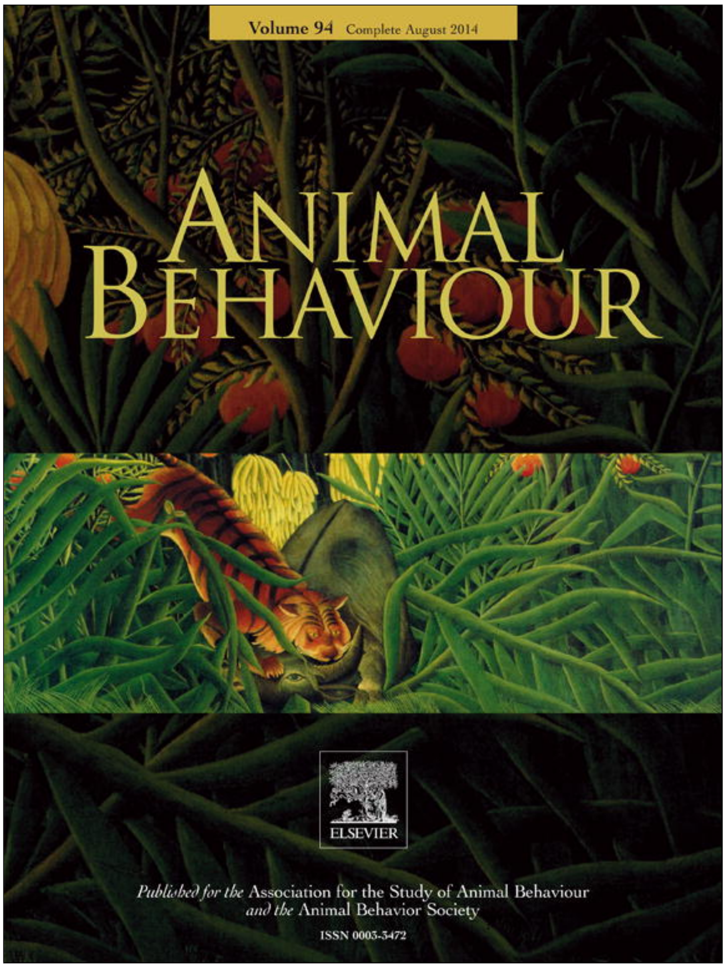
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Sexy voices – no choices: male song in noise fails to attract females

Rouven Schmidt, Aoibheann Morrison, Hansjoerg P. Kunc*

Institute for Global Food Security, Queen's University Belfast, School of Biological Sciences, Medical Biology Centre, Belfast, U.K.

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Anthropogenic noise affects species relying on acoustic communication. Signals used in acoustic communication are important for reproduction as females are often attracted by signalling males and base their mate choice on male song. Previous studies on the impact of anthropogenic noise on behaviour have focused on the sender and mostly on vertebrates. However, we have little understanding of how potential receivers, e.g. females, are affected by noise. Using playback experiments, we investigated the response of female field crickets, *Gryllus bimaculatus*, to male song in the presence and absence of anthropogenic noise. We found that anthropogenic noise resulted in less effective phonotaxis towards signalling males. Thus, our study provides experimental evidence that anthropogenic noise affects females by limiting their ability to locate potential mates. Since male songs were not energetically masked by anthropogenic noise, signal masking cannot explain the difference in response. The reduced ability to locate singing males may be explained by distraction caused by the broad stimulus filtering of *G. bimaculatus*. The behavioural adjustments at the individual level may be passed to higher ecosystem processes, owing to invertebrates' fundamental role as part of a functioning ecosystem.

Urbanization and the associated increase in transport networks and industry have caused an evolutionarily sudden rise in anthropogenic noise in terrestrial habitats (Barber, Crooks, & Fristrup, 2010). Anthropogenic noise creates habitats with novel environmental selection pressures, and may lead to a decline of individuals and species, resulting in a loss of biodiversity (Bayne, Habib, & Boutin, 2008; Francis, Ortega, & Cruz, 2009). Initial responses of individuals to novel selection pressures are often behavioural (Tuomainen & Candolin, 2011). Research on the impact of anthropogenic noise on individuals has concentrated on vertebrates (Kight & Swaddle, 2011; Slabbekoorn et al., 2010). However, invertebrates are a fundamental part of a functioning ecosystem (Wilson, Morris, Arroyo, Clark, & Bradbury, 1999), and changes in their abundance through behavioural changes in response to noise could have far-reaching consequences on higher ecosystem processes.

