

Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components

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Summary

1. Anthropogenic noise is known to affect acoustic signal production in birds, frogs and mammals. These animals use different mechanisms to adjust their signals to elevated background noise levels (increase in signal amplitude, shift to higher frequencies, etc.). Previous studies have concentrated on behaviourally plastic changes in signal production as a result of elevated background noise levels. To our knowledge, long-term effects of anthropogenic noise on signal production have not yet been investigated. Moreover, strategies of invertebrate species to ensure acoustic signal transmission under anthropogenic noise have not been examined, so far.

2. We tested whether and how male *Chorthippus biguttulus* grasshoppers from noisy roadside habitats may adjust acoustic courtship signals to elevated background noise levels, compared with conspecifics from quiet control habitats. In this species, sexually selected male courtship signals serve to attract potential mating partners, which make the undisturbed transmission of signals in habitats with increased background noise levels crucial for male reproductive success.

3. Compared to males from control populations, males from roadside habitats produced songs with a significantly higher local frequency maximum under standardized, quiet recording conditions. This local frequency maximum (in the range of c. 6–9 kHz) overlaps with low-frequency road noise that has the potential to degrade or mask this part of the signals' frequency spectrum.

4. To our knowledge, this is the first evidence that insects from noisy habitats produce different acoustic signals than conspecifics from quiet habitats, possibly using a more permanent mechanism for signal adjustment than behavioural plasticity, which was found in different bird species adjusting to high background noise levels. Such an effect of anthropogenic noise has not been shown for any invertebrate species before, and our results suggest that similar strategies to avoid degradation or masking by noise (i.e. increase in carrier frequency) are used over a wide range of taxa, including both, vertebrates and invertebrates.

Key-words: acoustic communication, anthropogenic noise, *Chorthippus biguttulus*, sexual selection, signal masking

Introduction

Exposure to anthropogenic noise increasingly affects the acoustic communication of animal species in their natural habitats (Slabbekoorn & Peet 2003; Bee & Swanson 2007; Barber, Crooks & Fristrup 2009; Halfwerk *et al.* 2011; Parks *et al.* 2011). Anthropogenic noise has the potential to degrade or even completely mask acoustic signals and to affect efficient intraspecific communication (Barber,

Crooks & Fristrup 2009; Halfwerk *et al.* 2011). Road noise is one of the major noise sources in urban environments (Warren *et al.* 2006; Barber, Crooks & Fristrup 2009). It is the spatially most extensive type of noise (Barber, Crooks & Fristrup 2009), and thus, it has the potential to affect the acoustic communication of many different species. For example, frogs from noisy habitats were found to call at higher pitches than conspecifics in more rural habitats (Parris, Velik-Lord & North 2009). Furthermore, it has been shown that birds inhabiting urban areas shift their songs to higher frequencies or use higher-pitched song

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types, as compared to conspecifics from rural habitats (Slabbekoorn & Peet 2003; Nemeth & Brumm 2009; Dowling, Luther & Marra 2011).

Up to date, research has mainly focused on the effects of urban or anthropogenic noise on acoustic communication in vertebrates, whereas there is not much known about potential effects on communication in natural populations of invertebrates. Studies addressing the impact of noise on insect communication have focused on the effects of artificial signals, such as white noise of different frequency bands, on signal perception in the laboratory (Bailey & Morris 1986; Ronacher & Hoffmann 2003; Samarra *et al.* 2009; Einhupl *et al.* 2011). Samarra *et al.* (2009) found that *Drosophila montana* females decrease their response rate to male courtship songs in the presence of background noise. Bailey & Morris (1986) demonstrated that random noise, as well as male signals of a closely related species, significantly disrupted female phonotaxis in the bush cricket *Conocephalus brevipennis*. Einhupl *et al.* (2011) showed that male courtship songs of the grasshopper *Chorthippus biguttulus* (Fig. 1) that were more robust against broad band white noise (1–40 kHz) were also judged as more attractive by females: The most attractive songs still elicited a female duet response song at 4 dB higher noise levels than the least attractive songs (Einhupl *et al.* 2011). Hence, interference of anthropogenic noise sources with insect communication signals seems also likely in natural populations in those cases where frequency bands of signal and noise overlap.

