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Sender–receiver dynamics in leafhopper vibrational duetting

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A coordinated reciprocal exchange of acoustic signals (duetting) is common in arthropods relying on substrate-borne vibrational signalling. Communication between partners is under evolutionary pressures resulting from ecological and sexual selection and reciprocal effects arising from such dynamic interactions may influence the sender's and receiver's mating success. We investigated the influence of female reply duration on male mate-searching effort in the leafhopper *Aphrodes makarovi* in which the female reply is essential for successful location of the female. In a duet, the beginning of a female reply overlaps the end of the male call and males evaluate only the nonoverlapped duration of the female reply. In playback experiments we varied the duration of female replies within the natural range. The duration of a female reply was negatively correlated with the male calling effort. By increasing her reply duration a female may significantly reduce the male's direct and indirect costs associated with signalling and searching, thus, ultimately, affecting male reproductive success. Males showed high adaptability in signalling behaviour and when female replies were short, searching males shortened the last section of their advertisement calls. This strategy allows the nonoverlapped part of the female reply to be longer irrespective of its overall duration. Despite its deceptively simple form, vibrational duetting may entail more complex interactions than just temporal coordination.

Communication between partners is an essential part of reproductive behaviour (e.g. Shuster & Wade, 2003). Signals used in sexual communication enable identification (species, sex, condition, receptivity), as well as the location of a potential partner (Mendelson & Shaw, 2012; Wilkins, Seddon, & Safran, 2013), and therefore provide cues that are involved in mate choice and play an important role in promoting and maintaining reproductive isolation (Kraaijeveld, Kraaijeveld-Smit, & Maan, 2011; Ritchie, 2007).

Sexual communication often involves a reciprocal exchange of signals between partners (Bailey, 2003; Hall, 2009; Lewis & Cratsley, 2008; Rodríguez & Barbosa, 2014). Duets are characterized by a predictable temporal association between the partners' airborne or substrate-borne acoustic signals, and temporal coordination between the initiating call and a reply is expressed in reply latency, as well as in alternation or overlapping of signals (Bailey, 2003; Hall, 2009). The coordinated exchange of airborne or substrate-borne acoustic signals has been described in many taxa including arthropods (Bailey, 2003; Uhl & Elias, 2011), amphibians (Emerson & Boyd, 1999), birds (Hall, 2009) and mammals (Geissmann 2000). While duetting between partners appears to be relatively rare in airborne sound communication (Cooley & Marshall, 2001; Emerson & Boyd, 1999; Hall, 2009; Robinson & Hall, 2002), it is common in arthropods relying on vibrational signalling (Bailey, 2003; Boumans & Johnsen, 2015; Henry et al., 2013; Rodríguez & Barbosa, 2014). In arthropods, where partners establish only a temporary bond prior to copulation, the function of a duet has been associated with mate recognition and mate choice (Rodríguez & Barbosa, 2014), as well as with location of a partner (Derlink, Pavlovčič, Stewart, & Virant-Doberlet, 2014; Legendre, Marting, & Cocroft, 2012; Polajnar et al., 2014).

Duetting is a complex and dynamic interaction in which both partners modify their signals and behaviour according to the partner's reply (de Groot et al., 2012; Polajnar et al., 2014; Rodríguez & Barbosa, 2014; Rodríguez, Haen, Cocroft, & Fowler-Finn, 2012). Detailed studies of reciprocal effects arising from signal exchange that influence the sender's and receiver's individual mating success may improve our understanding of the function and evolution of duets and their role in sexual and ecological selection (Rodríguez & Barbosa, 2014; Wilkins et al., 2013). Furthermore, they may provide valuable insights into the mechanisms of animal communication in general (Bailey, 2003; Hall, 2009).

Here, we investigated the role of the duration of a female reply in sender–receiver dynamics in the leafhopper *Aphrodes makarovi*.

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Sexual communication is based on a species-specific vibrational duet initiated by a male advertisement call to which a sexually receptive female responds and the beginning of a female reply overlaps with the last section of the male call (Fig. 1; Bluemel et al., 2014; de Groot et al., 2012). While in this species a higher calling rate increases the probability of the male locating the female (Kuhelj, de Groot, Pajk, Simčič, & Virant-Doberlet, 2015), it also has a detrimental effect on the male's survival, due to eavesdropping predators (Virant-Doberlet, King, Polajnar, & Symondson, 2011) and indirect costs arising from high energy expenditure (Kuhelj, de Groot, Pajk, et al., 2015).

