-noise levels. The signal-to-noise -ratio between experimental and control background noise differ around 5 dB for the low-note and are similar for the peak-note in this example recording.

the experiment). The observers were switched between treatments every other day to correct for inter-observer differences. The observers noted the song perch at one-minute intervals to determine the nearest song post. After the dawn chorus, the horizontal distance to the nest box was measured with a yard stick and the vertical distance was estimated to the nearest meter to get a combined distance measure to the nearest song post.

We scored female behavior using the automatic dawn chorus recordings, including the time of nest box emergence, call rate and response latency (Figure 5.1). Inter-individual female call variation is high and we therefore selected only the first and second call bout from a recording for the latency analysis. We measured the time (in ms) between start of female calling and start of male song or call bout (Figure 5.1).

Male song behavior was analyzed by assessing the beginning of the dawn chorus and by identifying the different song types sung by the male until the female emerged. We estimated for each song type the proportion of time it was sung on a particular morning and selected for each song type the longest bout for further analysis. From each song type bout we selected two strophes from the start, mid and end of the bout. We determined the peak frequencies, as well as the onset and offset times of each note within a strophe in the program Luscinia (Figure 5.2; [37]) and averaged the measurements over the lowest notes (here after low-note) and loudest notes (here after peak-note) for each song type strophe.

We band-pass filtered each note (150 Hz above and below peak frequency of the note, which corresponds to the critical bandwidth of the great tit; Figure 5.2; [38]) and calculated the root-mean-square (RMS)-value in Matlab (the Mathworks). We selected a noise sample of similar length after the song type strophe and used the same band-pass filter settings to calculate the RMS-value of the noise for each individual note. RMS-values of notes and noise were transformed to a dB-scale and adjusted according to microphone gain. Noise amplitude was subtracted from note amplitude (dB(note) – dB(noise) to get signal-to-noise ratios for both low-note and peak-note. In addition we determined maximum song amplitude (loudest song type based on dB-values, Figure 5.1). Song frequency and signal-to noise ratio measurements were averaged over song type, adjusted for the percentage of time sung. For the signal-to-noise measurements we used recordings made inside the nest box and for the frequency and song amplitude measurements we used recordings made outside the nest box.



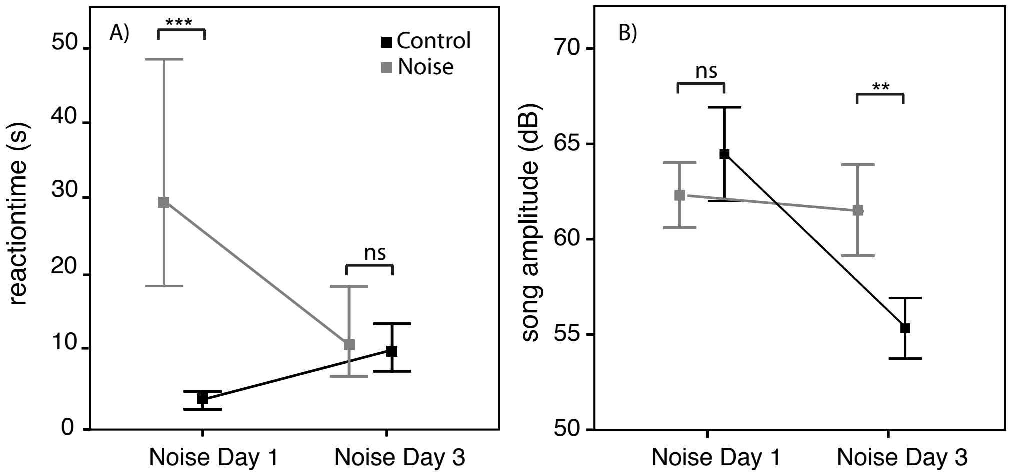


Figure 5.3. Intra-pair communication in anthropogenic noise. (**A**) Female response behaviour in noise. Females call much later in response to start of male song or call bout on the first day of full noise exposure (GLMM; pairwise – comparison: control vs. noise on Noise day 1; ***p < 0.001). Difference in reaction time between noise and control groups have disappeared after two days (Noise day 3; p = 0.88). (**B**) Male change song behavior when females are exposed to noise. The amplitude of the loudest recorded song type (e.g. ST B in Figure 1) did not differ on Noise day 1, but was lower in the control group on Noise day 3 (**p = 0.01). Maximum song amplitudes decreased in the control group, whereas in the noise group the amplitude did not change on average.

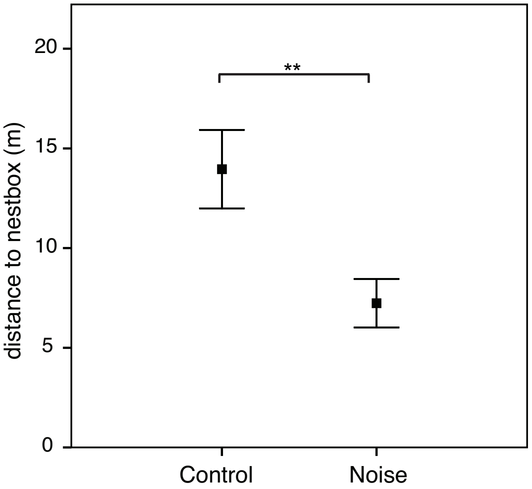


Figure 5.4. Males sing closer when females are exposed to noise. The distance between nest box and the nearest song post occupied by males differs between noise and control group after three experimental days (LMM: p = 0.005).

Data analyses

We analyzed male and female acoustic behavior on the first day (Noise Day 1) of full noise exposure (which was the third day of the experiment for the control treatment group) and compared this with measurements taken three days later (Noise Day 3). When a female had not started calling by the third morning of the experiment, we selected the first morning of calling as Noise Day 1. Additionally, we analyzed female emergence times and call rates, as well as male song frequency and signal-to-noise ratio's on day one, four and seven from the start of laying as these variables have been shown to co-vary strongly with egg-laying phase[29]. Male song perch was only analyzed on Noise day 3.

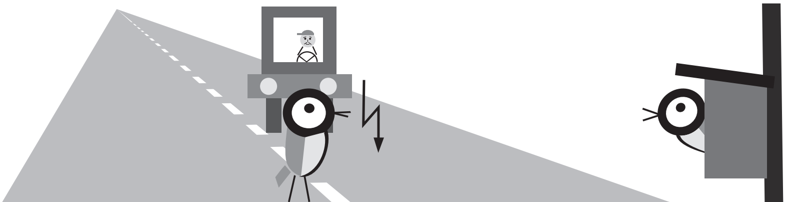
An impact of continuous noise exposure on male and female behavior was tested using full factorial generalized linear mixed models (GLMM, SPSS 17.0), with loglink-function for response latency (log-transformed) and call rate. Treatment and noise day, or treatment and egg-day were included as fixed effects and site, year and date as random effects. Song post distance (log-transformed) was compared in a linear mixed model (LMM) with treatment as fixed factor and site and date as random factors.

RESULTS

Noise levels at the position of the female inside the nest box differed substantially between treatment groups (noise = 67.7±1.8 s.d., control = 36.9±3.2 s.d. dB SPL, A-weighted), but the majority of spectral energy of the experimental noise was largely outside the frequency range of great tit song (see Figure 5.2 for an example of a song under both noise and control conditions). As a result, noise levels differed more subtle in the low-note frequency range (3.74±0.30 s.d. kHz), by 5.5 dB (Anova; $F_{1,28} = 10.1$; $p = 0.004$; see also Figure 5.2) and noise levels in the peak-note frequency range (4.29±0.28 s.d. kHz) differed non-significantly by 3.3 dB (Anova; $F_{1,28} = 3.09$; $p = 0.09$).

Female response latencies to songs or calls of their social male increased on the first morning of full noise exposure (Figure 5.3A), but differences with females in control boxes disappeared within two days (GLMM; interaction day/treatment: N = 29; d.f. = 1; $\chi^2 = 10.2$; $p = 0.001$; Figure 5.3a). Noise exposure had no effect on the moment of female emergence or female call rate (all $p>0.3$).

Male maximum song amplitude recorded at the position of the nest box showed an opposite pattern (GLMM; interaction day/treatment: N = 29; d.f. = 1; $\chi^2 = 10.2$; $p = 0.001$;



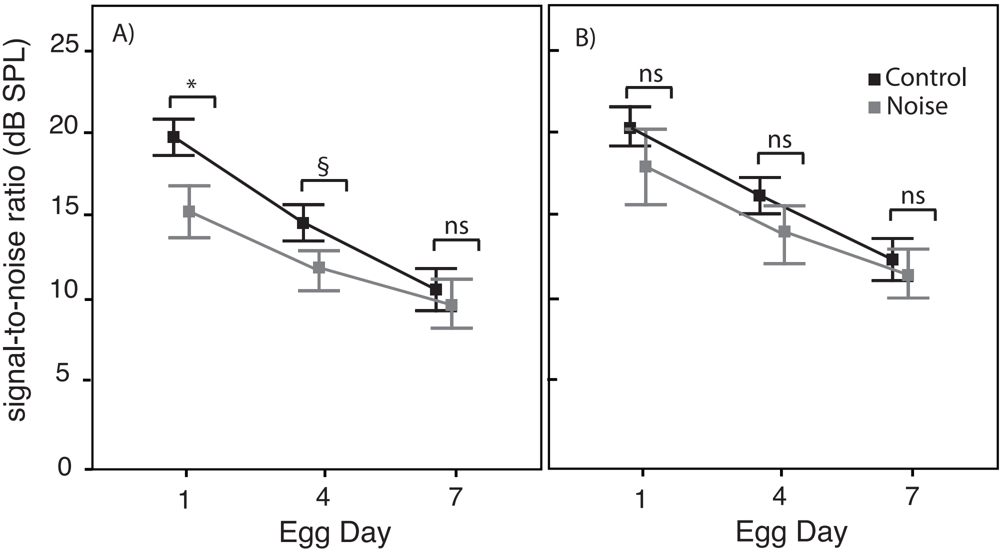


Figure 5.5. Changes in male song signal-to-noise ratio in relation to noise treatment, laying date and note type. Signal-to-noise (S2N) ratios decrease with egg-laying (GLMM; all p < 0.001). (**A**) S2N ratios in the low-note frequency range differ between treatment groups (GLMM; p = 0.044), but the differences decrease with days after start of laying (day 1: p = 0.14; day 4: p = 0.06; day 7: p = 0.64). (**B**) S2N ratios in the peak-note range do not differ significantly (GLMM; p = 0.19).

Figure 5.3B), with amplitudes only differing between treatments after three days of full noise exposure (Figure 5.3B). The interaction effect was mainly due to a decrease in amplitude in the control group (15 out of 16 males decreased in recorded amplitudes), whereas in the noise group the amplitude either increased (4 out of 13), decreased (5 out of 13) or remained the same (4 out of 13, change of less than 1 dB). The noise treatment had no effect on the start of male dawn singing or the low-note or peak-note frequency (all $p>0.6$).

The difference in recorded amplitude levels at the position of the nest boxes were related to song posts occupancy found in a different subset of males. After three days of exposure (on average on egg-day 3.6±1.1 s.d.) Males in the noise treatment group sang at closer distance during the dawn chorus compared to males in the control group (LMM; $N = 22$; $F_{1,20} = 10.12$; $p = 0.005$; Figure 5.4).

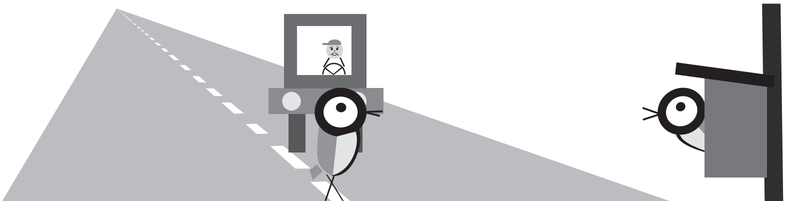
The overall decrease in amplitude between noise days suggests that males moved away from the nest box, which can also explain why signal-to-noise ratios generally decreased with egg-laying (Figure 5.5). The signal-to-noise ratios differed between noise and control treatment groups for the low-notes (GLMM; $N = 29$; d.f. = 1; $\chi^2 = 4.07$; $p = 0.044$), but these differences disappeared at later stages in the laying phase (Figure 5.5A). We did not find significant differences in signal-to-noise ratios between treatment groups for the peak-notes. ($\chi^2 = 1.70$; $p = 0.19$; Figure 5.5B).

DISCUSSION

We examined the role of female feedback on noise-dependent male song behavior during the great tit dawn chorus ritual. We exposed females to artificial traffic noise inside their nest box, while leaving the singing male outside unaffected. We found females to delay their calling response in the noise treatment, which was related to increased song masking levels. Males, not directly exposed, nevertheless responded in the noise treatment by vocalizing from closer song perches. Consequently, the change in spatial song behavior resulted in higher song amplitudes recorded at the position of the nest box in the noise treatment, which was related to restored signal-to-noise ratios as well as female calling response in the noise treatment.

Internal or external feedback

We found males to sing at closer distance in the noise condition, thereby restoring signal-to-noise ratios, even though males did not receive exposure directly. This suggests that males relied on a cue from the females to adjust their signaling behavior appropriately. We did not find females



to change call rate or emergence behavior, but males could have used the increased response latencies to move closer to the females. Alternatively, males may have relied on a visual cue, provided by subtle movements of females, for instance at the nest box entrance. A similar social feedback mechanism was found in brown cowbirds, for which it was shown that selective female response tendencies played a determinant role in shaping male songs[39].

Short-term noise-dependent signaling strategies have been proposed to be the result of an internal or external feedback mechanism (chapter 2 & 3)[27]. Males can use direct auditory feedback from their own perception of noise or signal-to-noise level (internal) and change singing behavior accordingly or use indirect social feedback (external) from conspecific receivers, such as females or neighbors, to adjust their songs in response to changing noise conditions[27]. Our study suggests that noise-dependent spatial song behavior is driven by an external mechanism in great tits.

Most knowledge on noise-dependent feedback mechanisms comes from studies on amplitude regulation, which is generally presumed to reflect an internal mechanism, known as the Lombard effect[8]. The Lombard effect specifically refers to an involuntarily control of amplitude in response to noise [42,43], but animals can also adjust signal amplitude outside the context of noise, as male birds have been shown to sing louder when their mates are further away[40]. Males may have an internal mechanism that matches information on receiver-distance to song amplitude, but it seems more likely that males relied in this experiment on an external feedback mechanism in the form of female response. Although noise-dependent amplitude regulation has been shown to occur in many animals in the absence of a receiver (e.g.[19,41]), it does not prove that individuals are not affected by external cues while fine-tuning vocal amplitude as well. Interestingly, this latter possibility has never been adequately tested and our study shows how distinguishing between the two types of feedback mechanisms can be more complex than we would expect at first sight.

Exposing only senders to noise, or only receivers as in our experimental setup, seems a useful tool to study whether birds adopt an internal or external mechanism when singing higher, louder or faster in response to noise during intra-pair communication. Males responded in our experiment by moving closer to females, a simple yet effective way to increase signal-to-noise ratios at the receiver's side[24]. Males could also have produced songs at higher amplitudes, or changed the radiation pattern of their songs by aiming their songs at the nest-box[42], but it is likely that the theoretical increase of ~6 dB, related to half the distance between song post and nest box, was sufficient to overcome the 5.5 dB masking impact on low notes.

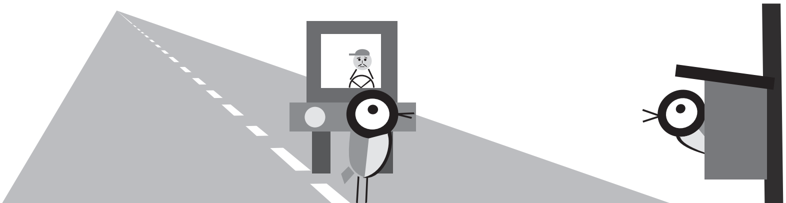
We do know that great tit males did not change the frequency of their songs in the noise treatment, despite the fact that great tit females can provide frequency-dependent feedback to males (chapter 4)[29]. The lack of frequency change in the present study suggests that noise-dependent frequency use in great tits is not driven by an external feedback, or at least not during male – female communication.

Costs of communication in noise

We found an impact of anthropogenic noise on intra-pair communication and although birds were rapidly able to restore communication, such an impact may still have negative fitness consequences as found in a previous study (chapter 6). The masking of the acoustic interaction can affect synchronization of reproductive behavior between pair members and can have a negative impact on the pair bond between males and females[43]. The negative impact of masking may be crucial even for short periods of exposure, especially when they coincide with the peak of female fertility, as it did in our experiment. Such impact will have crucial fitness consequences as it may reduce the pair's reproductive investment, for instance during food provisioning to the chicks[44] and my explain our previous findings (chapter 6).

We also found male great tits to change song perches during noise treatment. Males occupied songs posts that were closer to the nest box in both horizontal and vertical direction. As a result, males could have been singing from more exposed branches and suffer higher predation risks[45]. Furthermore, a change of song post can affect a song's spatial ecology[3,24]. During the peak in female fertility, great tit male dawn song is typically delivered from a song post that is close to the roosting cavity of the social mate[31]. However, males also interact with neighboring males around dawn during so- called song type matching contests[30]. Under normal circumstances, a trade-off related to signal detection for different types of receiver determines optimal signal design, including song post choice[3,46]. A noise-dependent change in song post affects this trade-off and especially a reduction in song post height can have a dramatic effect on long-range transmission for male-male communication and territory defense[25].

Anthropogenic noise can additionally affect an animal's cognitive demands, either through distraction[47] or through increased sensory processing[23]. Consequently, anthropogenic noise has the potential to shift allocation of cognitive capacity with crucial fitness consequences. For instance, shifting attention away or towards predator risk assessment immediate



affects survival probabilities as many species face a trade-off between vigilance and foraging behavior[48] and anthropogenic noise has been found to reduce predator detection[47] and to reduce feeding efficiency as a result of increased vigilance[49]. Interestingly, as sensory processing is often multi-modal[50], it is very likely that acoustic noise affects behaviors that depend on other sensory modalities as well[51].

CONCLUSIONS

We have experimentally shown that females can provide noise-dependent acoustic feedback on male song performance during intra-pair communication, which may have caused males to decrease singing distance and increase signal-to-noise ratios. Males did not adjust song frequency in response to the feedback from females, but the spatial adjustment of song perch may have been already sufficient to mitigate song masking and restore critical communication conditions. Our findings suggests that great tits have a suit of strategies to compensate detrimental noise impact, which may explain why this species survives well in the urban habitat, despite some loss in reproductive success[36] and limitations in terms of information transfer associated with signal adjustment[29]. The experimental approach testing noisy urban conditions on just the receiver side strongly suggest an active role for female birds in steering male communicative behavior and reveals the critical role of ecology in shaping animal interactions.

REFERENCES

1 Bradbury, J.W. & Vehrencamp, S.L., *Principles of Animal Communication*. (Sinauer Associates, Sunderland, MA, 1998).

2 Helm, B. *et al.*, *Animal Behaviour* 72, 245-262 (2006).

3 Naguib, M. *et al.*, in *Adv in the Study of Behavior, Vol 43*, edited by H. J. Brockmann *et al.* (Elsevier Academic Press Inc, San Diego, 2011), Vol. 43, pp. 239-271.

4 Endler, J.A., *Am. Nat.* 139, S125-S153 (1992).

5 Wiley, R.H. & Richards, D.G., *Beh Eco and Soc* 3 (1), 69-94 (1978).

6 Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

7 Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

8 Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

9 Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

10 Bee, M.A. & Swanson, E.M., *Animal Behaviour* 74, 1765-1776 (2007).

11 Lengagne, T., *Biological Conservation* 141 (8), 2023-2031 (2008).

12 Brumm, H. *et al.*, *J of Experimental Biology* 207 (3), 443-448 (2004).

13 Parks, S.E. *et al.*, *Biology Letters* 7 (1), 33-35 (2011).

14 Vasconcelos, R.O. *et al.*, *J of Experimental Biology* 210 (12), 2104-2112 (2007).

15 Slabbekoorn, H. *et al.*, *TREE* 25 (7), 419-427 (2010).

16 Codarin, A. *et al.*, *Marine Pollution Bulletin* 58 (12), 1880-1887 (2009).

17 Gross, K. *et al.*, *Am. Nat.* 176 (4),

456-464 (2010).

[18] Habib, L. *et al.*, *J of Applied Ecology* 44 (1), 176-184 (2007).

[19] Potash, L.M., *Psychonomic Science* 26 (5), 252-254 (1972).

[20] Zelick, R. & Narins, P.M., *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 156 (2), 223-229 (1985).