In many grasshopper species acoustic communication plays a major role, as it serves to attract mating partners and thus directly links with reproductive success and fitness (von Helversen & von Helversen 1997; von Helversen, Balakrishnan & von Helversen 2003; Klappert & Reinhold 2005). To attract females, males of the acridid grasshopper *C. biguttulus* produce courtship songs by rubbing a toothed file on their hind legs against a protruding vein on the front wings (Klappert & Reinhold 2005; for detailed descriptions of *C. biguttulus* signals see von Helversen &

von Helversen 1997; von Helversen, Balakrishnan & von Helversen 2003; and Fig. 2). Females respond to attractive males with shorter, predominantly low-frequency acoustic signals that are much more variable than male signals with respect to carrier frequency and temporal structure (von Helversen & von Helversen 1997). Males approach females that have answered previous callings to mate with them (von Helversen, Balakrishnan & von Helversen 2003). Whether a female will respond to male song depends on the attractiveness of male song characteristics (Klappert & Reinhold 2003), on the female recognizing the male as a conspecific (Safi, Heinzle & Reinhold 2006), as well as on the females' motivation to mate, which may change during the course of her lifecycle (Wirmer, Faustmann & Heinrich 2010).

In the present study, we analyse long-term effects of traffic noise on the production of male *C. biguttulus* courtship signals. Road noise usually peaks around 1 kHz, but reaches amplitudes of 55–65 dB_A in the 6–9 kHz frequency range (Sandberg 2003), which marks the lower-frequency local maximum of male *C. biguttulus* signals (Meyer & Elsner 1996; von Helversen & von Helversen 1997). As the absence of low-frequency components in artificially generated male signals was shown to significantly decrease the response probability of females (von Helversen & von Helversen 1997), males should avoid degradation or masking of these frequency bands. We expect male grasshoppers to produce different signals under high background noise levels than under more quiet conditions, as successful signal transmission is essential in the context of mate choice and male fitness in this species. This includes the capability of males to convey information on their attractiveness, under elevated noise levels. We hypothesize that *C. biguttulus*

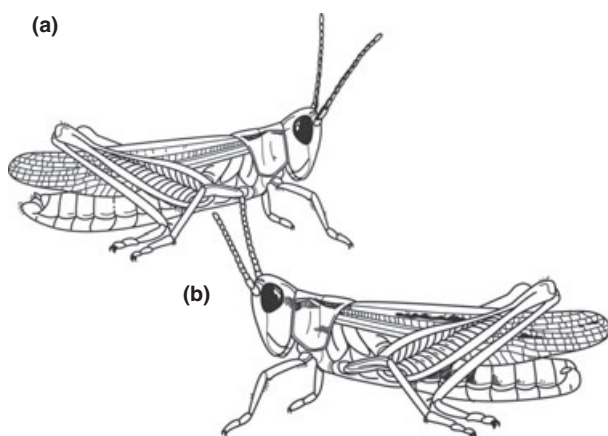


Fig. 1. *Chorthippus biguttulus* male (a) and female (b) (Sketch: Nils Cordes).

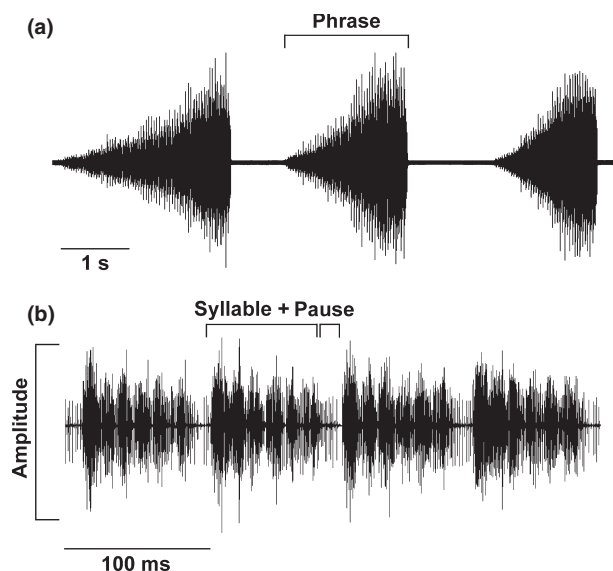


Fig. 2. (a) Temporal structure of an exemplary *Chorthippus biguttulus* song, consisting of three phrases. Amplitude is depicted over time. Male signals usually include 2–6 phrases. (b) Temporal structure of four exemplary syllables of a *C. biguttulus* phrase. A phrase consists of c. 20–60 syllables.

