Animal Behaviour 95 (2014) 15–22

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 14 January 2014
Initial acceptance 27 February 2014
Final acceptance 28 April 2014
Published online
MS. number: A14-00032R

Keywords:
acoustic signal
anthropogenic noise
communication
invertebrate behaviour
masking effect
Oecanthus
phonotaxis
playback
tree cricket

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.

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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http://dx.doi.org/10.1016/j.anbehav.2014.05.009
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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

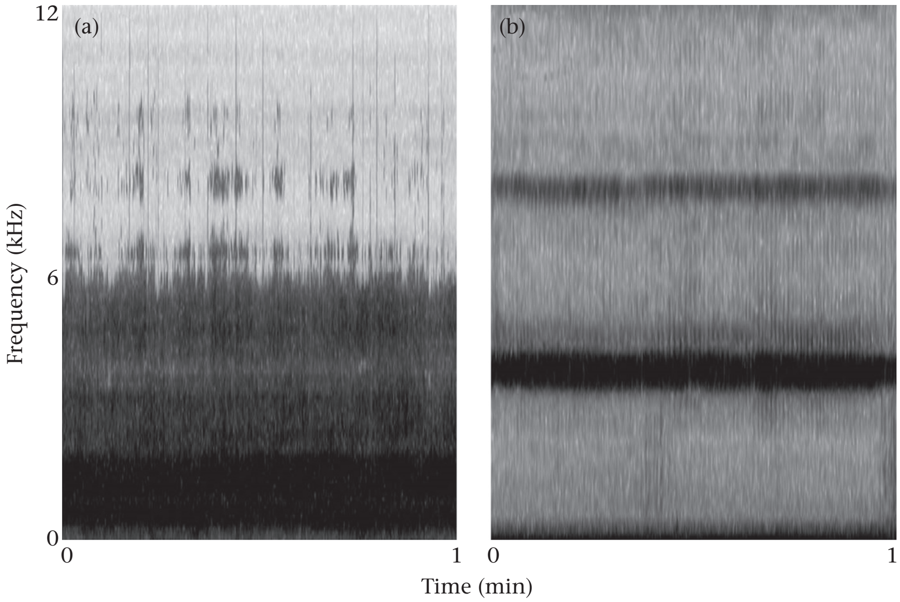

Figure 1. Spectrograms of (a) road noise and (b) calling signal of a male *Oecanthus argentinus*, a continuously calling tree cricket. Sound intensity is represented on a greyscale with white representing low sound intensity and black representing high sound intensity. (a) Road noise is primarily composed 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).