[21] Potvin, D.A. *et al.*, *Proc R Soc B*(2011).

[22] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[23] Bee, M.A. & Micheyl, C., *J of Comparative Psychology* 122 (3), 235-251 (2008).

[24] Slabbekoorn, H., in *Nature's music: The Science of Birdsong*, edited by P. Marler & H. Slabbekoorn (Elsevier Academic Press, 2004).

[25] Mathevon, N. *et al.*, *Ethology* 102 (5), 397-412 (1996).

[26] Blumenrath, S.H. *et al.*, *Bioacoustics* 14 (3), 209-223 (2004).

[27] Halfwerk, W. & Slabbekoorn, H., *Animal Behaviour* 78 (6), 1301-1307 (2009).

[28] Gorissen, L. & Eens, M., *Auk* 121 (1), 184-191 (2004).

[29] Halfwerk, W. *et al.*, *PNAS* 108 (35), 14549-14554 (2011).

[30] Krebs, J. *et al.*, *Nature* 271 (5645), 539-542 (1978).

[31] Mace, R., *Nature* 330 (6150), 745-746 (1987).

[32] Kluyver, H.N., *Ardea* 39 (1), 1 - 135 (1951).

[33] Lambrechts, M. & Dhondt, A.A., *Beh Eco and Soc* 19 (1), 57-63 (1986).

[34] Rivera-Gutierrez, H.F. *et al.*, *Animal Behaviour* 80 (3), 451-459 (2010).

[35] Franco, P. & Slabbekoorn, H., *Animal Behaviour* 77 (1), 261-269 (2009).

[36] Halfwerk, W. *et al.*, *J of Applied Ecology* 48 (1), 210-219 (2011).

[37] Lachlan, R.F., Luscinia: a bioacoustics analysis computer program (2007).

[38] Langemann, U. *et al.*, *Animal Behaviour* 56, 763-769 (1998).

[39] King, A.P. *et al.*, *Ethology* 111 (1), 101-117 (2005).

[40] Brumm, H. & Slater, P.J.B., *Animal Behaviour* 72, 699-705 (2006).

[41] Manabe, K. *et al.*, *J. Acoust Soc Am* 103 (2), 1190-1198 (1998).

[42] Brumm, H. *et al.*, *Animal Behaviour* 81 (3), 653-659 (2011).

[43] Swaddle, J.P. & Page, L.C., *Animal Behaviour* 74, 363-368 (2007).

[44] Johnstone, R.A., *Behavioral Ecology* 22 (2), 436-444 (2011).

[45] Moller, A.P. *et al.*, *Behavioral Ecology* 17 (2), 155-163 (2006).

[46] Naguib, M. *et al.*, *Behavioral Ecology* 19 (5), 1034-1040 (2008).

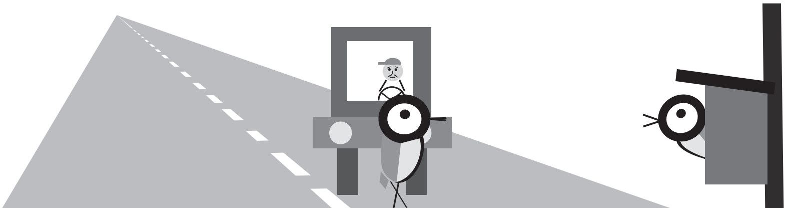
[47] Chan, A.A.Y.-H. *et al.*, *Biology Letters* 6 (4), 458-461 (2011).

[48] Bernays, E.A. & Funk, D.J., *Proc R Soc B* 266 (1415), 151-156 (1999).

[49] Quinn, J.L. *et al.*, *J of Avian Biology* 37 (6), 601-608 (2006).

[50] Driver, J. & Spence, C., *Trends Cogn Sci* 2 (7), 254-262 (1998).

[51] Chan, A.A.Y.-H. & Blumstein, D.T., *Applied Animal Behaviour Science* 131 (1-2), 1-7 (2011).



Chapter 6

Negative impact of traffic noise on avian reproductive success

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Lessells K & Slabbekoorn H. 2011, 48: 210 -219

ABSTRACT

Traffic affects large areas of natural habitat worldwide. As a result, the acoustic signals used by birds and other animals are increasingly masked by traffic noise. Masking of signals important to territory defense and mate attraction may have a negative impact on reproductive success. Depending on the overlap in space, time and frequency between noise and vocalizations, such impact may ultimately exclude species from suitable breeding habitat. However a direct impact of traffic noise on reproductive success has not previously been reported. We monitored traffic noise and avian vocal activity during the breeding season alongside a busy Dutch highway. We measured variation in space, time and spectrum of noise and tested for negative effects on avian reproductive success using long-term breeding data on great tits *Parus major*. Noise levels decreased with distance from the highway, but we also found substantial spatial variation independent of distance. Noise also varied temporally with March being noisier than April, and the day time being noisier than night time. Furthermore, weekdays were clearly noisier than weekends. Importantly, traffic noise overlapped in time as well as acoustic frequency with avian vocalization behavior over a large area. Traffic noise had a negative effect on reproductive success with females laying smaller clutches in noisier areas. Variation in traffic noise in the frequency band that overlaps most with the lower frequency part of great tit song best explained the observed variation. Additionally, noise levels recorded in April, when eggs are laid and incubated, had a negative effect on the number of fledglings, independent of clutch size, and explained the observed variation better than noise levels recorded in March. *Synthesis and applications*. We found that breeding under noisy conditions carries a cost, even for species common in urban areas. Such costs should be taken into account when protecting threatened species, and we argue that knowledge of the spatial, temporal and spectral overlap between noise and species-specific acoustic behavior will be important for effective noise management. We provide some cost-effective mitigation measures such as traffic speed reduction or closing of roads during the breeding season.

INTRODUCTION

Anthropogenic noise currently affects large areas of natural habitat worldwide[1,2]. Masking by noise interferes with the use of the acoustic signals critical to many animal species[3,4]. As a consequence, animals living in areas exposed to anthropogenic noise may suffer reduced reproductive success, which may ultimately lead to the exclusion of species from otherwise suitable habitat[5].
The majority of areas affected by noise are situated along major transport links, such as highways and railways[1,2]. The impact of traffic noise has been explored in a diverse range of taxa (bats; [6,]frogs; [7]), but has been studied most intensively in birds (e.g.[8,9]). Many studies have shown a reduction in breeding numbers in the vicinity of highways (e.g.[10,11]), but no study to date has been able to exclude confounding factors associated with roads and thus identify traffic noise as the key threat to birds[12].

An impact of anthropogenic noise on breeding numbers[13] and species richness[14] without confounding factors has been demonstrated in the vicinity of noisy gas compressor stations. However, extrapolating these findings to highway noise is far from straightforward. For instance, noise at gas compressor stations is constant in amplitude throughout the day and year[14], whereas most anthropogenic noise levels show strong daily, weekday versus weekend, and seasonal variation[12,15].

The negative effect of traffic noise on birds depends on the temporal and spectral overlap with relevant acoustic sounds[4]. Birds use a variety of vocalizations throughout the day but many species restrict the use of song, which is important in both territorial defense and female attraction, to the period around dawn[16]. The overlap between dawn song and peaks in traffic activity (e.g. the rush hour) may be an important factor in determining negative effects, and depends primarily on the time of year in combination with longitude and latitude[12]. Assessing temporal variation in noise levels is therefore an important step in understanding when noise overlaps most with the vocal activity of birds[2,5].
Spectral overlap is most dramatic for birds vocalizing at low frequencies (e.g. cuckoos, owls, woodpeckers and grouse) as traffic noise is typically loudest at lower frequencies[17] and low sounds attenuate less with distance and vegetation density[18,19]. Furthermore, fluctuations in low frequency transmission can change dramatically with weather conditions[20] resulting in unpredictable overlap levels.
Even when there is clear temporal and spectral overlap between traffic noise and birdsong, assessing whether there is a negative impact

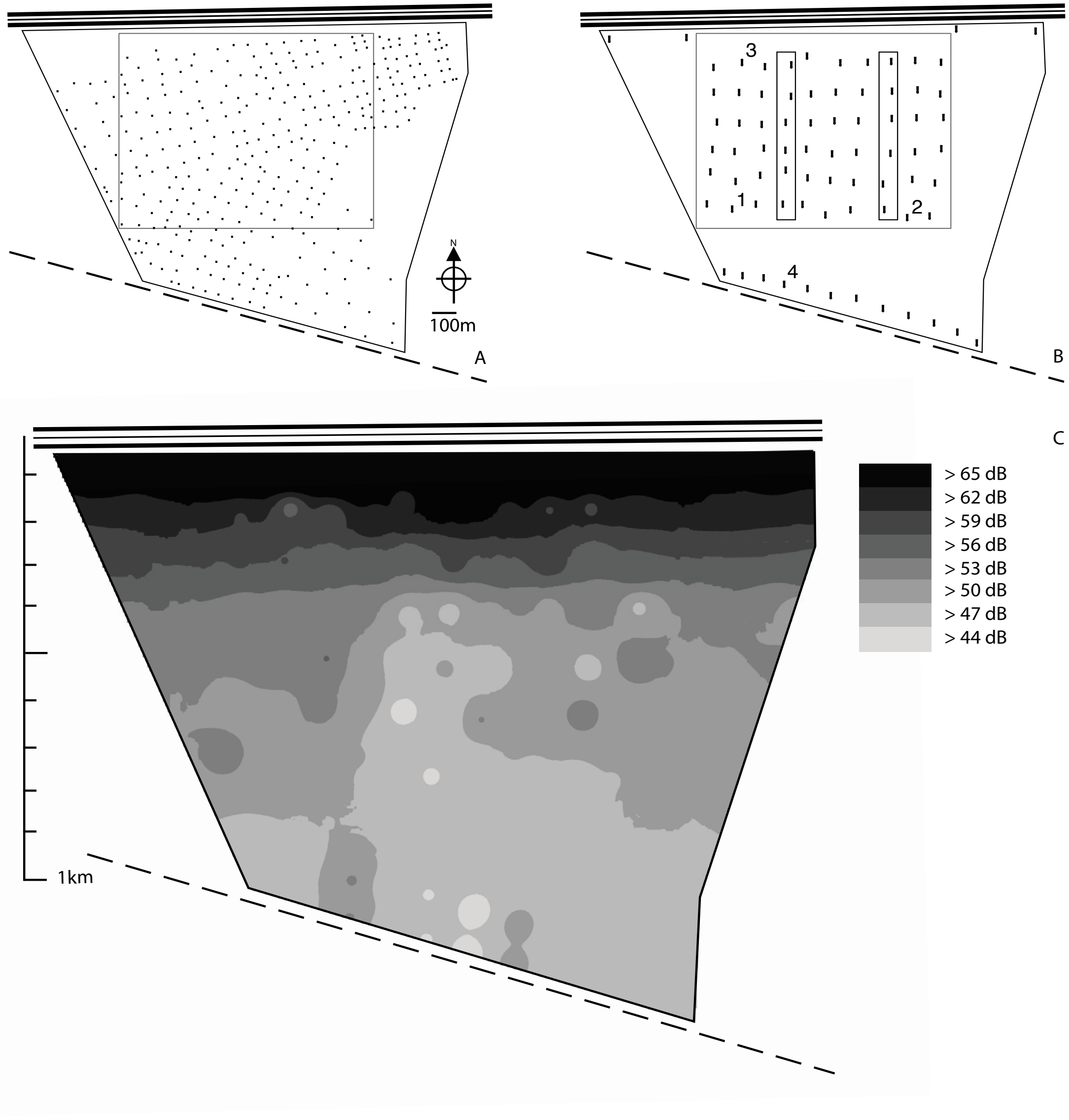


Figure 6.1. Maps of the Buunderkamp area showing nest-boxes, sampling locations and noise levels. Motorway (triple line) and railway (dashed line) are shown. (**A**) nest-box distribution (small dots). Only breeding data from nest-boxes within the rectangle was used. (**B**) sampling locations (filled rectangles) along 10 transects (open rectangles, 2 of them shown). Numbers refer to locations of example recordings used in Figure 6.2. (**C**) GIS-map showing spatial variation in sound levels. Traffic noise shows a strong decrease with distance from the motorway (absolute range at sampling locations 46.5–67.8 dB SPL, A-weighted), but there is substantial spatial variation in this decline.

on reproductive success in the field is not straightforward. The effect on breeding numbers may underestimate the impact and provides little insight into the mechanisms by which birds are affected. For example, breeding success and welfare may be impaired, but breeding densities remain high because of compensating effects of noise on predation rates[14] or competition for food[21]. Furthermore, inexperienced or low quality birds may be more likely to occupy noisy areas[11,22]. Therefore, understanding the mechanisms underlying the negative effects of noise is best achieved by focusing on individual life history traits that are components of reproductive success.

The great tit (*Parus major;* Linneaus 1758) is a common species that is currently not under threat, but the availability of long-term data from a population bordering a major highway provides a rare opportunity to investigate whether noise has more subtle effects than simply excluding birds from otherwise suitable habitat. This species prefers artificial nest-boxes to natural cavities[23] even when they are situated in suboptimal habitat. This is probably one reason why great tits breed in substantial numbers in areas adjacent to highways[24], allowing collection of breeding data in noisy areas. Great tit singing behavior has been repeatedly related to noise at both the population[25,26] and individual level[27]. We know that relatively low frequency songs are detected less well when there is traffic-like noise[17], and great tits can switch between song types when exposed to experimental noise (chapter 2)[28]. However, it is unknown whether such behavioral flexibility prevents any negative effects of anthropogenic noise.

We studied spatial, temporal and spectral variation in the loudness of traffic noise and bird acoustic behavior in a nest-box population of great tits adjacent to a Dutch highway with a heavy traffic load. Traffic noise and bird song were recorded during two important breeding stages: March, when territories are formed, and April, when eggs are laid and incubated. We used these data, together with habitat and long-term breeding data to explore the following questions: How does traffic noise in habitat adjacent to a highway vary in space? To what extent do traffic noise and bird vocal activity overlap in time and frequency, and does the amount of overlap differ between breeding stages? Is there an impact of traffic noise levels on breeding success? Does seasonal variation in traffic noise affect particular breeding stages? And does spectral overlap between great tit song and traffic noise play a role in the effect on reproductive success? Answers to these questions will be valuable in identifying conservation measures and applying effective noise management in natural areas polluted by traffic noise.

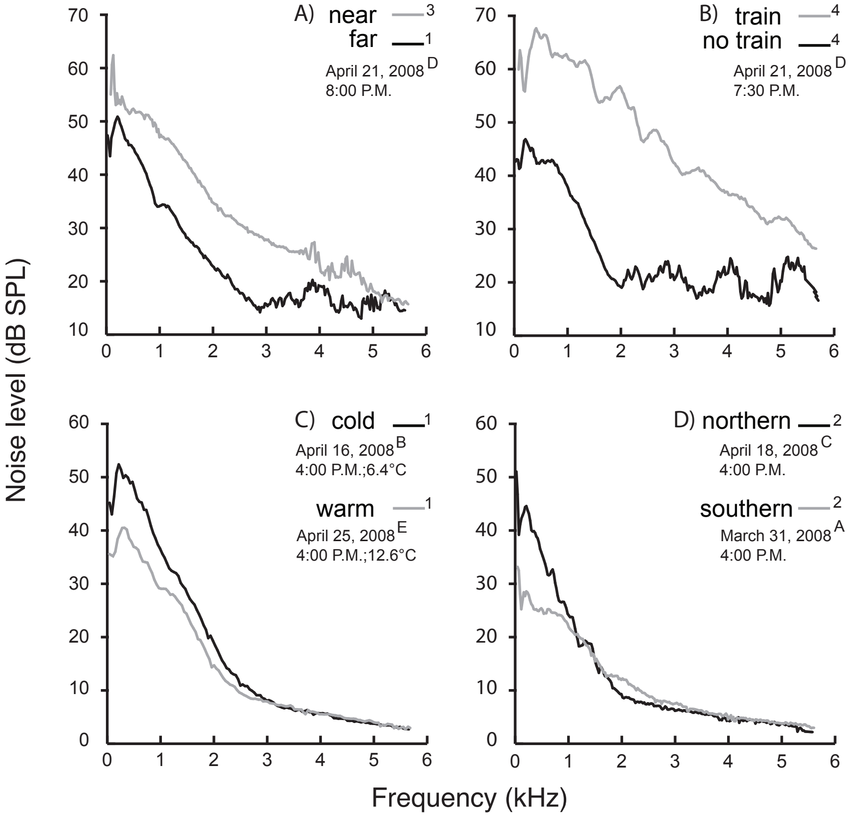


Figure 6.2. Variation in sound profiles across different environmental conditions. (**A**) powerspectrographic example comparing sound profiles near to (±100 m), and far from (±700 m), the motorway. At larger distances, the high-frequency components of traffic noise are more attenuated and even disappear above ±3 kHz. (**B**) recordings made near the railway (±100 m from the track and ±1 km from the motorway) shortly before and during the passage of a train. (**C**) comparison of sound profiles on days with different temperatures, but similar wind conditions illustrates large effect of weather conditions on noise levels. (**D**) comparison of sound profiles on days with opposite wind directions, but similar temperature and wind speed. Small numbers refer to locations illustrated in Figure 6.1. Capital letters refer to recording days illustrated in Figure 6.3.

MATERIALS AND METHODS

Study site & species

We collected data from a nest-box population of great tits *Parus major* breeding at the Buunderkamp (05º45′E; 52º01′N) in the Netherlands (Figure 6.1A). The area is bounded in the north by a four-lane highway and in the south by a railway line (about 20 trains/hour). The habitat is mixed woodland consisting of plots of varying sizes, and age and species of trees, with *Pinus sylvestris* and *Quercus rubra* dominant (see[29] for further description of the area).

The great tit is a hole-nesting passerine that sings in the frequency range of 2 - 9 kHz[28]. Territory defense starts in mid-January and peaks towards the end of March[23]. Egg-laying in the study population starts in April and is accompanied by a strong increase in dawn singing activity. We used long-term breeding data on great tits for the period 1995 - 2009 during which no major changes have been made in the area that would have affected the spatial spread of noise coming from the highway.

Noise data acquisition

We made sound recordings between March and May 2008, before major leafing of the deciduous trees. We sampled sound levels along ten transects perpendicular to the highway (Figure 6.1B), with automatic SongMeter recorders (16 bit, 24 kHz sample rate; Wildlife Acoustics Inc.). Exact sampling locations were determined with a GPS (Garmin 60CSx). The sampling transects started 100 m from the mid-line of the highway and six sampling locations at approximately 100 m intervals were chosen within each transect. The transects were spaced 80 - 100 m apart and two transects were sampled simultaneously for 3 - 5 consecutive days. Transects were each sampled twice in a random order, once between 8th and 30th of March, and once between 31st of March and 1st of May. The sampling grid encompassed most of the area, but we used two additional SongMeters to monitor the remaining area. Recorders were attached to large trees (> 40 cm in diameter) at 2 m above the ground with the recording microphone directed towards the highway. Recording levels for the microphones were adjusted to a sensitivity ranging from 0.0 - 1.5 dBV/pa (reaching full scale between 92.5 - 94.0 dB SPL) and amplitude levels were adjusted according to the effective sensitivity of each individual Song Meter recorder. Recorders were randomly swapped between sampling locations to control for any remaining variation in recording levels. Recorders were scheduled to record for 30 seconds at 30 minute intervals, day and night.