males from noisy habitats produce signals with a particular temporal, spectral or energetic structure to avoid signal degradation or signal masking through traffic noise.

Materials and methods

We caught a total of 188 *C. biguttulus* males during the mating season between mid-July and early September 2010, originating from 16 populations in eight locations in Northwestern Germany (Table 1). Grasshoppers from two populations in close proximity were caught on the same day, with one of the populations inhabiting a noisy habitat next to a major highway (German *Autobahn*), the other one a quiet control habitat. Noisy and quiet habitats were located in a mean distance of 2.71 km (SE = ± 0.47) from each other, whereas the mean distance from one noisy habitat to the nearest other noisy habitat was 22.55 km (± 5.91). Paired habitats are significantly closer to each other than roadside habitats (paired *t*-test: $t = 3.56$; d.f. = 7; $P < 0.01$).

Background noise levels were measured with a sound-level meter (PeakTech 5035; 4 in 1 Multifunction environment tester by Conrad Electronic GmbH, Hirschau, Germany) in dB_A. Ambient noise in roadside habitats was significantly louder than in the respective control habitats (paired *t*-test, on mean values of four measurements per habitat: $t = 14.22$; d.f. = 7; $P < 0.01$) (Table 1). Additional to our own background noise measurements, we obtained ambient noise data for all roadside habitats from the state road maintenance services of Lower Saxony and North Rhine-Westphalia. These data were calculated based on traffic counts from 2010, for a height of 1 m above the ground and a distance of 1 m from the road (directly behind the crash barrier, where we caught grasshoppers) (road maintenance services, personal communication). A mean ambient noise level of 80.7 dB_A (SD = ± 2.2) was calculated for roadside habitats during daytime. A pairwise comparison between the data provided by road maintenance services and our own measurements from noisy habitats (means per site as documented in Table 1) demonstrates no significant difference between the two data sets (paired *t*-test, on mean dB_A values for roadside habitats: $t = -1.2$; d.f. = 7; $P = 0.27$).

Grasshoppers from noisy habitats were caught by sight, as it was hardly possible to hear male signals right next to the highway, much less to locate them accurately. Males from quiet control sites were caught by sight and by hearing. All animals were brought to the laboratory, where they were kept in cages at room temperature and fed *ad libitum* with a mixture of different *Poaceae* grasses.

Song recordings took place between 10 AM and 5 PM in a dark, sound-isolated room constantly held at 29 °C (± 0.5), 24–72 h after the animals were caught. Grasshoppers show phototactic response to light sources (Kral 2008) and prefer to sit within illuminated patches in dark surroundings. Therefore, we placed males in our recording setup onto a small tripod platform that was located in an illuminated wooden box (70 cm \times 135 cm \times 60 cm), to keep them on the spot. As males of this species produce their courtship signals during daytime, our recording setup does not interfere with the animals' natural signalling behaviour. A Bruel & Kjaer 4939 microphone (Nærum, Denmark; ¼ Microphone Free Field with a NC*MX-HD cable connector by Neutrik, Charlotte, NC, USA) that was connected to a standard desktop PC was positioned at a distance of 10 cm to the male. This recording distance was strictly adhered to with the aid of a 10-cm-long metal bar that was attached to the microphone in such a way that the free end of the bar was positioned right at the (lateral) side of the male's body closest to the microphone. Males were stimulated to produce courtship songs by exposing them to a randomly chosen adult female from their own population. Females were placed directly in front of the males, but mating was prevented by the experimenter to maintain male motivation to sing.

