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

Halfwerk, W.

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Author: Halfwerk, Wouter

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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 success¹. However, rapid worldwide urbanization² 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 areas³⁻⁵. 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 frequencies⁷⁻⁹, 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 frequencies¹⁴. 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 sufficient¹⁹ or come at a considerable cost⁵.

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.



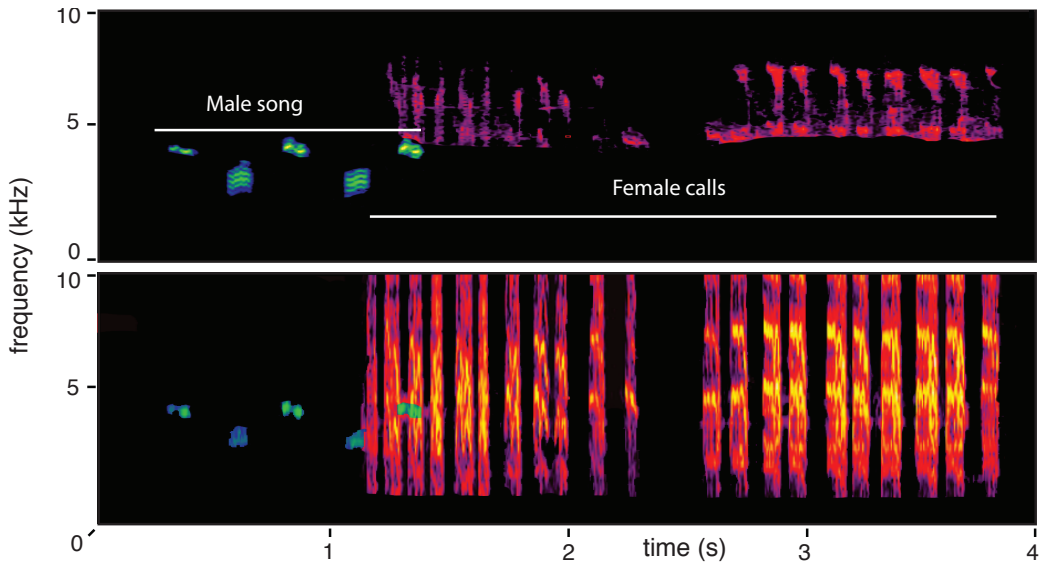


Figure 4.1. The dawn chorus ritual of great tits (*Parus major*). Sonogram of a stereo recording shows the acoustic interaction between a male (song in blue) and a female (calls in red). Males continuously sing or call close to the nest box during dawn and females can call in response. Females call most 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.