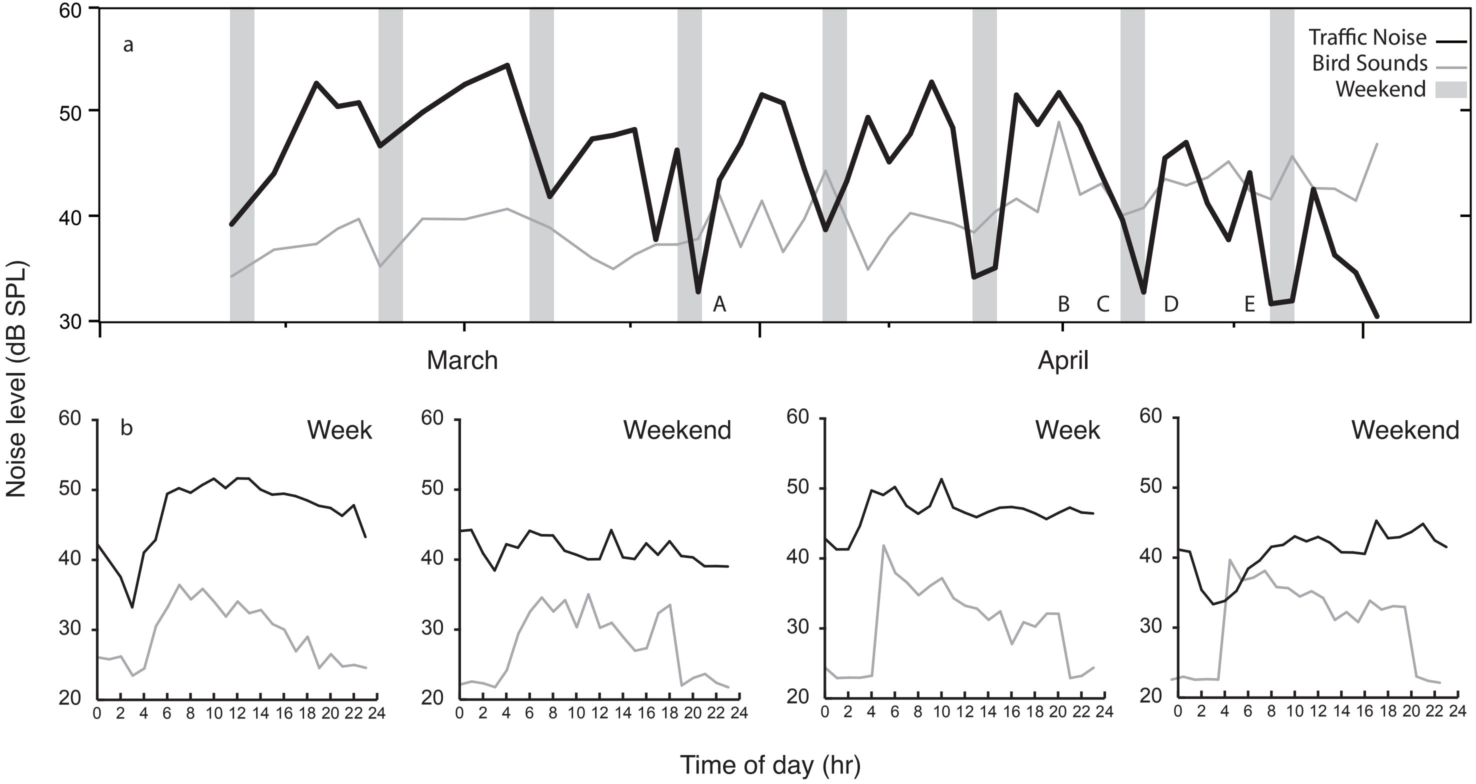


Figure 6.3. Temporal patterns in traffic noise levels and bird vocal activity. Recordings made at distances of 400–700 m from the motorway, averaged over 1 or 24 h intervals. We compared amplitude fluctuations in the 1 and 4 kHz band, which are mainly influenced by traffic and bird vocal activity respectively. (**A**) seasonal pattern in sound levels between March and May 2008. Recordings made at dawn during peak singing activity. Traffic noise levels decrease throughout the season, but show substantial variation due to changes in traffic activity (week days being noisier than weekend days) and changes in weather conditions. Bird vocal activity increases throughout the season. (**B**) daily pattern in traffic noise and bird sound levels during either the period of great tit territory defense (8–16 of March, left two graphs) or egg-laying (19–27 of April, right two graphs), on weekdays or at the weekend.

We analyzed sound recordings in the computer program Matlab (Mathworks Inc.). We measured overall sound levels (using an A-weighted filter), and also sound levels in four adjacent octave-bands, centered at frequencies of 0.5, 1.0, 2.0, and 4.0 kHz. Sound measurements were averaged over either 30-minute or 24-hour intervals, and/or sampling locations, depending on the type of analysis.

We used 76 sampling locations to visualize spatial variation in noise levels for the Buunderkamp in the computer program ArcGis (version 9.0, ESRI). Sixty locations from the sampling transects and 16 additional sampling locations were plotted onto a geo-annotated reference map from which noise maps were derived with the Spatial Analyst toolbox. Spatial resolution was set at 5m and raster values between sampling locations were calculated with a weighted distance interpolation tool (IDW). Additionally we calculated distances for all nest boxes and sampling locations to the nearest mid-point on the highway.

We assessed the temporal overlap between traffic noise and vocal bird activity throughout the season and at different times of day. At our study site most of the non-anthropogenic sound comes from vocalizing birds with the majority of acoustic energy in the range of 2 - 8 kHz. We selected a subset of sampling locations at distances over 400 m from the highway where there is little traffic noise present in the 4 kHz octave band so temporal variation in sound levels was mainly related to the vocal activity by birds. For these locations, we compared sound levels, averaged over 1 or 24 hour intervals, in the 1 kHz band (mainly due to traffic noise) with those in the 4 kHz band (mainly due to bird activity, including great tits).

Long-term breeding data

Great tit breeding data were collected between 1995 and 2009 by the Netherlands Institute of Ecology (NIOO-KNAW). We used data from both large and small nest-boxes within the sampling grid (Figure 6.1A) on laying date, clutch size, number of hatchlings, number of fledglings and fledging mass (average weight of chicks for the brood when chicks are 15 days old) for all first great tit clutches over this period, except for 2007 and 2008 when data were excluded because of an unrelated experiment. Additional data on female identity, female age and fledging mass were only available for 1995-1999, 2001 and 2009.

For analysis of breeding performance we used only first clutches (categorized using female identity or because laying date was within 30 days of the first laying date for a given year). For

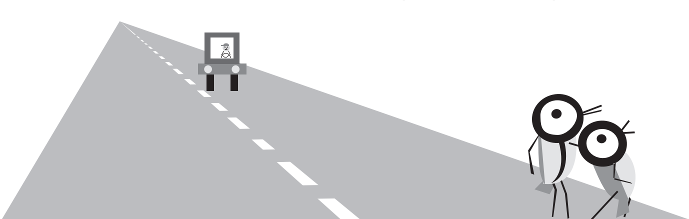


Table 1. Results from mixed model showing effect of weather condition on overall noise levels. Sampling location (N = 60) was added as random factor. Only first order interactions are reported.

Source	d.f.	F	P
Distance	5	6.61	<0.001
Wind direction (N vs S)	1	10.92	0.001
Daily Temperature	1	9.65	0.002
Wind speed*	1	29.30	<0.001
Distance x Wind direction	5	3.81	0.002
Distance x Daily Temperature	5	2.73	0.019
Distance x Wind speed*	5	1.75	0.12
Wind direction x Daily Temperature	1	1.32	0.25
Wind direction x Wind speed*	1	10.38	0.001
Daily Temperature x Wind speed*	1	11.26	0.001
* log-transformed			

analyses of laying date we used only clutches for which this could be reliably calculated. We were interested in the mechanisms underlying breeding success and therefore focused on life history traits that reflected decisions made by the birds. For the analysis of clutch size we therefore excluded clutches that were not incubated, because including nests that were abandoned (either through a decision by the parents, or predation of the parents) would introduce unwanted heterogeneity in the data. Similarly, we excluded nests where no chicks hatched or fledged from the analyses of the number of hatchlings and fledglings, respectively, because it was usually unknown whether failure was caused by death of all the embryos or chicks, abandonment by the parents or predation of the parents (away from the nest).

Weather & habitat data

We assessed habitat characteristics, including tree density, tree diameter and species composition, at the level of woodland plots (0.2-1.0 ha). We measured tree density and diameter and noted tree species at each of the 60 sampling locations, and at the two nest boxes nearest to these locations. We calculated the percentage of deciduous trees per plot and averaged tree density and diameter over all locations within a plot. We used weather data on daily wind direction and speed, and temperature, recorded by the Royal Netherlands Meteorological Institute (KNMI) at de Bilt (situated ± 50 km to the west of the Buunderkamp).

Statistical analysis

We analyzed all data using SPSS (version 17.0) and log-transformed variables when necessary to meet model assumptions. Temporal variation in daily and seasonal sound levels were explored using repeated measures ANOVAs with sound level grouped by sampling location as the dependent variable and time of day or date as an explanatory variable. Additionally, we compared recordings made on weekdays with recordings from weekends with type of day as a fixed factor.

We examined the effect of daily weather conditions on the propagation of noise with full factorial linear mixed models. To test for the effect of wind direction we discriminated between days with northerly (coming from the direction of the highway) and southerly winds (going towards the direction of the highway). Wind direction was included as a fixed factor, and sample location as a random factor. Distance to the highway, wind speed, and daily temperature were included as covariates.

We constructed a set of linear mixed models for each life history trait and compared them using a model selec-

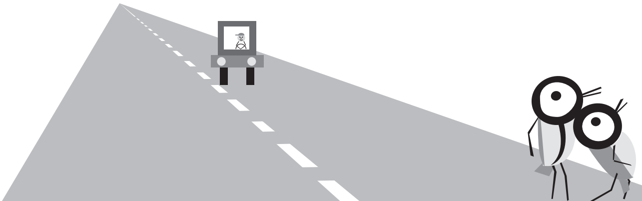


Table 2. Life history model selection procedure based on traffic noise, distance and/or habitat features using Akaike's information criterion. Overall noise level (**Noise**), distance to the highway (**dH**), tree diameter (**d**), tree density (**t**) and percentage of deciduous trees (**%d**) were entered as main effects in mixed models. Only models with a Δ AIC < 4.0 are shown for each life history trait.

Dependent trait	Model	AIC	Δ AIC	Akaik weight
Laying date	d+t	3523.81	0.00	0.52
(N = 542)	d	3525.61	1.80	0.21
	Noise+d+t	3526.86	3.06	0.11
Clutch size	Noise+d	1727.51	0.00	0.32
(N = 505)	Noise+d+t	1727.92	0.41	0.26
	Noise	1729.43	1.92	0.12
	d	1730.05	2.54	0.09
	d+t	1730.41	2.90	0.07
	Noise+t	1730.41	2.90	0.07
Number of hatchlings	d	917.53	0.00	0.36
(N = 470)	d+t	917.71	0.18	0.33
	Null	920.18	2.65	0.10
	t	921.05	3.53	0.06
	Noise+d	921.19	3.66	0.06
	Noise+d+t	921.38	3.85	0.05
Number of fledglings	d	1956.24	0.00	0.29
(N = 387)	d+t	1956.65	0.42	0.24
	Noise+d	1957.61	1.37	0.15
	Noise+d+t	1958.08	1.85	0.12
	Null	1958.98	2.74	0.07
	t	1959.22	2.99	0.07
Fledging mass	Noise+d+t+%d	2070.29	0.00	0.52
(N=215)	Noise+d+t	2072.26	1.96	0.19
	Noise+d+t+dH+%d	2072.86	2.57	0.14

tion approach based on Akaike's information criterion[30]. Models always included nest-box type (large or small), sampling location and breeding year as random factors. Depending on the model, we also included other reproductive traits as explanatory variables (cf. [31]). For instance, clutch size can correlate with laying date and an effect of noise on clutch size could be indirectly caused by an effect of noise on laying date. Including laying date in the clutch size model therefore allows us to test for a direct effect of noise. For the number of hatchlings we included clutch size and for the number of fledglings we included number of hatchlings in the models. For the fledging mass model we included both clutch size and laying date as these factors are known to have a large effect on fledging mass (e.g.[31]).

In a first analysis we compared models that included overall noise levels, distance to the highway, tree density, tree diameter and percentage deciduous trees as explanatory factors. Models contained single factors or in combination with other factors as main effects as we had no a priori knowledge that interactions among factors would be of importance. The total set contained 32 models to be compared for each trait, including the Null model. We calculated for each explanatory factor the probability that it would be in the best approximating model using Akaike weights (see e.g.[32,33]). We used the subset of models with a delta-AIC < 4.0 from the top model to get model-averaged estimates and standard errors each factor (cf. [30]). In a second analysis we focused on temporal overlap between noise sampling period and breeding stage. We used the models with delta-AIC < 4.0 from the previous analysis and only exchanged the overall noise with noise levels sampled either in March or in April. In a third analysis, we repeated this procedure, but focused on the spectral overlap with song and explored whether noise in a certain frequency range (0.5, 1.0, 2.0, or 4.0 octave band, or overall noise) better explained variation of the data.

Breeding performance is known to be age-dependent[23,31] and we therefore re-ran analyses for which we found strong support using the subset of data for which female age was known. Female identity was added as a random factor and female age (first year or older) as a fixed factor.

RESULTS

Spatial patterns in noise levels

Overall sound levels gradually decreased with distance from the highway ($F_{5,54} = 200.5$, $P < 0.001$) with an average drop of 20 dB SPL (A-weighted) over less than 500 m (Figure 6.1C). Furthermore, high frequencies attenuated faster than low

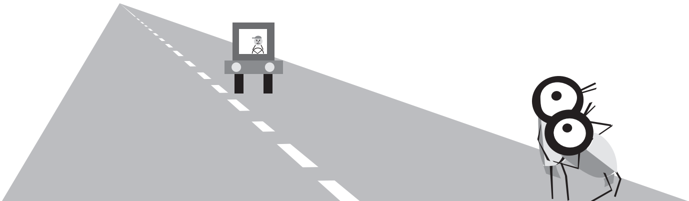


Table 3. Results from model selection procedure showing selection probabilities (calculated across the whole model set) and parameter estimates (using a subset of the models with Δ AIC < 4.0 and model averaging procedures; see text and Table 2). Only factors that were used for model averaging are shown.

Dependent trait/ independent parameter	Selection probability	B	SE
Laying date			
Tree diameter	0.92	-1.07	3.92
Tree density	0.70	0.34	0.93
Noise	0.18	0.044	0.075
Clutch size			
Noise	0.80	-0.053	0.021
Tree diameter	0.75	0.18	1.23
Tree density	0.42	0.17	0.25
Number of hatchlings			
Tree diameter	0.81	0.72	1.64
Tree density	0.46	-0.05	0.35
Noise	0.14	-0.039	0.030
Number of fledglings			
Tree diameter	0.80	-0.75	0.83
Tree density	0.45	-0.18	0.15
Noise	0.33	-0.044	0.020
Fledging mass			
Tree diameter	0.99	145.1	151.7
Tree density	0.99	-10.87	26.96
Noise	0.93	-3.14	2.67
Distance to highway	0.22	0.005	0.11
Percentage deciduous	0.16	0.56	0.39

frequencies ($F_{3,59} = 12.03$, $P < 0.001$; Figure 6.2A). There was substantial spatial variation in traffic noise, independent of distance to the highway (Figure 6.1C): different locations at medium (>300 m) to large (>700 m) distances from the highway differed by more than 9 dB SPL (A-weighted) in noise level (Figure 6.1C). Train noise can be very loud (see e.g. Figure 6.2B) but, in contrast to highway noise, is transient and average daily noise levels near the railway line were among the lowest (Figure 6.1C).

Weather-dependent noise levels

Wind direction, wind speed and daily temperature all had an effect on overall sound levels (see Table 1). Furthermore, wind direction and temperature interacted with distance to the highway (Table 1). We reanalyzed a subset of recordings made at distances of 400 – 700 m from the highway to explore the effect of weather conditions on sounds in different octave bands. Both temperature ($F_{1,59} = 27.78$; $P < 0.0001$) and wind direction ($F_{1,59} = 5.27$; $P = 0.001$) interacted with frequency, with the strongest effect at lower frequencies and large distances from the highway. For instance, at 700 m from the highway, sound levels below 1 kHz could increase by over 10 dB SPL on cold days or days with northerly winds (Figure 6.2C,D).

Temporal fluctuations in traffic noise overlap with bird activity

Traffic noise levels changed throughout the season ($F_{1,59} = 7.57$ $P = 0.008$) with March being noisier and more variable than April (Figure 6.3A). Additionally, noise levels on weekdays were significantly higher than at the weekend ($F_{1,59} = 4.87$ $P = 0.032$; Figure 6.3). Noise levels showed a strong daily pattern ($F_{1,59} = 8.776$ $P = 0.005$), with a clear drop between 0:00 and 4:00 AM, but no distinct rush-hour peaks (Figure 6.3B).

Screening of recordings revealed that, at distances over 400 m from the highway, variation in sound levels in the 4 kHz band was indeed mainly influenced by bird vocal activity, and we therefore used recordings at these distances to assess seasonal and daily overlap of traffic noise and bird vocal behavior. Bird vocal activity as measured at the peak of the dawn chorus increased throughout the season (4 kHz-band; $F_{1,59} = 7.88$, $P < 0.001$) whereas traffic noise during this time period decreased (1 kHz-band; $F_{1,59} = 5.13$, $P < 0.001$; Figure 6.3A). Bird vocal behavior showed a temporal shift between early March and late April due to changes in the time of sunrise, but despite this, the temporal overlap with traffic noise remained remarkably high on weekdays (Figure 6.3B), probably due to the change from winter to summer time (i.e. clock time advancing by

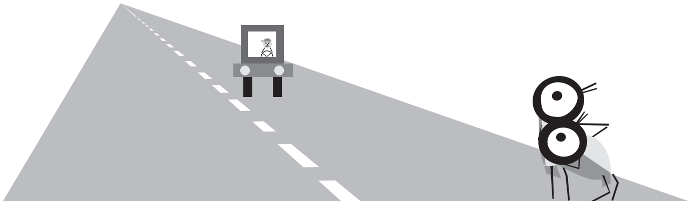


Table 4. Results from model selection procedure focusing on temporal variation in noise. Models as used in Table 2 were adjusted to include noise levels recorded either in March or April.

Dependent trait	Model	AIC	Δ AIC	Akaike weight
Laying date	d+t	3523.81	0	0.52
(N = 542)	d	3525.61	1.80	0.21
	Noise April+d+t	3527.03	3.23	0.10
	Noise March+d+t	3527.30	3.49	0.09
	Noise April+d	3528.85	5.05	0.04
	Noise March+d	3529.14	5.34	0.04
Clutch size	Noise March+d	1725.97	0	0.25
(N = 505)	Noise April+d	1726.20	0.23	0.22
	Noise April+d+t	1726.56	0.59	0.19
	Noise March+d+t	1726.79	0.82	0.17
	Noise March	1728.05	0.17	0.09
	Noise April	1728.11	2.08	0.09
Number of hatchlings	d	917.53	0	0.36
(N = 470)	d+t	917.71	0.18	0.33
	Null	920.18	2.65	0.09
	t	921.05	3.53	0.06
Number of fledglings	Noise April+d	1955.34	0	0.32
(N = 387)	Noise April+d+t	1956.08	0.74	0.22
	d	1956.24	0.89	0.21
	d+t	1956.65	1.31	0.17
Fledging mass	Noise April+d+t+%d	2070.16	0	0.39
(N=215)	Noise Marchl+d+t+%d	2071.12	0.96	0.24
	Noise April+d+t	2072.30	2.14	0.13
	Noise March+d+t	2073.01	2.85	0.09
	Noise April+d+t+dH+%d	2073.13	2.97	0.09
	Noise March+d+t+dH+%d	2073.84	3.68	0.06

one hour on 30 March). Peak activity of avian vocal behavior showed the least overlap with traffic noise during the weekends, especially in late April (Figure 6.3B).

Negative effect of traffic noise on breeding performance

Overall noise levels received strong support in the model selection procedure for clutch size and fledging mass models and moderate support for the number of fledglings model (Table 2 and 3). Tree diameter and tree density received strong support in all life history models (Table 2 and 3), but the effect was not consistent across models and the variance was high (Table 3). Distance to the highway and percentage deciduous trees received weak support in the fledging mass model (Table 2 and 3) and virtually no support in the remaining life history models.

Overall noise levels had an independent negative effect on clutch size, with females laying on average about 10% fewer eggs across a noise gradient of 20 dB SPL (A-weighted) (Table 3). Reanalyzing the top clutch size model to include female identity and age confirmed the effect of noise ($F_{1,268} = 7.82$, $P = 0.007$), but failed to show an effect of female age on clutch size ($F_{1,268} = 0.20$, $P = 0.82$). Noise levels had a negative effect on fledging mass (Table 3), but in none of the top models was the effect significant (all $P > 0.2$).

Temporal and spectral variation in noise predicts smaller clutches and fewer fledglings

Refining the models with noise sampled either in March or in April did not change the level of support, except for the number of fledglings model (Tables 4 and 5). Noise sampled in April was about 7 times more likely to explain variation of the data compared to noise sampled in March (Table 5). Higher noise levels in April correlated with lower numbers of fledglings (Table 5). We re-ran the top model to include clutch size instead of the number of fledglings as fixed factor. Clutch size had a large effect on the number of fledglings ($B = 0.57 \pm 0.070$; $F_{1,364} = 65.51$, $P < 0.0001$), but we found noise sampled in April to have an additional negative effect ($B = -0.061 \pm 0.027$; $F_{1,364} = 5.09$, $P = 0.028$) as well.

