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

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Chapter 5

Female control over noise-dependent song perch adjustment

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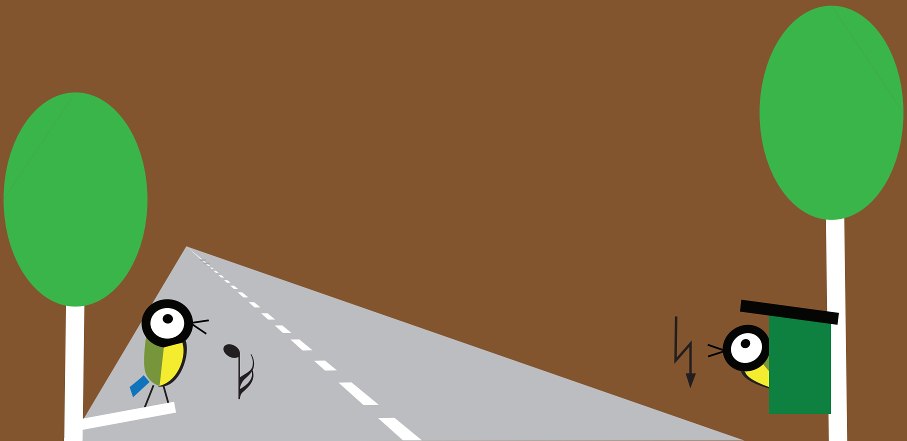