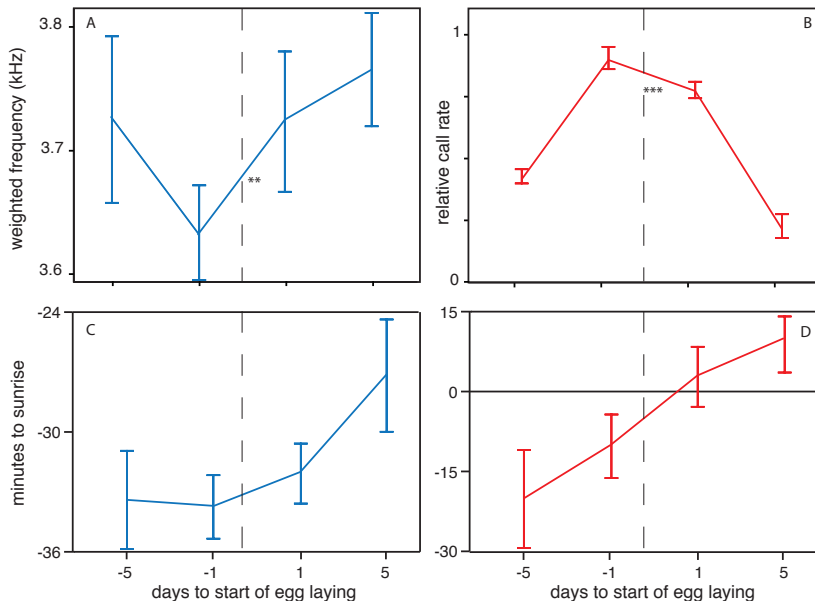


Figure 4.2. Within-individual variation of male and female behavior during the dawn chorus. **(A)** Male song performance peaks with female fertility (GLMM; $***P < 0.001$) and males sing lowest when fertility is highest (egg-day -1). **(B)** Female calling changes with egg-laying (GLMM; $***P < 0.001$) 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 \pm 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 birds²⁵⁻²⁷, 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 experimentally¹⁷, 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 conditions³²⁻³⁴, outside a context meaningful to signal efficacy and reproductive success.

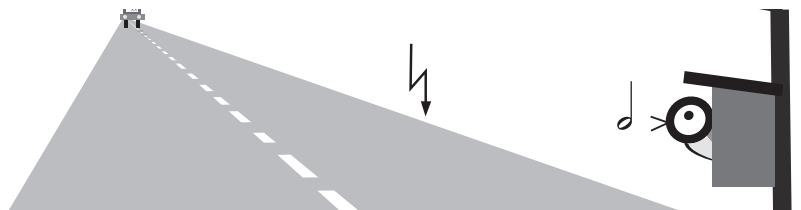
Here we studied acoustic courtship interactions in a natural woodland area among male and female great tits during the courtship ritual at dawn. We studied breeding great tit pairs at their nest box, which allowed us to document close-range male-female interactions. We used pairs of microphones, one 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-day²; $\chi^2 = 18.76$; d.f. = 3; $P < 0.001$), as individual males sang lowest just before the start of egg-laying (Figure 4.2A). In contrast, males