Finally, we found that variation in noise levels in the 2 kHz octave band best explained variation in clutch size, although overall noise and noise in the 0.5 and 1.0 kHz band also received moderate support (Table 6a). Noise in the 2 kHz band frequency range overlaps the lower part of great tit song in our study population and had a negative effect on the number of eggs laid by females (Table 6b).

Table 5. Temporal variation in noise is related to breeding performance. Selection probabilities and parameter estimates of noise recorded either in March or April from model selection procedures are shown (see text and Table 4).

Dependent trait	Noise parameter (sampling period)	Selection probability	B	SE
Laying date	March	0.13	0.007	0.050
	April	0.14	0.024	0.059
Clutch size	March	0.50	-0.038	0.020
	April	0.50	-0.040	0.020
Number of hatchlings	March	0.07	-0.027	0.027
	April	0.09	-0.032	0.029
Number of fledglings	March	0.08	-0.033	0.019
	April	0.55	-0.051	0.019
Fledging mass	March	0.39	-1.97	1.80
	April	0.61	-3.16	2.48

Table 6. Spectral overlap between noise and song predicts clutch size. (**A**) model selection using clutch size models with strong support in previous analysis (see text and Table 2). Only models with a Δ AIC < 4.0 are shown. (**B**) Selection probabilities for noise in different frequency ranges and parameter estimates after model averaging. Only results for noise variables are shown.

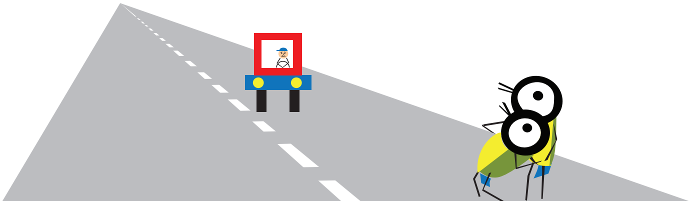
A

Model (Noise frequency range)	AIC	Δ AIC	Akaike weight
2 kHz band+d+t	1726.59	0	0.28
overall (A-weighted)+d+t	1727.92	1.33	0.15
0.5 kHz band+d+t	1728.14	1.54	0.13
1 kHz band+d+t	1728.62	2.02	0.10
4 kHz band+d+t	1729.57	2.98	0.06
2 kHz band+d	1730.27	3.67	0.05

B

Noise frequency range	Selection probability	B	SE
2 kHz band	0.38	-0.058	0.016
overall (A-weighted)	0.20	-0.053	0.021
0.5 kHz band	0.18	-0.070	0.022
1 kHz band	0.15	-0.064	0.018
4 kHz band	0.09	-0.069	0.027

Collecting field data; clockwise: female incubating on nest during weekly routine check; finished clutch containing 12 eggs, measuring chicks, blood sample for genetic paternity analysis.



DISCUSSION

We recorded high traffic noise levels in forest bird breeding habitat related to the proximity of a highway. However, we also found spatial variation in noise levels independent of distance to the highway that allowed us to demonstrate a negative relationship between noise levels and the reproductive success of great tits. Furthermore, noise levels varied substantially with the time of day, season and weather conditions, and both temporal and spectral overlap with vocalizing birds is high under a wide range of conditions. Finally, we found noise levels in April to have a negative effect on the number of fledglings, while noise variation in the frequency with most spectral overlap with great tit song best predicted a negative effect on clutch size.

Explaining noise impact on reproductive success

We found an impact of traffic noise on avian reproductive success manifest by smaller clutches and fewer fledged chicks in the noisier areas. We also explored relationships between breeding traits and temporal and spectral overlap of noise, which could provide some insight into the mechanisms by which birds are affected. We believe there are at least four possible mechanisms, all related to signal masking to some degree, which could explain how anthropogenic noise has a negative impact on avian reproductive success.

The first explanation is related to interference with acoustic assessment of mate quality. Female birds are known to rely on song in assessment of male quality and subsequent investment decisions[34]. High noise levels could reduce perceived song quality and cause females to breed later, allocate less energy to the eggs or provide less maternal care to the chicks. Our data show that spectral overlap between noise and great tit song best predicts patterns in clutch size, suggesting that noise may indeed interfere with song-based assessment of male quality and subsequently lower female investment.

The second explanation for the effect of traffic noise on reproductive success could be related to the non-random distribution of individuals across the habitat. Birds may perceive a noisy territory as being of lesser quality[5] and therefore try to avoid these areas. For instance, both Reijnen & Foppen[11] and Habib, *etal*[22] found less experienced birds breeding in more noisy territories. We did not find traffic noise or clutch size to covary with female age and we have no insight into distribution and performance of lower quality individuals (e.g. immigrants, who are known to produce smaller clutches;[23]), but it is likely that noise may play an important role at the time that individuals are settling and defending territories.

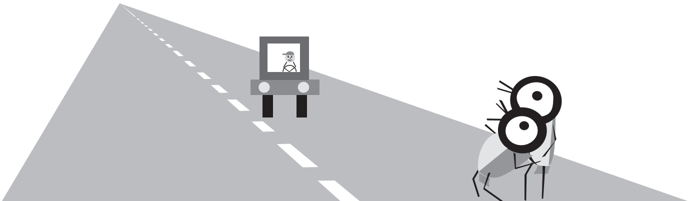
The third explanation is that increased noise levels could also cause physiological stress due to reduced foraging opportunities, because prey are less easy to detect[6], or because more time has to be spent scanning for predators[35]. Individuals living in noisy areas may therefore have less energy to invest in their eggs and offspring.

And finally, the fourth explanation could be that noise can have an impact on parent-offspring communication and adults may therefore not be able to meet their chicks' demands[36]. We did not find a significant effect on fledging mass, but we did find that high noise levels in April have a negative effect on the number of fledglings, independent of clutch size. Whether this is related to higher stress levels, reduced foraging or decreased communication is difficult to disentangle, but it does suggest that noise interference could affect food provisioning to the chicks.

Explaining traffic noise heterogeneity

The opportunity to test for an impact of traffic noise on avian reproductive success relied on the heterogeneity of noise levels independent of distance to the highway. Many earlier studies have designed ways to predict spatial and temporal variation of traffic noise, using a combination of field data and theoretical modeling[37]. However, these models have tended to focus either on noise data at the source (taking traffic and road variables into account; e.g.[38,39]) or on transmission data (e.g.[20]). The few models that have integrated these aspects have assumed that the areas adjacent to highways are environmentally homogeneous[37]. In contrast, our study reveals a high level of heterogeneity at a local scale that should be taken into account when trying to understand the impact of noise on bird breeding populations.

In addition to revealing the pattern of noise heterogeneity, we were able to provide some insight into the causal explanations for the noise variation in space, time, and frequency. We found substantial spatial variation throughout our study area that was not related to the distance to the highway. The effect was most pronounced at a few hundred meters from the highway, with nearby areas differing by over 9 dB in mean noise levels. Transmission of traffic noise is known to depend on highway architecture, and ground and vegetation structure[40]. However, the architecture of the highway does not vary over the length adjacent to our study area and the spatial noise heterogeneity that we found is most likely to be caused by variation in tree densities in the areas close to the highway[19]. Noise levels close to the highway source are known to depend on traffic load[39] which can vary between day and night, and between weekdays and the weekend[15]. Noise amplitude is also strongly related to traffic speed[41], which is probably why we did not detect a clear rush-hour peak in noise, because traffic during the rush-hour is often much slower



or even stationary. Finally, we not only confirmed that lower frequency sounds were transmitted over a larger area than higher frequency sounds but that relatively low frequencies were also more influenced by changing weather conditions.

CONCLUSIONS AND APPLICATIONS

We have shown that traffic noise levels in roadside forest vary substantially in space, time and frequency, which allowed us to reveal a negative relationship with reproductive success in a common species. Great tit females laid fewer eggs and pairs fledged fewer young in noisier areas. As the impact of noise is potentially even higher for species vocalizing at lower frequencies than great tits our data could have significance for the conservation of species that are less abundant or under threat. Consequently, we believe that integration of data on species-specific acoustic behavior with noise prediction models and actual field measurements could be a useful approach in exploring ways to protect threatened birds in noise-polluted wildlife sanctuaries.

Mitigation measures to reduce the negative impact of noise on breeding birds could include sound barriers[5], alternative, more sound-efficient transport by buses through nature reserves[42] or closing roads during acoustically critical phases in the breeding cycle[43]. Traffic noise could also be reduced by introducing a 'noise tax' for a given time of day or season based on the type of car or tires and the average vehicle speed - factors that are known to affect noise levels[41]. It is clear that the trade-off between ecological and economic values will play a crucial role in the implementation of these kinds of applications. Furthermore, sufficient insight into species-specific acoustic behavior and noise distribution data is typically still lacking. Nevertheless, we hope our results help to raise awareness of the potentially negative impact of anthropogenic noise on breeding birds in general.

REFERENCES

1 Forman, R.T.T., *Conservation Biology* 14 (1), 31-35 (2000).

2 Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

3 Bradbury, J.W. & Vehrencamp, S.L., *Principles of Animal Communication*. (Sinauer Associates, Sunderland, MA, 1998).

4 Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

5 Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

6 Schaub, A. *et al.*, *J of Experimental Biology* 211 (19), 3174-3180 (2008).

7 Bee, M.A. & Swanson, E.M., *Animal Behaviour* 74, 1765-1776 (2007).

8 Reijnen, R. *et al.*, *J of Applied Ecology* 32 (1), 187-202 (1995).

9 Stone, E., *Anthrozoos* 13 (4), 225-231 (2000).

10 van der Zande, A.N. *et al.*, *Biological Conservation* 18 (4), 299-321 (1980).

11 Reijnen, R. & Foppen, R., *J Fur Ornithologie* 132 (3), 291-295 (1991).

[12] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[13] Bayne, E.M. *et al.*, *Conservation Biology* 22 (5), 1186-1193 (2008).

[14] Francis, C.D. *et al.*, *Current Biology* 19 (16), 1415-1419 (2009).

[15] Bautista, L.M. *et al.*, *Conservation Biology* 18 (3), 726-732 (2004).

[16] Catchpole, C.K. & Slater, P.J.B., *Bird Song: Biological themes and Variations*. (Cambridge University press, Cambridge, 2008).

[17] Pohl, N.U. *et al.*, *Animal Behaviour* 78 (6), 1293-1300 (2009).

[18] Wiley, R.H. & Richards, D.G., *Beh Eco and Soc* 3 (1), 69-94 (1978).

[19] Padgham, M., *J Acoust Soc Am* 115 (1), 402-410 (2004).

[20] Ovenden, N.C. *et al.*, *J. Acoust Soc Am* 126 (1), 25-35 (2009).

[21] Slabbekoorn, H. & Halfwerk, W., *Current Biology* 19 (16), R693-R695 (2009).

[22] Habib, L. *et al.*, *J of Applied Ecology* 44 (1), 176-184 (2007).

[23] Kluyver, H.N., *Ardea* 39 (1), 1 - 135 (1951).

[24] Junker-Bornholdt, R. *et al.*, *J Fur Ornithologie* 139 (2), 131-139 (1998).

[25] Slabbekoorn, H. & den Boer-Visser, A., *Current Biology* 16 (23), 2326-2331 (2006).

[26] Mockford, E.J. & Marshall, R.C., *Proc R Soc B* 276 (1669), 2979-2985 (2009).

[27] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[28] Halfwerk, W. & Slabbekoorn, H., *Animal Behaviour* 78 (6), 1301-1307 (2009).

[29] Drent, P.J., *Ardea* 75 (1), 59-71 (1987).

[30] Burnham, K.P. & Anderson, D.R., *Model Selection and Multimodel Inference: A Practical-Theoretic Approach*, 2nd ed. (Springer-Verlag, Berlin, 2002).

[31] Wilkin, T.A. *et al.*, *J of Animal Ecology* 75 (2), 604-615 (2006).

[32] Whittingham, M.J. *et al.*, *J of Applied Ecology* 42 (2), 270-280 (2005).

[33] Garamszegi, L.Z. *et al.*, *Behavioral Ecology* 20 (6), 1363-1375 (2009).

[34] Holveck, M.J. & Riebel, K., *Proc R Soc B* 277 (1678), 153-160 (2009).

[35] Quinn, J.L. *et al.*, *J of Avian Biology* 37 (6), 601-608 (2006).

[36] Leonard, M.L. & Horn, A.G., *Behavioral Ecology* 19 (3), 502-507 (2008).

[37] Steele, C., *Applied Acoustics* 62 (3), 271-287 (2001).

[38] Li, B.G. *et al.*, *Applied Acoustics* 63 (6), 679-691 (2002).

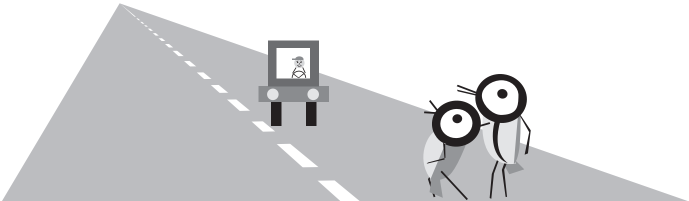
[39] Parris, K.M. & Schneider, A., *Ecology and Society* 14 (1) (2009).

[40] Bucur, V., *Urban Forest Acoustics*. (Springer-Verlag, Berlin, Heidelberg, 2006).

[41] Makarewicz, R. & Kokowski, P., *J. Acoust Soc Am* 122 (4), 2074-2081 (2007).

[42] Laube, M.M. & Stout, R.W., *Transit: Planning, Intermodal Facilities, Management, and Marketing* (1735), 59-69 (2000).

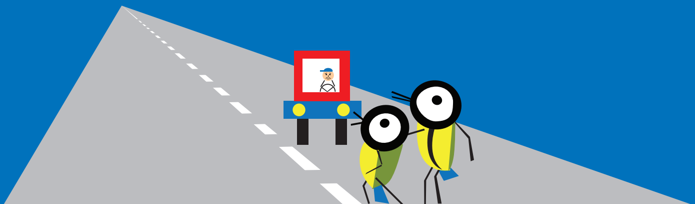
[43] Groot Bruinderink, G.W.T.A. *et al.*, 2002.



Chapter 7

Noise annoys at the community level

An adjusted version of this chapter is published in *Current Biology* as a commentary on Francis *et al.* 2009 (Slabbekoorn & Halfwerk, 2009, 19:R693-695)



ABSTRACT

A new study on the impact of anthropogenic noise on birds takes a behavioral discipline to the level of community ecology: noise can not only harm individual species but also alter species relationships. The new study examined avian communities at noisy and relatively silent natural gas extraction sites, thereby avoiding the typical confounding factors associated with highways or cities. The study not only confirmed that anthropogenic noise can have negative effects on breeding density for several species, but also demonstrated positive effects on other species that seem to benefit from a noise-associated decline in their major nest-predator. Noise may affect predator-prey interactions or heterospecific competition and may thereby have an indirect positive effect species. We describe a case study on nest site competition between two related species, the great tit (*Parus major*) and the blue tit (*Cyanistes caeruleus*). We found great tits to occupy quiet control nest boxes, whereas blue tits were found breeding more often in noisy nest boxes. The most likely explanation for these results are noise avoidance of great tits leading to competitive release for blue tits, who are normally subordinate to the bigger great tits. Our results may explain why blue tits are not, or positively affected by the proximity of a highway. These studies on the impact of noise go beyond the perils for single species and indicate anthropogenic infiltration at community level, but also show that an effect on species interactions may lead to complex, and sometimes counterintuitive, results.

INTRODUCTION

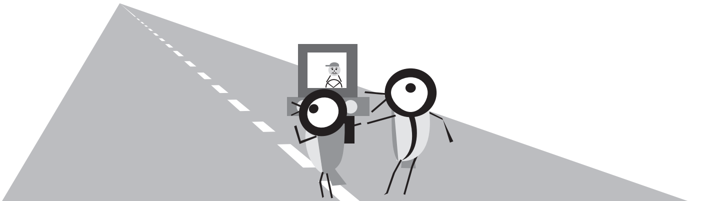
Elevated noise levels through anthropogenic activity is a global phenomenon[1,2] and probably only hearing-impaired people can say they have never experienced it. Noise is so common that most of us are habituated to unnaturally high levels and genuine city-dwellers may even prefer urban loudness above rural quietness. But when the transmission of an important message depends on acoustics, the appreciation of noisy 'soundscapes' changes dramatically. Just imagine a situation in which masking noise renders your ability to communicate the dangers of car approaching at high speed to a pedestrian.

Singing birds depend continuously on acoustics for communicating a message that can be critical to survival in a territory providing food, shelter, and nesting opportunities[3]. Also, mate attraction is typically guided by acoustic signals: female birds often find a male of the right species and of the preferred quality by ear[4,5]. Other important acoustic interactions concern begging by nestlings or fledglings, food and alarm calling, and production of contact calls that can be critical to group cohesion[3]. Being able to hear rustling prey or hunting predators will also heavily affect chances of survival and reproduction, adding to the potential impact of masking noise on individual success and population viability[1,2].

Confounding factors associated with noise

The effect of anthropogenic noise on birds is typically studied in a context of dramatic habitat conversion associated with building roads and cities. Indeed, highways show a negative impact on bird breeding density and diversity, which may be attributed to the road-associated rise in noise level[6,7]. Urbanization leads to the same set of common bird species present in cities everywhere, largely independent of the locality-specific original avifauna[8,9]. This homogenization may also be partly due to urban noise excluding sensitive species and providing opportunity to behaviorally flexible species[10,11]. However, there are many factors that are potentially playing a role in species decline and community change, most notably landscape turnover, but also chemical pollution, visual disturbance by people or car traffic, and introduction of human-associated food (for example, bread and peanuts) or predators (such as cats and dogs). Studies excluding all such confounding factors, either statistically, or experimentally, are required to confirm that anthropogenic noise itself is really harmful to birds[7,12].

Natural areas exploited for soil resources by the gas industry provide



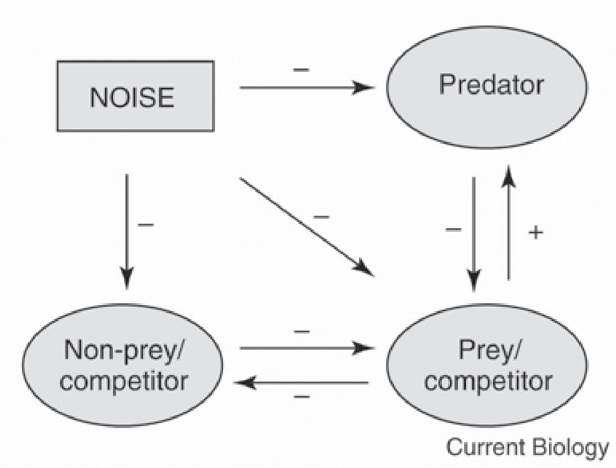


Figure 7.1. A species interaction web for three model bird species, including a predator–prey and a two-competitor relationship. Arrows indicate either negative (–) or positive impact (+) on each other between species, and a negative impact of noise on all three species.

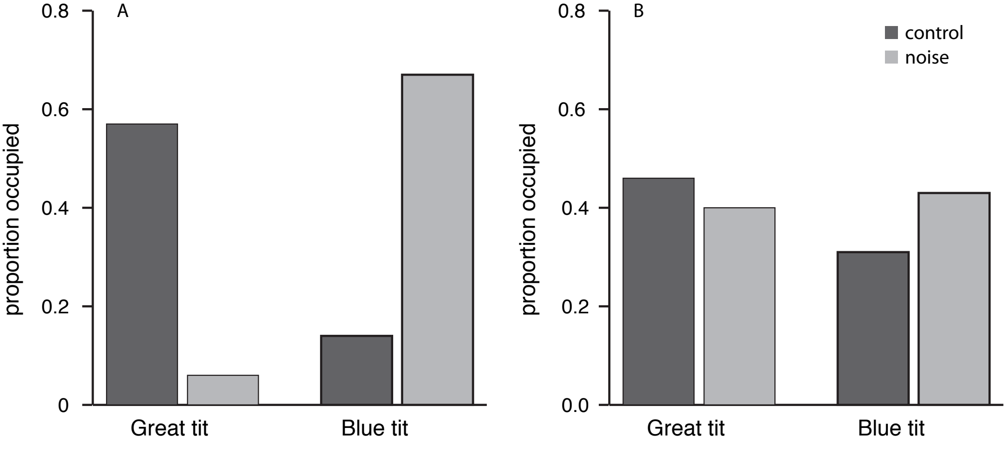


Figure 7.2. Occupancy patterns for two related species that are known to compete over nest sites. The percentage of occupied nest boxes for both great tit and blue tit pairs is shown. (**A)** Only nest boxes that were located inside a great tit territory with a choice between two treatment type nest boxes were included in this analysis. Great tits avoid the noisy nest box when they have choice. Blue tits do not prefer noisy nest boxes, but as they are subordinate to great tits, simply occupy the remaining boxes, as shown in (**B**) in which nest boxes occupied by great tits with a choice of nest box in their territory were excluded from analysis.

an interesting and unique model system to study the impact of noise pollution on birds. Typically, gas extraction stations are numerous and scattered throughout a large geographic area. Interestingly, only a subset of these stations are equipped with compressors that generate a loud low-frequency noise 24/7(13). The decision to place a compressor at a certain site is based on gas well pressure and is made irrespective of above-ground variation in vegetation and other micro-climatic characteristics. Therefore, any difference between noisy compressor stations and relatively silent well pads, in bird density, diversity, or breeding success, can be attributed solely to the impact of noise.