Across the animal kingdom, a striking example of behaviour is communication, i.e. the transfer of information from a sender to a receiver through the environment. Communication plays a crucial role in many species in the context of sexual selection, through both female choice and male–male competition, among parents and their offspring, and in predator–prey interactions (Bradbury & Vehrencamp, 2011). Therefore, anthropogenic noise is specifically a problem for species relying on acoustic communication (Rabin & Greene, 2002). In many species, females are attracted by males using acoustic signals on which females base their mate choice (Andersson, 1994). Anthropogenic noise impairs male–female communication (Bee & Swanson 2007; Halfwerk et al., 2011; Huet des Aunay et al., 2014; Samarra, Klappert, Brumm, & Miller, 2009), which may translate to lower reproductive output. Thus, changes in species abundance may derive from negative effects that increasing noise levels may have on an individual's behaviour.

The aim of this study was to investigate how anthropogenic noise affects the behaviour of potential receivers, such as females. As a model, we chose the field cricket, *Gryllus bimaculatus*, in which males sing in choruses to attract females (Simmons, 1988). We exposed females to two playbacks of singing males: one without and one with noise (Fig. 1). If noise affects the ability of females to locate singing males, female behaviour should differ between the two playbacks.

METHODS

Study Animals

We studied final moult *G. bimaculatus* females, which were kept individually in cylindrical plastic containers with a diameter of 9.5 cm and a height of 5.5 cm. Containers were equipped with pieces of cardboard egg box and crickets were provided with

* Correspondence: H. P. Kunc, Institute for Global Food Security, Queen's University Belfast, School of Biological Sciences, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, U.K.

E-mail address: kunc@gmx.at

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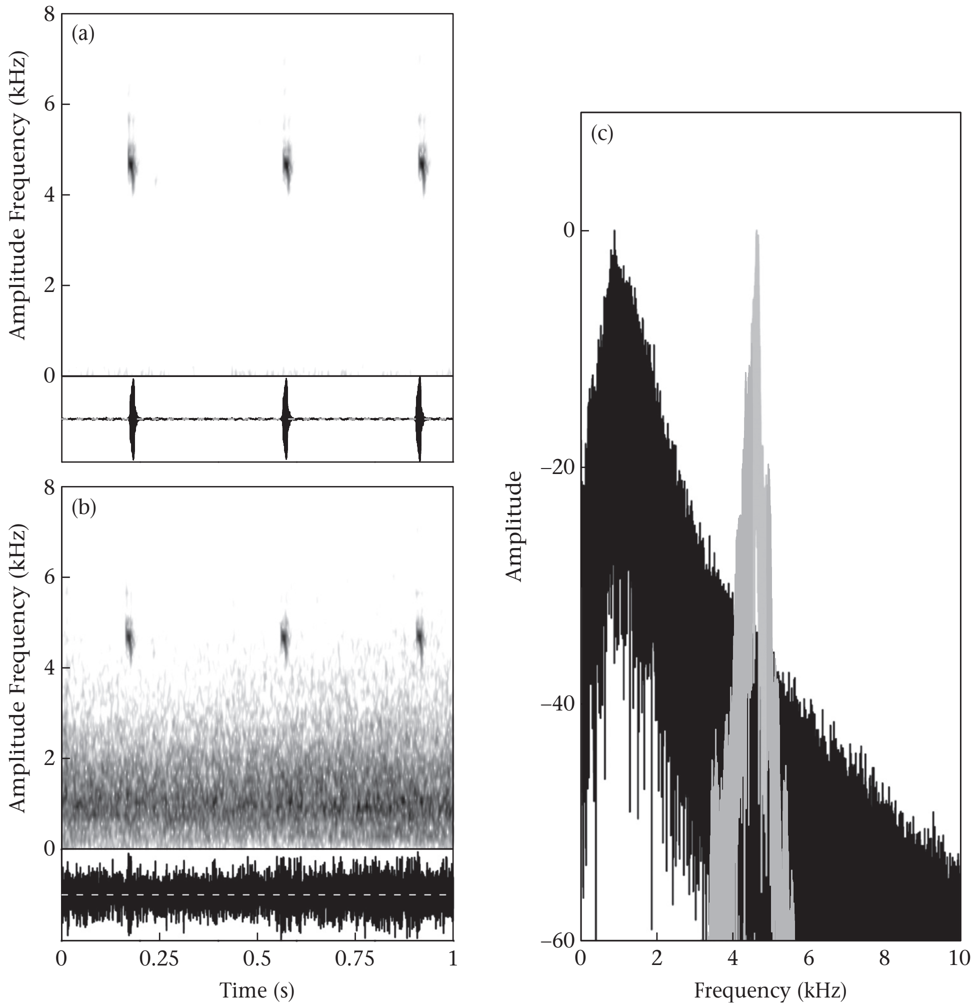