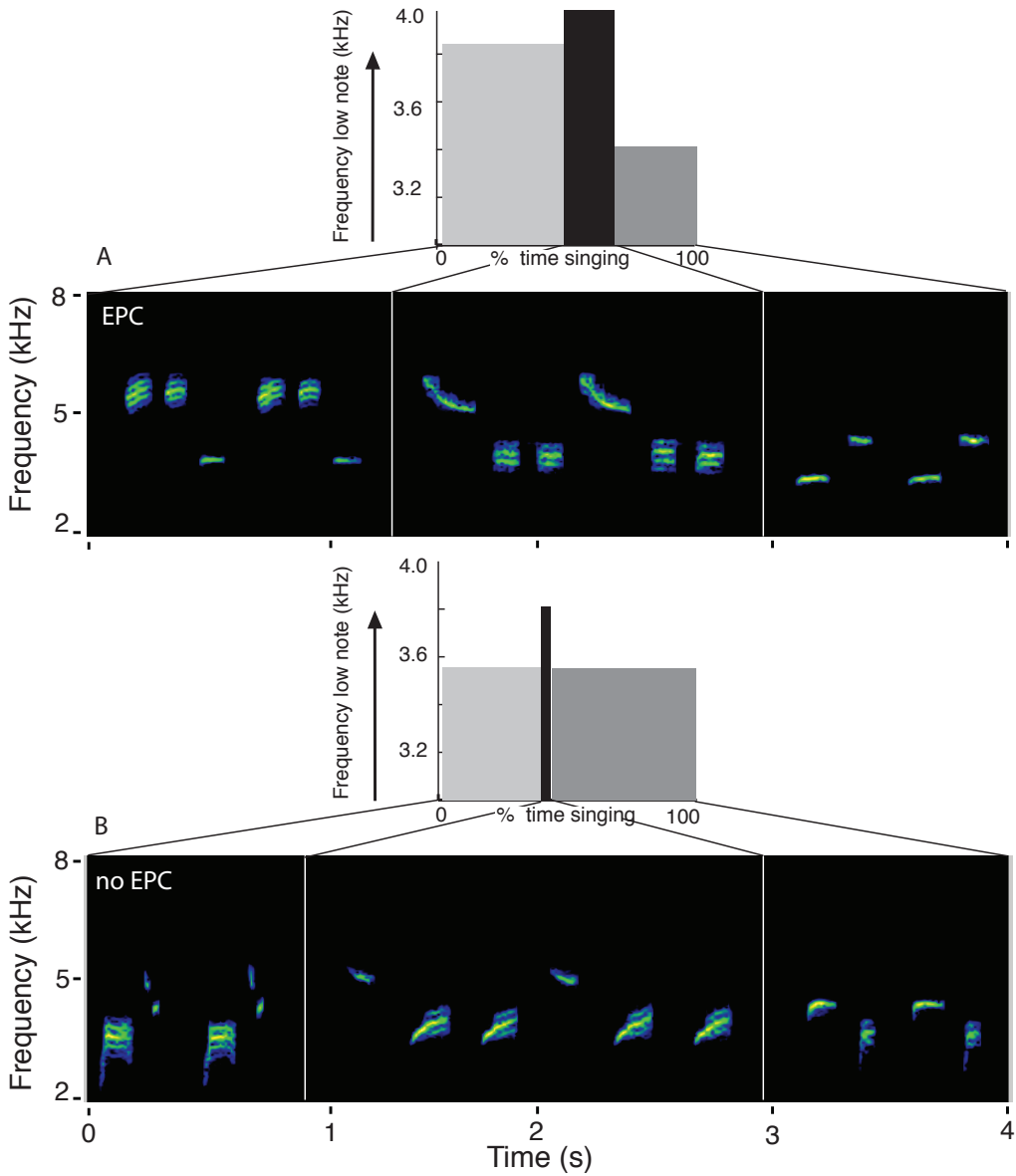


Figure 4.3. Males singing low frequency songs suffer less paternity loss. (**A,B**) Examples of song type repertoires and song type use for two neighboring males in relation to paternity loss. The cuckolded male (**A**, EPC) has similar song types compared to the non-cuckolded male (**B**, No EPC) and 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-day²: $\chi^2 = 1.43$; 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 ($\chi^2 = 8.75$; 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 ($\chi^2 = 18.34$; 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; $\chi^2 = 19.71$; d.f. = 1; $P < 0.001$; [Figure 4.2D](#)).

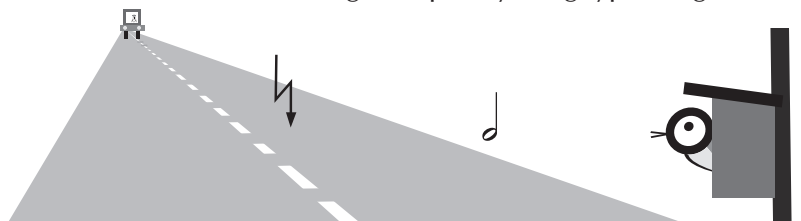
Low-singing males get cuckolded less

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; $\chi^2 = 7.14$; 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 \pm 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; $\chi^2 = 8.63$; 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