Table 1. Geographic coordinates and mean maximum background noise (\pm SD) of all 16 grasshopper populations. Maximum background noise [dB]_A for all populations was measured over four 1 min intervals during a time span of 10 min on respective catch days. Two background noise measurements were carried out on a Sunday (both Bad Eilsen populations). All other measurements were taken on weekdays (Monday–Friday). All measurements were conducted between 10 AM and 3 PM on weekdays (Monday–Friday)

Location (name of nearest settlement)	Population	Geographic coordinates	Mean maximum background noise [dB] _A	N
Bad Eilsen	Roadside	52°13'08.98"N 09°03'24.58"E	83.0 (± 0.7)	12
Bad Eilsen	Control	52°13'56.16"N 08°59'36.92"E	54.2 (± 1.1)	12
Beckum	Roadside	51°43'27.66"N 07°58'48.24"E	87.0 (± 0.4)	12
Beckum	Control	51°42'44.78"N 07°57'13.86"E	37.5 (± 3.2)	12
Geseke	Roadside	51°35'50.23"N 08°31'51.58"E	82.4 (± 0.7)	12
Geseke	Control	51°36'18.64"N 08°29'52.32"E	50.5 (± 3.2)	12
Haaren	Roadside	51°33'13.50"N 08°48'02.50"E	78.9 (± 0.9)	12
Haaren	Control	51°33'48.58"N 08°47'42.22"E	49.2 (± 1.7)	12
Dissen	Roadside	52°10'14.82"N 08°09'21.34"E	81.6 (± 1.9)	12
Dissen	Control	52°07'37.66"N 08°09'42.28"E	50.0 (± 5.2)	11
Oelde	Roadside	51°49'35.76"N 08°12'07.32"E	83.0 (± 0.9)	11
Oelde	Control	51°49'42.89"N 08°10'14.16"E	45.8 (± 1.5)	12
Paderborn	Roadside	51°37'36.34"N 08°43'31.00"E	83.2 (± 1.3)	12
Paderborn	Control	51°37'38.28"N 08°44'43.20"E	43.9 (± 8.5)	12
Velpe	Roadside	52°15'40.20"N 07°50'55.40"E	79.1 (± 1.1)	11
Velpe	Control	52°17'08.84"N 07°50'52.66"E	47.4 (± 0.5)	11

N, number of males recorded

Avisoft-SASLab Pro bioacoustics software 4.3 (Berlin, Germany, <http://www.avisoft.com/>) was used to record male grasshopper signals with a sampling rate of 192 kHz. For the analysis of temporal patterns and sound pressure level (SPL) of the signals, a custom-built MATLAB-based GUI was used. To calibrate signal amplitudes we used a reference signal of 79.7 dB_A (SPL). We selected the loudest male song recorded from the present data set to obtain the reference signal and recorded the amplitude of the same signal again in a distance of 10 cm to the loud speaker (Ultrasonic Dynamic Speaker ScanSpeak by Avisoft Bioacoustics) with a sound-level meter (PeakTech 5035, 4 in 1 Multifunction environment tester by Conrad Electronic GmbH). All other signals were then referenced to the signal of the loudest male.

The mean peak frequency of the low-frequency local maximum was determined with Audacity 1.3.13 β (Boston, MA, USA, <http://audacity.sourceforge.net>). Based on well-documented

mechanisms of signal adjustment in response to background noise that were found in other taxa (Brumm, Schmidt & Schrader 2009), four song parameters were included in the comparison of noisy vs. control habitat songs: (1) phrase length, (2) syllable to pause ratio, (3) mean maximum amplitude (calculated over all syllables for each song) and (4) local frequency maximum (for illustrations of signal parameters see Figs 2 and 3). Parameters (1) and (2) were included to detect potential changes in the temporal structure of signals. Parameter (3) was included to test for increased signal amplitude as a response to elevated background noise levels, whereas (4) was analysed to test whether male grasshoppers are capable of adjusting potentially degraded or masked parts of their signals' frequency spectrum to higher background noise levels by changing frequency. We specifically included the lower local frequency maximum (6–9 kHz) of grasshopper courtship songs because low-frequency traffic noise has the potential to degrade this part of the frequency spectrum (Fig. 3; Sandberg 2003). We did not consider other spectral song parameters like maximum song frequency or the absolute frequency maximum (the loudest part of the frequency spectrum for each song), as these parameters are ultrasonic (30–40 kHz) and thus cannot be masked by low-frequency traffic noise.