Figure 1. Song stimuli of *Gryllus bimaculatus* played back as (a) song without anthropogenic noise and (b) song with anthropogenic noise (sonograms on top and oscillograms below); (c) power spectra of anthropogenic noise (black) and cricket song (grey).

carrots ad libitum and water supplied on a sponge. Laboratory temperature was maintained at 19 °C and the light:dark cycle was 17:7 h. Subjects were obtained from a local supplier (City Reptiles, Belfast, U.K.).

Playback Stimuli

We created playback stimuli from recordings of different groups of crickets, each consisting of five males and five females housed in plastic containers of 15.5 × 7.5 cm and 5 cm high. Groups were held under the same conditions as the focal females. We recorded each group for 60 min using a solid state recorder (Marantz PMD660, .wav format, sample frequency 48 kHz, resolution 16 bit) connected to a Sennheiser ME 66/K6 directional microphone. From each recording, a continuous section of 15 min was selected using Audacity 2.0 (http://audacity.sourceforge.net) and normalized to the peak amplitude (see English, Kunc, Madden, & Clutton-Brock, 2008; Kunc, Amrhein, & Naguib, 2006, 2007; Kunc, Madden, & Manser, 2007). The resulting 17 unique stimuli served as the 'song' treatment. A copy of each 15 min playback stimulus was merged with a traffic noise recording and served as the stimulus in the 'song and noise' treatment. Anthropogenic noise was recorded at a distance of about 10 m from motorways during rush hours with the same equipment as described above and then standardized to 70 dB (McMullen, Schmidt, & Kunc, 2014). This experimental setup ensured that attractiveness of signals was the same for both treatments. Spectrograms, oscillograms and power spectra were generated using the package 'seewave 1.7.2' (Sueur, Aubin, & Simonis, 2008) in R 3.0.1 (R Development Core Team, 2013) with the following settings: FFT size = 512, window function = Hanning, overlap = 75%, resulting in a frequency resolution of 94 Hz and a temporal resolution of 8.0 ms. The peak frequency for the song was 4.69 kHz and for the noise 0.94 kHz, and the signal-to-noise ratio at 4.69 kHz was −34 dB.

Playback Protocol

To test whether noise had an effect on female behaviour, the container with a female was transferred to the centre of an experimental arena (90 × 45 cm and 38 cm high) equipped with a loudspeaker (Saul Mineroff Electronics, NY, U.S.A., www.mineroff.com) at each narrow side. The arena was divided into four equally sized sections, i.e. a section closest to the loudspeaker on each narrow side, and a neutral zone of the remaining two central sections subdivided by a central line. Females were released in the centre of the arena. After the first playback, presented randomly from either the left or the right speaker, females were returned to the centre and kept in the container again. After 3 min, females were released again and the other playback treatment was started, again randomly from either speaker. Treatment order was randomized, with the constraint that treatments were balanced (Milinski, 1997).

Statistical Analyses

Statistical tests were carried out in R 3.0.1. We analysed (1) the initial movement of the 17 females towards or away from the broadcasting speaker using chi-square tests, and (2) the percentage of time females spent in the section either closest to or furthest away from the speaker broadcasting sound, using the lme function in 'MASS' (Venables & Ripley, 2002). We transformed the percentage of time females spent in each of the two sections using arcsine transformation, and analysed it as a function of section and treatment. Our hypothesis was that the time females spent in the sections depended on the treatment, i.e. statistically we were interested in the interaction term of treatment and section. A significant interaction between the two factors indicates that the main effects are not independent of each other (Quinn & Keough, 2002), i.e. time spent in a section depends on the playback treatment. To account for the repeated sampling of the same individuals we included individual identity as a random factor.

RESULTS

During the 'song' treatment, more females initially approached the loudspeaker broadcasting songs than the quiet loudspeaker ($\chi^2_1 = 13.24$, $P < 0.001$; Fig. 2a). However, during the 'song and noise' treatment females did not show this pattern in approach ($\chi^2_1 = 1.47$, $P = 0.23$; Fig. 2a).