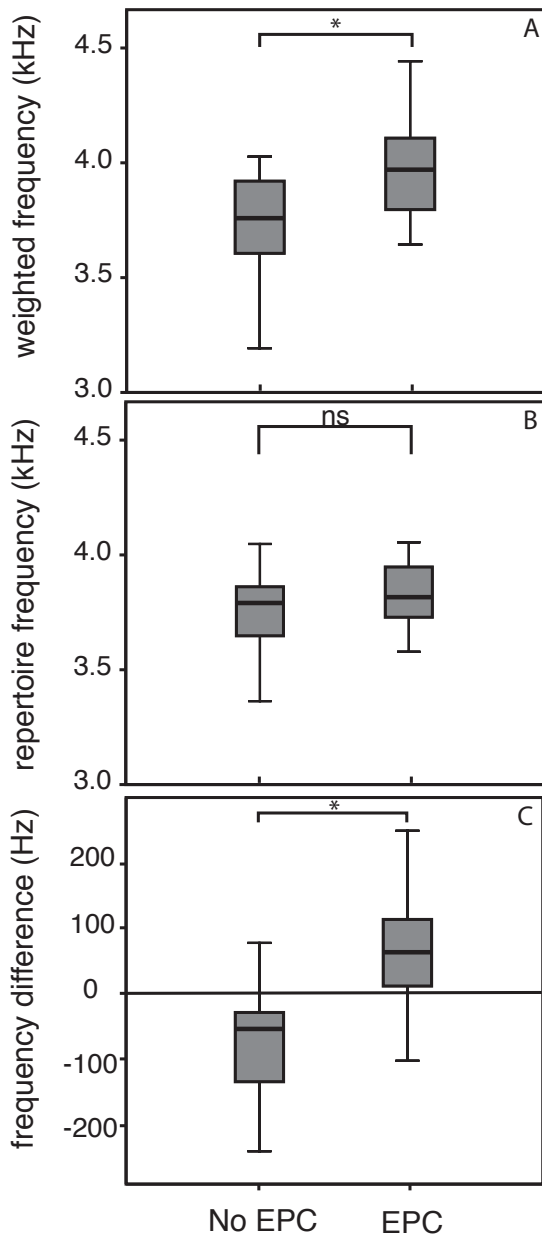


Figure 4.4. Males singing low frequency songs suffer less paternity loss. **(A)** Non-cuckolded males sing on average lower than cuckolded males during the dawn chorus at the peak of female fertility (LMM; $F_{1,21} = 6.84$; $*P = 0.018$). **(B)** Differences cannot be ascribed to non-cuckolded males 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.

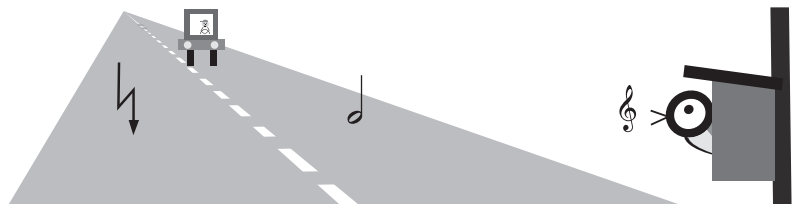
Sexual selection for low-frequency songs is in line with the fact that acoustic variation among singing birds concerns the most reliable information on male qualities under poor light conditions. The females in our study seem to actively sneak away before

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 features³⁸. For instance, females could prefer broad-banded song types that can be physically demanding to produce³⁸.

Low-frequency songs could also be favored by natural selection pressures such as the transmission properties of the acoustic environment²², including the complex acoustic structure of a nest box²³. 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.