ABSTRACT

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

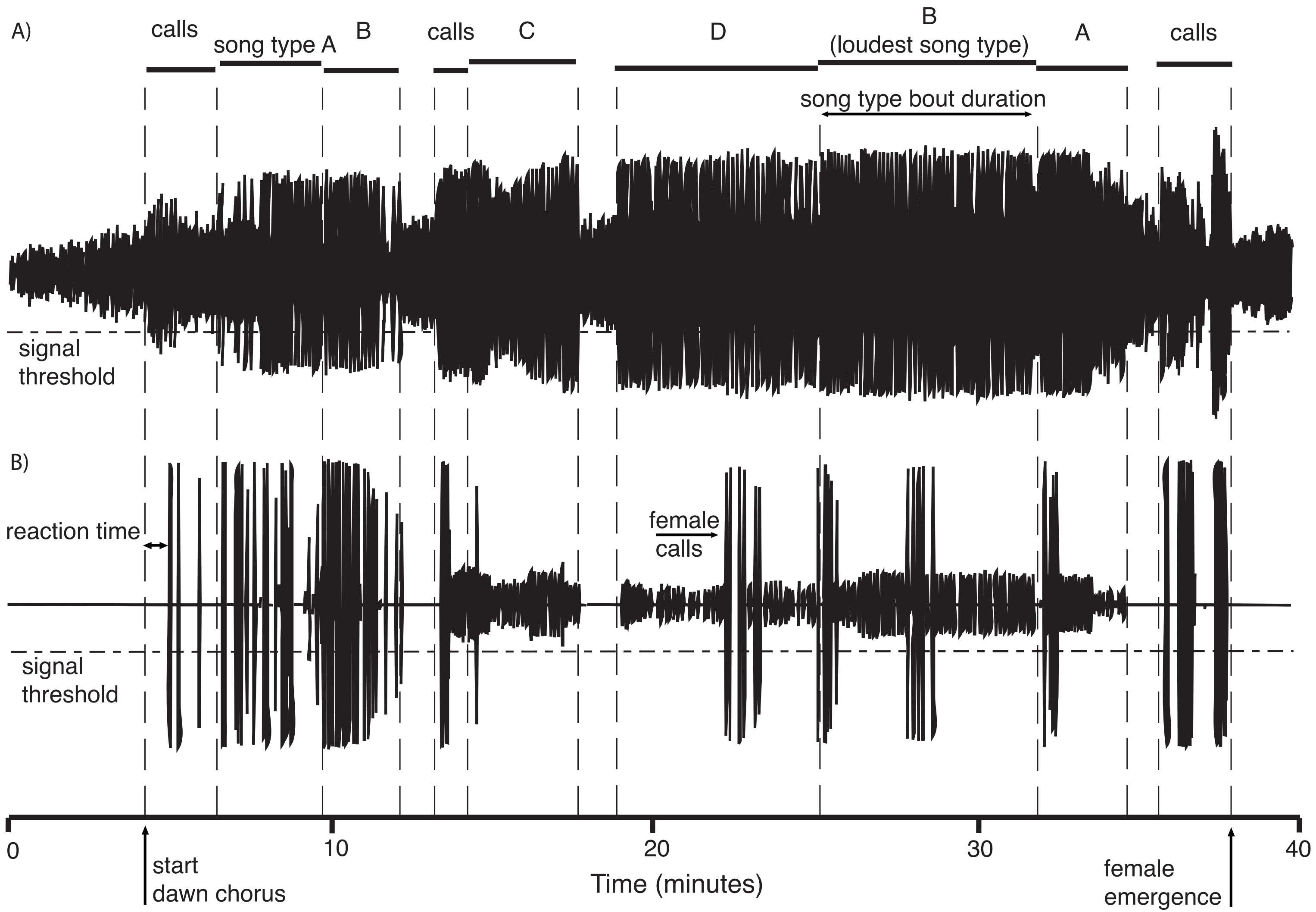

A)
calls
song type A
B
calls
C
D
B
(loudest song type)
A
calls
song type bout duration
signal threshold
B)
reaction time
female calls
signal threshold
0
10
20
30
40
start dawn chorus
Time (minutes)
female emergence

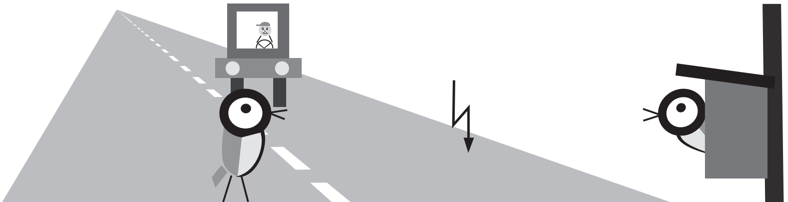
Figure 5.1. Male and female acoustic interactions during a complete dawn chorus bout. (**A**) an amplitude wave of a recording made outside the nest box, starting 40 minutes prior to sunrise. The male typically initiates the dawn chorus with a few calls towards the female after which he starts singing 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