Independent noise impact on avian biodiversity

A few years ago, the first study on this 'natural' experiment was conducted in a boreal mixed woodland forest in northeastern Alberta, Canada. In a single-species study, male ovenbirds (*Seiurus aurocapilla*) were shown to have a 17% reduction in mate attraction probability at noisy compressor sites compared to noiseless well pads[14]. Furthermore, the authors also monitored the avian communities near (100–300 m) and far (400–700 m) from gas extraction stations. Several species revealed the lowest densities in the 'near-noisy' condition, and this condition also turned out to have significantly lower overall breeding densities than 'far-noisy', 'near-quiet', and 'far-quiet' conditions[15].

The study of an impact of anthropogenic noise on avian communities was repeated by an other research group at gas extraction stations in pinyon-juniper woodlands of northwestern New Mexico, USA[13]. In contrast to the earlier study, the analysis was not broken down to monitoring groups that were near and far away from stations, nor was there an overall decline in breeding density for the avian community near noisy compressor sites. Nevertheless, several species were shown to nest at larger distances from the station at noisy sites (monitored within a 400 m radius) compared to noiseless control sites. Interestingly, in this study a significant reduction in species diversity at noisy compressor sites indicated a dramatic change in the avian community which was not reported for the Canadian location.

Noise-dependent changes at the community level

While several species showed an expected decline in breeding density at noisy sites compared to noiseless sites, there were, remarkably, also species that showed the opposite pattern[13]. The authors argued that this noise-associated incline for several small songbird species may be explained by an indirect positive

response through predator-release. The main reason for nest failure across species was nest predation by the Western scrub-jay (*Apheocoma californica*). The jay is also one of the species not doing well in noisy conditions and the probability of depredation turned out to be significantly lower in the noisy sites with less jays. This indirect positive effect may explain why some small songbird species do relatively well at compressor sites, not excluding the possibility of a direct negative impact of noise.

Besides the typical predator–prey relationship, in which high predator numbers negatively affect the prey population and high prey numbers positively affect the predator population (e.g.[16,17]), there could be more relationships pushed out of balance by noise (see Figure 7.1). Although it may not be very obvious in the current model system, two or more species may compete for the same resources, such as nest sites, food sources, or hiding places (e.g.[18,19]). Two such competitor species can negatively affect each other through competitive exclusion (Figure 7.1). Consequently, detrimental effects of anthropogenic noise that hit one species harder than the other may lead to improved conditions for the other through competitive release (see below). Again, this may explain a noise-associated incline in one species (or the lack of a decline) despite a potentially direct negative impact on both competitor species.

CASE STUDY: HETEROSPECIFIC COMPETITION UNDER URBAN NOISE CONDITIONS

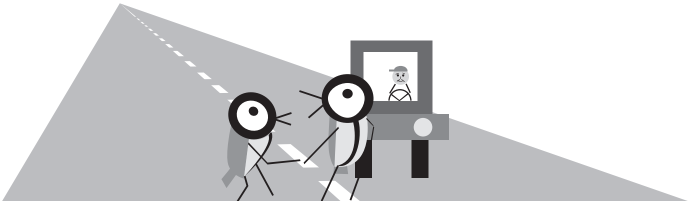
We collected experimental data on the impact of noise on competition over nesting sites by two related tit species. The great tit (*Parus major*) and the blue tit (*Cyanistes caeruleus*) are two European hole-breeding passerines that are known to compete over nest cavities[20,21]. Coexistence negatively affects reproductive success of both species, but the effect is asymmetrical, as great tits are dominant over blue tits and are known to exclude them from nest boxes[21,22]. We tested whether anthropogenic noise affected heterospecific competition by providing artificial nest boxes with and without experimental noise exposure through small in-box speakers (see chapter 5 for details on experimental exposure). This experiment was part of a larger study on the effect of anthropogenic noise on breeding great tits (see chapter 5), but as blue tits also used the boxes, we were able to look at species interactions as a byproduct of the main study.

We provided 78 nest boxes (equal number per treatment) divided over a grid of 10 rows, at two different sites (see for a description of the population chapter 5). A noise or control treatment was randomly assigned to the first nest box in a row and we alternated treatments across the remaining nest boxes of the row. The experiment was conducted between March and May 2010 and started prior to nest building. We regarded a nest box as occupied by either great tit or blue tit once an egg was laid and nest boxes that were taken over after an egg had been laid, or that were occupied by other species (nuthatch or tree sparrow) were left out of the analyses.

We calculated the probability that a nest box was occupied dependent on the treatment for the two tit species separately. Great tits were found significantly more often in a quiet control box (GLM; binomial error distribution, probit link-function; GLM: N = 69; LR = 4.0; $p = 0.047$), whereas blue tits showed a trend in the opposite direction (GLM: N = 69; LR = 3.5; $p = 0.060$). Competition dynamics over nest boxes may change over the breeding season[23], but we did not find occupancies early in the season to differ with late in the season, nor did we found lay date to differ between species (all $p > 0.29$).

Noise seemed to affect nest box choice by great tits, but a large number of birds nevertheless settled for a noisy nest boxes, despite the availability of 10 unoccupied control nest boxes. Some of these nest boxes were occupied by other hole-breeding passerines (5 nuthatches and 1 tree sparrow), but it also suggests that settling for a noisy nest box may outweigh other factors associated with nest box choice.

We had mapped territories of great tits at the start of the noise exposure and found several resident pairs (N = 13) to defend areas with both types of nest boxes available to them. We reran the analysis including only nest boxes that were located in a great tit territory with a choice between treatments and found a strong effect of noise on occupancy for both tit species (Figure 7.2A). Great tits almost exclusively occupied the quiet boxes (GLM: N = 38; LR = 14.5; $p < 0.0001$), suggesting that individuals avoid noise when given a choice. Blue tits that occupied a nest box inside a great tit territory were more often found in noisy nest box (GLM: N = 38; LR = 14.5; $p < 0.0001$), but when we excluded all the nest boxes in our study area that were occupied by great tits from the analysis, the effect of treatment disappeared (GLM: N = 56; LR = 0.5; $p = 0.47$; (Figure 7.2B), which suggests that blue tits did not prefer noisy nest boxes, but simply settled for the nest box that was available to them. Great tit individuals that settled for a noisy nest box did also seem to have no choice, unless they postponed breeding after territoriality ceased during which they would have been able to secure one of the remaining quiet boxes.



DISCUSSION

The integration of the behavioral study of noise impact on animal communication with community ecology reveals clearly how much anthropogenic noise can affect the ecological integrity of whole ecosystems. The new insights not only confirm that noise can be harmful, independent of confounding factors, but also tell us that we should not be surprised to find inconsistent results for single species when studied in different communities.

Community ecology involves direct and indirect effects in species relationships; the associated complexity is a well-known problem, for example with multi-level trophic cascades or multi-species competitive interactions (e.g.[24-26]). There are some community-level studies addressing human impact on birds, for example showing a shift from specialist to generalist species adjacent to walking trails[27]. However, the unique sampling opportunities unintentionally provided by the gas industry yield an interesting tool to study avian community ecology in a way similar to classic fertilizer experiments in plants[28,29].

Our experimental case-study showed that great tits avoid settling in a noisy nest box and suggests that blue tits may indirectly benefit from anthropogenic noise through heterospecific competition release. We know that breeding densities of blue tits increase when great tits are experimentally excluded from an area[21] and that an increase in blue tit abundance can be related to a decrease in great tit numbers close to highways[30]. However, two other studies that assessed abundance or breeding patterns of blue and great tits did not find an effect of highway vicinity[31,32] and when calculated noise levels were related to the abundance of blue tits, one study even found a negative correlation for this species[31]. This indicates that an impact of traffic noise on (breeding) densities and heterospecific competition as confirmed by our experimental approach does not always translate to observational data with many unidentified confounding factors associated with noise and highways.

From now on, we should realize that noise impact studies can involve complex relationships and that a thorough insight into local community ecology is required. This certainly means that translating data to conservation implications will be more challenging, but makes it all the more important.

REFERENCES

[1] Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

[2] Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

[3] Bradbury, J.W. & Vehrencamp, S.L., *Principles of Animal Communication*. (Sinauer Associates, Sunderland, MA, 1998).

[4] Marler, P. & Slabbekoorn, H., *Nature's music: The Science of Birdsong*. (Elsevier Academic Press, 2004).

[5] Catchpole, C.K. & Slater, P.J.B., *Bird Song: Biological themes and Variations*. (Cambridge University press, Cambridge, 2008).

[6] Reijnen, R. & Foppen, R., in *The Ecology of Transportation: Managing Mobility for the Environment*, edited by J. Davenport & J.L. Davenport (Springer-Verlag, Heidelberg, 2006), pp. 255–274.

[7] Halfwerk, W. *et al.*, *J of Applied Ecology* 48 (1), 210-219 (2011).

[8] Clergeau, P. *et al.*, *Biological Conservation* 127 (3), 336-344 (2006).

[9] McKinney, M.L., *Biological Conservation* 127 (3), 247-260 (2006).

[10] Slabbekoorn, H. & Peet, M., *Nature* 424 (6946), 267-267 (2003).

[11] Halfwerk, W. & Slabbekoorn, H., *Animal Behaviour* 78 (6), 1301-1307 (2009).

[12] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[13] Francis, C.D. *et al.*, *Current Biology* 19 (16), 1415-1419 (2009).

[14] Habib, L. *et al.*, *J of Applied Ecology* 44 (1), 176-184 (2007).

[15] Bayne, E.M. *et al.*, *Conservation Biology* 22 (5), 1186-1193 (2008).

[16] Nystrom, J. *et al.*, *Ibis* 147 (3), 587-597 (2005).

[17] Angerbjorn, A. *et al.*, *J of Animal Ecology* 68 (1), 34-49 (1999).

[18] Kemmerer, E.P. *et al.*, *Forest Ecology and Management* 255 (7), 2094-2102 (2008).

[19] Kappes, J.J. & Davis, J.M., *Condor* 110 (3), 441-449 (2008).

[20] Minot, E.O. & Perrins, C.M., *J of Animal Ecology* 55 (1), 331-350 (1986).

[21] Dhondt, A.A. & Eyckerman, R., *Ecology* 61 (6), 1291-1296 (1980).

[22] Kempenaers, B. & Dhondt, A.A., *Ornis Scandinavica* 22 (1), 73-75 (1991).

[23] Both, C., *ARDEA* 92 (1), 107-111 (2004).

[24] Batzer, D.P. *et al.*, *Wetlands* 20 (2), 307-312 (2000).

[25] Van Bael, S.A. & Brawn, J.D., *Oecologia* 143 (1), 106-116 (2005).

[26] Berger, K.M. *et al.*, *Ecology* 89 (3), 818-828 (2008).

[27] Miller, S.G. *et al.*, *Ecological Applications* 8 (1), 162-169 (1998).

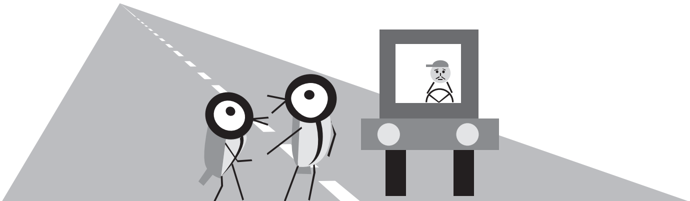
[28] Bakelaar, R.G. & Odum, E.P., *Ecology* 59 (4), 660-665 (1978).

[29] Inouye, R.S. & Tilman, D., *Ecology* 76 (6), 1872-1887 (1995).

[30] Rheindt, F.E., *J Fur Ornithologie* 144 (3), 295-306 (2003).

[31] Reijnen, R. *et al.*, *J of Applied Ecology* 32 (1), 187-202 (1995).

[32] Junker-Bornholdt, R. *et al.*, *J Fur Ornithologie* 139 (2), 131-139 (1998).



Chapter 8

Summary and general discussion

Urbanization and the associated rise in noise levels affect many animals in their struggle to survive and reproduce[1,2] . Animals have been found to respond to urban noise by changing their communication signals, or by avoiding noisy areas during breeding[1,3] . For instance, great tits in cities have faster songs that are also higher in frequency compared to their forest counterparts[4] and urban nightingales sing louder songs during noisy weekdays compared to quiet weekends[5] . However, the precise causes and consequences of these noise-dependent behavioral adjustments are far from being understood[6] .

This thesis addresses the impact of anthropogenic noise on avian communication and its reproductive consequences by using carefully conducted field experiments in combination with breeding data obtained from an area with varying noise levels (see for an overview Figure 1.1). The focus of the thesis is on communication between members of a breeding pair, looking at the impact of noise on the sender's side, the receiver's side and the interaction between these two. The sender's side is experimentally exposed to noise to assess the mechanism underlying noise-dependent frequency use. Furthermore, the receiver's side is experimentally exposed to noise to assess the impact of song frequency change on signal detection and signal attractiveness and to examine the role of females in providing noise-dependent feedback to singing males. Finally, the consequences of breeding in noise are addressed in a field study relating local noise levels to long-term breeding data and by providing noise-exposed nest boxes to birds during the period of nest-site choice.

Studying the mechanisms of noise-dependent frequency use

The impact of noise on animal communication systems depends on the overlap in acoustic energy, in time and frequency, between signal and noise (i.e. masking). To avoid urban noise interference, birds can change the frequency of their songs by upward shifting of song elements or their whole song, or by selective song type use when they possess a repertoire[7] . We exposed singing male great tits (*Parus major*) during the dawn chorus to artificial low- and high-frequency noise and found song type duration to be affected by the amount of noise masking (chapter 2). Males sang low song types for shorter duration in low-frequency noise compared to high song types and showed an opposite trend when confronted with high-frequency noise. Consequently, birds singing a relative low song type, switched earlier to another, on average higher song type, although this was not specifically the optimal song type for masking reduction.

As an additional control, we exposed singing males to a white noise treatment, with a flat amplitude level across all frequencies. We did not find birds to change their song frequencies consistently, but we did find an impact on song rate, mainly because some individuals ceased singing. This result suggests that there could be performance constraints on singing in noise, or point to the importance of acoustic feedback (see below).

Male great tits could have assessed the spectral overlap with their songs directly, or they could have monitored their own song output as a feedback mechanism to adjust song type bout duration (chapter 2). Monitoring of own signal-to-noise ratios may have caused great tits to increase song amplitude during noise exposure (a taxonomically widespread phenomenon, known as the Lombard effect), which could have increased song performance or energy demands and led to an early switch to another song type to reduce motor fatigue[8] . If such auditory feedback mechanism is masking-dependent, it could explain the increased use of high-frequency songs in urban noise (chapter 3). Singing males may also have relied on social feedback, from males during matched counter-singing contests, or from females during acoustic dawn chorus interactions (chapter 4 & 5). Feedback from noise-exposed females did not lead to a change in their mate's song frequency during the dawn chorus, but we did find males to sing from a closer perch in response to the experimental treatment (chapter 5).

Consequences of communicating in noisy urban environments

Urban noise causes males to use high-frequency songs, which probably increases signal detection, but may come at the cost of reduced attractiveness to females. Vocal performance can be related to male size or condition, and females could favor low songs, when the use of these songs reflects bigger, healthier or stronger males[9] . We studied great tit vocal performance during the dawn chorus ritual and found males to peak with their lowest songs at the height of female fertility. Furthermore, females with social mates singing relatively high-frequency songs from their repertoire turned out to be more involved with extra-pair copulations than those with social mates that hit their low notes more often (chapter 4). We did not find other song parameters to vary with fertility or paternity, except for the start of the dawn chorus, which increased progressively with laying stage. The moment of female nest box emergence also increased across egg-laying, but more interestingly, we found very early emergence to be related to extra-pair copulation engagement of females.

Males may only be able to rely on very low songs to secure female fidelity under poor light conditions, but these songs may suffer increased loss of detection in urban noise. We examined this apparent trade-off in signal efficiency experimentally by exposing females inside their nest boxes to artificial urban noise and found low-

TO BE LOVED OR TO BE HEARD IN A NOISY WORLD

Male Great Tits, as well as other male birds found in cities, are faced with a dilemma: how can they make sure they are heard above the noise of people and traffic? Results from earlier research suggested that they can achieve this by singing their songs at higher pitch. In chapter 4 we show that this is an effective approach for being heard better, but the downside could be that females find these songs less impressive, resulting in an modern trade-off between signal detection and signal attractiveness.

frequency songs to suffer reduced attractiveness, favoring high-frequency songs in noise (chapter 4). These results suggest that high-quality males have lost the potential to stand out acoustically in noisy urban environments by using low-frequency songs and that females, living under these conditions, may have shifted their preferences towards high-frequency songs, or towards songs reflecting other characteristics of quality-related vocal performance.

Anthropogenic noise can also affect interactions between members of a breeding pair, which may have consequences for reproductive investments by males and females[10] . We exposed females inside their nest box to artificial urban noise during the dawn chorus, while leaving the singing male unaffected, to test for an impact on intra-pair communication at the receiver side. We found females to respond later to male song in the noisy condition (chapter 5). Furthermore, we found males from the noise treatment group to sing closer to the nest box within several days of exposure, which led to higher song amplitudes at the position of the nest box. The increased song amplitudes restored the inside signal-to-noise ratios and consequently brought back communication to equal levels between treatment and control groups. These results show the importance of intra-pair communication and provide yet another strategy of noise-dependent signaling in birds. Males may change spatial singing to increase male-female efficiency in urban noise, although we have little insight into potentially negative consequences of this behavior, such as, a decrease of male-male communication or an increase in predation risk, associated with song post exposure.

Reproductive consequences of living in a noisy world

Noise can have a negative effect on reproductive success and ultimately cause bird breeding populations to decline. Noise can affect the individual directly by disturbance, deterrence, and masking or indirectly by changing interactions with conspecifics as well as heterospecifics[2,11] . We studied the impact of anthropogenic noise on avian reproductive success in a nest box population situated close to a highway with high traffic load (A2 in the Netherlands, between Utrecht and Arnhem). We monitored fluctuations in traffic noise throughout the great tit's breeding season and found a significant temporal and spectral overlap over a large spatial range (chapter 6). Noise levels were high when singing activity peaked and remained high throughout most of the day. Furthermore, noise levels changed with season as well as traffic load (noise levels were higher during weekdays compared to weekends). High frequencies attenuate faster compared to low frequencies, especially in forests[12] , but noise levels in the frequency range overlapping song of the great tit were nevertheless detectable throughout the whole population.

We related temporal, spatial and spectral noise patterns to available long-term breeding data. Traffic noise levels were negatively related to reproductive success through an independent impact on clutch size as well the number of produced fledglings (chapter 6). The impact was best explained by seasonal overlap between noise and the start of egg-laying, as well as by a spectral overlap between song and noise. The negative correlation could have been directly caused by an impact of noise on individual stress levels, or through the masking impact of noise on the communication between male and female, or between parent and offspring in great tits. Alternatively, the negative correlation could be caused by social-ecological factors related to interactions with individuals of own and different species.

Traffic noise fluctuations may result in a heterogenic breeding distribution through an effect on the interaction between individuals of different quality. For instance, high-quality birds who can produce large clutches could avoid noisy areas, which will subsequently be occupied by low-quality individuals, leading to a correlation between reproductive success and noise levels. Anthropogenic noise can also affect interactions between species, altering predator-prey interactions or heterospecific competition. We tested the latter possibility by providing noise-exposed nest boxes prior to nest site settlement in an area occupied by two competing species, the great tit and the blue tit, and found a species-specific nest box occupancy pattern (chapter 7). Great tits were more often found to breed in quiet control nest boxes, whereas blue tits settled more for noisy nest boxes, most likely because these boxes were released from competition with the larger, dominant great tits. These results show that noise affects breeding distribution of individual birds, which ultimately can alter processes at the community level.

