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Effects of anthropogenic noise on male signalling behaviour and female phonotaxis in *Oecanthus* tree crickets

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Communication is vital to the survival and reproductive success of organisms. There is growing evidence that anthropogenic noise interferes with acoustic communication. While recent studies have tested whether signallers behaviourally modify their signals to prevent masking from noise, studies have only recently begun to test whether noise in fact interferes with the perception of acoustic signals. In this study, we investigated how road noise affects both male signalling and female phonotaxis in *Oecanthus* tree crickets. Acoustic signals of tree crickets, which are relatively low amplitude and composed primarily of low frequencies, are likely to be masked by road noise. To determine whether males alter their calls in the presence of road noise, we assessed how a playback of recorded road noise changed four male calling characteristics: dominant frequency, call amplitude, total time spent calling and latency to begin calling. We then used response trials to test the ability of females to localize and respond to male calls in the presence of road noise. Unlike studies in other organisms, which detected quantifiable differences in male signal characteristics, male tree crickets were less likely to call but did not change signal characteristics. Surprisingly, female response to male signals was not affected by the presence of road noise, despite the potential masking effects of road noise. Because tree crickets often communicate in environments with many species of calling insects, tree crickets may be adapted to tolerate novel sources of acoustic interference. This study presents a case where male signals and female responses are not affected by road noise. Since species are differentially affected by noise, detailed understanding of behaviour and sensory systems may be necessary for predicting the effect of acoustic interference on trophic interactions and population dynamics.

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Communication efficacy is vital to the survival and reproductive success of many species of animals. Because animals communicate to defend territories, warn of approaching predators and attract mates (Bradbury & Vehrencamp, 2011), changes to the transmission environment that render a signal unable to reach the intended receiver and maintain information content may negatively affect individual fitness and population persistence (Barber, Crooks, & Fristrup, 2010; Seehausen, van Alphen, & Witte, 1997). One recent, dramatic and pervasive change to the environment that may impair signal transmission is an increase in anthropogenic noise in both urban and, increasingly, natural areas (Barber et al., 2010).

Effective communication in high-interference environments can be maintained if signallers modify their signal structure or if receivers adjust their perception (Rabin & Greene, 2002). Studies demonstrate that animals can change their signalling behaviour to decrease the amount of acoustic masking by anthropogenic noise (reviewed in Barber et al., 2010). Because the extent of masking depends on the intensity (perceived as volume) and the frequency composition (perceived as pitch composition) of the signal and noise (Rabin & Greene, 2002), one strategy to decrease the effect of masking is to increase the intensity of the signal (Lombard, 1911). This strategy has been observed in male urban nightingales, *Luscinia megarhynchos*, which sing with greater intensity when recorded in noisy urban environments (Brumm, 2004). Because anthropogenic noise is primarily composed of low frequencies, another strategy to decrease the effect of masking is to shift the acoustic signal towards higher frequencies. Both observational and experimental studies have shown that songbirds sing with higher minimum frequencies in noisy areas and treatments as compared to songbirds in quiet areas and treatments (Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2009; Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2011; Dowling, Luther, & Marra, 2012; Gross, Pasinelli, & Kunc, 2010; Halfwerk & Slabbekoorn, 2009; McLaughlin & Kunc, 2012; Montague, Danek-Gontard, & Kunc,

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2012; Slabbekoorn & Peet, 2003; Slabbekoorn, Yeh, & Hunt, 2007; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010; Wood, Yezerinac, & Dufty, 2006). Similarly, grasshoppers (*Chorthippus biguttulus*) produce courtship signals with elevated frequency components when collected from environments near highways and when reared in road noise environments, which suggests that shifting frequency to decrease masking by noise occurs in a wide range of taxa (Lampe, Reinhold, & Schmoll, 2013; Lampe, Schmoll, Franzke, & Reinhold, 2012). Additionally, signallers have been documented to change signal duration (Montague et al., 2012; Penna, Pottstock, & Velasquez, 2005; Wiley, 2006) or change the timing of their signals to decrease noise interference (Fuller, Warren, & Gaston, 2007).