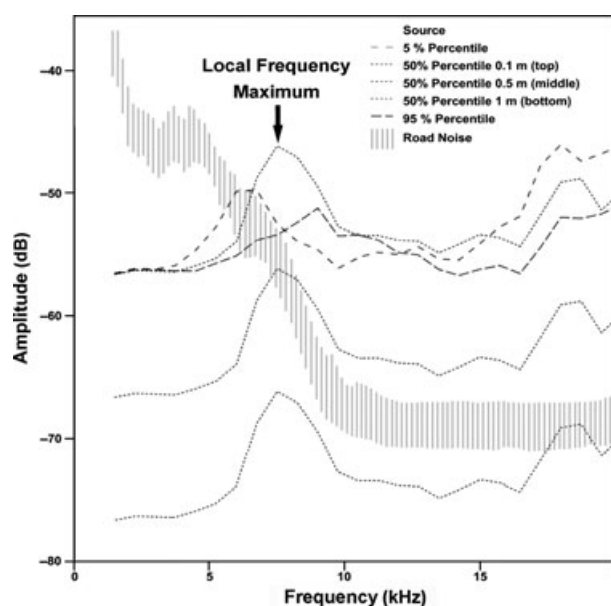


Fig. 3. Power spectra of road noise recordings (maximum amplitude range = grey bars) and three *Chorthippus biguttulus* courtship songs (located at the 5%, 50% and 95% percentiles of the local frequency maximum). We used 40 one-minute samples of road noise recordings from four roadside habitats located in close proximity to our sampling sites. Noise samples were recorded from a distance of c. 10–15 m from the highway, where grasshoppers can be found behind the crash barrier. The local frequency maxima of the three grasshopper signals shown in the graph are located at 6362 Hz (5% percentile), 7450 Hz (50% percentile) and 8849 Hz (95% percentile). *C. biguttulus* signals were recorded in the laboratory with a distance of 10 cm to the microphone. Here, we shifted the 50% percentile signal on the y-axis to illustrate spectra for two additional distances (0.5 and 1 m). The graph illustrates that road noise in the *C. biguttulus* roadside habitats reached relatively high amplitudes in a frequency band, which has been shown to be important in the context of female mate choice (von Helversen & von Helversen 1997).

In total, 952 songs of 188 males from 16 different populations from eight locations were recorded (Table 1). All song parameters were log-transformed to approximate normality. Linear mixed effect (LME) ANCOVA models were fitted in R 2.13.1 (R Development Core Team 2011), using the function `lme` (library `nlme`). Likelihood ratio tests were run for significance testing, using a stepwise backward model selection procedure, as described by Crawley (2005). Reported *P* values refer to the increase in deviance when respective terms are removed from the more complex models. All statistical tests were two-tailed, and we rejected the null hypothesis at $P < 0.05$. We used Bonferroni-Holm correction for the analyses of the four song parameters to keep the experiment-wise error rate at an alpha of 0.05.

All models included acoustic background (noisy vs. control) as a fixed effect two-level factor. Catch day and body mass (taken immediately after signal recordings) were included as fixed effect covariates to control for seasonal variation in signal properties and variation due to body size (Whitman 2008). In models (3) and (4) we included an interaction term between acoustic background and body mass to detect the magnitude of a potential effect of body mass on mean maximum amplitude and local frequency maximum, respectively. Individuals within population within location were included as nested random effects in all models to account for non-independency of the data.

In addition to the analyses of song parameters, we also calculated a mixed effect (LME) ANCOVA model with body mass as the dependent variable to test whether individuals from the two habitat types differed in body mass. Catch day was included into this model as a fixed covariate, and population within location were included as nested random effects.

