



Vibrational signalling, an underappreciated mode in cricket communication

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Abstract

Signalling via substrate vibration represents one of the most ubiquitous and ancient modes of insect communication. In crickets (Grylloidea) and other taxa of tympanate Ensifera, production and detection of acoustic and vibrational signals are closely linked functionally and evolutionarily. Male stridulation produces both acoustic and vibrational signal components, the joint perception of which improves song recognition and female orientation towards the signaller. In addition to stridulation, vibrational signalling mainly through body tremulation and/or drumming with body parts on the substrate has long been known to be part of crickets' close-range communication, including courtship, mate guarding and aggression. Such signalling is typically exhibited by males, independently or in conjunction with stridulation, and occurs literally in all cricket lineages and species studied. It is further also part of the aggressive behaviour of females, and in a few cricket groups, females respond vibrationally to acoustic and/or vibrational signals from males. The characteristics and function of these signals have remained largely unexplored despite their prevalence. Moreover, the communication potential and also ubiquity of cricket vibrational signals are underappreciated, limiting our understanding of the function and evolution of the cricket signalling systems. By providing a concise review of the existing knowledge of cricket perception of vibrations and vibrational signalling behaviour, we critically comment on these views, discuss the communication value of the emitted signals and give some methodological advice respecting their registration and control. The review aims to increase awareness, understanding and research interest in this ancient and widespread signalling mode in cricket communication.

Keywords Biotremology · Vibrational communication · Courtship · Multimodal communication · Signalling evolution · Grylloidea

Communication by substrate-borne vibrations

Signals and cues generated as mechanical oscillations of a medium provide one of the most ubiquitous modes of information exchange among animals. Such energy can be transmitted in two ways: as longitudinal (i.e., acoustic or sound) waves travelling through air or water, or as various types of mechanical waves at the solid or water boundary (i.e., surface- or substrate-borne vibrations; Hill and Wessel 2016).

Although signalling by sound and substrate vibration are functionally closely related (Caldwell 2014), signals from these two modalities differ largely in their properties and potential information content, and are typically detected by different sensory organs (or different functional parts of a compound organ). Because of the human perceptual preference for hearing, sound has long been considered the predominant means of mechanosensory communication and has been studied extensively in insects and vertebrates (Gerhardt and Huber 2002; Narins et al. 2006; Hedwig 2014a; Pollock et al. 2016; Ladich and Winkler 2017). However, recent advances in biotremology (i.e., the study of animal interactions via substrate-borne waves, Hill and Wessel 2016) have shown that the use of substrate vibrations is of great importance for animal communication and survival (Cocroft et al. 2014a; Hill 2009; Hill et al. 2019; *in press*), and is second in phylogenetic presence only to reliance on chemical signals and cues (Endler 2014). Particularly in insects, which

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are ubiquitously equipped with sensilla to detect substrate surface deflections (while only a subset of insects possess hearing organs; Lakes-Harlan and Strauß 2014; Strauß and Lakes-Harlan 2014), and also as energetically more efficient signalers through the substrate than through the air (Bennet-Clark 1998), vibrational signalling largely exceeds and evolutionarily predates the use of sound in communication (Cocroft and Rodríguez 2005). Signals are produced by specific movements of the body, or some of its parts, with or without striking the substrate (drumming and tremulation, respectively), or by specialised structures for rubbing or buckling to produce vibrations (stridulation and tymbal mechanisms, respectively; Virant-Doberlet and Čokl 2004; Hill 2012). Not only because some of these mechanisms excite both airborne and substrate-borne vibrations, insects can use both types of signals in communication (Cocroft and Rodríguez 2005). In such cases, the two signalling channels would merit joint experimental attention; however, so far bioacoustic and biotremological research in insects and other animals have been conducted largely independently (Cocroft et al. 2014b).