Implications for other species

The great tit is one of the most abundant species throughout Europe and has been shown to breed readily in cities as well as in the proximity of busy highways. Clearly, great tit populations are not under threat of extinction through a negative impact of noise. However, several issues addressed in this thesis may be valuable to predict an impact of noise for other species, whether or not they are locally or globally threatened at the moment. Furthermore, even great tits show reduced breeding output in relation to noise (chapter 6), and their behavior is affected at low levels of song masking (less than 6 dB, chapter 5) which shows that having some prerequisites to adapt may not be sufficient to cope completely with high levels of anthropogenic noise.

A first step to make predictions about noise impacts on other species would be to determine the set of characteristics important in adaptation to anthropogenic noise, using great tits as a yardstick, and to assess which species lack one or more of these characteristics. Focusing on the topics addressed in this thesis, it seems that, 1) singing low-frequency songs, 2) lacking signal flexibility, 3) relying on long-distance communication, are key ingredients for susceptibility to noise masking. The latter issue may be especially important for conservation as threatened species are typically found at relatively low-densities. Those species that have to communicate over very large distances with sound will be disproportional affected by anthropogenic noise.

A second step would be to determine the distance from a source over which noise can affect species, incorporating insights from the first step. In this thesis, great tit reproductive behavior was found to be most affected by noise in the 2-kHz range, overlapping the lower part of this species song (chapter 6). At our highway site, noise in the 2-kHz range could be detected at distances of 400 – 800 m from the centre of the highway (chapter 6), which may correspond to the upper limit at which both behavior and reproduction of great tits are affected. Species that use similar frequency range for communication as great tits are will probably be affected over a similar distance, whereas species that are affected by noise in a lower frequency range are likely to be affected over larger distances.

Potentially affected species

Vocalizing at low frequencies has been found to be an important predictor of an impact of anthropogenic noise[13,14] . Among birds that show reduced numbers close to noisy structures, such as highways or gas compressor stations are various species of grosbeak, nuthatch, cuckoo, owl, pigeon, oriole and sage-grouse[11,15-18] , all of which vocalize at low frequencies (majority of their song < 2 kHz). Several of these taxa contain globally threatened species in areas with high anthropogenic activity (grouse, owls, pigeons) and it is likely that these species are severely affected by anthropogenic noise over much larger distances than great tits[19] , especially when noise is not obstructed by vegetation, or when a noise source is located opposite the predominant wind direction (chapter 6).

Other characteristics of acoustic behavior that may determine whether species will be affected by anthropogenic noise are signal plasticity or other constraints on signal change. Taxonomic groups that contain currently threatened species, such as tyrant flycatchers, vireos, pipits and wood- and leaf-warblers have been found to show reduced breeding numbers in areas with high levels of low-frequency anthropogenic noise, despite their relatively high frequency songs. The effect may be related to a lack in frequency plasticity (tyrant-flycatchers;[20]), or constraints on song attractiveness through sexual selection and extra-pair paternity (wood-and leaf-warblers;[21,22-24]).

Finally, migratory bird species may be more affected by noise compared to resident species for several reasons. Migratory birds typically have to broadcast their song over a range as wide as possible to attract overflying females[21] and any reduction in signal detection may negatively affect pairing success[15]. Migratory species are also more time constraint to attract mates, especially in forests, as breeding has to coincide with the pronounced peak in food availability in these habitats and because migratory birds have already difficulties catching up with phenologic shifts due to climate change[22,23]. Migratory species of forested habitats have been shown to be affected by anthropogenic noise[15,17], including several species which have shown strong population declines over the last two decades throughout Europe, including the Netherlands[23], and including a non-songbird species, the common cuckoo (*Cuculus canorus*), that probably lacks sufficient acoustic plasticity and also vocalizes at very low frequencies.

Future directions

Urbanization is expected to increase in the coming decades and it is unlikely that the world will get quieter soon. More traffic will also move into natural areas, leading to a global increase in anthropogenic noise levels, despite the current trend towards electric or hybrid transport engines. The need to understand the nature and magnitude of potential problems for animals, in air and underwater, will therefore only grow in the near future. The current thesis provides some initial answers and describes new approaches to address the most urgent questions with respect to its impact on birds. However, it also shows that studying the consequences of communicating under noisy urban conditions requires more detailed knowledge on causes related to noise-dependent signal strategies, in particular on the mechanism underlying the use of high-frequency songs in response to low-frequency noise. Furthermore, more work on signal evolution and sexual selection is needed, as well as on long-term fitness consequences of living under noisy conditions.

The role of social feedback in noise-dependent frequency use may be assessed in a playback experiment with singing males, mimicking matching contests with high and low song types, either in quiet and noisy areas, or by using artificial urban noise. Additionally, an interactive experiment with playback of calls from within the nest box towards males, in the absence of females (temporarily removed), would be an ideal approach to study the role of feedback-dependent singing behavior. Whether song type switching by male great tits is related to song amplitude and motor fatigue may be studied in a respiratory chamber[24], but it would be better to do this in the field, during the peak in territory defense and female fertility, as assessment of song performance constraints requires highly motivated birds. Although challenging, heart rate telemetry, which has been successfully applied in a similar-sized passerine, may be used in combination with urban noise exposure to singing great tits[25] . Furthermore, masking-dependent motor fatigue may also occur in species that do not display their songs with eventual variety and these species may be exposed with low-frequency, as well as high-frequency noise to test whether song frequencies change immediately with a rise in amplitude, or after some time, as suggested for noise-exposed great tits.

The consequences in terms of sexual selection pressures on particular song characteristics may be studied by comparing female preference or male aggression in birds from noisy urban, as well as quiet forest populations. A playback experiment using songs with varying levels of vocal performance, such as song frequency, song consistency, or singing speed,[26-28] , may be designed to test the role of noise in sensory drive. Furthermore, the extra-pair paternity rates may be correlated to song behavior and local noise levels to gain insight into the process of signal evolution in rapidly changing environments.

Finally, long-term experimental noise exposure to males in the field is required to get a full understanding of the consequences of singing high songs, by looking at production constraints, as well as a potential reduction of signal strength in territory defense or female attraction. Similarly, both members of a breeding pair would have to be exposed at different periods of the breeding cycle, to understand the mechanisms underlying the impact of anthropogenic noise on avian reproductive success. The female may be exposed inside the nest box, while the male is simultaneously exposed to noise in the proximity of the nest box. However, such an experiment may only start when females have chosen a particular nest site, whereas an impact of noise may arise prior to this, for instance during pair formation, a process for which surprisingly little is known in great tits. To assess fitness consequences of noise therefore requires a solid experimental approach throughout the breeding season and ultimately throughout an individual's life and may perhaps be achieved by equipping bird's with headphones, a procedure which has already been used in the lab[29] and which, in time, may be applied in the field as well.

Concluding remark

The alteration of natural areas into urban habitat at an unprecedented global scale may be viewed as a natural experiment that will generate new insights on environmental causes for evolutionary change. However, understanding the individual components of these processes ultimately requires a true experimental approach, excluding confounding variables, such as the ones described in this thesis. These experiments preferably mimic the ecological setting in which animals and their behaviors have evolved, which can often only be achieved in the field, although manipulation of the sensory environment can be methodologically challenging. Finally, we can observe animals in our own backyard and as more and more people will live in similar urban habitat it is likely that studies on urban ecology and evolution will continue to grasp public attention, but they should also raise awareness of the consequences of human behavior.

REFERENCES

[1] Barber, J.R. *et al.*, *TREE* 25 (3), 180-189 (2009).

[2] Slabbekoorn, H. & Ripmeester, E.A.P., *Molecular Ecology* 17 (1), 72-83 (2008).

[3] Brumm, H. & Slabbekoorn, H., in *Adv in the Study of Behavior, Vol 35* (2005), Vol. 35, pp. 151-209.

[4] Slabbekoorn, H. & den Boer-Visser, A., *Current Biology* 16 (23), 2326-2331 (2006).

[5] Brumm, H., *J of Animal Ecology* 73 (3), 434-440 (2004).

[6] Warren, P.S. *et al.*, *Animal Behaviour* 71, 491-502 (2006).

[7] Patricelli, G.L. & Blickley, J.L., *Auk* 123 (3), 639-649 (2006).

[8] Lambrechts, M. & Dhondt, A.A., *Animal Behaviour* 36, 327-334 (1988).

[9] Gil, D. & Gahr, M., *TREE* 17 (3), 133-141 (2002).

[10] Hall, M.L., *Adv in the Study of Behavior, Vol 40* 40, 67-121 (2009).

[11] Francis, C.D. *et al.*, *Current Biology* 19 (16), 1415-1419 (2009).

[12] Richards, D.G. & Wiley, R.H., *Am. Nat.* 115 (3), 381-399 (1980).

[13] Francis, C.D. *et al.*, *PLoS ONE* 6 (11), e27052 (2011).

[14] Herrera-Montes, M.I. & Aide, T.M., *Urban Ecosystems* 14 (3), 415-427 (2011).

[15] Bayne, E.M. *et al.*, *Conservation Biology* 22 (5), 1186-1193 (2008).

[16] Doherty, K.E. *et al.*, *J of Wildlife Management* 72 (1), 187-195 (2008).

[17] Reijnen, R. *et al.*, *J of Applied Ecology* 32 (1), 187-202 (1995).

[18] Goodwin, S.E. & Shriver, W.G., *Conservation Biology* 25 (2), 406-411 (2011).

[19] Copeland, H.E. *et al.*, *PLoS ONE* 4 (10), e7400 (2009).

[20] Francis, C.D. *et al.*, *Proc R Soc B* 278 (1714), 2025-2031 (2011).

[21] Catchpole, C.K. & Slater, P.J.B., *Bird Song: Biological themes and Variations*. (Cambridge University press, Cambridge, 2008).

[22] Both, C. & Visser, M.E., *Nature* 411 (6835), 296-298 (2001).

[23] Both, C. *et al.*, *Proc R Soc B* 277 (1685), 1259-1266 (2010).

[24] Oberweger, K. & Goller, F., *J of Experimental Biology* 204 (19), 3379-3388 (2001).

[25] Bisson, I.A. *et al.*, *Proc R Soc B* 276 (1658), 961-969 (2009).

[26] Podos, J., *Nature* 409 (6817), 185-188 (2001).

[27] Rivera-Gutierrez, H.F. *et al.*, *Biology Letters* 7 (3), 339-342 (2011).

[28] Rivera-Gutierrez, H.F. *et al.*, *Animal Behaviour* 80 (3), 451-459 (2010).

[29] Osmanski, M.S. & Dooling, R.J., *J. Acoust Soc Am* 126 (2), 911-919 (2009).

Jac P. Thijsse had meer dan een eeuw geleden al oog voor veranderingen in het gedrag van merels in de stad Amsterdam:

“Zijn zang is maar zoo zoo. Doch buiten zijn er ook merels, die slecht zingen. Ik twijfel er evenwel niet aan, of deze stadsvogels zullen in den loop der tijden alle anders gaan zingen en zich anders gaan gedragen, dan vogels van het vrije veld. De stadsornithologen zullen hierover binnenkort interessante dingen te vertellen hebben.”

Uit ‘*Het intieme leven der vogels*’, 1906.

Nederlandse samenvatting

De wereld verstedelijkt in een snel tempo. Overal verschijnen nieuwe gebieden, zoals steden en industriegebieden, die weer onderling verbonden zijn met wegen, treinlijnen en vliegroutes. Deze verstedelijking gaat gepaard met een toename van achtergrondlawaai, voornamelijk afkomstig van verkeer en industrie. Dit kan voor allerlei diersoorten mogelijk problemen opleveren. Veel dieren vertrouwen immers op hun gehoor om te overleven en op akoestische communicatie om tot voortplanting te komen. Het voortbestaan van bepaalde diersoorten zou dus verstoord kunnen worden door lawaai afkomstig van menselijke activiteiten.

Verschillende studies hebben laten zien dat soorten in lawaaiige gebieden achteruit gaan. Dit bedreigt de biodiversiteit. De onderliggende redenen voor deze bevindingen zijn tot nu toe echter onduidelijk gebleven. Tegelijkertijd laten studies zien dat dieren op allerlei manieren hun gedrag veranderen als ze worden blootgesteld aan lawaai. Vogels op locaties met hoge lawaainiveaus zingen bijvoorbeeld anders; op een manier waarmee de kans op detectie door partners of rivalen vergroot wordt. Echter, of een verandering van zang voldoende is om alsnog gehoord te worden door soortgenoten en of dat voldoende is om de negatieve effecten op het broedgedrag teniet te doen, is tot nu toe weinig onderzocht. Daarnaast zijn de meeste gegevens over individuele aanpassingen aan lawaai afkomstig uit laboratoriumstudies, terwijl het begrijpen van de invloed van lawaai op het individu, op de populatie en uiteindelijk op de gemeenschap vraagt om veldonderzoek, waarbij gedrag en ecologische omstandigheden worden geïntegreerd.

Dit proefschrift behandelt de gevolgen van lawaaiproductie door de mens op de communicatie en op de voortplanting van de koolmees (*Parus major*). Het zwaartepunt ligt bij de communicatie binnen een broedpaar, waarbij gekeken wordt naar de invloed van lawaai op het zingende mannetje (de zender van de boodschap), het luisterende vrouwtje (de ontvanger van de boodschap) en de interactie tussen deze beide. Zenders zijn blootgesteld aan lawaai om te onderzoeken of en op welke manier koolmezen hun zang aanpassen. Vrouwtjes zijn blootgesteld aan lawaai om te onderzoeken hoe ontvangers reageren op een verandering in zang onder verschillende omstandigheden en om te kijken of vrouwtjes aanwijzingen kunnen geven, waarmee de mannen zich het beste kunnen aanpassen aan lawaai. En tot slot is de invloed van verkeerslawaai op het broedgedrag van vogels onderzocht in een veldstudie door experimenteel gemanipuleerde lawaai-nestkasten aan te bieden.

Hoe passen vogels hun zang aan?

Het effect van lawaai op communicatie hangt af van de overlap in akoestische energie tussen signaal (zang) en ruis (lawaai), een fenomeen dat bekend staat als ‘maskering’. Lawaai geassocieerd met steden en

snelwegen is veelal laag van toon en vogels op lawaaiige plekken kunnen voorkomen dat hun zang gemaskeerd wordt door onder andere hoger te gaan zingen. Om dit te bereiken, kunnen vogels een gedeelte van hun zang of een geheel zangtype opschuiven naar een hoger frequentie bereik. Of ze kunnen een ander (en hoger) zangtype zingen als ze beschikken over een repertoire van verschillende liedjes.

Wij hebben zingende mannen blootgesteld aan twee typen kunstmatig lawaai om te onderzoeken wat het mechanisme is dat koolmezen gebruiken om hoog te zingen op lawaaiige plekken (zie hoofdstuk 2). Tijdens lawaai dat vooral laag van toonhoogte was, zongen koolmezen gemiddeld hoger. Terwijl ze tijdens omgekeerd lawaai (dus vooral hoog in toon) gemiddeld juist lager zongen. Deze verandering werd voornamelijk veroorzaakt door die individuen die tijdens het lawaai van zangtype veranderden.

Koolmeesmannen hebben gemiddeld 2 – 6 verschillende zangtypen in hun repertoire die onderling sterk van toonhoogte kunnen verschillen. We vonden dat, wanneer een zangtype sterk gemaskeerd werd door lawaai, een individu sneller overstapte op een ander zangtype. Als gevolg hiervan werden met laag lawaai hoge liedjes langer gezongen, terwijl met hoog lawaai het omgekeerde het geval was (hoofdstuk 2). Dus, door de duur dat een bepaald zangtype gezongen wordt te verlengen of te verkorten kan een koolmees de gemiddelde toonhoogte van zijn zang veranderen.

Een individu kan zijn zang aanpassen door naar zichzelf te luisteren of door gebruik te maken van feedback van andere individuen. Als de signaal-ruis-verhouding van de eigen zang onder een bepaald niveau komt, kan een vogel besluiten van zangtype te wisselen. Een individu kan ook het volume van zijn zang verhogen (een algemeen principe, bekend als het Lombard-effect). Als hij hierdoor eerder uitgeput raakt dan kan dat er ook voor zorgen dat hij van zang verandert (hoofdstuk 3). Zingende mannen kunnen ook gebruik maken van sociale feedback, bijvoorbeeld door de effectiviteit van een zangtype tijdens vocale interactie met een naburige rivaal te bepalen aan de hand van de reactie van die rivaal. Daarnaast kunnen vrouwen ook feedback geven (hoofdstuk 4) en hoewel we niet vonden dat mannen hoger gingen zingen als hun vrouwen vanuit een lawaaiige nestkast zaten te luisteren en terug te roepen, vonden we wel dat deze mannen dichterbij gingen zitten zingen (hoofdstuk 5). Hiermee konden ze op een andere manier de communicatie herstellen.

Gevolgen van aanpassen aan lawaai

Wanneer vogels hoger gaan zingen door lawaai afkomstig van menselijke activiteiten zorgt dat ervoor dat ze beter hoorbaar zijn, maar dat kan wellicht ten koste gaan van de aantrekkelijkheid voor vrouwen.

Bij veel diersoorten vallen vrouwen namelijk voor lage noten, vermoedelijk omdat laag vaak betekent dat een mannetje groot, sterk, of beide is. We hebben de zangprestaties van koolmeesmannen over het broedseizoen gevolgd en vonden dat mannen gemiddeld het laagst zingen als hun partner het meest vruchtbaar is. Daarnaast vonden we dat vrouwen, die een partner hadden die gemiddeld hoger zong, vaker vreemd gingen (hoofdstuk 4). Ook interessant, vrouwen die vreemd gingen, bleken tijdens hun vruchtbare periode een stuk vroeger uit de nestkast te komen. Mogelijk omdat het toen nog zo donker was dat ze ongezien naar een buurman konden vliegen om te paren?

Dat vrouwen die vreemd gaan in het donker naar de buurman vliegen, suggereert dat mannen voor een groot deel op hun zangkwaliteiten moeten rekenen om te voorkomen dat hun partners vreemdgaan. Echter, het gebruik van hoge zangtypes in lawaaiige urbane gebieden kon wel eens conflicteren met het voorkomen van overspel. Wij onderzochten deze mogelijke tegenstelling door vrouwen in de nestkast bloot te stellen aan lawaai en vervolgens hun reactie te scoren op hoge en lage zangtypes van hun partner. We vonden dat lage zangtypes hun aantrekkingskracht verloren in lawaai en dat hoge zangtypes het beste presteerden (hoofdstuk 4). Deze resultaten suggereren dat koolmeesmannen van hoge kwaliteit in stedelijke gebieden niet meer de mogelijkheid hebben om zich met lage zang te onderscheiden van andere individuen. Verder moeten vrouwen waarschijnlijk hun voorkeur verschuiven naar hoge tonen of naar andere zangeigenschappen die informatie over de kwaliteiten van de zender verschaffen.

Antropogeen geluid kan ook van invloed zijn op interacties binnen een broedpaar, hetgeen gevolgen kan hebben voor reproductieve investeringen van zowel mannen als vrouwen. We stelden vrouwen in de nestkast bloot aan kunstmatig verkeerslawaai rond zonsopkomst, wanneer een broedpaar veelvuldig communiceert. We vonden dat vrouwen in lawaai veel later reageerden op de zang van hun eigen mannetje (hoofdstuk 5). Dit effect van lawaai was echter al na twee dagen verdwenen en viel samen met een toename in signaal-ruis-verhouding ter hoogte van de nestkast. Dit kan op drie manieren worden veroorzaakt door een individu: harder zingen, hoger zingen of dichterbij zingen.

We vonden niet dat mannen hoger gingen zingen in reactie op veranderde respons van vrouwen in lawaaikasten, maar wel dat mannen dichterbij zaten te zingen na drie dagen van experimentele blootstelling. Deze resultaten tonen het belang aan van de communicatie tussen leden van een broedpaar en geven ook aan dat vogels alternatieve strategieën kunnen gebruiken om in lawaai te communiceren. Koolmezen kunnen het gebruik van hun zangposten aanpassen in lawaai om de communicatie met hun eigen vrouwtje te verbeteren, maar we hebben te weinig zicht op de gevolgen voor hun reproductief succes. Het zou bijvoorbeeld ten koste kunnen gaan van het verdedigen van het territorium met zang, of de kans op predatie verhogen.

Gevolgen voor het broedgedrag

Lawaai kan een negatief effect hebben op het reproductief succes van individuen en kan uiteindelijk tot afname van vogelpopulaties leiden. Lawaai kan vogels verstoren, afschrikken, belangrijke signalen maskeren, of indirect de interacties met soortgenoten of andere soorten beïnvloeden. We bestudeerden de gevolgen van antropogeen lawaai op het reproductief succes van vogels in een nestkastpopulatie naast een drukke snelweg (A2, tussen Utrecht en Arnhem). We namen dag en nacht geluidsniveaus op gedurende het broedseizoen en vonden dat het vrijwel altijd lawaaiig is over een groot gebied als vogels actief zijn. We vonden dus niet een duidelijke piek in lawaainiveaus tijdens de spits, wat waarschijnlijk te maken heeft met een afname in de gemiddelde snelheid als het aantal auto's toeneemt. We vonden ook dat lawaai in het hoge frequentie bereik sneller afnam naarmate we verder van de snelweg het geluid opnamen en naarmate de temperatuur steeg.