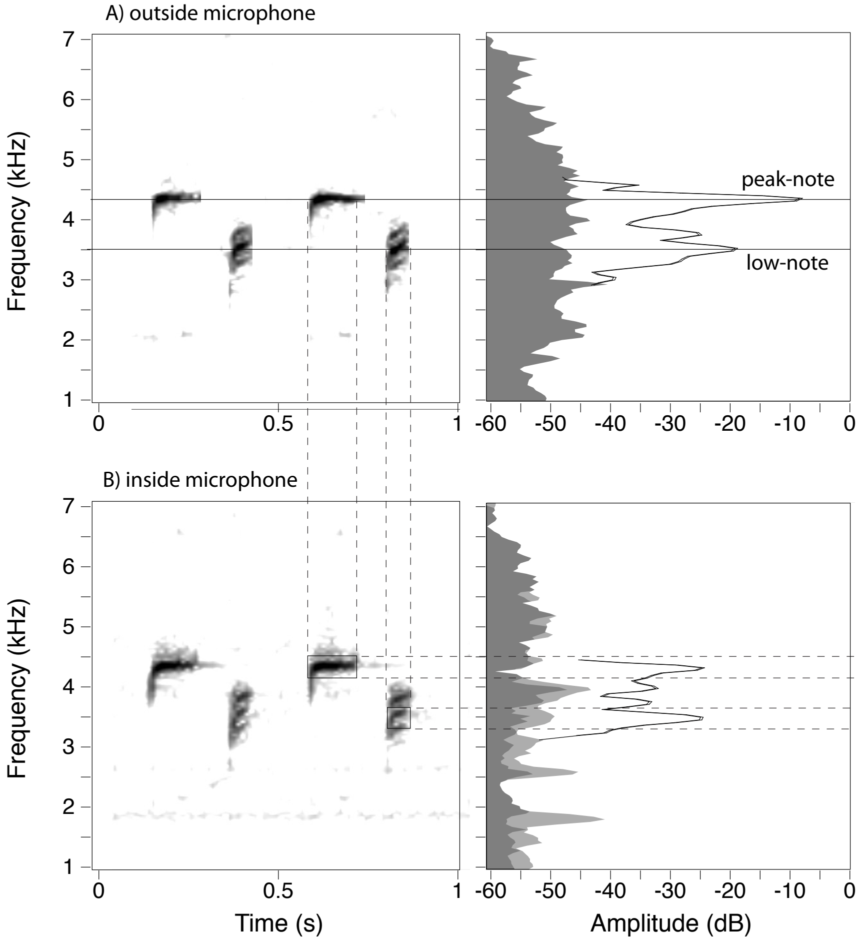


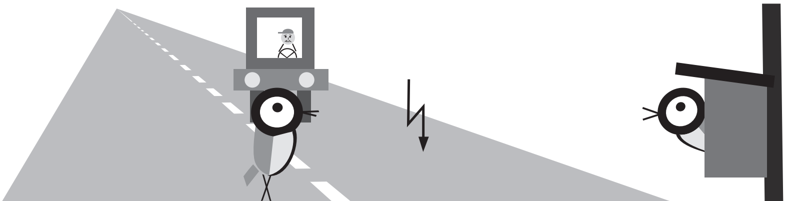
Figure 5.2. Examples of male song and noise profiles inside and outside the nest box (**A**) a sonogram of a recording made on the outside microphone of a two-note song type (left panel, time on the x-axes, frequency on the y-axes) and a powerspectrogram (right panel, relative amplitude level on the 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.



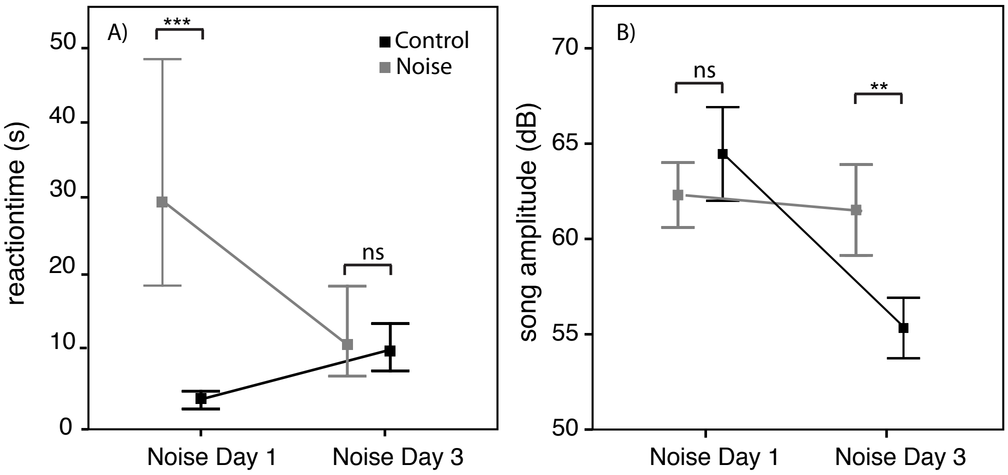


Figure 5.3. Intra-pair communication in anthropogenic noise. (**A**) Female response behaviour in noise. Females call much later in response to start of male song or call bout on the first day of full noise exposure (GLMM; pairwise – comparison: control vs. noise on Noise day 1; ***p < 0.001). Difference 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.

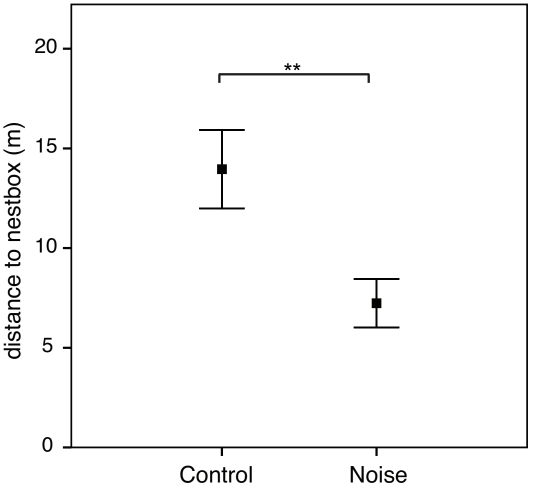


Figure 5.4. Males sing closer when females are exposed to noise. The distance between nest box and the nearest song post occupied by males differs between noise and control group after three experimental days (LMM: p = 0.005).

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.