Vibrational signalling in cricket communication

Crickets (Orthoptera, Grylloidea) have been studied for their acoustic communication for over a century and are now established as one of the most important invertebrate models for studying mating systems and communication (Huber et al. 1989; Zuk and Simmons 1997; Robinson and Hall 2002; Hedwig 2014b; Horch et al. 2017; Shöeneich 2020). Male crickets produce sound signals by rubbing specialised regions of the forewings together (tegmenal stridulation), which is their principal mode of long-distance signalling, in the context of mate attraction and territoriality (Alexander 1961; Alexander and Otte 1967). In addition to stridulation, which involves the release of mechanical energy into both air and substrate, crickets exhibit several other types of behaviours related to vibration production (Table 1, Fig. 1). These behaviours may be considered of particular importance for short-range communication, but have received very little attention in experimental research. Here, we provide a concise overview of knowledge of cricket vibratory perception and vibrational behaviour, highlight its documented distribution and communication potential, and critically comment on the commonly held views regarding its importance and evolution. Finally, we provide some methodological advice on vibrational signal registration and control. In doing so, we hope to increase awareness, understanding and research interest in this ancient and widespread signalling mode in cricket communication.

Stridulation and neuroethology of signal detection

The properties of stridulatory vibrations, their sensory detection, the neuronal (co-)processing of sound and vibration signals and its behavioural significance were studied more widely in crickets (and other Ensifera) in the last decades of the previous century, before research focused almost exclusively on the airborne channel. In these insects, the vibratory sense is functionally and evolutionarily tightly related to hearing. Ensifera possess complex mechanosensory organs for substrate vibration detection, situated in all legs (Lakes-Harlan and Strauß 2014; Strauß et al., 2014). In the forelegs, a subset of these sensilla, primitively vibrosensory, have in the course of evolution specialised for sound detection (Meier and Reichert 1990; Rössler 1992; Strauß and Lakes-Harlan, 2009). Consequently, a set of post-synaptic vibratory interneurons of Ensifera have been exploited for the newly developed audition, as well (Stritih and Stumpner 2009). In hearing species, the homology of auditory and vibratory senses is evident by the convergence of both types of information partly at the same interneurons of the ventral nerve cord (Kühne 1982; Kühne et al. 1984), implicitly suggesting a high behavioural relevance of combined acoustic and vibrational stimuli. In a subset of first-order auditory interneurons of crickets, this convergence improves encoding of calling and courtship song patterns and reduces habituation, or otherwise shapes neuronal responses through combined excitatory and inhibitory inputs (Wiese 1981; Kühne et al. 1984). During phonotaxis, female crickets prefer a simultaneously vibrating substrate when approaching the sound source (Weidemann and Keuper 1987). Since stridulatory vibration as a highly correlated signal occurring simultaneously with sound improves encoding of song and orientation, it could be interpreted merely as an ‘efficacy backup’ (Hebets and Papaj 2005). However, vibratory inhibition of the auditory AN2 neuron (Kühne et al. 1984), for example, which mediates avoidance to high-intensity ultrasound during flight, may help switch its function to intraspecific communication associated with the emission of lower-intensity sound and substrate vibration (Kühne et al. 1984). Thereby, the function of concurrent vibrational signals may also be, among others, to facilitate context interpretation for the receiver (see Hebets and Papaj 2005). These data highlight the importance of the simultaneously available auditory and vibratory components of songs for the receiver, and also of other concurrent vibrational signals (see below) in eliciting natural behavioural responses. As discussed in more detail in later parts of this paper, this view should also be considered when designing bioacoustic experiments.