We koppelden de fluctuaties in lawaainiveaus aan de verzamelde broedgegevens van de afgelopen 15 jaar en vonden dat lawaai een negatieve invloed had op het broedsucces (hoofdstuk 6). Koolmezen op lawaaiige plekken legden gemiddeld minder eieren en produceerden gemiddeld minder jongen dan koolmezen in stillere delen van het gebied. De relatie tussen lawaai en broedgedrag kon het best verklaard worden als we variatie in het seizoen en variatie met betrekking tot frequentiebereik meenamen in onze statistische modellen. Lawaai in april verklaarde sterk de afname in het aantal jongen dat werd grootgebracht, terwijl lawaai dat overlapt met het lage gedeelte van de zang van de koolmees het beste verklaarde waar koolmezen minder eieren legden (hoofdstuk 6). Deze gegevens suggereren dat de maskerende werking van lawaai op de zang van de koolmees er voor zorgt dat vrouwen minder eieren produceren. Een mogelijk, andere verklaring zou kunnen zijn dat individuen van hoge kwaliteit de lawaaiige gebieden vermijden, waardoor individuen van lage kwaliteit hier meer kans hebben om tot broeden te komen.
Als vrouwen van lage kwaliteit gemiddeld minder eieren leggen dan kan dat ook de negatieve relatie met het lawaai niveau verklaren.

Lawaai kan ook de interacties tussen soorten beïnvloeden. De verhouding tussen roofdieren en hun prooi kan verstoord worden of de competitie met andere soorten kan veranderen als de ene soort meer beïnvloed wordt door lawaai dan de ander. Wij hebben de laatste mogelijkheid getest door nestkasten met en zonder lawaaiblootstelling in een bosgebied te plaatsen voordat vogels waren begonnen met nestelen. In dit gebied kwamen twee concurrerende soorten voor: de koolmees en de pimpelmees, die dezelfde nestkasten kunnen bezetten. Tijdens het experiment bleken de koolmezen veelal in de stille controlekasten te broeden, terwijl we pimpelmezen vaker in de lawaai- nestkasten aan troffen (hoofdstuk 7). Pimpelmezen hadden niet een specifieke voorkeur voor lawaai, maar hadden waarschijnlijk minder last van de grotere en dominante koolmezen in de lawaaikasten. Deze resultaten laten zien dat antropogeen lawaai kan bepalen waar bepaalde individuen zich vestigen en hoe dit uiteindelijk processen binnen een gemeenschap van verschillende soorten vogels kan beïnvloeden.

Afsluitende opmerking

De grote schaal en snelheid waarmee natuurlijk gebieden plaats moeten maken voor stedelijke gebieden is historisch gezien ongekend en kan gezien worden als een buitengewoon interessant experiment om de invloed van de omgeving op evolutionaire verandering te onderzoeken. Echter, het begrip van de individuele componenten van deze processen die met verstedelijking geassocieerd kunnen worden, vraagt uiteindelijk om een echte, experimentele benadering zoals die bijvoorbeeld in dit proefschrift worden beschreven. Deze experimenten zullen bij voorkeur de natuurlijke omgeving, waarin de dieren en hun gedrag zich hebben ontwikkeld, moeten nabootsen, wat vaak alleen kan worden bereikt in het veld.

Ten slotte zien we de meeste dieren in onze eigen achtertuin en zolang meer en meer mensen in een stadse omgeving komen te wonen, zullen studies over stedelijke ecologie en evolutie de publieke aandacht blijven grijpen. Dit biedt niet alleen mogelijkheden voor onderzoekers, maar ook verantwoordelijkheden om de bewustwording van de gevolgen van het menselijke gedrag tot stand te brengen (en te doen wat in ons vermogen ligt om de uitwerking van ons gedrag op andere soorten te verminderen).

Bibliography

Angerbjorn A., Tannerfeldt M. & Erlinge S. (1999). Predator-prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, 68, 34-49.

Bakelaar R.G. & Odum E.P. (1978). Community and population level responses to fertilization in an old-field ecosystem. *Ecology*, 59, 660-665.

Barber J.R., Crooks K.R. & Fristrup K.M. (2009). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, 25, 180-189.

Batzer D.P., Pusateri C.R. & Vetter R. (2000). Impacts of fish predation on marsh invertebrates: Direct and indirect effects. *Wetlands*, 20, 307-312.

Bautista L.M., Garcia J.T., Calmaestra R.G., Palacin C., Martin C.A., Morales M.B., Bonal R. & Vinuela J. (2004). Effect of weekend road traffic on the use of space by raptors. *Conservation Biology*, 18, 726-732.

Bayne E.M., Habib L. & Boutin S. (2008). Impacts of Chronic Anthropogenic Noise from Energy-Sector Activity on Abundance of Songbirds in the Boreal Forest. *Conservation Biology*, 22, 1186-1193.

Bee M.A. & Micheyl C. (2008). The cocktail party problem: What is it? How can it be solved? And why should animal behaviorists study it? *Journal of Comparative Psychology*, 122, 235-251.

Bee M.A. & Swanson E.M. (2007). Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, 74, 1765-1776.

Bergen F. & Abs M. (1997). Etho-ecological study of the singing activity of the Blue Tit (Parus caeruleus), Great Tit (Parus major) and Chaffinch (Fringilla coelebs). *Journal Fur Ornithologie*, 138, 451-467.

Berger K.M., Gese E.M. & Berger J. (2008). Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology*, 89, 818-828.

Bermudez-Cuamatzin E., Rios-Chelen A.A., Gil D. & Garcia C.M. (2010). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, 7, 36-38.

Bernays E.A. & Funk D.J. (1999). Specialists make faster decisions than generalists: experiments with aphids. *Proc. R. Soc. B-Biol. Sci.*, 266, 151-156.

Bisson I.A., Butler L.K., Hayden T.J., Romero L.M. & Wikelski M.C. (2009). No energetic cost of anthropogenic disturbance in a songbird. *Proc. R. Soc. B-Biol. Sci.*, 276, 961-969.

Blumenrath S.H., Dabelsteen T. & Pedersen S.B. (2004). Being inside nest boxes: Does it complicate the receiving conditions for great tit Parus major females? *Bioacoustics-the International Journal of Animal Sound and Its Recording*, 14, 209-223.

Blumenrath S.H., Dabelsteen T. & Pedersen S.B. (2007). Vocal neighbour-mate discrimination in female great tits despite high song similarity. *Animal Behaviour*, 73, 789-796.

Botero C.A., Rossman R.J., Caro L.M., Stenzler L.M., Lovette I.J., de Kort S.R. & Vehrencamp S.L. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, 77, 701-706.

Both C. (2004). Does mate-guarding give non-territorial birds the chance to settle? *ARDEA*, 92, 107-111.

Both C., Van Turnhout C.A.M., Bijlsma R.G., Siepel H., Van Strien A.J. & Foppen R.P.B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1259-1266.

Both C. & Visser M.E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411, 296-298.

Bradbury J.W. & Vehrencamp S.L. (1998). *Principles of Animal Communication*. Sinauer Associates, Sunderland, MA.

Brommer J.E., Alho J.S., Biard C., Chapman J.R., Charmantier A., Dreiss A., Hartley I.R., Hjernquist M.B., Kempenaers B., Komdeur J., Laaksonen T., Lehtonen P.K., Lubjuhn T., Patrick S.C., Rosivall B., Tinbergen J.M., van der Velde M., van Oers K., Wilk T. & Winkel W. (2010). Passerine Extrapair Mating Dynamics: A Bayesian Modeling Approach Comparing Four Species. *Am. Nat.*, 176, 178-187.

Brumm H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73, 434-440.

Brumm H., Lachlan R.F., Riebel K. & Slater P.J.B. (2009). On the function of song type repertoires: testing the 'antiexhaustion hypothesis' in chaffinches. *Animal Behaviour*, 77, 37-42.

Brumm H. & Naguib M. (2009). Environmental Acoustics and the Evolution of Bird Song. *Advances in the Study of Behavior, Vol 40*, 40, 1-33.

Brumm H., Robertson K.A. & Nemeth E. (2011). Singing direction as a tool to investigate the function of birdsong: an experiment on sedge warblers. *Animal Behaviour*, 81, 653-659.

Brumm H. & Slabbekoorn H. (2005). Acoustic communication in noise. In: *Advances in the Study of Behavior, Vol 35*, pp. 151-209.

Brumm H. & Slater P.J.B. (2006a). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology*, 60, 475-481.

Brumm H. & Slater P.J.B. (2006b). Animals can vary signal amplitude with receiver distance: evidence from zebra finch song. *Animal Behaviour*, 72, 699-705.

Brumm H. & Todt D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, 63, 891-897.

Brumm H., Voss K., Kollmer I. & Todt D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *Journal of Experimental Biology*, 207, 443-448.

Bucur V. (2006). *Urban Forest Acoustics*. Springer-Verlag, Berlin, Heidelberg.

Burnham K.P. & Anderson D.R. (2002). *Model Selection and Multimodel Inference: A Practical-Theoretic Approach*. 2nd edn. Springer-Verlag, Berlin.

Byers B.E. (2007). Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology*, 18, 130-136.

Cardoso G.C. & Atwell J.W. (in press). On the relation between loudness and the increased song frequency of urban birds. *Animal Behaviour*.

Catchpole C.K. & Slater P.J.B. (2008). *Bird Song: Biological themes and Variations*. Cambridge University press, Cambridge.

Chan A.A.Y.-H. & Blumstein D.T. (2011). Attention, noise, and implications for wildlife conservation and management. *Applied Animal Behaviour Science*, 131, 1-7.

Chan A.A.Y.-H., Giraldo-Perez P., Smith S. & Blumstein D.T. (2011). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, 6, 458-461.

Chiver I., Stutchbury B.J.M. & Morton E.S. (2008). Do male plumage and song characteristics influence female off-territory forays and paternity in the hooded warbler? *Behavioral Ecology and Sociobiology*, 62, 1981-1990.

Clergeau P., Croci S., Jokimaki J., Kaisanlahti-Jokimaki M.L. & Dinetti M. (2006). Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation*, 127, 336-344.

Codarin A., Wysocki L.E., Ladich F. & Picciulin M. (2009). Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare, Italy). *Marine Pollution Bulletin*, 58, 1880-1887.

Copeland H.E., Doherty K.E., Naugle D.E., Pocewicz A. & Kiesecker J.M. (2009). Mapping oil and gas development potential in the US Intermountain West and estimating impacts to species. *PLoS ONE*, 4, e7400.

Darwin, C. R. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London.

Davies N.B. & Halliday T.R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, 274, 683-685.

de Kort S.R., Eldermire E.R.B., Valderrama S., Botero C.A. & Vehrencamp S.L. (2009). Trill consistency is an age-related assessment signal in banded wrens. *Proceedings of the Royal Society B-Biological Sciences*, 276, 2315-2321.

Dhondt A.A. & Eyckerman R. (1980). Competition between the great tit and the blue tit outside the breeding-season in field experiments. *Ecology*, 61, 1291-1296.

Dingle C., Halfwerk W. & Slabbekoorn H. (2008). Habitat-dependent song divergence at subspecies level in the grey-breasted wood-wren. *Journal of Evolutionary Biology*, 21, 1079-1089.

Dingle C., Poelstra J.W., Halfwerk W., Brinkhuizen D.M. & Slabbekoorn H. (2010). Asymmetric response patterns to subspecies-specific song differences in allopatry and parapatry in the gray-breasted wood-wren. *Evolution*, 64, 3537-3548.

Doherty K.E., Naugle D.E., Walker B.L. & Graham J.M. (2008). Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management*, 72, 187-195.

Dooling R.J., Lohr B. & Dent M.L. (2000). Hearing in birds and reptiles. In: *Comparative hearing in birds and reptiles*. Springer Berlin.

Double M. & Cockburn A. (2000). Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 267, 465-470.

Drent P.J. (1987). The importance of nestboxes for territory settlement, survival and density of the great tit. *Ardea*, 75, 59-71.

Driver J. & Spence C. (1998). Attention and the crossmodal construction of space. *Trends Cogn. Sci.*, 2, 254-262.

Endler J.A. (1992). Signals, Signal Conditions, and the Direction of Evolution. *Am. Nat.*, 139, S125-S153.

Falls J.B., Krebs J.R. & McGregor P.K. (1982). Song matching in the great tit (parus-major) - the effect of similarity and familiarity. *Animal Behaviour*, 30, 997-1009.

Fernández-Juricic E., R. , Poston K., De Collibus T., Morgan B., Bastain C. & Martin K. (2005). Microhabitat selection and singing behavior 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.

Forman R.T.T. (2000). Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology*, 14, 31-35.

Forman R.T.T., Reineking B. & Hersperger A.M. (2002). Road traffic and nearby grassland bird patterns in a suburbanizing landscape. *Environmental Management*, 29, 782-800.

Forstmeier W., Kempenaers B., Meyer A. & Leisler B. (2002). A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 269, 1479-1485.

Francis C.D., Ortega C.P. & Cruz A. (2009). Cumulative consequences of noise pollution: noise changes avian communities and species interactions. *Current Biology*, 19, 1415-1419.

Francis C.D., Ortega C.P. & Cruz A. (2011a). Noise Pollution Filters Bird Communities Based on Vocal Frequency. *PLoS ONE*, 6, e27052.

Francis C.D., Ortega C.P. & Cruz A. (2011b). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B-Biological Sciences*, 278, 2025-2031.

Franco P. & Slabbekoorn H. (2009). Repertoire size and composition in great tits: a flexibility test using playbacks. *Animal Behaviour*, 77, 261-269.

Garamszegi L.Z., Calhim S., Dochtermann N., Hegyi G., Hurd P.L., Jorgensen C., Kutsukake N., Lajeunesse M.J., Pollard K.A., Schielzeth H., Symonds M.R.E. & Nakagawa S. (2009). Changing philosophies and tools for statistical inferences in behavioral ecology. *Behavioral Ecology*, 20, 1363-1375.

Gil D. & Gahr M. (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, 17, 133-141.

Gil D., Slater P.J.B. & Graves J.A. (2007). Extra-pair paternity and song characteristics in the willow warbler Phylloscopus trochilus. *Journal of Avian Biology*, 38, 291-297.

Goodwin S.E. & Shriver W.G. (2011). Effects of Traffic Noise on Occupancy Patterns of Forest Birds. *Conservation Biology*, 25, 406-411.

Gorissen L. & Eens M. (2004). Interactive communication between male and female Great Tits (Parus major) during the dawn chorus. *Auk*, 121, 184-191.

Gould S.J. & Lewontin R.C. (1979). Spandrels of san-marco and the panglossian paradigm - a critique of the adaptationist program. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 205, 581-598.

Grimm N.B., Faeth S.H., Golubiewski N.E., Redman C.L., Wu J.G., Bai X.M. & Briggs J.M. (2008). Global change and the ecology of cities. *Science*, 319, 756-760.

Groot Bruinderink G.W.T.A., Brandjes G.J., van Eekelen R., Niewold F.J.J., ten Den P.G.A. & Waardenburg H.W. (2002). Faunabeheerplan Nationaal Park Sallandse Heuvelrug i.o. In. Alterra, Research Instituut voor de Groene Ruimte Wageningen.

Gross K., Pasinelli G. & Kunc H.P. (2010). Behavioral Plasticity Allows Short-Term Adjustment to a Novel Environment. *Am. Nat.*, 176, 456-464.

Gummbah (2000). *De tijd vliegt slecht*. De Harmonie, Amsterdam.

Habib L., Bayne E.M. & Boutin S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. *Journal of Applied Ecology*, 44, 176-184.

Halfwerk W., Bot S., Buikx J., van der Velde M., Komdeur J., ten Cate C. & Slabbekoorn H. (2011a). Low songs lose potency in urban noise conditions. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 14549-14554.

Halfwerk W., Holleman L.J.M., Lessells C.M. & Slabbekoorn H. (2011b). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48, 210-219.

Halfwerk W. & Slabbekoorn H. (2009). A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour*, 78, 1301-1307.

Hall M.L. (2009). A Review of Vocal Duetting in Birds. *Advances in the Study of Behavior, Vol 40*, 40, 67-121.

Hamao S., Watanabe M. & Mori Y. (2011). Urban noise and male density affect songs in the great tit Parus major. *Ethol. Ecol. Evol.*, 23, 111-119.

Hasselquist D., Bensch S. & vonSchantz T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, 381, 229-232.

Helm B., Piersma T. & Van der Jeugd H. (2006). Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour*, 72, 245-262.

Herrera-Montes M.I. & Aide T.M. (2011). Impacts of traffic noise on anuran and bird communities. *Urban Ecosystems*, 14, 415-427.

Holveck M.J. & Riebel K. (2009). Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B-Biological Sciences*, 277, 153-160.

Hu Y. & Cardoso G.C. (2009). Which birds adjust the frequency of vocalizations in urban noise? *Animal Behaviour*, 79, 863-867.

Hunter M.L. & Krebs J.R. (1979). Geographic variation in the song of the great tit (*Parus Major*)in relation to ecological factors. *Journal of Animal Ecology*, 48, 759-785.

Inouye R.S. & Tilman D. (1995). Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology*, 76, 1872-1887.

Johnstone R.A. (2011). Load lightening and negotiation over offspring care in cooperative breeders. *Behavioral Ecology*, 22, 436-444.

Junker-Bornholdt R., Wagner M., Zimmermann M., Simonis S., Schmidt K.H. & Wiltschko W. (1998). The impact of a motorway in construction and after opening to traffic on the breeding biology of Great Tit (Parus major) and Blue Tit (P-caeruleus). *Journal Fur Ornithologie*, 139, 131-139.

Kalinowski S.T., Taper M.L. & Marshall T.C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16, 1099-1106.

Kappes J.J. & Davis J.M. (2008). Evidence of positive indirect effects within a community of cavity-nesting vertebrates. *Condor*, 110, 441-449.

Kemmerer E.P., Shields J.M. & Tidemann C.R. (2008). High densities of bell miners Manorina melanophrys associated with reduced diversity of other birds in wet eucalypt forest: Potential for adaptive management. *Forest Ecology and Management*, 255, 2094-2102.

Kempenaers B., Borgstrom P., Loes P., Schlicht E. & Valcu M. (2010). Artificial Night Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds. *Current Biology*, 20, 1735-1739.

Kempenaers B. & Dhondt A.A. (1991). Competition between blue and great tit for roosting sites in winter - an aviary experiment. *Ornis Scandinavica*, 22, 73-75.

Kight C.R. & Swaddle J.P. (2011). How and why environmental noise impacts animals: an integrative, mechanistic review. *Ecology Letters*.

King A.P., West M.J. & Goldstein M.H. (2005). Non-vocal shaping of avian song development: Parallels to human speech development. *Ethology*, 111, 101-117.

Kirschel A.N.G., Blumstein D.T., Cohen R.E., Buermann W., Smith T.B. & Slabbekoorn H. (2009). Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. *Behavioral Ecology*, 20, 1089-1095.

Klump G.M. (1996). Bird communication in the noisy world. In: *Ecology and Evolution of Acoustic Communication in Birds* (eds. Kroodsma DE & Miller EH). Cornell University Press Ithaca, pp. 321–338.

Kluyver H.N. (1951). The population ecology of the great tit, Parus major L. *Ardea*, 39, 1 - 135.

Kociolek A.V., Clevenger A.P., Clair C.C.S. & Proppe D.S. (2011). Effects of Road Networks on Bird Populations. *Conservation Biology*, 25, 241-249.

Krebs J., Ashcroft R. & Webber M. (1978). Song repertories and territory defence in great tit. *Nature*, 271, 539-542.

Kroodsma D.E. (2004). the diversity and plasticity of bird song. In: *Nature's Music: The Science of Bird Song* (eds. Marler P & Slabbekoorn H). Elsevier Academic Press London, pp. 108-130.

Lachlan R.F. (2007). Luscinia: a bioacoustics analysis computer program. In.

Lambrechts M. & Dhondt A.A. (1986). Male quality, reproduction, and survival in the great tit (Parus major). *Behavioral Ecology and Sociobiology*, 19, 57-63.

Lambrechts M. & Dhondt A.A. (1988). The anti-exhaustion hypothesis - a new hypothesis to explain song performance and song switching in the great tit. *Animal Behaviour*, 36, 327-334.

