Low-frequency songs lose their potency in noisy urban conditions

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Many animal species communicate with their mates through acoustic signals, but this communication seems to become a struggle in urbanized areas because of 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 tradeoff between signal strength and signal detection in a successful urban bird species, the great tit (Parus major). We show 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, whereas 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, because they provide evidence for low-frequency songs being linked to reproductive success and to be affected by noise-dependent signal efficiency.

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 it is typically biased to low frequencies (3, 6). Interestingly, several urban bird species have been found to reduce the spectral overlap with 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 (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 and cuckoos) (11, 14). However, even species that have been shown to immediately adjust song frequency in the presence of experimental noise (15–18) may suffer reduced breeding success when potential benefits of a spectral adjustment are not sufficient to avoid negative masking impact (19) or when spectral adjustment comes at a cost of reduced attractiveness (5).

Low frequencies can play a crucial role in female attraction, because they have the potential to convey a message of male quality (20, 21); they also 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 tradeoff between frequencies that are optimal for signal strength in terms of mate attraction or optimal for signal detection in terms of masking avoidance. Noisy human activities may interfere in this way 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 (i) a lack of insight into whether singing low matters in avian mate attraction and (ii) a lack of evidence from the field for frequency-dependent signal efficiency related to the presence of anthropogenic noise.

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 for the bird—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 efficiency 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 simultaneously, one inside and one outside the nest box, to record male song behavior and female response behavior (Fig. L4) (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-vs. 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 variation varied over time within individuals and peaked with the moment of highest fertility [generalized linear mixed model (GLMM): egg day$^2$; $\chi^2 = 18.76$, degrees of freedom ($df$) = 3, $P < 0.001$], because individual males sang lowest just before the start of egg laying (Fig. 1B). In contrast, males did not change the spectral frequency of their song types in relation to egg laying (GLMM: egg day$^2$; $\chi^2 = 1.43$, $df = 3$, $P = 0.70$), 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: $P = 0.31$), although start of dawn singing increased with progress in the laying stage ($\chi^2 = 8.75$, $df = 3$, $P = 0.033$) (Fig. S1). Female calling activity level peaked synchronously with male spectral song performance at the start of egg laying ($\chi^2 = 18.34$, $df = 3$, $P < 0.001$) and rapidly dropped after the first few eggs had been laid (Fig. 1C). Furthermore, females left the nest box earlier than after egg laying (GLMM: egg day; $\chi^2 = 19.71$, $df = 1$, $P < 0.001$) (Fig. S1).

Low-Singing Males Get Cuckolded Less Often. We tested whether performing with low-frequency songs at the peak in fertility was related to female sexual fidelity and found that noncuckolded males sang lower songs compared with cuckolded males [linear mixed models (LMM); $F_{1,21} = 6.84$, $P = 0.018$] (Fig. 2). Non-cuckolded males did not have lower-frequency song types (Fig. 2D) but used the low-frequency song types from their repertoire for a larger proportion of time (Fig. 2E). Interestingly, female fidelity was also related to nest box emergence [generalized linear model (GLM); $\chi^2 = 7.14$, $df = 1$, $P = 0.008$]. Unfaithful females, at the peak of fertility, left their nest box earlier (17.5 ± 4.8 min before sunrise; mean ± SD) compared with females who did not engage in extra-pair copulations (0.04 ± 5.71 min after sunrise).

Low Songs Lose Signal Efficiency in Anthropogenic Noise. We measured female response to playback of high- and low-frequency song types from the repertoire of their own mate under noisy and control conditions (Fig. S2 shows an example of signal-to-noise ratios of both song types under both noise conditions). Females are known to emerge from the nest box in response to dawn

![Figure 1](https://www.pnas.org/ cgi/doi/10.1073/pnas.1109091108 Halfwerk et al.)

**Fig. 1.** The dawn chorus ritual of great tits (*Parus major*) peaks with female fertility. (A) 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 mostly at the start of male dawn singing, during song type switches, and shortly before emergence from the nest box. Upper and lower show recordings made with the outside and inside microphones, respectively. (B) Within individual variation of great tit song behavior is related to egg laying (GLMM; $***P < 0.001$), and males sing lowest when fertility is highest (egg day −1). (C) Female calling changes with egg laying (GLMM; $***P < 0.001$), and females call most on days around the start of laying. The graphs show means ± 1 SE. The x axes show days related to start of laying (egg day 0; indicated by barred line), and y axes show male average weighted frequency of low notes and female calling (number of calls produced during dawn chorus, normalized per female).
singing, after which they typically immediately copulate with their mates (28), and female calling is related to fertility (this study); therefore, we used these two measures, emerging and calling from the nest box, as a proxy for female preference. Both song types (high and low) were played on 2 subsequent d with and without noise exposure inside the nest box. Female emergence from the nest box differed across tests (GLMM; $\chi^2 = 8.63$, $df = 3$, $P = 0.035$) (Fig. 3), depending on noise and the song type played. Females emerged 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 emerge more often during playback of low-frequency song types than high-frequency song types under control conditions (low control–high control: $P = 0.22$; peak frequencies of low notes averaged over song types of an individual’s repertoire). (E) Differences are the result of using the lower song types more often [LMM, $F_{1,71} = 7.39$, *$P = 0.014$; difference between average weighted song frequency (C) and frequency averaged over repertoire (D) per individual.]