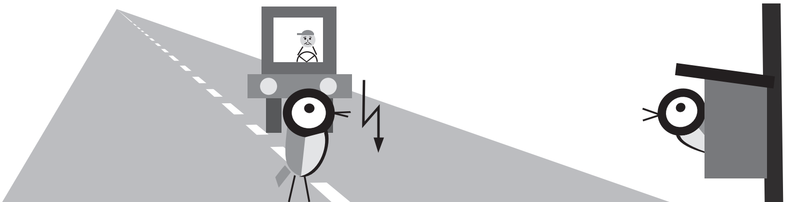
An impact of continuous noise exposure on male and female behavior was tested using full factorial generalized linear mixed models (GLMM, SPSS 17.0), with loglink-function for response latency (log-transformed) and call rate. Treatment and noise day, or treatment and egg-day were included as fixed effects 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; $\chi^2 = 10.2$; $p = 0.001$;



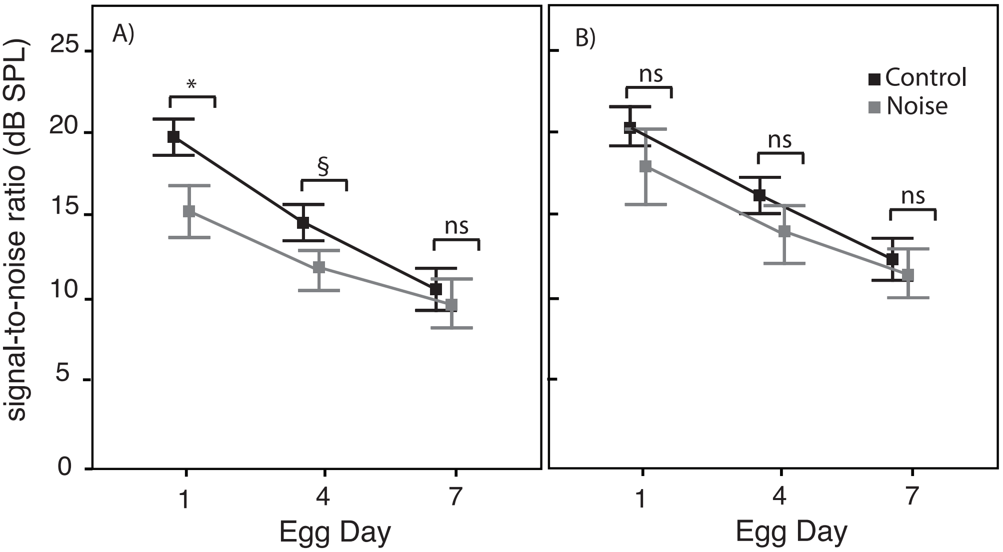


Figure 5.5. Changes in male song signal-to-noise ratio in relation to noise treatment, laying date and note type. Signal-to-noise (S2N) ratios decrease with egg-laying (GLMM; all $p < 0.001$). (**A**) S2N ratios in the low-note frequency range differ between treatment groups (GLMM; $p = 0.044$), but 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).

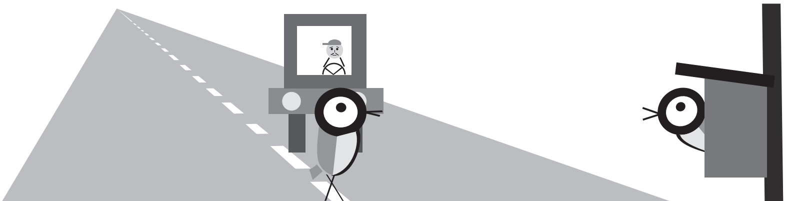
The overall decrease in amplitude between noise days suggests that males moved away from the nest box, which can also explain why signal-to-noise ratios generally decreased with egg-laying (Figure 5.5). The signal-to-noise ratios differed between noise and control treatment groups for the low-notes (GLMM; $N = 29$; 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.

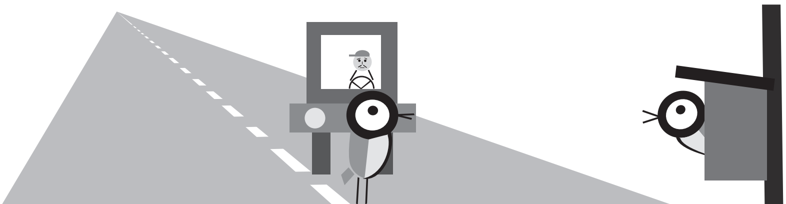
We do know that great tit males did not change the frequency of their songs in the noise treatment, despite the fact that great tit females can provide frequency-dependent feedback to males (chapter 4)[29]. The lack of frequency change in the present study suggests that noise-dependent frequency use 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.

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