Results

Controlling for body mass and catch day, neither phrase length ($\chi^2 = 2.65$; d.f. = 1; $P = 0.1$), syllable to pause ratio ($\chi^2 = 3.79$; d.f. = 1; $P = 0.05$) nor mean maximum amplitude ($\chi^2 = 0.2$; d.f. = 1; $P = 0.66$) differed significantly between noisy and control habitats. However, the local frequency maximum was located at higher frequencies in songs of males collected from noisy habitats ($7622 \text{ Hz} \pm 81 \text{ SE}$) compared to songs of control habitat males ($7319 \text{ Hz} \pm 74 \text{ SE}$; $\chi^2 = 7.35$; d.f. = 1; $P = 0.0067$, Fig. 4). This effect remained significant after Bonferroni-Holm correction (critical $P = 0.0125$). Controlling for catch day, there was no difference in body mass between individuals from roadside and control habitats ($\chi^2 = 0.01$; d.f. = 1; $P = 0.93$).

Discussion

We found that male grasshoppers from noisy roadside habitats produced signals with higher local frequency maxima compared to males from nearby control sites. This result suggests that grasshoppers use higher frequencies in the presence of elevated background noise levels to avoid signal degradation or masking, representing the first evidence that anthropogenic noise affects acoustic communication signals in natural insect populations. Similar findings were obtained in other taxa, such as mammals (Parks *et al.* 2011), birds (Slabbekoorn & Peet 2003; Parris & Schneider 2009; Dowling, Luther & Marra 2011) and anurans (Parris Velik-Lord & North 2009), indicating that

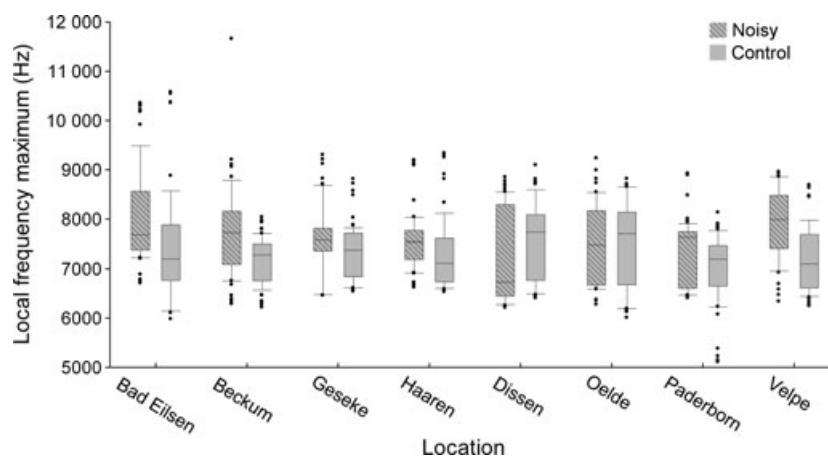


Fig. 4. Locations of the low-frequency amplitude maxima [Hz] of *Chorthippus biguttulus* signals from eight noisy and eight adjacent control sites. Black bars denote medians, boxes represent quartiles, and whiskers symbolize maximum and minimum, or 1.5 times the interquartile range in case of outliers.

animals across a wide range of taxa may use similar means for dealing with anthropogenic noise.

Although we cannot rule out the possibility that factors other than noise associated with proximity to major roads (e.g. soil chemistry, food plant quality and species composition) could have caused the observed differences, we consider it unlikely that these would produce a difference in one of the very signal properties shown to be affected by anthropogenic noise in a similar way in other taxa. Furthermore, we demonstrate the difference in song parameters while accounting statistically for body mass. Thus, to a large degree, we control for potentially confounding effects that may result from different food plant or habitat quality in general.

A behaviourally plastic response to noise exposure was shown in several vertebrate species (Bermúdez-Cuamatzin *et al.* 2011; Roy *et al.* 2011) and in the context of timing and synchronization of male bushcrickets in aggregations (Hartbauer, Stabentheiner & Römer 2011). However, in the present study, individuals from both habitat types were recorded under the same (i.e. quiet) conditions, 24–72 h after they were removed from their habitat, which leads us to the conclusion that the detected differences cannot be explained by behavioural plasticity. Short-term adjustment of frequency spectra can be considered unlikely in *C. biguttulus* signals, as the carrier frequency range probably is caused by structural traits. In addition, the stridulating behaviour has been proposed to be mainly hardwired, potentially because it requires precise neuronal coordination (Gottsberger & Meyer 2007; Einhäupl *et al.* 2011).