Table 1 Distribution of acousto-vibrational signalling mechanisms in crickets

| Taxon | | Context | | | | | | Reference | | |
|----------------------|-------------------------------|---|---------------------------------|-----------|---------------|--------|-------------|--------------|---|------------------------------|
| | | Male | | | | Female | | | | |
| Family | subfamily | Species | Call | Court | Guard | Aggr | Call/accept | Aggr/reject | | |
| Mogoplistidae | | <i>Cycloptiloides canariensis</i> | S | S | | S | T | | Dambach and Beck (1990) | |
| | | <i>Ornebius aperta</i> | S | S, T | | | | | Andrade and Mason (2000) | |
| Trigonidiidae | | <i>Balamara (Trigonidium) gydia</i> | -, aD | S, aD, pD | T, aD | aD | aD, pD | aD | Evans (1988) | |
| | | <i>Laupala cesarina</i> | S | S, T | | | | | Shaw and Khine (2004) | |
| | | <i>Trigoniduim</i> 'lineage A' (6 sp.) | S* | S, T | T | | T | | de Carvalho and Shaw (2010); de Carvalho and Otte (2006)* | |
| | | <i>Trigoniduim</i> 'lineage B' (2 sp.) | S* | S, T | | | | | | |
| | | <i>Laupala</i> (3 sp.) | S* | S, T | | | | | | |
| | | <i>Prolaupala</i> (2 sp.) | S* | S, T | | | | | | |
| | | <i>Anele ulia</i> | S* | S, T | | | | | | |
| | | <i>Phyllopalpus pulchellus</i> | S | S, T, pD | | S, T | | | Funk (2016) | |
| | | <i>Cranistus colliurides</i> | S | S, T | S, T | | | | Centeno and Zefa (2019) | |
| | Phalangopsidae | | <i>Vanzoliniella sambophila</i> | - | S, ID | | | | | de Mello and dos Reis (1994) |
| | | <i>Izecksohniella aimore</i> | Mute | ID, wF | | | | | Heidelbach and Dambach (1997) | |
| | | <i>Phaeophyllacris spectrum</i> | Mute | T, wF | | | | | Prado (2006) | |
| | | <i>Eidmanacris corumbatai</i> | Mute | T, ID, aV | | | | | Zefa et al. (2008) | |
| | | <i>Adelosgryllus rubricephalus</i> | | S, T, aV | | | | | | |
| | | <i>Phaeophilacris bredoides</i> | Mute | T, wF | | T | | T | Lunichkin et al. (2016) | |
| | | <i>Endecous (Endecous) chape</i> | S* | S, T | | | | | Fianco et al. (2018); Souza-Dias et al. (2017)* | |
| Gryllidae | | | <i>Oecanthus nigricornis</i> | S | S, T, aT, wV | | | | | Bell (1980) |
| | | Oecanthinae | <i>Oecanthus latipennis</i> | S | S, T, aD | | | | | Funk (1989) |
| | | <i>Neoxabea bipunctata</i> | S | S, T, aD | T | | | | | |
| | <i>Leptogryllus elongatus</i> | Mute | T, aV | T | | | | Brown (2016) | | |
| Nemobiinae | | <i>Nemobius sylvestris</i> | S | S, T | | T | | | Gabutt (1954) | |
| | | <i>Hygronemobius alleni</i> | S | S, T | | | | | Mays (1971) | |
| | | <i>Pteronemobius-Allonemobius</i> (4 sp.) | S | S, T | | | | | | |
| | | <i>Pteronemobius-Neonemobius</i> (2 sp.) | S | S, T | | | | | | |
| | | <i>Pteronemobius-Eunemobius</i> (2 sp.) | S | S, T | | | | | | |
| | | <i>Bobilla victoriae</i> | S | S, aV | | T | | | Evans (1988) | |
| | | <i>Bobilla gullanae</i> | S | S, T | | T | | | Su and Rentz (2000) | |
| | | <i>Allonemobius socius</i> | S | S, T | | | | | Sadowski et al. (2002) | |
| | Eneopterinae | | <i>Nisitrus sp.</i> | S | S, IW, aV, wV | | | | | Preston-Mafham (2000) |
| | | | <i>Lebinthus santoensis</i> | S | S, T | | | | | Narvaez and Robillard (2012) |
| | | <i>Lebinthus luae</i> | S | ? | | | T | | ter Hofstede et al. (2015) | |
| | | <i>Cardiodactylus muria</i> | S | ? | | | T | | | |
| | | <i>Agnotecous obscurus</i> | S | ? | | | T | | | |
| | | <i>Ponca hebaridi</i> | S | ? | | | T | | Benavidez-Lopez et al. (2020) | |

Table 1 (continued)

| Taxon | | Context | | | | | Reference | |
|-----------|-----------|-------------------------------|------|-----------|---------|---------|-------------|---|
| | | Male | | | Female | | | |
| Family | subfamily | Species | Call | Court | Guard | Aggr | Call/accept | Aggr/reject |
| Gryllinae | | <i>Acheta domesticus</i> | S | S, T, ID* | S,T | S, T | T* | Alexander and Otte (1967); Hack (1997); Khalifa (1950); own unpublished data* |
| | | <i>Gryllus campestris</i> | S | S, T | S,T, aV | S,T | T | Alexander (1961), Alexander and Otte (1967), Rillich et al. (2009) |
| | | <i>Gryllus bimaculatus</i> | S | S, T | S,T, aV | S,T | T | Adamo and Hoy (1994, 1995), Simmons (1986) |
| | | <i>Teleogryllus commodus</i> | S | S | S,T, aV | S,T, aV | T | Loher and Rentz (1978), Evans (1983) |
| | | <i>Teleogryllus oceanicus</i> | S | S, ID | | S, T | T, wV | Fuentes and Shaw (1986), Broder et al. (2021) |