Discussion

Our findings show that male great tits sing their lowest songs at the peak of female fertility with a reward of sexual fidelity. The females involved in extra-pair copulations in our study also seem to sneak away before sunrise, which is suggestive for an active mate choice decision (cf. 37). Acoustic variation among singing birds concerns the most reliable information on male qualities under poor light conditions, and sexual selection for low-frequency songs yields, therefore, a feasible explanation for the well-timed spectral performance of males. We also show 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 thereby, are less effective than high-frequency songs, showing that it pays urban birds to increase song frequencies when confronted with noisy conditions.

There are several not mutually exclusive explanations for the relationship between song frequency and female fidelity. Female songbirds make song-based reproductive decisions during the dawn chorus (26, 27), and female great tits in our study could have used 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, because low frequencies can co-vary with more complex spectral features (38). For instance, females could prefer broad-banded song types that can be physically demanding to produce (38) and will, on average, be lower in frequency compared with small-banded song types. 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 ratios 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.

However, another interpretation of the female preference for males shifting their singing efforts to the low-frequency song types in their repertoire could be that different song types serve different functions. Low-frequency song types could play an explicit role in male–female communication, whereas high-frequency song types could be more important in male–male communication. 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 forth between territory boundaries and matching song types. If males selectively sing low-frequency songs to females and high-frequency songs to males and if the amount of interaction time spent with females varies with laying stage and mate guarding, this finding could also explain the observed patterns in frequency use in relation to female fertility and sexual fidelity. Alternatively, low-frequency songs could be used in song contest among males to guard paternity and be indirectly related to female preference if females use the outcome of the contest in extra-pair mating decisions (26).

Our playback results show experimental evidence for a noise-dependent advantage of high-frequency songs under natural field conditions. Low-frequency songs suffer reduced efficiency in male–female communication under noisy conditions, favoring the use of high-frequency songs. This finding is in line with experimental data showing that great tits actively avoid spectral overlap with background noise (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 opposite during exposure to high-frequency inverse city noise. Many species have now been observed to raise song frequencies up 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 concomitantly with other signaling strategies, such as raising song amplitude (41), or it can be used as an alternative for those species for which raising amplitude above a certain level is too energetically demanding.

The evolutionarily 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 tradeoff 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 therefore, for species in which females make sound-based reproductive decisions, we would expect signal detection to prevail over signal strength under high-noise conditions. A focus on detection of conspecifics rather than discrimination among them, which has been observed in female frogs exposed to natural chorus noise (42), can result in a preference shift from the low to the high frequencies. Consequently, the tradeoff 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 that may explain urban divergence through sensory drive to, for example, higher and faster songs (30, 38). Great tits living in noisy territories in cities have already been found to respond more strongly 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 expanding 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, reduced reproductive success (12, 44), or they may end up with low-quality or at least, less-productive mates, laying smaller clutches and raising fewer offspring close to noisy highways (13). The masking impact by traffic noise will be highest for those species that use low frequencies to attract females, which is shown by our field playback experiment, and this finding 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-frequency song types to be related to reproductive success through female fidelity, which shows that low-frequency singing is under direct or indirect sexual selection. These findings also show that benefits of masking release through singing higher frequencies in cities are constrained by a potential loss in signal strength and point to the existence of a modern tradeoff. It would be interesting to examine further how anthropogenic noise can alter the strength, direction, or specific target of selection pressures acting on bird song. Studies on urban acoustics will likely continue to provide both scientific opportunity and
conservation concern. They generate new insights on environmental causes for evolutionary change, but they should also raise awareness of the consequences of noisy human behavior.

Materials and Methods
The study was conducted in a nest box population of great tits situated in the National Park Dwingelderveld in 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 (see below) began when nests were near completion to minimize nest desertion because of our activities. All males and females were included only one time in this study. The Leiden Committee for animal experimentation approved the study under number 08073.

Acoustic Recordings and 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, whereas 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 (1 h before until 1 h after sunrise) across the laying phase. We identified song types of the social male and determined start of dawn singing, total time spent 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) to determine song spectral performance. Low-note frequency was multiplied with bout duration and divided by the total amount of time spent singing to get an average weighted measure of song frequency per day.

Paternity Analysis. Chicks were sampled for blood on the second day and parents were sampled on the seventh day posthatching for DNA extraction. To assign paternity, we used the six microsatellite loci (described in ref. 49). A female mating with two males would produce four offspring, whereas the offspring of a single male would be identical. We selected a subset of pairs (n = 15) for which we had suitable recordings before (egg days –5 and –1) and during laying (egg days 1 and 5). We tested whether within individual vocal performance peaked at fertility using a generalized linear mixed model (GLMM) with a power link function, a normal error distribution (or Poisson distribution 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 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, log link function, and noise treatment, and song type (high or low), stimulus order, and day were fixed factors.

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Fig. S1. Male and female behavioral timing changes with egg laying. (A) Onset of dawn song is related to egg laying (generalized linear mixed model; $P = 0.033$), and males start singing later after females have laid several eggs. (B) Females also emerge later from their nest box in relation to egg laying (generalized linear mixed model; $P < 0.001$), with the biggest shift observed around the start of laying.

Fig. S2. Noise profiles of anthropogenic noise and great tit song types. Shown are power spectrographic examples of a recording made inside and outside a nest box situated ~70 m from a major highway as well as a recording of the experimental noise and a high and low song type inside the nest box. Traffic noise is typically louder toward the lower frequencies, and noise levels are reduced inside the nest box compared with the outside. Sound is resonated inside the nest box, causing the rugged noise profile. Note that the high song type has a higher signal to noise ratio overall compared with the low song type.