Females spent more time close to the playback speaker during the 'song' treatment whereas they did not show a preference when exposed to 'song and noise' (treatment: $F_{1,48} = 1.26$, $P = 0.27$; section: $F_{1,48} = 1.1$, $P = 0.3$; interaction between treatment and section: $F_{1,48} = 6.42$, $P = 0.015$; Fig. 2b). This significant interaction indicates that females preferred the section nearest to the loudspeaker only during the 'song' treatment.

DISCUSSION

Anthropogenic noise affected the behaviour of female crickets to signalling males. Females approached the side of the experimental arena where the singing males were simulated without anthropogenic noise, demonstrating that females are attracted to the songs of males. However, during the 'song and noise treatment' we did not find a clear pattern for either the initial approach or the time spent in the sections closest to or furthest away from the loudspeaker.

Regarding the difference in approach to the speaker when noise was absent or present, a number of possible nonmutually exclusive mechanisms may be involved: First, noise may mask male songs and females may not be able to locate acoustically signalling males when noise levels are high. However, the frequency band of *G. bimaculatus* songs was well above that of anthropogenic noise (Fig. 1c). Thus, signal masking cannot explain the different response of females to song when anthropogenic noise was present or absent.

Second, phonotaxis to male song in a noise-polluted environment might be less effective. A solution to cope with complex acoustic environments is stimulus filtering, which occurs when the sensitivity range of auditory organs is narrowed to a species-specific range of emitted sound frequencies (Roemer, 2013; Schmidt, Riede, & Roemer, 2011). In fruit flies, *Drosophila montana*, females are able to detect male song in the presence of noise

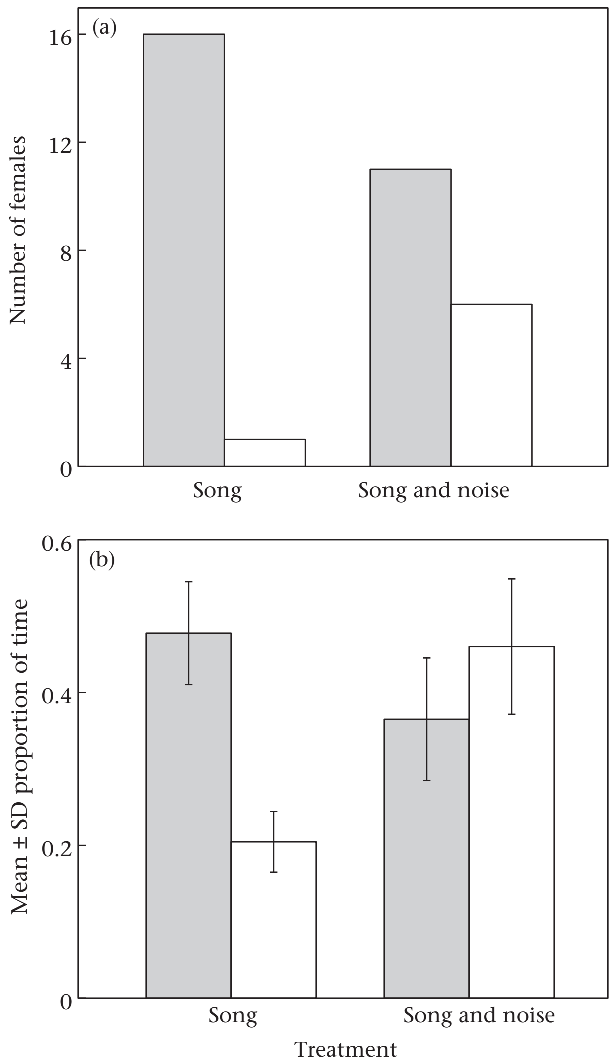

Figure 2. Responses of female crickets during playback of male 'song' and 'song and noise': (a) number of females initially approaching the broadcasting loudspeaker (grey bars) or the silent loudspeaker (white bars); (b) proportion of time females spent during playback at either the broadcasting loudspeaker (grey bars) or the silent loudspeaker (white bars).

