



The process of pair formation mediated by substrate-borne vibrations in a small insect



Jernej Polajnar^{a,*}, Anna Eriksson^{a,b}, Marco Valerio Rossi Stacconi^a, Andrea Lucchi^b, Gianfranco Anfora^a, Meta Virant-Doberlet^c, Valerio Mazzoni^a

^a Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, San Michele all' Adige, Italy

^b Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, Pisa, Italy

^c Department of Entomology, National Institute of Biology, Večna pot 111, Ljubljana, Slovenia

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ABSTRACT

The ability to identify and locate conspecifics depends on reliable transfer of information between emitter and receiver. For a majority of plant-dwelling insects communicating with substrate-borne vibrations, localization of a potential partner may be a difficult task due to their small body size and complex transmission properties of plants. In the present study, we used the leafhopper *Scaphoideus titanus* as a model to investigate duetting and mate searching associated with pair formation. Studying these insects on a natural substrate, we showed that the spatio-temporal structure of a vibrational duet and the perceived intensity of partner's signals influence the mating behaviour. Identification, localization and courtship stages were each characterized by a specific duet structure. In particular, the duet structure differed in synchronization between male and female pulses, which enables identification of the partner, while the switch between behavioural stages was associated with the male-perceived intensity of vibrational signals. This suggests that males obtain the information about their distance from the female and optimize their strategy accordingly. More broadly, our results show that even in insects smaller than 1 cm, vibrational signals provide reliable information needed to find a mating partner.

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1. Introduction

Substrate-borne vibrational signalling is an ancient communication channel that is widely used by both invertebrates (Virant-Doberlet and Čokl, 2004; Cocroft and Rodriguez, 2005) and vertebrates (Hill, 2008). In insects alone, it is used by an estimated 195,000 species (Cocroft and Rodriguez, 2005), often exclusively, but has so far received much less attention than airborne sound communication.

The first step of mating sequences in sexually reproducing insects is pair formation that is achieved by identification and localization of a potential partner in the habitat (Alexander et al., 1997). Species-specific vibrational signals used in sexual communication enable identification of the emitter and provide directional information (e.g. Virant-Doberlet et al., 2006; Hill, 2008; Legendre et al., 2012; De Groot et al., 2012). In some insects that rely on vibrational communication, the searching for a mating partner has been described as “trial and error” (e.g. Gillham, 1992) while in others,

individuals travelled a shorter path than they would during pure random search (Stewart and Sandberg, 2006; Legendre et al., 2012), suggesting that they extracted directional information from signals themselves.

Plants are the most common signalling substrate for invertebrates (Barth, 1998; Čokl and Virant-Doberlet, 2003; Cocroft and Rodriguez, 2005); however, they are complex structures and due to signal degradation and frequency filtering during transmission (Michelsen et al., 1982; Barth, 1998; Magal et al., 2000; Cocroft et al., 2006), signals may be distorted in the frequency and time domains (Michelsen et al., 1982; Miklas et al., 2001). Differences in amplitude and time of arrival of the vibrational signal to spatially separated vibration receptors in legs are the most obvious directional cues that insects may use (Virant-Doberlet et al., 2006). In insects, most vibration receptors are located in the legs (Čokl et al., 2006) and therefore the size (i.e. maximal leg span) of the

* Corresponding author. Tel.: +39 0461 615 509.

E-mail address: jernej.polajnar@fmach.it (J. Polajnar).

a reliable cue due to amplitude oscillations of vibrational signals during transmission (Michelsen et al., 1982; Čokl et al., 2007; Polajnar et al., 2012) and the role of amplitude in orientation behaviour is still under debate (Virant-Doberlet et al., 2006; Mazzoni et al., 2014). Furthermore, the majority of insects that rely on vibrational communication are smaller than 1 cm. In this case, deriving directional cues by directly comparing amplitude or time differences between sensory inputs may not be possible (Virant-Doberlet et al., 2006). Some small insects may instead be able to extract directional information from the mechanical response of the whole body (Cocroft et al., 2000), but solutions have been insufficiently studied.

In the present work, we describe pair formation and searching in a small plant-dwelling insect for which obtaining directional information may be difficult. We used the Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae), which communicates with substrate-borne signals (Mazzoni et al., 2009a), as a model species. The body length of this leafhopper is around 5 mm, with a leg span that is probably too small to enable orientation by direct comparison of sensory inputs (Virant-Doberlet et al., 2006). Like other leafhoppers, *S. titanus* does not rely on chemical signals (Claridge, 1985; Mazzoni et al., 2009a), which allowed us to focus on vibrational cues alone.