While recent studies have tested whether signallers can behaviourally modify their signals to reduce or prevent masking from road noise, the effect of anthropogenic noise on receiver perception of signals has only recently begun to be explored. Playback studies on grey tree frogs, *Hyla chrysoscelis*, and great tits, *Parus major*, suggest that traffic and urban noise decrease conspecific signal detection (Bee & Swanson, 2007; Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012; Pohl, Slabbekoorn, Klump, & Langemann, 2009). While recent studies on the European robin, *Erithacus rubecula*, suggest that noise affects songs of both signallers and receivers (McLaughlin & Kunc, 2012; McMullen, Schmidt, & Kunc, 2014; Montague et al., 2012), to our knowledge, no study has investigated how anthropogenic noise affects both mating signals and the ability of female receivers to detect and respond to signals. The present study explores how road noise affects male mating signals and the response of females to those signals in tree crickets (Orthoptera: Gryllidae: *Oecanthus*).

Tree crickets are likely candidates to experience acoustic communication masking from road noise. The majority of the energy in the tree cricket signal falls in a narrow and low frequency range (3.5—5.5 kHz). This range overlaps with road noise, which is likewise composed predominantly of low frequencies (Fig. 1). Furthermore, tree crickets have a lower call intensity than many larger-bodied calling insects (Counter, 1977; Galliart & Shaw, 1996). In addition to producing low-intensity signals with frequencies that

overlap with road noise, tree crickets may be unable to decrease interference from road noise by altering their call characteristics behaviourally. Unlike birds and anurans, singing insects produce calls in a morphologically fixed and mechanistic way (Lampe et al., 2012; Mhatre, Montealegre-Z, Balakrishnan, & Robert, 2012). Given the possibility that male tree crickets cannot alter their calls, understanding how female response to unaltered male calls is affected by road noise is especially important.

To test how road noise affects both male calling behaviour and female phonotaxis in *Oecanthus* tree crickets, we performed road noise playback experiments. We recorded male calls in the presence and absence of high levels of road noise and measured whether males shifted the dominant frequency of their calls, increased the intensity of their calls, or changed their time spent calling to decrease interference. To test how female response to male calls is affected by road noise, we performed female response trials and measured whether females were less likely or slower to respond to male calls in the presence of road noise.

METHODS

Male Calling Behaviour and Characteristics

We collected 79 male crickets of the genus *Oecanthus* (Orthoptera: Gryllidae) in nine locations throughout the United States between 12 May and 10 September 2012 (Supplementary Table S1). Six species of tree cricket were collected and studied: *O. argentinus*, *O. celerinictus*, *O. forbesi*, *O. fultoni*, *O. quadripunctatus* and *O. texensis*. Crickets were collected from different locations to ensure that we tested the response of male crickets from different populations with different environmental and genetic histories. All locations where males were collected were less than 200 m from a road, excluding the three crickets collected from Idaho. Two collection locations in Texas were located on medians in commercial parking lots. Males were caught either by sight as nymphs or by acoustic localization as adults. All males were held in the same room but were maintained singly in plastic containers 8 cm tall with a diameter of 12 cm, permitting individual identification. Each
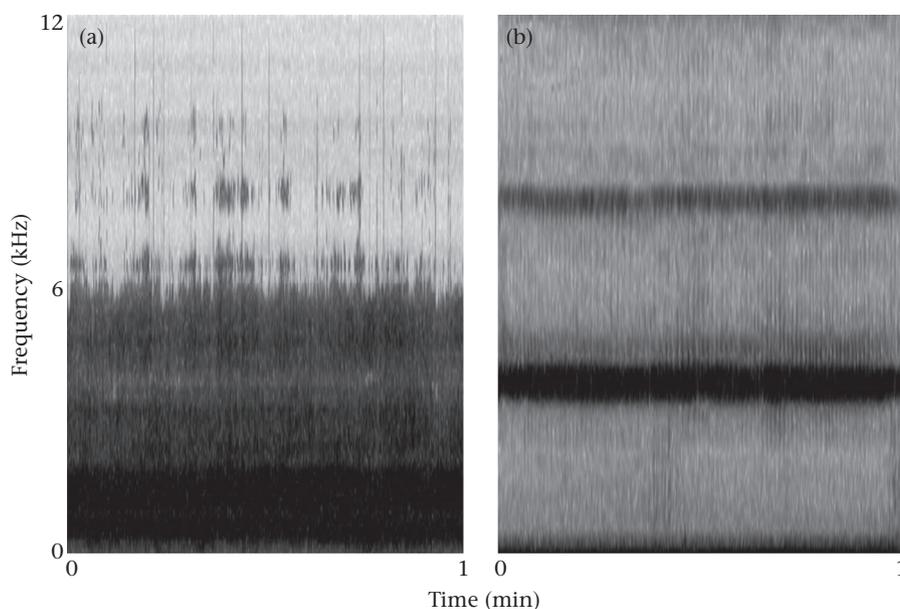
Figure 1. Spectrograms of (a) road noise and (b) calling signal of a male *Oecanthus argentinus*, a continuously calling tree cricket. Sound intensity is represented on a greyscale with white representing low sound intensity and black representing high sound intensity. (a) Road noise is primarily composed of high-intensity low frequencies. (b) Tree cricket signals are narrowband (3.5—5.5 kHz) with harmonics that contain approximately 5% of the total energy of the call. The peak frequency occurs in a narrow frequency band (3.7—4.2 kHz).