outside the frequency band of the song, but not in the presence of in-band noise above a certain amplitude (Samarra et al., 2009). If females had an auditory tuning to a broad frequency range, the presence of out-of band noise would also have impaired signal detection. Thus, the underlying mechanism of stimulus filtering reduces the influence of noise outside the sensitivity range of the filter (Samarra et al., 2009; Schmidt et al., 2011). Accordingly, in habitats with high acoustic competition, auditory sensitivity is sharply tuned to conspecific song whereas in habitats with lower acoustic competition a broader auditory tuning can be found (Schmidt et al., 2011). Our study species, *G. bimaculatus*, has been shown to have a broad auditory tuning range (Schmidt et al., 2011). Therefore, our results suggest that species with a broader auditory tuning are more susceptible to distraction caused by acoustic interference through anthropogenic noise. Distraction arises when an animal's attention suddenly shifts involuntarily (Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Chan and Blumstein, 2011) and anthropogenic noise might act as distraction (Francis & Barber, 2013). At this stage, the combination of auditory tuning and distraction provides a parsimonious explanation for our results.

Finally, individuals might simply avoid the noise. In our experiment, avoidance does not explain the results because the females should have shown a clear preference for the opposite side of the arena if they had actively avoided the noise. A cause and effect relationship between increasing noise levels and avoidance behaviour has been demonstrated in birds. Individuals experimentally exposed to short-term anthropogenic noise avoid the noise by moving away from it (McLaughlin & Kunc, 2013). Long-term noise exposure experiments have shown that birds avoid noise-polluted areas (Blickley, Blackwood, & Patricelli, 2012), which can translate into observed changes in settlement patterns (Bayne et al., 2008; Francis et al., 2009). To our knowledge there are no studies on avoidance behaviour in insects in response to anthropogenic noise.

The difference in response to male songs in the absence or presence of anthropogenic noise could have consequences at both the individual and the population level (e.g. Gross, Pasinelli, & Kunc, 2010; Habib, Bayne, & Boutin, 2007). At the individual level, noise may limit the reproductive output of both males and females by reducing their ability to locate a mate, leading to a decrease in abundance at the population level. Females of *G. bimaculatus* search for sedentary calling males, which may make females particularly susceptible to predation (Simmons, 1986). Under natural conditions, an increase in the time females have to invest to find a mate increases the risk of predation (Simmons, 1986). Thus, by increasing the time for mate search, anthropogenic noise may lead to a sex-biased mortality rate through an increased predation risk. Such sex-biased mortality rates could lead to changes in the operational sex ratio of invertebrate populations. It is important to note that our experiments, albeit short-term, reveal a clear effect of noise on female behaviour. Thus, chronic noise exposure is likely to have a more pronounced effect on individuals and populations.

The consequences outlined above at the individual and population level may then have a wider impact on ecological processes. Anthropogenic noise has the potential to reduce population sizes and species diversity of birds (Barber et al., 2010). Although, to our knowledge, no study has investigated how noise affects insect diversity, our study, together with previous work on signalling male crickets (Lampe, Reinhold, & Schmoll, 2014; Lampe, Schmoll, Franzke, & Reinhold, 2012) and cicadas (Shieh, Liang, Chen, Loa, & Liao, 2012), suggests similar effects on insects. Invertebrates are a crucial component of food webs and fulfil many ecosystem services, such as decomposition, nutrient release and pollination (Morley, Jones, & Radford, 2013). Thus, a decrease in invertebrate abundance could have a wider impact on ecological processes. First, it seems invertebrates and vertebrates are affected by noise directly, which may lead to a decrease in abundance and a loss in biodiversity. Second, invertebrates are prey for many predatory species, which may abandon noise-polluted areas due to a decrease in prey. Third, anthropogenic noise may have long-term effects on ecosystem structure and diversity (Francis, Kleist, Ortega, & Cruz, 2012), and a decrease in invertebrate species can affect ecosystem function (Mulder, Koricheva, Huss-Danell, Hogberg, & Joshi, 1999). Therefore, noise may affect species not only directly through masking or distraction, but also indirectly by lowering the availability of potential prey and changes in ecosystem services.

In conclusion, our study provides experimental evidence that anthropogenic noise affects female invertebrates by limiting their ability to locate potential mates effectively. Our results are remarkable, as male songs were not masked by anthropogenic noise. The reduced ability to locate singing males can be explained by the broad stimulus filtering of *G. bimaculatus* which increases distraction. Thus, if species differ in their sensitivity to anthropogenic noise based on their auditory tuning, those species with broader auditory tuning might suffer more from increasing noise levels than species with sharper auditory tuning. Behavioural adjustments at the individual level could affect larger ecological processes, as invertebrates are potential prey for many other species and provide ecosystem services.

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