The major taxonomic groups are listed from basal to terminal, following the phylogeny of Chintauan-Marquier et al. (2016). Abbreviations: *Call*, calling; *Court*, courtship; *Guard*, guarding; *Aggr*, aggression; *Call/accept*, calling/acceptance; *Aggr/reject*, aggression/rejection; *S*, stridulation; *T*, body tremulation; *aT*, abdominal tremulation; *aD*, abdominal drumming; *ID*, leg (foreleg) drumming; *pD*, palpal drumming; *aV*, antennal vibration/waving; *lW*, leg waving; *wV*, wing vibration; *wF*, wing flicking; -, lacks calling song; mute, lacks stridulation apparatus; ?, no reference on courtship behaviour. In *P. breoides* (Lunichkin et al. 2016), female tremulation was reported in undefined context; we included it in the category of ‘Aggr/Reject’ for convenience of table organization and as the most likely context. The list shows examples with species-specific descriptions available at least for pre-mating behaviour. Data on species described for mate guarding or aggressive behaviour only are not included. For details on individual signalling mechanisms, see Fig. 1

Tremulation, drumming and other vibration-producing behaviours

Crickets also produce vibrational signals by mechanisms other than stridulation, which produces substrate vibration along with sound as an inevitable part of their song (Fig. 1). In their pioneering behavioural studies of crickets, Alexander (1961) and Alexander and Otte (1967) described body tremulation (termed ‘rocking’, ‘shaking’, ‘jerking’, ‘swaying’ or ‘vibrating’ by the authors) as a ubiquitous display during short-range courtship and aggressive behaviour of males. This has been confirmed to date by a large number of behavioural reports from species of all major cricket lineages (Table 1). These studies showed that, especially during courtship, tremulation is often combined with (and in some cases apparently replaced by) drumming or ‘tapping’ of various body parts on the substrate, and/or additional vibration-producing behaviours such as antennal, wing or leg waving or vibration (Table 1, Fig. 1). Such signals are mostly, although not exclusively, exhibited by males, independently or in combination with stridulation, and occur largely in the same form and context in singing and non-singing species, as well as in ground- and plant-dwelling species of crickets (Table 1). However, examples of the most diverse or extensive use of vibrational signalling are found in non-singers and in crickets inhabiting vegetation

(e.g., Bell 1980; Prado 2006; Brown 2016; Table 1), both aspects presumably facilitating vibrational communication. Whether the specific functions of vibrational signals might differ among crickets inhabiting different substrates (due to their known constraints on vibrational communication, e.g., Cocroft and Rodríguez, 2005; Elias and Mason 2014) would be an interesting aspect to investigate in the future.

Evolution of vibrational signalling

The prevalence of tremulation behaviour across different cricket lineages strongly suggests that this signalling mode must have been present in the early crickets ancestors, most likely before the evolution of their acoustic communication (see also Stumpner and von Helversen 2001; Stritih and Stumpner 2009; Stritih and Čokl 2012; Desutter-Grandcolas et al. 2017). However, this view does not seem to be generally appreciated. Recently, the evolutionary transition of a startle response into an intraspecific communication signal has been hypothesised for Eneopterinae crickets (Lebintini: ter Hofstede et al. 2015; Benavidez-Lopez et al. 2020). Males of this group emit calling songs at unusually high frequencies (for crickets), and stationary females respond to these signals with tremulation that prompts the male to find the mate on a plant. Because high-frequency acoustic signals at high intensity normally elicit a reflex startle