container had a screen lid and a piece of plastic plant for structure. Crickets were fed an ad libitum diet of Fluker's Cricket Chow (available from pet stores or Fluker Farms, Port Allen, LA, U.S.A.) until natural senescence.

To create road noise stimuli to play to crickets in the laboratory, we recorded traffic while standing 3 m from State Route 72 (a two-lane road with a speed limit of 72 km/h) in Clifton, OH, on 4 July 2012. Recorded traffic noise was obtained with a Marantz 661 solid-state recorder at a sampling rate of 48 kHz and 24-bit depth connected to a Sennheiser ME 62 microphone with a K6 power module. Birdsongs and silence between passing vehicles were removed using Raven Pro 1.4 software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A., http://www.birds.cornell.edu/brp/raven/ravenoverview.html). The edited 20 min recording was then looped using R 2.15.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) and the Sound and Seewave packages. The same recording was used in all experiments. However, the recording included 146 different vehicles, capturing a variety of traffic sound.

To assess the effect of road noise on male calling behaviour and call characteristics, we randomly assigned 72 collected male crickets to either a silence (0 dB) or a road noise (116.4 dB) treatment. The sound level of the road noise treatment (116.4 dB) was selected to match the sound level that would be experienced by a cricket 3 m from Ohio State Route 21 in Clinton, OH (a four-lane highway separated by a grassy median with a speed limit of 97 km/h) (Supplementary Table S1). This stimulus falls at the upper end of naturally occurring road noise, testing whether even intense road noise has the potential to impact male tree cricket calling behaviour and characteristics. We measured the sound level of Route 21 by recording with a Marantz 661 recorder and a Sennheiser ME62 microphone at 3 m from Route 21. At the completion of the recording, we recorded a 94 dB sound standard (ND9 Calibrator IEC942). To determine the sound level of the recorded road noise, we used Raven Pro 1.4 to measure the road noise level on the recording as well as the sound level of the sound standard. By using these measurements, we were able to normalize the road noise level to obtain an accurate estimate of road noise sound level. This approach allowed us to determine the intensity of specific frequency bands of road noise and reduced concerns about frequency weighting biases in sound level meters that are weighted for human hearing (Nilsson, 2007).

Each male was assigned haphazardly to one of the two treatments and was placed individually in an acoustically isolated environment and recorded for 8 h with a small hand-held recorder. Before being recorded in experimental trials, males were kept in the laboratory for a mean ± SD of 30.5 ± 18.6 days. During the trial, crickets were recorded with one of two models of recorder: Sony ICD-PX720 (sampling rate of 11 kHz and 16-bit depth) or Olympus VN-5200PC (sampling rate of 44 kHz and 16-bit depth). All Olympus VN-5200PC recordings were converted into wave audio files with AVS Audio Converter 7.0 at a sampling rate of 11 kHz before analysing male call characteristics in Raven Pro 1.4. For the road noise treatment, an iLuv i209 speaker connected to an MP3 played the recorded road noise (see above) for the duration of an 8 h trial at 116.4 dB. Male crickets were placed 8 cm from the speaker during the trial.

The number of males from each collection site and the number of species represented in each treatment were approximately equal. Likewise, the mass of the male insects did not differ significantly between treatments (two-sided t test: $t_{70} = 0.83$, $P = 0.37$). For male crickets caught as nymphs in the field and with known moult dates, age since final moult did not differ significantly between treatments (two-sided t test: $t_{47} = 0.61$, $P = 0.55$). For crickets caught as adults, time since final moult cannot be known,

and these crickets were assigned to treatments haphazardly. Because of logistical constraints, trials were performed at a range of temperatures (18.5–30.5 °C), and temperature is included as a covariate in all analyses. In addition, median temperature was not significantly different between treatments (two-sided t test: $t_{70} = 2.61$, $P = 0.11$).