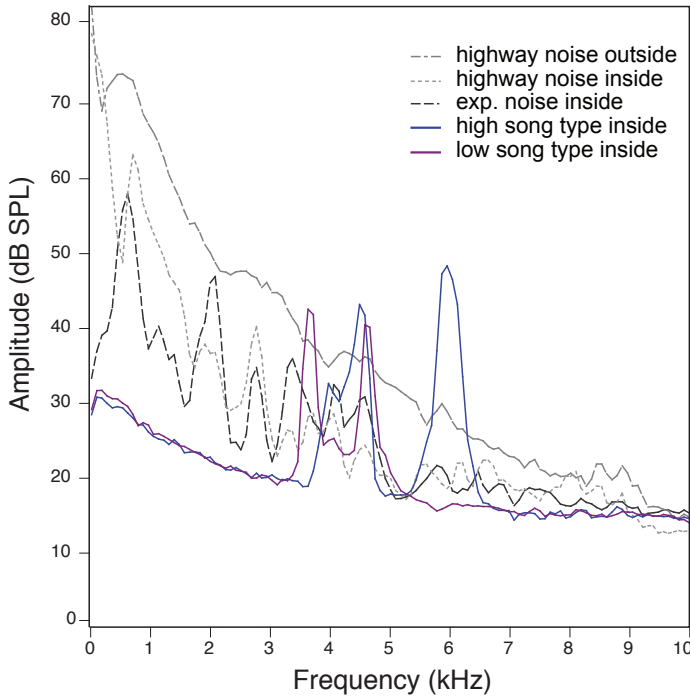


Figure 4.5. Noise profiles of anthropogenic noise and great tit song types. Shown are power spectrographic examples of a recording made inside and outside a nestbox situated ~70m from a major highway, as well as a recording of the experimental noise and a high and low song type inside the nestbox. Traffic 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.

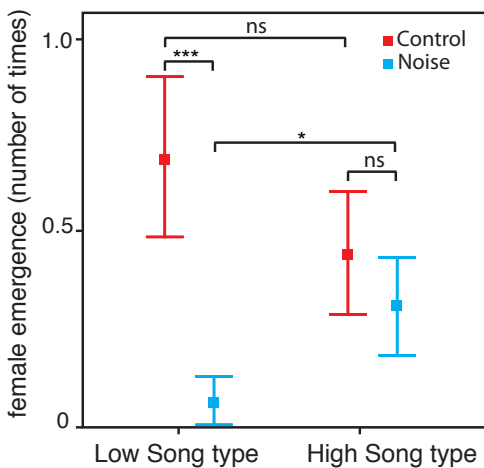


Figure 4.6. Reduced female response to low male songs in noise. Females were played the lowest and highest song type from their mate's repertoire on days with and without experimental noise exposure. Shown is the number of trials during which females emerged from their nest box as the response measure. 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 inter-sexual signaling³⁹ and song frequency of great tits has been shown to be positively related to male density⁴⁰. 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 settings^{7,8,15} and, although the benefits in terms of masking release have been debated recently¹⁹, 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 amplitude⁴¹, 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 frequencies⁴². 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 territories³¹ and although familiarity remains to be excluded as a factor⁴³ 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 densities⁴⁴⁻⁴⁷. 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

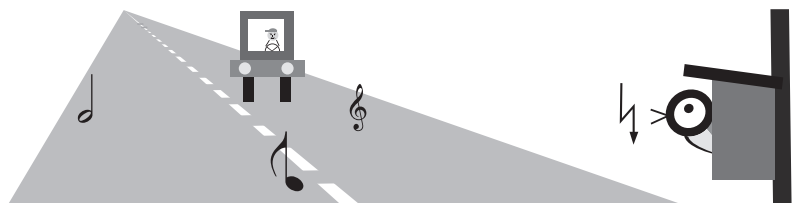
1.3. Bout duration and low-note frequency were measured for each song type independently¹⁷ and were used to calculate a weighted song frequency per day (adjusting frequency with percentage used before averaging over song type).

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 3.0⁵¹ 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 highway¹³ 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 \pm 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 noise⁵² 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

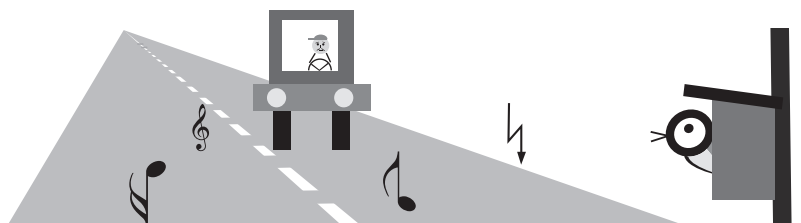
All multivariate analyses were carried out in SPSS 17.0 and data were transformed when necessary to meet model assumptions. We used different subsets of males and females for the observational analyses depending on the availability of suitable recordings and paternity data.

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.



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