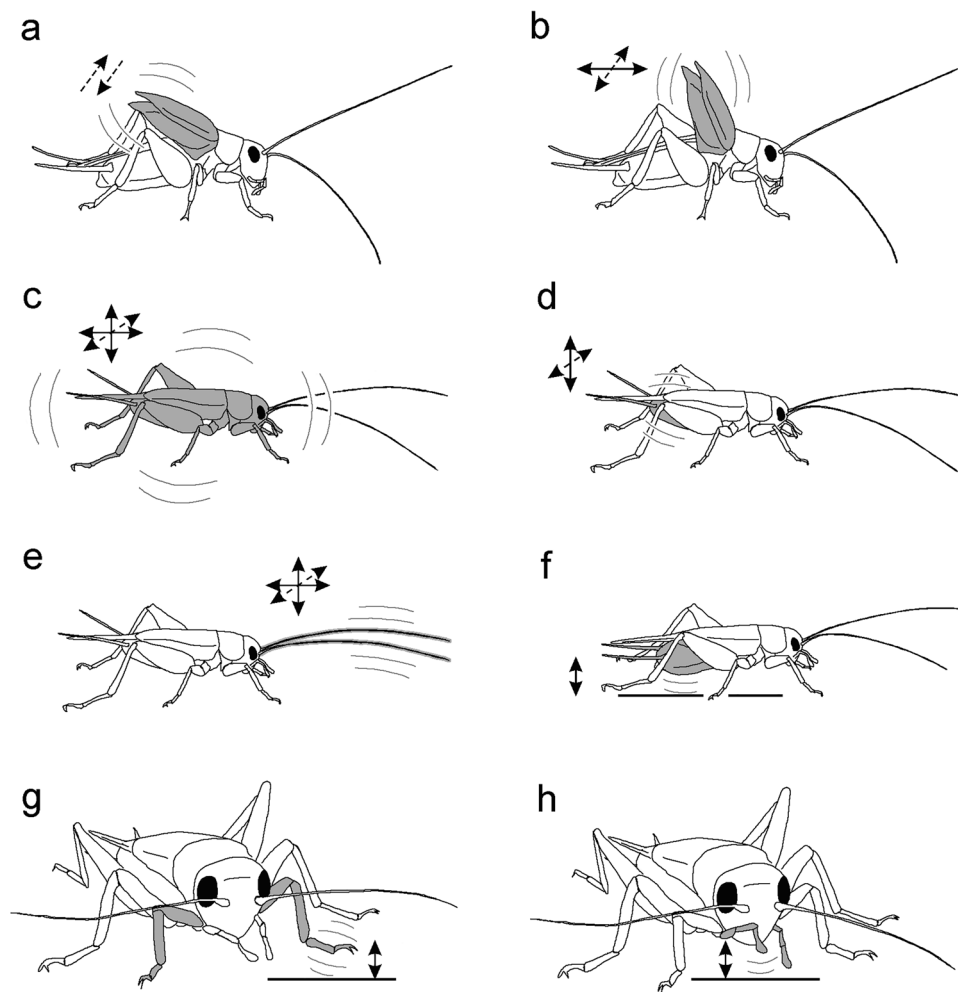


Fig. 1 Schematic representation of acousto-vibrational signalling mechanisms in crickets. Gray coloration indicates body parts primarily involved in signal production. Arrows indicate the described directions of movement. **a** Stridulation (tegmina stridulum), **b** wing vibration (lateral vibration without friction, or antero-posterior ‘flicking’ of tegmina), **c** body tremulation (antero-posterior, lateral or dorso-ventral vibration of the entire body, without a percussive impact of the substrate), **d** abdominal tremulation (dorso-ventral or lateral vibration of the abdomen), **e** antennal vibration (dorso-ventral or lateral vibration, or larger-scale antero-posterior ‘waving’ of antennae),

f abdominal drumming, **g** foreleg drumming and **h** palpal drumming, which include impacts of respective body parts against the substrate (schematized by a horizontal line). Note that tremulation/vibration mechanisms are soundless, and typically emit low-frequency signals into the substrate. Drumming typically induces broadband substrate vibration and at least a weak acoustic signal component. Stridulation produces intense sound and high-frequency/broadband substrate vibrations. In crickets, these signalling mechanisms are often combined, simultaneously or subsequently, in a complex mechanosensory display

response (expressed as a jerky contraction of the body in a sedentary animal), it has been proposed that female startle response to male calls evolved into a signal by sensory exploitation (ter Hofstede et al. 2015; Benavidez-Lopez et al. 2020). The recently documented tremulatory responses of males to male calls in the context of rivalry are also proposed to have evolved via the same mechanism (Benavidez-Lopez et al. 2020). While this hypothesis is appealing and the authors provided some neuroethological support for it (but also presented some disconfirming behavioural data in the study; ter Hofstede et al. 2015), it seems highly unlikely that tremulatory signalling, as found in literally