To measure whether crickets were able to adjust the dominant frequency of their calls to minimize the effects of masking on low frequencies, we used Raven Pro 1.4 to measure the fundamental frequency of the first three calling bouts and found the average of these values. Because previous research has demonstrated that the dominant frequency is repeatable in a male's call (Deb, Bhattacharya, & Balakrishnan, 2012), we measured the dominant frequency of only three calls from each individual. To determine whether crickets differed in their time spent calling or their proclivity to begin calling between noise and silence treatments, we measured the total call duration and the time to first call using Raven Pro 1.4.

To test whether the number of Oecanthus crickets that remained silent during 8 h of recording differed between road noise and silence treatments, we used a generalized linear model with a binomial link function and included treatment, species, temperature and the interaction of species and temperature as fixed effects. For ease of interpretation, results are presented as proportion of crickets that called. This analysis was performed with JMP v.11.1 statistical software (SAS Institute, Cary, NC, U.S.A.).

A second level of analysis was performed on the call characteristics of males that did call. We used general linear models to compare dominant frequency, total call duration and time to first call between road noise and silence treatments. Time to first call was log transformed and total call duration was square-root transformed to achieve normality. Treatment, species, temperature and the interaction of species and temperature were included as fixed effects in each model. We did not include collection site in the models because of the small sample size at some collection sites and the high covariance between species and collection site. Models were analysed in R 2.15.2 statistical software (R Development Core Team). Results from JMP v.11.1 were qualitatively similar to results from R 2.15.2. Because the Olympus dictaphone recorders produced compressed files with uneven frequency representation, we included only crickets recorded with the Sony ICD-PX720 recorders, which had a flat frequency response to the frequencies analysed, in the dominant frequency analysis.

In addition to the 8 h trials, we also conducted short trials to determine whether call sound level changed in the presence of road noise. Call sound level was recorded 0.4 m from the cricket with a Sennheiser microphone and Marantz 661 recorder sampling at 96 kHz and 24-bit depth. To minimize absorption or reflection of the sound, we recorded crickets in suspended mesh containers. Because a male cricket's call is propagated directly in front of and behind the male's raised wings (Forrest, 1991), recordings were retained only if the cricket was facing directly towards or directly away from the recorder, as observed by a red headlight in a dark room. After 1 min of recording the call without background noise, an iLuv i209 speaker connected to an MP3 player then played the recorded road noise at 116.4 dB. Normally, turning on the speaker disrupted the cricket's call. Once the cricket resumed calling with the road noise playing, the call was again recorded with a Marantz 661 recorder for 1 min. The sound level of the recorded calls were measured in Raven Pro 1.4 and calibrated with a 94 dB tone as an internal standard. The temperature of the room where the recordings were made was kept constant throughout the recording session.

The sound levels of calls both with and without road noise in the background were obtained for 14 male crickets of seven species of

Oecanthus. We used a two-sample matched pairs *t* test to compare the peak sound level in calls with and without road noise. Statistical tests were two tailed and performed using R 2.15.2 statistical software (R Development Core Team).

Female Response Behaviour

We collected 42 female *Oecanthus* crickets in seven locations in the United States between 12 May and 10 July 2012 (Supplementary Table S1). Crickets were collected from different locations to ensure that the responses of multiple populations were represented. All locations were less than 516 m away from a road. Five species of female tree crickets were collected and studied: *O. argentinus*, *O. celerinictus*, *O. forbesi*, *O. nigricornis* and *O. quadripunctatus*. All females were caught by sight as nymphs. Female crickets were reared singly in the laboratory in the same manner as the male crickets (see above). Females were housed in a separate room from males, which helped dampen the sound level of male cricket calls but did not completely isolate females from male calls.

To test whether female tree cricket response to male calls changed with increasing levels of road noise, we performed female response tests. Female crickets were placed under a cup in the centre of a 1 m diameter ring with sound-absorbing foam walls. Two Genelec 6010A speakers were embedded into the foam wall, positioned directly next to each other. One speaker played a synthetic call while the other speaker played the recording of road noise recorded 3 m away from State Route 72 in Clifton, OH (see above). To control for variation in male call attractiveness, the synthetic calls were modelled on the mean calls of males from the same population as the focal female and were created in R 2.15.1 (Symes, 2014; code available on request). Not all males caught and recorded for synthetic call modelling were used in the experiments described above. The artificial call stimulus and the road noise playback were initiated simultaneously and the cup was lifted immediately after. We then measured the time a female took to respond to the male's call, determined by when the female contacted one of the speakers. Trials lasted a maximum of 120 s.