Previous studies have found that female preferences for male acoustic signals (Bailey & Zuk 2008), as well as male mating tactics and reproductive investment (Bailey, Gray & Zuk 2010) in crickets showed developmental plasticity. In both of these studies, early acoustic environment determined the later behaviour of adult insects. Whether such within-generation developmental adjustments could be a

potential cause of the differences in signal production found between grasshopper males from noisy and quiet habitats needs to be tested experimentally. A *post-hoc* analysis of ‘highway presence’ (i.e. the period of time a highway section has been open for traffic) in the present data set gives us an idea about alternative explanations for the effect of noise on the local frequency maximum of grasshopper signals. We found a trend towards higher local frequency maxima, produced by males from ‘older’ highways (LME: $\chi^2 = 3.48$; d.f. = 1; $P = 0.06$). Thus, genetic differentiation resulting from local adaptation seems a likely explanation of the effect in *C. biguttulus* signal production. Alternatively, differential epigenetic or maternal effects in noisy and quiet habitats could as well explain the results obtained in the present study.

The analysis of ‘highway presence’ might also explain the opposing trend of the location of local frequency maxima in the Dissen population pair to a certain degree. The roadside habitat of the Dissen population pair was located at the ‘youngest’ highway section of all roadside habitats of our data set (personal communication, road maintenance services Lower Saxony and North Rhine-Westphalia). Assuming that local adaptation of grasshopper signals to noisy conditions offers an explanation for the overall effect, the reverse trend of the Dissen population may appear less surprising. We did not detect any peculiarities concerning the control habitat of this population pair, which is located at the edge of a field, similar to the other control sampling sites we used. Our background noise recordings show that we measured the third highest background noise levels of all control populations at this sampling site (Table 1). In the end we can only speculate about potential explanations for the reversing trend in this pair, as we could not identify a single factor that is exclusive to either of the two habitats.

In *C. biguttulus*, temporal structure and amplitude of male songs largely determine male mating success (von

Helversen & von Helversen 1997; Klappert & Reinhold 2005; Einhupl *et al.* 2011). So far, carrier frequency of male signals has not been considered in much detail in terms of attractiveness as evaluated by females. In the study of von Helversen & von Helversen (1997), the response rate of females to artificially manipulated male signals increased significantly, if the signals included both, high and low-frequency components, indicating that the lower-frequency maximum of male signals is essential in the context of female mate choice and/or species recognition. Females show a response threshold minimum in the frequency band between 4 and 8 kHz, and the vibration spectra of female tympanal membranes peak around 8 kHz (Meyer & Elsner 1997), which further indicates the relevance of this part of the male signal spectrum for females. To our knowledge, frequency discrimination in *C. biguttulus* females has not been investigated thus far, and we can therefore make no predictions with respect to the potential impact of the mean difference of 300 Hz between roadside and control habitats on female mate choice. However, in our data set, heavier males produced louder signals with lower local frequency maxima. As male signals with higher maximum amplitudes were found to be more attractive to females (Klappert & Reinhold 2003), it seems plausible, based on our data, that male signals with a lower local frequency maximum might be more attractive to females. If females do show preferences for the location of local frequency maxima in male signals under relatively quiet conditions, the strength and direction of their preferences will determine how female choice affects selection pressure induced by the males' acoustic environment. Female preferences may oppose signal adjustment to anthropogenic noise, if females prefer heavier, louder males that produce a lower local frequency maximum. To further determine the potential strength of selection pressures driven by the acoustic environment, it is crucial to test whether carrier frequency is relevant for the attractiveness of male signals. If this is the case, a potential interaction between female mate choice and acoustic environment in *C. biguttulus* needs to be addressed, as well. If females do not show preferences for the location of male local frequency maxima, it might still be advantageous for males under noisy conditions to produce signals with relatively high local frequency maxima to avoid degradation of their signals and still be heard and recognized by females.

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