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Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*



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Keywords: acoustic signalling anthropogenic noise behavioural plasticity tree cricket urbanization Noise pollution is a world-wide phenomenon and its effects on animal behaviour have been investigated by numerous studies focusing mostly on vertebrate taxa. However, studying how insects are impacted by human-made noise is indispensable, because of their ecological importance and in order to gain a more comprehensive knowledge of how animals can cope with this new challenge. The few studies that have examined the effects of noise pollution on the acoustic signalling of insects have characterized noise over long timescales. In this study we examined whether males of the tree cricket Oecanthus pellucens modify their calling song in response to the fluctuation in traffic noise over a short timescale. To examine this question we carried out (1) noise level measurements over a short time window (200 ms) paired with song parameter measurements on sound recordings of males singing in their noise-polluted habitats and (2) laboratory playback experiments in which each singing male was recorded during a silent control period and during noise playback. Our results show that males shortened their calls (echemes) and paused singing with a higher probability with increasing noise level. However, males did not modify the fundamental frequency of their song and did not adjust the duration of the interecheme interval in response to noise. These results suggest that crickets decrease signalling effort during high levels of noise and, at least for the song parameters we examined, do not modify their signals, as do birds and frogs, to reduce masking by anthropogenic noise.

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Animals often rely on sounds to survive and reproduce: a wide range of species use the acoustic channel to scan their environment for cues revealing, for example, the presence of predators or prey or to emit and receive signals that convey information about potential mates or rivals (Bradbury & Vehrencamp, 2013; Smith & Harper, 2003). Anthropogenic noise may mask these important acoustic patterns, presenting a new challenge for animals living in habitats with high levels of noise pollution (Brumm, 2013; Farina, 2014). Recognizing this problem, a rapidly increasing number of studies have started to investigate the effects of human noise emission in a widening range of taxa (Barber, Crooks, & Fristrup, 2010; Laiolo, 2010; Slabbekoorn et al., 2010). Results show that animals may avoid human-made noise by spatial (Bayne, Habib, & Boutin, 2008) or temporal shift (Fuller, Warren, & Gaston, 2007; Shirley et al., 2001) of their acoustic activity. Other studies have reported

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adjustments in acoustic signal parameters to decrease the effect of masking, for example increasing the amplitude (Brumm & Todt, 2002; Brumm, Voss, Köllmer, & Todt, 2004; Potvin & Mulder, 2013) or shifting the frequency components of the signals (Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2009; Nemeth & Brumm, 2009; Parris, Velik-Lord, & North, 2009; Slabbekoorn & Boer-Visser, 2006; Wood & Yezerinac, 2006) to avoid masking by the dominant, low-frequency components of noise. However, even in species in which noise-related adaptive modifications are known, these modifications may be costly (Read, Jones, & Radford, 2014) and noise may significantly reduce reproductive success or survival (Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011).

Most published work on the effect of noise pollution on animals has focused on vertebrate taxa and only a handful of studies have investigated insects (Costello & Symes, 2014; Lampe, Reinhold, & Schmoll, 2014; Lampe, Schmoll, Franzke, & Reinhold, 2012; Schmidt, Morrison, & Kunc, 2014; Shieh, Liang, Chen, Loa, & Liao, 2012; Shieh, Liang, & Chiu, 2015). However, the necessity to gather information on how insects are impacted by human-made noise is clear (Morley, Jones, & Radford, 2014). Insects are

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important components of natural and urban ecosystems because of their fundamental role in food webs, nutrient cycles, pollination and seed dispersal (Schowalter, 2011). Many species occur in large numbers and constitute a major component of biodiversity of animal communities. Moreover, their study may yield results complementing those obtained for vertebrate taxa (Schmidt & Balakrishnan, 2015). Acoustic communication evolved independently in arthropods and vertebrates (Greenfield, 2002) with very different physiological backgrounds, physical constraints and levels of behavioural plasticity (e.g. learning is a dominant process in the acoustic communication of certain groups of vertebrates); therefore we expect to learn a lot from studying how insects respond to noise pollution.