Different sound levels of both the road noise (loud = 116.4 dB, quiet = 92.8 dB, silent = 0 dB) and the synthetic male call (loud = 89.8 dB, quiet = 76 dB) were presented to the female. The loud road noise sound level corresponds to the sound level of the road noise recorded 3 m away from State Route 21 in Clinton, OH (see above). For the quiet road noise stimulus, we calculated the expected sound level that would be experienced by a cricket at 45 m away from State Route 21. To make this calculation, we first calculated the sound intensity (the energy transported by a sound wave per unit time across a unit area perpendicular to the energy flow) of the road noise at 3 m, using the equation $\beta = 10\log(I/I_0)$ where β is the sound level in dB, I is the intensity of the road noise 3 m away from the road, and I_0 is the intensity of a reference level (10^{-12} W/m²). From this, we calculated the power (the energy per unit time) of the road noise as $I = P/4\pi r^2$ where P is power, and r is distance. Once we knew the power of the road noise, we were able to use both equations to solve for $r = 45$ m. To make this calculation, we assumed that no sound was absorbed by the air and that the medium of sound propagation was uniform in all directions. Thus, the road noise sound level is approximately 92.8 dB and corresponds to a distance of 45 m from a four-lane highway with a speed limit of 97 km/h. Using the same approach, we calculated the sound levels of the synthetic male calls. The loud synthetic male call (89.8 dB) corresponds to a male 0.2 m away, and the quiet synthetic male call (76 dB) corresponds to a male 1 m away from the female.

Table 1
Calling behaviour of individual male *Oecanthus* crickets by noise treatment

	Silent	Road noise	Total
Call	34	20	54
No call	5	13	18
Total	39	33	72

Each female was presented with all combinations of synthetic male call sound levels and road noise sound levels in a random order (a total of six trials). To ensure that females remained responsive throughout the trials, each testing session contained no more than three trials and sessions were separated by a minimum of 1 h. All females were tested when they had been adults for several weeks but had not had the opportunity to mate. Thus, females were likely to be highly motivated to respond to the mean male call. Females were kept in the laboratory for a mean ± SD of 51.6 ± 21.9 days before experimentation. Before using females in the experiment, we presented females with a synthetic population-mean call without road noise. If females failed to respond to this stimulus within 120 s, they were considered nonresponsive and were excluded from the trials. All trials were performed between 24 and 26.5 °C and were observed in a dark room with a red headlight.

To test whether the proportion of female crickets that responded in each trial was significantly different among trials, we used a generalized linear model that included the sound level of the male call stimulus, road noise sound level and their interaction as fixed effects and species and female nested within species as random effects. For females that did respond, we used a general linear model to compare the response time (the time it took the female to make contact with one of the speakers) among the trials. The model included male call stimulus sound level, road sound level and their interaction as fixed effects and species and female nested within species as random effects. Statistical tests were performed in SAS v.9.3 statistical software (SAS Institute).

RESULTS

Male Calling Behaviour and Characteristics

A total of 54 crickets called during individual 8 h recordings (Table 1). The number of *Oecanthus* crickets that initiated calling was significantly lower in the road noise treatment compared to the silence treatment (generalized linear model: $\chi^2_1 = 8.20$, $P = 0.004$; Supplementary Table S2). In the silence treatment, 87% of *Oecanthus* tree crickets called, whereas, in the road noise treatment, 61% of *Oecanthus* tree crickets called. In addition, probability of initiating calling differed between the four *Oecanthus* species tested in this experiment (generalized linear model: $\chi^2_2 = 8.33$, $P = 0.040$; Supplementary Table S2).