every cricket species, would evolve de novo in Lebinthini via the exploitation of a startle reflex. This is especially of concern since similar communication between males and females is also known from primitive cricket lineages, suggesting that females were capable of producing vibrational responses to male calls early in cricket evolution. Females that respond to male calling and/or courtship signals within a regular male–female vibrational or acousto-vibrational duet are known from species of the Trigonidiinae and Mogoplantinae (Evans 1988; Dambach and Beck 1990; de Carvalho and Shaw 2010; Table 1). As in Lebinthini (ter Hofstede et al. 2015), these females do not perform phonotaxis but are

stationary while the male calls and searches for them, conditions that apparently facilitate the evolution of bidirectional signalling in crickets. Moreover, female crickets have also been found tremulating in the context of aggression, at least whenever this has been explicitly studied (mostly in field crickets: Fuentes and Shaw 1986; Adamo and Hoy 1995; Rillich et al. 2009; see also Table 1), which suggests their common ability to emit vibrational signals.

Vibrational signalling in courtship

Evaluation of the function of cricket vibrational signalling has been limited so far to aggressive tremulation constituting agonistic and guarding behaviour, and has been based exclusively on the assessment of behavioural context (e.g., Adamo and Hoy 1995; Hofmann and Schildberger 2001; Parker and Vahed 2009; Bertram et al. 2010; but see Vedenina and Shestakov 2018, for correlation between aggressive tremulation and expression of courtship behaviour). However, understanding the function of vibrational signals would be particularly relevant in cricket courtship, a multimodal communication process that influences female choice. In field crickets, this process has been studied extensively for the quality of the exchanged information and the associated female preferences in the acoustic, and recently also the contact chemical channel, but is still not completely understood (see also below). The importance in courtship initiation and its success has also been studied for tactile mechanosensory and for visual signals and cues (Loher and Rence 1978; Adamo and Hoy 1994; Balakrishnan and Pollack 1997), while the role of vibrational signals in this aspect has never been studied experimentally. This is surprising given the well-documented cricket vibratory sense and behaviour, as even the elevated body temperature of males resulting from singing has recently been studied (though not confirmed) as a putative short-range signal to influence female choice (Erreger et al. 2018). The lack of experimental focus on vibration in cricket communication may in part be related to the challenge of isolating vibrational signals or removing them from the behavioural context, which may be more difficult to achieve than with other sensory modalities. However, this lack also seems to be a sign that the importance of vibrational signals in communication is generally underappreciated.

Even those studies explicitly addressing the role of non-acoustic modalities in complementing sound during courtship largely focused on chemical cues (Rebar et al., 2009; Leonard and Hedrick 2010; Stoffer and Walker 2012; Simmons et al. 2013; but see Wegerhaupt and Wagner 2017, suggesting the role of vibration, as well). Chemical signals were also investigated as an alternative to compensate for the evolutionary loss of sound among the Pacific field cricket *T. oceanicus* (without providing evidence for this; Gray et al.

2014), although both vibrational and chemical signals have previously been recognised as pre-existing modalities underlying the still high mating success of the silent males (Bailey et al. 2008). Nevertheless, the first insight into substrate-borne information in courtship has just been provided for the intermediate, ‘purring’ morph of this species, which emits quieter but still functional songs (Broder et al. 2021). This study documented leg drumming signals for the first time in field crickets, and showed that vibrations emitted by purring individuals are similar in amplitude to that of typical ones and may influence mating decisions (Broder et al. 2021). Facilitated by the present review, we hope that research interest in cricket vibrational signals will gradually increase, especially after a better understanding of their communication potential in courtship, which is discussed in more detail below.

In field crickets, it has been shown that despite strong directional preferences of females for certain courtship song parameters, acoustic information alone is not a reliable indicator of male quality. The song lacks condition dependence (Wagner and Reiser 2000; Gray and Eckardt, 2001; Harrison et al. 2013) and also weakly reflects the male's immunocompetence tested as an alternative quality index (Rantala and Kortet 2003; Tregenza et al. 2006; Simmons et al. 2010). This suggests that females would benefit from simultaneous assessment of song with other available signals. We would like to highlight the particularly high potential of vibratory information to functionally complement sound in this regard. This is not only because these two signalling channels are closely linked at the behavioural and sensory levels of crickets but also because signals of both modalities are costly and are produced dynamically in time (see below). As a result, vibrational signals may increase the reliability of auditory information differently than the more static chemical signals (which inform females about male identity, sex, status, genetic compatibility, etc., e.g., Tregenza and Wedell 1997; Thomas and Simmons 2009; 2011; Tyler et al. 2015).