In *S. titanus*, the male is searching for the female, and mating sequence is always initiated by the male emitting a calling signal (MCS) to which the stationary females respond with pulses emitted in gaps between the male pulses (Mazzoni et al., 2009a). A successful copulation is preceded by a male–female courtship duet (CrD), which can be disrupted by a rival male emitting a disturbance noise (DN) and taking over the duet. Duetting systems are common in arthropod communication (Claridge, 1985; Bailey, 2003; Virant-Doberlet and Čokl, 2004), often involving complex interactions where signalling is modified by the perception of the partner's reply (De Groot et al., 2012; Mazzoni et al., 2009a; Rodríguez et al., 2012). In such a system, replies by the stationary individual (usually the female) provide information needed for localization by the searching partner, but also by potential eavesdropping competitors (Bailey, 2003). Therefore, a male should optimize the process of gathering the necessary information from the female signals in order to reduce both the energetic costs and competition. To achieve this, a male should perform (1) accurate identification and (2) rapid localization, and should only begin with more complex and demanding courtship after these tasks have been accomplished. The same general principle has been recognized in numerous other animals before (Alexander et al., 1997), but the apparent monomodality of sexual communication in leafhoppers and the ability to accurately measure signals using laser vibrometry allow us to identify the cues that guide behaviour in these stages and trigger transitions between them. Understanding this process may then shed light on the problem of extracting information from vibrational signals by small insects.

In the present work, we therefore tested the following assumption: during pair formation, sexual behaviour progresses through different stages that are characterized and triggered by specific vibrational cues, favouring reliability of recognition and speed of localization before the onset of the most complex advertising stage of courtship. The process is facilitated by the ability of *S. titanus* males to use information in female signals to make directional decisions and detect female proximity despite their small body size.

2. Material and methods

2.1. Insects

Rearing of *S. titanus* from egg to adult followed the method described in Eriksson et al. (2011). All experiments were done with

virgin and sexually mature males and females at least 8 days after their emergence (Mazzoni et al., 2009a). Each leafhopper was tested only once.

2.2. Experimental setup

We used grapevine cuttings with two different geometries as substrate. In each case the bottom of the stem was put in a glass vial filled with water to prevent withering and the vial was placed on an anti-vibration table (Astel s.a.s., Ivrea, Italy). In one case the cutting had two leaves (surface 6 cm × 10 cm) with petioles separated by a 10-cm long stem section (Fig. 1A), while in the other the cutting had three leaves with petioles separated by 5-cm long stem sections (Fig. 1B). For the purpose of analysis, the cuttings were divided into sections, each with a measuring point in the middle. For cuttings with two leaves, those were: (1) basal leaf, (2) basal petiole, (3) stem between the two leaves, (4) apical petiole and (5) apical leaf (Fig. 1A). For cuttings with three leaves, the section labelling was equivalent, but followed the position of male and female (Fig. 1B). The cuttings were replaced with equivalently shaped fresh ones as they wilted.

To prevent the insects from escaping, the setup was contained within a clear Plexiglass cylinder (50 cm × 30 cm). Mating behaviour was observed for 20 min or until the male reached the female, whichever came first. The experiments were performed at 23 ± 1 °C between 5 pm and 9 pm local time to obtain highest sexual activity from *S. titanus* (Mazzoni et al., 2009a), except in tests 1.2 and 1.4 where the temperature was 28 ± 1 °C.

Movement was recorded with a Canon MV1 miniDV camera (50 FPS). Vibrational signals were recorded with a laser vibrometer (Ometron VQ-500-D-V) and digitized with 48 kHz sample rate and 16-bit resolution, then stored directly onto a hard drive through a LANXI data acquisition device (Brüel and Kjær Sound & Vibration A/S, Nærum, Denmark). The laser beam was focused on a small piece of a reflective tape glued to each measuring point.

2.3. Data analysis and terminology

Spectral and temporal parameters of the recorded signals were analyzed with Pulse 14.0 (Brüel and Kjær) after applying Fast Fourier Transform (FFT) with window length of 400 samples and 66.7% overlap. The equipment was calibrated, which enabled direct measurements of the actual substrate velocity.

The terminology used for description of vibrational signals in *S. titanus* follows Mazzoni et al. (2009a). Vibrational signals not previously described were labelled according to their behavioural context.

2.4. Test 1. Signal parameters involved in pair formation

2.4.1. Test 1.1. Male–female synchrony in the course of mating behaviour

Pair formation was studied using a male and a female of *S. titanus* ($N = 20$ pairs), each placed on a different leaf of the same grapevine cutting with two leaves. Vibrational signals were registered from the measuring point on the lamina of the basal leaf with the male (Fig. 1A, point 1).

To analyze the synchrony of male–female pulses within vibrational duets, we measured pulse repetition time (=period) in male signal in presence and absence of female reply (i.e. female pulse), and female pulse latency (the interval between onsets of the male and the female pulse). Each of these parameters was analyzed throughout the whole male–female communication sequence, from the starting position when a male was on a different leaf than a female, through the male's searching phase to his arrival to the leaf with the female. To quantify the effect of female reply on

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