Male calling characteristics and behaviour did not differ between road noise and silence treatments: dominant frequency of the call (general linear model: $F_{1,18} = 2.68$, $P = 0.12$; Supplementary Table S3), total call duration in an 8 h recording (general linear model: $F_{1,45} = 1.39$, $P = 0.25$; Supplementary Table S4), and time to first call (general linear model: $F_{1,45} = 2.14$, $P = 0.15$; Supplementary Table S5). There was no significant difference between *Oecanthus* species in call characteristics (general linear model: total call duration: $F_{3,45} = 0.023$, $P = 0.995$; time to first call: $F_{3,45} = 2.50$, $P = 0.07$; Supplementary Tables S4 and S5), except species differed in dominant frequency (general linear model: $F_{3,18} = 5.59$, $P = 0.007$; Supplementary Table S3). Peak sound level of *Oecanthus* calls did not change in response to road noise (paired *t* test: $t_{13} = -0.27$, $P = 0.80$).
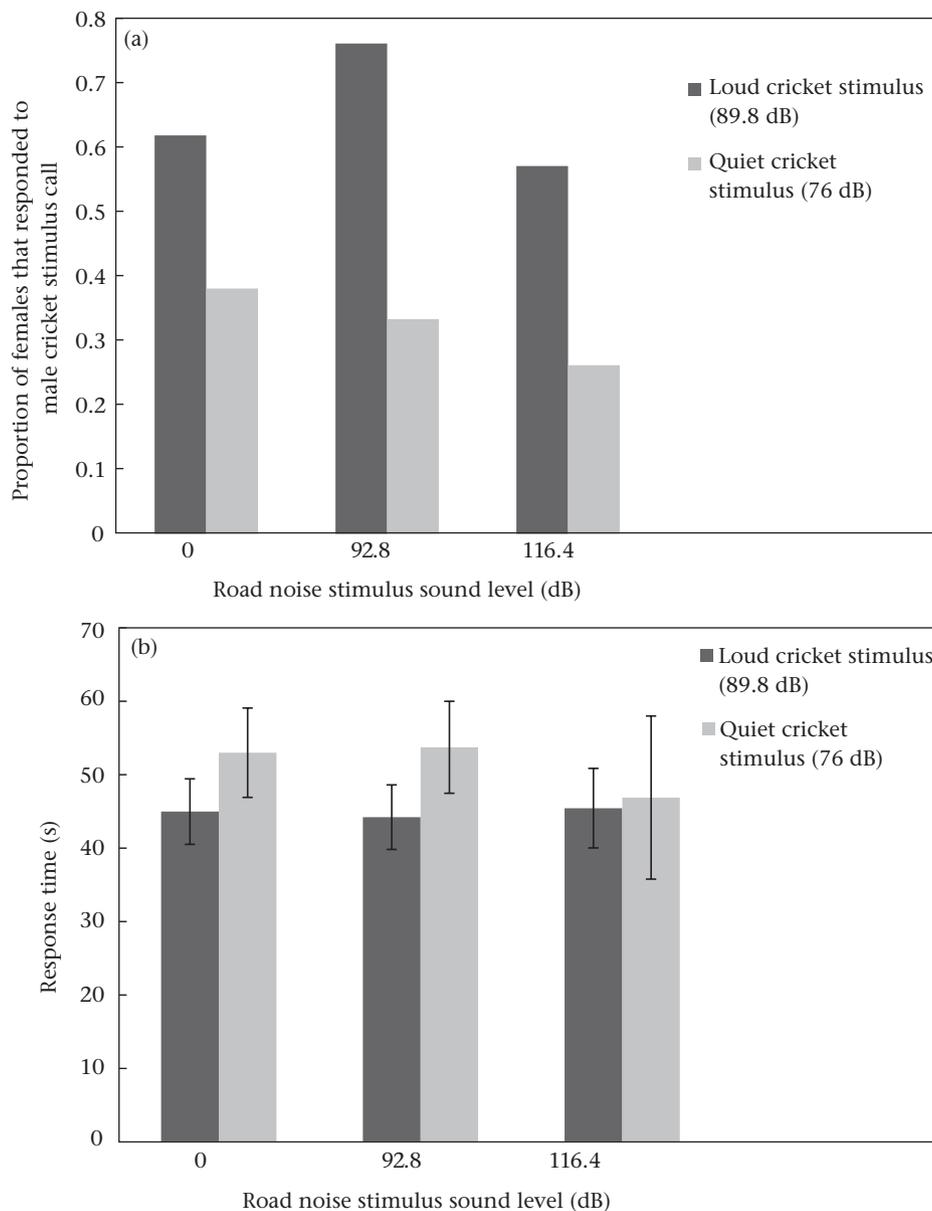
Female Response Behaviour