Presently available studies on the effects of noise pollution on insect acoustic communication have examined the relationship of noise level and acoustic behaviour over long timescales. However, one of the most characteristic features of traffic noise (a dominant source of noise pollution in urban environments) is its widely and rapidly fluctuating sound pressure level. The possible response of animals to such rapid changes in noise level by the immediate adjustment of acoustic signal characteristics has been examined in frogs (Sun & Narins, 2005; Vargas-Salinas, Cunnington, Amézquita, & Fahrig, 2014), birds (Potvin & Mulder, 2013; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010) and mammals (Miller, Biassoni, Samuels, & Tyack, 2000), but not yet in any insects. In this study, we examined whether males of a cricket species modify their calling song in response to fluctuations in traffic noise over short timescales. We chose to examine the Italian tree cricket. Oecanthus pellucens, which is a common species in Europe even in urban areas where it often occurs in roadside hedges with high levels of noise pollution. Males perching in bushes or sitting on tall plants emit their acoustic signals (Fig. 1) to attract conspecific females; therefore the effectiveness of these signals is an important component of their reproductive success (Brown, 1999). This species uses a calling song with a relatively low fundamental frequency between 2000 and 3700 Hz (Ragge & Reynolds, 1998) making its signal potentially sensitive to the masking effect of traffic noise dominated by low-frequency components (e.g. Warren, Katti, Ermann, & Brazel, 2006). We examined

whether males modify their calling song in response to the short timescale fluctuation in noise level caused by passing cars, trucks and trams in their roadside habitats. To examine this question we carried out (1) noise level measurements over a short time window paired with song parameter measurements on the sound recordings of males singing in noise-polluted habitats, and calculated generalized linear mixed-effect regression models (GLMMs) to see whether momentary noise level had an effect on the song parameters, and (2) laboratory playback experiments in which the song of each male was recorded during a silent control period and during noise playback. The main aim of the noise playback experiment was to clarify whether the GLMM results of the field recordings showed responses to noise or were due to some uncontrolled, unknown confounding variable (e.g. the light and gas emission or air movements caused by passing vehicles).

METHODS

Recording Songs and Measuring Noise Levels

To examine whether O. pellucens males modify their songs in relation to short timescale fluctuations in ambient noise (caused mainly by passing vehicles), we recorded the calling songs of males in roadside habitats in Budapest (Hungary) and its suburban area (Supplementary Table S1). Singing males were approached as close as possible without disturbing them and their song was recorded using portable digital solid-state recorders (ZoomH4n and M-Audio MicroTrack II). Microphone orientation in relation to the road (the main source of noise) varied between males causing some variation in the measured noise level between males. This variation was statistically handled using random intercept models. However, microphone orientation was held strictly fixed during the recording of each male. Therefore no microphone orientation-related variation in noise level is present in our data at the within-male level. We used only recordings in which the acoustic signal of the focal male could be measured precisely even during noise level peaks. Noise level values were measured in 200 ms long time windows just before the measured echemes of the singing male (N = 16males; Fig. 2): the end of each 200 ms noise measurement window

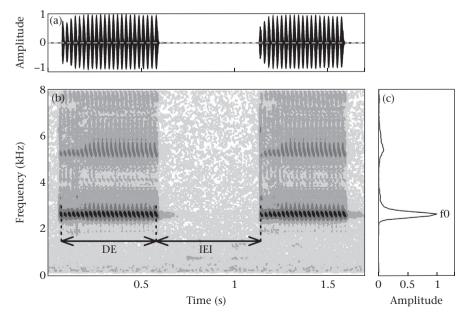


Figure 1. (a) An oscillogram and (b) a sonogram showing two echemes of the calling song of *Oecanthus pellucens* and (c) the frequency spectrum of the first echeme. Three of the four call parameters examined are indicated: DE = duration of echeme, IEI = interecheme interval, f0 = fundamental frequency of the signal.

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