Cricket tremulation provides an example of an energetically highly costly signalling behaviour. In agonistic interactions of house crickets, the oxygen consumption of tremulation exceeds that of stridulation by more than fivefold (Hack 1997; similar findings were obtained when comparing long-range acoustic signalling and tremulation in a neotropical katydid; Römer et al. 2010). Such energetic demands offer the emitted vibrational signals, and even more so the combined mechanosensory display of the courting male, the potential to convey much more relevant or ‘honest’ information to the female than acoustic signals alone (see Møller and Pomiankowski 1993). However, given the lack of condition dependence of courtship song, this is only true if the rates of vibrational and acoustic signals are not highly correlated, and may be particularly relevant for crickets that do not emit

both types of signals simultaneously. Indeed, in the scaly cricket *Ornebius aperta* (Mogoplistinae), which tremulate mostly upon the female retreat from courtship, high-condition males were more likely to produce tremulation signals that increased female receptivity to repeated mating attempts (Andrade and Mason 2000). To our knowledge, this is the only cricket study that discusses the function of courtship vibrational signals in more detail and also indicates them as reliable for female choice.

The information content of vibrational signals in relation to male quality and the related female preferences have rarely been studied in courtship rituals of insects in general. During precopulatory courtship of the red mason bee *Osmia rufa*, thoracic vibration bursts were significantly longer in males accepted for copulation, potentially informing the female about male health and vigour (Conrad et al. 2010). Courtship tremulations of the male katydid *Conocephalus nigropleurum* had a shorter inter-pulse interval in larger males, and such signals were preferentially selected by females in the two-choice stimulation paradigm (de Luca and Morris, 1998). The advertisement signals studied in treehoppers, heelwalkers and psyllids were also shown to contain information on male condition and/or age, but their primary function was confirmed in mate recognition and localisation, not in mate choice (de Luca and Coccoft 2009; Lubanga et al. 2016; Eberhard et al. 2019). This lack of data would make any future functional insights into the cricket vibratory courtship highly relevant also in the broader context of insect biotremology.

In the complex acousto-vibratory courtship of crickets, important messages about the signaller may be encoded not only in the vigour of motor performance (i.e., signalling rate, intensity or duration) but also in the signaller's ability to link a series of motor patterns in a precisely coordinated manner (Byers et al. 2010). Such motor skills are considered particularly reliable indicators of male health, genetic quality and developmental stability (Byers et al. 2010). In crickets, such information could be encoded, for example, in the degree of synchronisation of acoustic and/or vibrational signal components produced by various mechanisms (e.g., stridulation, tremulation and/or drumming), which may be difficult to achieve and maintain during a sustained, repetitive display typical of their courtship. This is suggested by examples of males from several animal groups, such as birds, frogs and spiders, known to perform courtship displays in a highly synchronised manner across modalities, and the high degree of synchronisation of signals is preferred by females (Taylor et al. 2011; LaRue et al. 2015; Kozak and Uetz 2016; reviewed in Mitoyen et al. 2019). The complex courtship display of crickets may provide another promising topic

to study from the view of multimodal communication and signal integration.

Recording and controlling vibrational signals

Several studies have analysed temporal parameters such as repetition rates of visually distinct tremulation by crickets (e.g., Heidelbach and Dambach 1997; Bertram et al. 2010; Narvaez and Robillard 2012; Brown 2016; Vedenina and Shestakov 2018), while descriptions of physical properties of the actual signals emitted into the substrate are scarce. Besides of a few sample oscillograms shown for female tremulation in Lebinthini (ter Hofstede et al. 2015) and leg drumming in a phalangopsid (i.e., the auditory component of the display; de Mello and dos Reis 1994), a quantitative insight into the frequency and amplitude characteristics of vibrations have only been given for two species of field crickets (by calling: Weidemann and Keuper 1987; and courtship signalling: Broder et al. 2021). Thus, for most species, contexts, mechanisms of signal production, as well as relevant (natural) substrates of crickets, a comprehensive analysis of temporal, spectral and intensity characteristics of vibrational signals is still lacking. Thus we may lack not only the basis to study the role of these signals in communication, but possibly also the presence of signals that are less obvious to our visual inspection. For example, combined substrate vibration and video recording has only recently revealed leg drumming as a mechanism of vibration production in field cricket courtship (Broder et al. 2021, for *T. oceanicus*; own unpublished data for *A. domesticus*), despite decades of behavioural study of these species.