Male cricket sound level affected the proportion of female crickets that responded to the male stimulus (generalized linear model: $\chi^2_1 = 32.15$, $P < 0.0001$; Fig. 2a), while road noise level and the interaction of road noise and synthetic male call did not (generalized linear model: road noise sound level: $\chi^2_2 = 4.30$, $P = 0.12$; road noise sound level*male cricket stimulus sound level: $\chi^2_2 = 2.90$, $P = 0.23$; Fig. 2a). Female crickets were more likely to respond to the loud synthetic male call than the quiet synthetic male call regardless of the road noise sound level (Fig. 2a). Likewise, female response times were faster when cricket calls were offered at higher sound levels (general linear model: $F_{1,37} = 35.47$, $P < 0.0001$; Fig. 2b) regardless of road noise sound level. There was no effect of road noise sound level or of the interaction of road noise and synthetic male call sound level on female response time

(general linear model: road noise sound level: $F_{2,37} = 1.29$, $P = 0.28$; road noise sound level*male cricket stimulus call sound level: $F_{2,37} = 1.31$, $P = 0.27$; Fig. 2b). There was no significant difference in response time between species (general linear model: $F_{4,37} = 1.14$, $P = 0.35$).

DISCUSSION

In playback experiments, male tree crickets of the four species used in this study were less likely to begin calling in the presence of road noise. This decrease in calling likelihood may be due to road noise interference with male tree cricket signals. Because male tree cricket calling is energetically costly (Prestwich & Walker, 1981; Symes, 2013), males may conserve energy by not calling in the presence of high background noise, when their calls could be masked, and by instead calling when background noise is lower.

Figure 2. Female response behaviour to the six male signal and road noise stimulus treatments. (a) Proportion of female tree crickets that responded to each cricket and road noise stimulus treatment. (b) Response time of responsive females to each cricket and road noise stimulus treatment. Error bars show means ± SE.

This explanation is most cogent when the female threshold for detection or discrimination of male signals is increased in the presence of road noise. In our experimental trials, however, the level of road noise did not affect the proportion of female tree crickets that responded or their response time. This suggests that road noise does not interfere with female perception of male calling signals, although it remains possible that road noise decreases the ability of females to assess and compare males on the basis of their call. Previous studies in other taxa suggest that observed changes in male calling behaviour decrease interference from anthropogenic noise and optimize communication effectiveness (Bermúdez-Cuamatzin et al., 2009, 2011; Brumm, 2004; Dowling et al., 2012; Gross et al., 2010; Halfwerk & Slabbekoorn, 2009; Lampe et al., 2012, 2013; McLaughlin & Kunc, 2012; Montague et al., 2012; Slabbekoorn & Peet, 2003; Slabbekoorn et al., 2007; Wood et al., 2006). However, the remarkable efficiency with which female tree crickets find males in loud environments suggests that the observed decrease in the likelihood of male tree cricket calling is not a mechanism that decreases the amount of acoustic masking by anthropogenic noise. To further test whether the decrease in male calling is due to frequency-specific masking or general interference from noise, future studies could measure whether male tree crickets show similar decreases in calling when presented with noise composed of frequencies that do not overlap with their call frequencies.

While males reduced calling likelihood in the presence of road noise, unlike male *Chorthippus biguttulus* grasshoppers (Lampe et al., 2012), they did not change call characteristics between noise and silence treatments in the playback experiment. Because high noise levels did not affect female perception of male calls, road noise likely does not alter the selective pressure that females impose on male calling characteristics. In addition, unlike birds and anurans, which use air flow through vocal cords and airsacs (Prestwich, 1994; Suthers, Goller, & Hartley, 1994), respectively, tree crickets produce sound by rubbing a file located on one wing against a vein located on the other wing (Alexander, 1967). This morphologically fixed way in which tree crickets produce sound may limit their capacity to manipulate call characteristics behaviourally (Lampe et al., 2012; Mhatre et al., 2012).

Given that high-intensity road noise did not influence male call characteristics and did not interfere with the females' ability to detect male signals, the logical question is how are females able to detect and respond to a male signal in the presence of road noise? One potential explanation is that females may adjust their perceptual apparatuses (Rabin & Greene, 2002). Römer, Bailey, and Dadour (1989) found that the Australian bushcricket, *Sciarasaga quadrata*, can open and close the auditory spiracle, allowing for frequency sensitivity to shift. Although 95% of tree cricket call energy is in the low fundamental frequencies, tree crickets do have high-frequency harmonics in their calls (Fig. 1), suggesting a possible avenue by which females could detect males even in the presence of low-frequency noise.