Lambrechts M.M. (1997). Song frequency plasticity and composition of phrase versions in Great Tits Parus major. *Ardea*, 85, 99-109.

Langemann U., Gauger B. & Klump G.M. (1998). Auditory sensitivity in the great tit: perception of signals in the presence and absence of noise. *Animal Behaviour*, 56, 763-769.

Laube M.M. & Stout R.W. (2000). Grand Canyon National Park - Assessment of transportation alternatives. *Transit: Planning, Intermodal Facilities, Management, and Marketing*, 59-69.

Lengagne T. (2008). Traffic noise affects communication behaviour in a breeding anuran, Hyla arborea. *Biological Conservation*, 141, 2023-2031.

Leonard M.L. & Horn A.G. (2008). Does ambient noise affect growth and begging call structure in nestling birds? *Behavioral Ecology*, 19, 502-507.

Li B.G., Tao S., Dawson R.W., Cao J. & Lam K. (2002). A GIS based road traffic noise prediction model. *Applied Acoustics*, 63, 679-691.

Lohr B., Wright T.F. & Dooling R.J. (2003). Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Animal Behaviour*, 65, 763-777.

Lombard E. (1911). Le signe de l'elevation de la voix. *Annales des maladies de l'oreille, du larynx du nez et du pharynx*, 37, 101-119.

Mace R. (1987). The dawn chorus in the great tit parus-major is directly related to female fertility. *Nature*, 330, 745-746.

Magrath M.J.L., Vedder O., van der Velde M. & Komdeur J. (2009). Maternal Effects Contribute to the Superior Performance of Extra-Pair Offspring. *Current Biology*, 19, 792-797.

Makarewicz R. & Kokowski P. (2007). Prediction of noise changes due to traffic speed control. *Journal of the Acoustical Society of America*, 122, 2074-2081.

Manabe K., Sadr E.I. & Dooling R.J. (1998). Control of vocal intensity in budgerigars (Melopsittacus undulatus): Differential reinforcement of vocal intensity and the Lombard effect. *Journal of the Acoustical Society of America*, 103, 1190-1198.

Marler P. & Slabbekoorn H. (2004). *Nature's music: The Science of Birdsong*. Elsevier Academic Press.

Mathevon N., Aubin T. & Dabelsteen T. (1996). Song degradation during propagation: Importance of song post for the wren Troglodytes troglodytes. *Ethology*, 102, 397-412.

Mayr E. (1983). How to carry out the adaptationist program. *American Naturalist*, 121, 324-334.

McGregor P.K. & Krebs J.R. (1982). Mating and song types in the great tit. *Nature*, 297, 60-61.

McGregor P.K. & Krebs J.R. (1989). Song learning in adult great tits (parus-major) - effects of neighbors. *Behaviour*, 108, 139-159.

McGregor P.K., Krebs J.R. & Perrins C.M. (1981). song repertoires and lifetime reproductive success in the great tit (parus-major). *Am. Nat.*, 118, 149-159.

McKinney M.L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247-260.

Mennill D.J., Ratcliffe L.M. & Boag P.T. (2002). Female eavesdropping on male song contests in songbirds. *Science*, 296, 873-873.

Miller S.G., Knight R.L. & Miller C.K. (1998). Influence of recreational trails on breeding bird communities. *Ecological Applications*, 8, 162-169.

Minot E.O. & Perrins C.M. (1986). Interspecific interference competition - nest sites for blue and great tits. *Journal of Animal Ecology*, 55, 331-350.

Mockford E.J. & Marshall R.C. (2009). Effects of urban noise on song and response behaviour in great tits. *Proceedings of the Royal Society B-Biological Sciences*, 276, 2979-2985.

Moller A.P. (1991). Why mated songbirds sing so much - mate guarding and male announcement of mate fertility status. *Am. Nat.*, 138, 994-1014.

Moller A.P., Nielsen J.T. & Garamszegi L.Z. (2006). Song post exposure, song features, and predation risk. *Behavioral Ecology*, 17, 155-163.

Morton E.S. (1975). Ecological sources of selection on avian sounds. *Am. Nat.*, 109, 17-34.

Naguib M., Kunc H.P., Sprau P., Roth T. & Amrhein V. (2011). Communication Networks and Spatial Ecology in Nightingales. In: *Advances in the Study of Behavior, Vol 43* (eds. Brockmann HJ, Roper TJ, Naguib M, Mitani JC & Simmons LW). Elsevier Academic Press Inc San Diego, pp. 239-271.

Naguib M., Schmidt R., Sprau P., Roth T., Florcke C. & Amrhein V. (2008). The ecology of vocal signaling: male spacing and communication distance of different song traits in nightingales. *Behavioral Ecology*, 19, 1034-1040.

Nelson B.S. (2000). Avian dependence on sound pressure level as an auditory distance cue. *Animal Behaviour*, 59, 57-67.

Nemeth E. & Brumm H. (2010). Birds and Anthropogenic Noise: Are Urban Songs Adaptive? *Am. Nat.*, 176, 465-475.

Nystrom J., Ekenstedt J., Engstrom J. & Angerbjorn A. (2005). Gyr Falcons, ptarmigan and microtine rodents in northern Sweden. *Ibis*, 147, 587-597.

Oberweger K. & Goller F. (2001). The metabolic cost of birdsong production. *Journal of Experimental Biology*, 204, 3379-3388.

Ohms V.R., Snelderwaard P.C., ten Cate C. & Beckers G.J.L. (2010). Vocal Tract Articulation in Zebra Finches. *PLoS ONE*, 5.

Osmanski M.S. & Dooling R.J. (2009). The effect of altered auditory feedback on control of vocal production in budgerigars (Melopsittacus undulatus). *Journal of the Acoustical Society of America*, 126, 911-919.

Ovenden N.C., Shaffer S.R. & Fernando H.J.S. (2009). Impact of meteorological conditions on noise propagation from freeway corridors. *Journal of the Acoustical Society of America*, 126, 25-35.

Padgham M. (2004). Reverberation and frequency attenuation in forests--implications for acoustic communication in animals. *J Acoust Soc Am*, 115, 402-10.

Parks S.E., Johnson M., Nowacek D. & Tyack P.L. (2011). Individual right whales call louder in increased environmental noise. *Biology Letters*, 7, 33-35.

Parris K.M. & Schneider A. (2009). Impacts of Traffic Noise and Traffic Volume on Birds of Roadside Habitats. *Ecology and Society*, 14.

Patricelli G.L. & Blickley J.L. (2006). Avian communication in urban noise: Causes and consequences of vocal adjustment. *Auk*, 123, 639-649.

Peake T.M., Matessi G., McGregor P.K. & Dabelsteen T. (2005). Song type matching, song type switching and eavesdropping in male great tits. *Animal Behaviour*, 69, 1063-1068.

Penna M., Pottstock H. & Velasquez N. (2005). Effect of natural and synthetic noise on evoked vocal responses in a frog of the temperate austral forest. *Animal Behaviour*, 70, 639-651.

Pick H.L., Siegel G.M., Fox P.W., Garber S.R. & Kearney J.K. (1989). inhibiting the lombard effect. *Journal of the Acoustical Society of America*, 85, 894-900.

Podos J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, 409, 185-188.

Podos J., Lahti D.C. & Moseley D.L. (2009). Vocal Performance and Sensorimotor Learning in Songbirds. In: *Advances in the Study of Behavior, Vol 40* (ed. Naguib M.), pp. 159-195.

Pohl N.U., Slabbekoorn H., Klump G.M. & Langemann U. (2009). Effects of signal features and environmental noise on signal detection in the great tit, Parus major. *Animal Behaviour*, 78, 1293-1300.

Potash L.M. (1972). Noise-induced changes in calls of the Japanese quail. *Psychonomic Science*, 26, 252-254.

Potvin D.A., Parris K.M. & Mulder R.A. (2011). Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (Zosterops lateralis). *Proceedings of the Royal Society B: Biological Sciences*.

Quinn J.L., Whittingham M.J., Butler S.J. & Cresswell W. (2006). Noise, predation risk compensation and vigilance in the chaffinch Fringilla coelebs. *Journal of Avian Biology*, 37, 601-608.

Rabin L.A. & Greene C.M. (2002). Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology*, 116, 137-141.

Reijnen R. & Foppen R. (1991). Effect of road traffic on the breeding site tenacity of male willow warblers (phylloscopus-trochilus). *Journal Fur Ornithologie*, 132, 291-295.

Reijnen R. & Foppen R. (1995). The effects of car traffic on breeding bird populations in woodland .4. influence of population-size on the reduction of density close to a highway. *Journal of Applied Ecology*, 32, 481-491.

Reijnen R. & Foppen R. (2006). Impact of road traffic on breeding bird populations. In: *The Ecology of Transportation: Managing Mobility for the Environment* (eds. Davenport J & Davenport JL). Springer-Verlag Heidelberg, pp. 255–274.

Reijnen R., Foppen R., Terbraak C. & Thissen J. (1995). The effects of car traffic on breeding bird populations in woodland .3. reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology*, 32, 187-202.

Rendell L.E., Matthews J.N., Gill A., Gordon J.C.D. & Macdonald D.W. (1999). Quantitative analysis of tonal calls from five odontocele species, examining interspecific and intraspecific variation. *Journal of Zoology*, 249, 403-410.

Rheindt F.E. (2003). The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal Fur Ornithologie*, 144, 295-306.

Richards D.G. & Wiley R.H. (1980). Reverberations and Amplitude Fluctuations in the Propagation of Sound in a Forest - Implications for Animal Communication. *Am. Nat.*, 115, 381-399.

Riebel K. & Slater P.J.B. (1999). Song type switching in the chaffinch, Fringilla coelebs: timing or counting? *Animal Behaviour*, 57, 655-661.

Riebel K. & Slater P.J.B. (2000). Testing the flexibility of song type bout duration in the chaffinch, Fringilla coelebs. *Animal Behaviour*, 59, 1135-1142.

Ripmeester E.A.P., Kok J.S., van Rijssel J.C. & Slabbekoorn H. (2010a). Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. *Behavioral Ecology and Sociobiology*, 64, 409-418.

Ripmeester E.A.P., Mulder M. & Slabbekoorn H. (2010b). Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behavioral Ecology*, 21, 876-883.

Rivera-Gutierrez H.F., Pinxten R. & Eens M. (2010). Multiple signals for multiple messages: great tit, Parus major, song signals age and survival. *Animal Behaviour*, 80, 451-459.

Rivera-Gutierrez H.F., Pinxten R. & Eens M. (2011). Songs differing in consistency elicit differential aggressive response in territorial birds. *Biology Letters*, 7, 339-342.

Ryan M.J. & Brenowitz E.A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist*, 126, 87-100.

Schaub A., Ostwald J. & Siemers B.M. (2008). Foraging bats avoid noise. *Journal of Experimental Biology*, 211, 3174-3180.

Seehausen O., vanAlphen J.J.M. & Witte F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, 277, 1808-1811.

Slabbekoorn H. (2004). Singing in the wild: the ecology of birdsong. In: *Nature's music: The Science of Birdsong* (eds. Marler P & Slabbekoorn H). Elsevier Academic Press.

Slabbekoorn H., Bouton N., van Opzeeland I., Coers A., ten Cate C. & Popper A.N. (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, 25, 419-427.

Slabbekoorn H. & den Boer-Visser A. (2006). Cities change the songs of birds. *Current Biology*, 16, 2326-2331.

Slabbekoorn H. & Halfwerk W. (2009). Behavioural Ecology: Noise Annoys at Community Level. *Current Biology*, 19, R693-R695.

Slabbekoorn H. & Peet M. (2003). Ecology: Birds sing at a higher pitch in urban noise *Nature*, 424, 267-267.

Slabbekoorn H. & Ripmeester E.A.P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology*, 17, 72-83.

Slabbekoorn H. & Smith T.B. (2002a). Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 357, 493-503.

Slabbekoorn H. & Smith T.B. (2002b). Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution* 56, 1849-58.

Slabbekoorn H., Yeh P. & Hunt K. (2007). Sound transmission and song divergence: A comparison of urban and forest acoustics. *Condor*, 109, 67-78.

Snow D. W., Perrins C. M., Gillmor R. & Hillcoat B (1998). *The birds of the Western Palearctic (concise edition)*. Oxford University Press, Oxford.

Smith T.B., Mila B., Grether G.F., Slabbekoorn H., Sepil I., Buermann W., Saatchi S. & Pollinger J.P. (2008). Evolutionary consequences of human disturbance in a rainforest bird species from Central Africa. *Molecular Ecology*, 17, 58-71.

Spruit, B. 2008. An experimental test of song frequency plasticity in adult great tits. BSc thesis, Leiden University.

Steele C. (2001). A critical review of some traffic noise prediction models. *Applied Acoustics*, 62, 271-287.

Stoddard P.K., Beecher M.D. & Willis M.S. (1988). Response of territorial-male song sparrows to song types and variations. *Behavioral Ecology and Sociobiology*, 22, 125-130.

Stone E. (2000). Separating the noise from the noise: A finding in support of the “Niche Hypothesis,” that birds are influenced by human-induced noise in natural habitats. *Anthrozoos*, 13, 225-231.

Svensson L., Zetterström D. & Mullarney K. (2010). *Birds of Europe (second edition)*. Princeton field guides.

Swaddle J.P. & Page L.C. (2007). High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. *Animal Behaviour*, 74, 363-368.

Thijsse J.P., (1906). *Het intieme leven der vogels*. Uitgeverij Veen, Amsterdam

Tinbergen N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410-433.

Tratalos J., Fuller R.A., Evans K.L., Davies R.G., Newson S.E., Greenwood J.J.D. & Gaston K.J. (2007). Bird densities are associated with household densities. *Global Change Biology*, 13, 1685-1695.

Van Bael S.A. & Brawn J.D. (2005). The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests. *Oecologia*, 143, 106-116.

van Dijk, L. E. 2010. Frequency-dependent transmission under noisy conditions between neighboring territories of great tits. BSc thesis, Leiden University.

van der Klugt, I. & Diepeveen, F. 2011. Does fearfulness affect song in male-male and male-female interactions in the great tit? BSc thesis, Leiden University.

van der Sluijs I., Gray S.M., Amorim M.C.P., Barber I., Candolin U., Hendry A.P., Krahe R., Maan M.E., Utne-Palm A.C., Wagner H.J. & Wong B.B.M. (2011). Communication in troubled waters: responses of fish communication systems to changing environments. *Evol. Ecol.*, 25, 623-640.

van der Zande A.N., ter Keurs W.J. & van der Weijden W.J. (1980). The impact of roads on the densities of four bird species in an open field habitat--evidence of a long-distance effect. *Biological Conservation*, 18, 299-321.

Vasconcelos R.O., Amorim M.C.P. & Ladich F. (2007). Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. *Journal of Experimental Biology*, 210, 2104-2112.

Verzijden M.N., Ripmeester E.A.P., Ohms V.R., Snelderwaard P. & Slabbekoorn H. (2010). Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. *Journal of Experimental Biology*, 213, 2575-2581.

Vignieri, S.N. (2011). Evolution: oh the noise! *Science*, 333,1360.

Vitousek P.M., Mooney H.A., Lubchenco J. & Melillo J.M. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494-499.

Walther G.R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.M., Hoegh-Guldberg O. & Bairlein F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389-395.

Warren P.S., Katti M., Ermann M. & Brazel A. (2006). Urban bioacoustics: it's not just noise. *Animal Behaviour*, 71, 491-502.

Weary D.M., Krebs J.R., Eddyshaw R., McGregor P.K. & Horn A. (1988). Decline in song output by great tits - exhaustion or motivation. *Animal Behaviour*, 36, 1242-1244.

Weary D.M., Lambrechts M.M. & Krebs J.R. (1991). Does singing exhaust male great tits. *Animal Behaviour*, 41, 540-542.

Whittingham M.J., Swetnam R.D., Wilson J.D., Chamberlain D.E. & Freckleton R.P. (2005). Habitat selection by yellowhammers Emberiza citrinella on lowland farmland at two spatial scales: implications for conservation management. *Journal of Applied Ecology*, 42, 270-280.

Wiley R.H. & Richards D.G. (1978). Physical constraints on acoustic communication in atmosphere - implications for evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, 3, 69-94.

Wilkin T.A., Garant D., Gosler A.G. & Sheldon B.C. (2006). Density effects on life-history traits in a wild population of the great tit Parus major: analyses of long-term data with GIS techniques. *Journal of Animal Ecology*, 75, 604-615.

Wollerman L. & Wiley R.H. (2002). Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour*, 63, 15-22.

Wood W.E. & Yezerinac S.M. (2006). Song sparrow (Melospiza melodia) song varies with urban noise. *Auk*, 123, 650-659.

Zelick R. & Narins P.M. (1985). characterization of the advertisement call oscillator in the frog eleutherodactylus-coqui. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology*, 156, 223-229.

Zollinger S.A., Goller F. & Brumm H. (2011). Metabolic and Respiratory Costs of Increasing Song Amplitude in Zebra Finches. *PLoS ONE*, 6.

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1994 – 1999	Vrije school, Zutphen, the Netherlands
2000 – 2003	BSc Biology/ philosophy, Nijmegen University, the Netherlands
2003 – 2006	MSc Biology, Utrecht University, the Netherlands
	MSc project studying binocular rivalry during biological motion perception to understand organization of human vision supervised by dr J. A. Beintema and prof. dr R.J.A. van Wezel
	MSc project studying the relationship between geographic variation in song and environmental selection pressures, supervised by dr H.W. Slabbekoorn (Leiden University) and dr C. Dingle (Cambridge University).
2006 – 2007	Research project Ecuador, Leiden/ Cambridge University, UK
2007 – 2012	PhD research, Behavioural Biology, IBL, Leiden University
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	During my PhD research I supervised several BSc and MSc students both in the field and in the lab and assisted several courses on animal behaviour and communication. I presented my work at several national (NVG ‘07/’08/’10/’11) and international scientific meetings (IEC ‘09, ISBE ‘10, IEC/ABS ‘11). I was invited to present my work during several seminars for professionals as well as amateurs. Furthermore, I participated in a documentary on the perception of noise and I gave several interviews for national and international media.
2012 – 2014	Post-doc project, Smithsonian Tropical Research Institute, PA

Publications

1. **Halfwerk, W.** Bot, S. Buikx, J.van der Velde, M. Komdeur, J. ten Cate, C. & Slabbekoorn, H. reply to Eens et al: urban noise can alter sexual selection on bird song. PNAS, *In press*.
2. Slabbekoorn, H. **Halfwerk, W.** & Yang, X. Birds and anthropogenic noise: singing higher may matter. American Naturalist. *In press*.
3. **Halfwerk, W.** Bot, S. Buikx, J.van der Velde, M. Komdeur, J. ten Cate, C. & Slabbekoorn, H. Low-frequency songs lose their potency in noisy urban conditions. PNAS, 2011.
4. **Halfwerk, W.** Holleman, L. Lessells, K. & Slabbekoorn, H. Negative impact of traffic noise on avian reproductive success. Journal of Applied Ecology, 2011.
5. Tobias, J.A. , Aben, J., Brumfield, R.T., Derryberry E.P., **Halfwerk, W.**, Slabbekoorn, H. & Seddon N. 2010. Song divergence by sensory drive in Amazonian birds. Evolution, 2010.
6. Dingle, C. Poelstra, J.W. **Halfwerk, W.** Brinkhuizen, D.M. & Slabbekoorn, H. Asymmetric response patterns to subspecies-specific song differences in allopatry and parapatry in the gray-breasted wood-wren. Evolution, 2010.
7. **Halfwerk, W.** & Slabbekoorn, H. A behavioural mechanism explaining noise-dependent pitch shift in urban birdsong. Animal Behaviour, 2009.
8. Slabbekoorn, H. & **Halfwerk, W.** Behavioural Ecology: Noise annoys at community level. Current Biology, 2009.
9. Dingle, C. **Halfwerk, W.** & Slabbekoorn, H. Habitat-dependent song divergence at subspecies level in the grey-breasted wood-wren. Journal of Evolutionary Biology, 2008.
10. Beintema, J.A. **Halfwerk, W.** & van Wezel, R.J.A. Less rivalry with more biological motion. Journal of Vision, 2004.

- **Halfwerk, W.** Bot, S. & Slabbekoorn, H. Female control over noise-dependent song perch adjustment. *In review*
- **Halfwerk, W.** Both, C. & Slabbekoorn, H. Anthropogenic noise alters heterospecific competition over nest sites. *In review*
- **Halfwerk, W.** Dingle, C. Brinkhuizen, D.M. Poelstra, J.W. Komdeur, J. & Slabbekoorn, H. Cultural and genetic transmission under avian contact. *In prep.*