A reciprocal exchange of vibrational signals in *A. makarovi* differs from the majority of other duetting systems studied so far, in that female replies are often longer than male calls (Bluemel et al., 2014; de Groot et al., 2012). Furthermore, the duration of the female reply varies substantially (5–60 s). This communication system provided an ideal opportunity to explore in more detail the influence of the duration of the female reply on male signalling and searching behaviour (Rodríguez & Barbosa, 2014). We hypothesized (1) that male mate-searching effort (which includes advertising signalling and walking to locate the female) is correlated with the duration of the female reply and (2) that in order to optimize his searching behaviour the male has to adjust his signalling according to the duration of the female reply. Males have to trigger every female reply and they are able to evaluate only the nonoverlapped duration of the female signal which depends also on the duration of the initiating call (Kuhelj, de Groot, Blejec, & Virant-Doberlet, 2015). Moreover, during his approach to the female, the male is motionless while calling; walking associated with searching behaviour is limited to the period of the nonoverlapped female reply and shortly afterwards (Kuhelj, de Groot, Pajk, et al., 2015). Consequently, a longer nonoverlapped duration of the female reply should enable males to walk longer distances before stopping and calling again. We predicted that longer female replies would be associated with lower male calling effort and that when the female reply is short, males would shorten the duration of their calls in order to obtain a longer nonoverlapped duration of the female reply.

METHODS

Study Species

Aphrodes makarovi (Hemiptera, Cicadellidae) is a relatively large representative of the leafhopper family (males around 6.5 mm, females around 7.5 mm; Bluemel et al., 2014). This species is widely distributed over the Palaearctic and has also been introduced to North America. *Aphrodes makarovi* is a phloem feeder and has been found on various host plants and in different habitats, often syntopically with other members of this genus (Bluemel et al., 2014). Field population densities vary greatly between localities as well as between years (Derlink et al., 2014). Males increase their signalling space by moving from plant to plant ('fly/jump-call' strategy) and a reply from a sexually receptive female triggers a more localized search on a plant. The female reply is essential for successful mating, since the male does not approach the female if she does not respond. A female mates only once in her lifetime (Bluemel et al., 2014). In rivalry situations (trio: two males and one female) males produce masking signals that overlap either the latter part of the female reply or, less frequently, the call of another male (Kuhelj, de Groot, Pajk, et al., 2015; Appendix Fig. A1).

Males of *A. makarovi* produce long and complex advertisement calls with a stereotyped structure composed of chirps and regularly repeated pulses (Bluemel et al., 2014; de Groot et al., 2012; Derlink et al., 2014; Fig. 1). The nonspecific and highly variable first section (makarovi element 0 (Me0)) is followed by species-specific elements Me1–Me3. The female reply is a series of regularly repeated pulses and there is no difference in the pulse repetition time between the last section of the male call (Me3) and the female reply. Both signals have broadband frequency characteristics; however, the dominant frequency of the male call usually lies between 100 and 300 Hz, while in the female reply most energy is

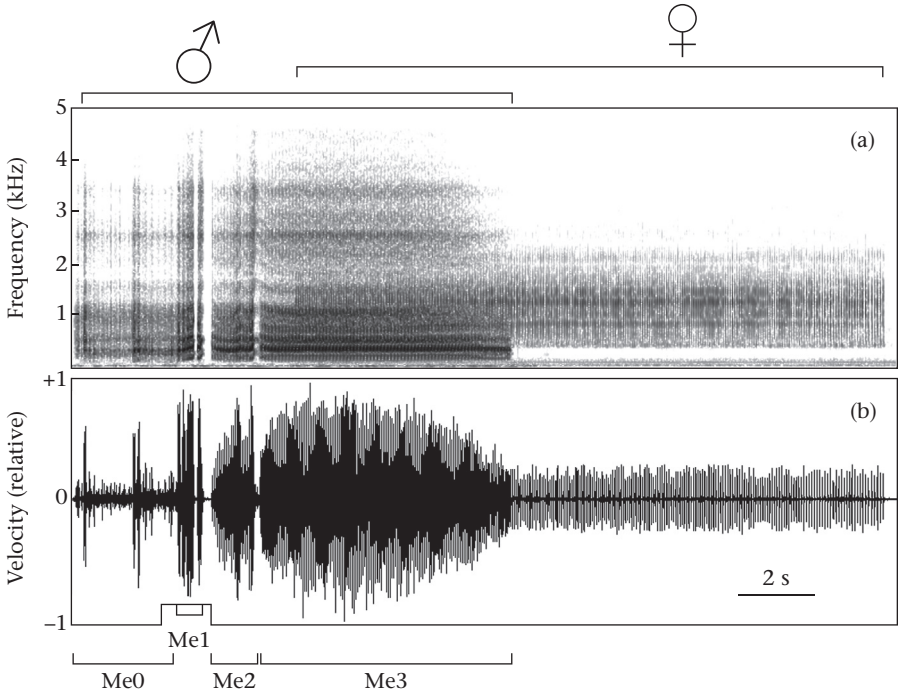

Figure 1. Representative male–female duet in *A. makarovi*. The (a) spectrogram (FFT, window size 4096 samples, 50% overlap) and (b) the corresponding waveform are shown. Me0–Me3: elements in male advertisement call as described in Derlink et al., 2014.