An alternative explanation for female tree crickets' perceptual abilities is that, having evolved in noisy insect communities, they may be adapted to environments with high levels of interference. Female tree crickets typically only respond to a relatively narrow range of species-specific pulse rates (Symes, 2014; Walker, 1957). Because they have evolved the capacity to respond to specific pulse rates, all other sounds without that pulse rate, including road noise, may produce minimal masking. Further research on the interaction between the female auditory system and anthropogenic noise will generate a more complete understanding of female perception in noisy environments. While road noise may mask acoustic communication in many organisms (Bee & Swanson, 2007; Lohr, Wright, & Dooling, 2003; Pohl et al., 2009; Pohl et al., 2012),

communication in some taxa, particularly taxa that have evolved to communicate in competitively noisy environments, may experience minimal masking.

Even though tree cricket signals are likely not masked by road noise, road noise may still affect tree cricket population dynamics by reducing the amount of time that male tree crickets spend signalling, possibly impacting mating, reproduction and the ability of females to assess and compare males. However, because road noise degrades (loses structural complexity) and attenuates (decreases in signal intensity) as sound waves travel from the road to the receiver (Rabin & Greene, 2002; Wiley & Richards, 1978), the observed decrease in the number of males calling may not occur in environments farther than 3 m from a highway. Still, why were male tree crickets less likely to call in environments with the upper level of naturally occurring road noise? Because male calling behaviour likely evolved in environments where the background noise was predominantly composed of calling insects, one potential explanation is that, historically, high noise levels indicated high levels of competition from conspecifics or potential masking from closely related heterospecifics. If a male monitors competition or masking from other insects by monitoring the level of background noise, at high levels of background noise, males may be predisposed to not call and instead wait for a quieter background noise level, even if the current source of noise does not represent competition or masking. In support of this argument, studies on katydids have demonstrated that followers in a chorus of a *Mecopoda* katydid species are more likely to call when competitors are quiet (Nityananda & Balakrishnan, 2008) and that males of *Neoconocephalus spiza* temporally adjust their calling patterns from calling at night to calling during the day to avoid acoustic interference from congeners (Greenfield, 1988).

Alternatively, fewer male tree crickets may call in the presence of road noise to decrease the risk of predation. Prey often use predator communication or movement sounds to detect predators (Bernal, Rand, & Ryan, 2007; Emmering & Schmidt, 2011; Magrath, Pitcher, & Dalziell, 2007; ter Hofstede and Fullard, 2008). However, when male crickets produce their calling signal, they suppress auditory sensitivity, protecting their hearing from damage (Poulet & Hedwig, 2002). Thus, a calling male has a decreased ability to detect an approaching predator and is more likely to be susceptible to predation. Road noise in the environment may further mask cues of an approaching predator, increasing the risk of predation (Barber et al., 2010). Alternatively, anthropogenic noise may distract male crickets by overstimulating their senses and prevent them from responding to predatory threats (Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Chan, Stahlman, et al., 2010). Under these hypotheses, even a silent male would be susceptible to predation in an environment with high noise levels. If a male cannot easily detect an approaching predator because of masking of predator signals or because of overstimulation and distraction, he may be less likely to initiate calling in order to increase vigilance.

While road noise in the environment may decrease the ability of prey to detect approaching predators, road noise may also decrease the ability of predators to localize prey. For example, a study on the greater mouse-eared bat, *Myotis myotis*, demonstrated that traffic noise can reduce foraging efficiency in acoustic predators (Siemers & Schaub, 2011). Thus, increasing levels of road noise may, in fact, decrease the risk of predation, especially for prey with acoustic signals that are likely to be masked by road noise. If road noise affects both the predator's ability to locate prey and the prey's ability to detect approaching predators, the outcome of these interactions may be complex and may depend on the sensory systems of the species involved, and their relative abundance and habitat characteristics. Investigating how road noise affects all taxa in their natural environments, where road noise follows natural

traffic patterns (i.e. rush hour) and where animals are free to move away from the noise source, represents an important direction for future work aimed at implementing informed conservation policies.

This study presents a case where male signals and female responses are not affected by road noise masking. Unlike studies on other species, male calling characteristics and female detection and response to male calls were unaffected in environments with high levels of road noise. Since different species are differentially affected by noise, detailed understanding of the behaviour and sensory systems of individual organisms and careful consideration of how altered acoustic environments shape trophic and social interactions will be required to understand the ecological and evolutionary consequences of increasing anthropogenic noise and changing signalling environments.

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2014.05.009.

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