For recording vibrational signals, we suggest preferential use of a species' natural substrate, or a non-resonant reference substrate such as a loudspeaker membrane, which would also facilitate interspecific comparison. Considering the high communication potential of vibrational signals to functionally backup or complement sound, we further argue that recording and control of vibrational signals available to the receiver should also be conducted in bioacoustic experiments. Control can be achieved primarily by choosing an experimental substrate that enables or prevents efficient vibration transmission, depending on the purpose of the experiment. So far, a variety of artificial substrates have been used (for example in mate choice experiments testing auditory courtship signals), from plastic or screen-bottomed arenas, wire mesh cages, Petri dishes covered with paper towels, to mineral wool chambers (e.g., Adamo and Hoy 1994; Libersat et al. 1994; Balakrishnan and Pollack 1996; Nelson and Nolen 1997; Vedenina and Pollack 2012). It is to be expected that these substrates differ greatly in both their sensitivity and frequency filtering to induced vibrations (Elias and Mason 2014). Although such experiments are typically conducted using signal isolation, i.e., with muted

males offered to females along with auditory playback, it should be noted that males with removed wings typically still perform all motor actions associated with courtship behaviour (the stridulatory movements of wing bases and other vibrational displays). This may affect female behaviour differently on different substrates, thus confounding study results. The apparent effectiveness of vibrational signalling by muted males has been highlighted, for example, by Balakrishnan and Pollack (1996) and Vedenina and Pollack (2012), who reported unexpected responses of females to partial songs with missing elements in the playbacks. Also, noteworthy is the rather high variability in courtship success of negative controls (i.e., muted males without auditory playback) between these experiments and especially when the same species was used (see Libersat et al. 1994; Balakrishnan and Pollack 1996; Bailey et al. 2008). This variability may reflect, at least in part, differential efficacy of male signalling through the substrate.

Concluding remarks

Because of human perceptual bias, we tend to think of auditory signals as a highly prevalent mode of communication via mechanical signals in animals. Crickets are not the only example where such a bias may have favoured the study of signals that we detect and intuitively understand much better than their substrate-borne counterparts. After decades of focusing only on the combination of visual and acoustic signals, substrate vibrations have been shown to be an additional and highly important means of information transfer in the multimodal courtship of fruit flies (Fabre et al. 2012; Mazzoni et al. 2013). Even in songbirds, such as finches, traditionally considered to be specialised acoustic and visual signallers, there is growing evidence for the use of substrate-borne signals as an additional means of information exchange important in short-distance courtship (Ota et al. 2015; Ota 2020).

While it is undisputed that acoustic signals represent the crucial means of long-distance communication in crickets, it is time to consider their so well-documented vibrational behaviour as important for short-distance communication and to consider these data in evolutionary scenarios, as well. In the review on cricket vibratory sense published three decades ago, Dambach (1989) pointed out that questions about cricket vibratory perception needed to be addressed primarily at the behavioural level, and this has not changed since then. We have learned since then, however, that the vibrational modality is much more complex than other sensory modalities due to the strong and variable effects of substrates as signalling media (Elias and Mason 2014; Mortimer 2017), which also relates to the challenges in signal recording, and especially playback,

that are not relevant in bioacoustics (Cocroft et al. 2014c; Nieri et al. *in press*). Since at the same time, many issues from bioacoustics are unknown to biotremologists, we propose that in the future, researchers from these two distinct but closely related sensory modalities combine their knowledge and expertise to jointly investigate the role of acoustic and vibrational displays, not only, but also, in cricket communication.

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Declarations

Ethics approval This manuscript is a theoretical paper that did not include experiments with animals or any other environmental influences.

Competing interests The authors declare no competing interests.

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