J Insect Behav (2026) 39:7
https://doi.org/10.1007/s10905-026-09901-9

RESEARCH

Complex Vibroacoustic Signalling During Pair Formation and Courtship in the Bushcricket *Ancistrura nigrovittata* (Orthoptera, Phaneropteridae)

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Received: 6 January 2025 / Revised: 4 November 2025 / Accepted: 1 February 2026

Abstract Many insects, including bushcrickets, use acoustic communication for mate finding and mate choice. These signals often produce simultaneous substrate vibrations, potentially aiding localization. However, independently produced vibratory signals are rarely documented in Orthoptera, despite their potential to enhance close-range communication. In the duetting bushcricket *Ancistrura nigrovittata*, acoustic communication has been extensively studied. We investigated whether any previously overlooked vibratory signals occur during close-range interactions in this species, and characterised their properties and interplay with acoustic signals. Combining laser vibrometry, audio and video recordings, we revealed soundless abdominal tremulation signals in both sexes during partner search and pair formation. Although subtle, these movements produce substrate vibration with amplitudes exceeding those induced by acoustic signalling (stridulation) by an order of magnitude. In both sexes, tremulation and acoustic signals can occur simultaneously or separately, demonstrating independent production mechanisms. Females combine song with tremulation during long-distance calling, use primarily tremulation after a male enters a plant, and typically cease signalling upon being found. Males add tremulation to the song after entering a plant and use it as the primary signal after partner contact. In both sexes, tremulation comprises mostly grouped pulses, emitted at a rate of about 2.5 Hz. Male tremulation exhibits a lower pulse number per train, higher dominant frequencies and amplitudes than female tremulation, and is typically accompanied by a short acoustic tick at the beginning of each pulse. Our findings reveal a previously unknown complexity of vibroacoustic communication in *A. nigrovittata*.

Keywords Tremulation · Vibration signal · Complex signal · Vibroacoustic duet

Introduction

Animal communication serves a number of purposes: social interaction, threatening potential predators, warning conspecifics about predators, territorial defence, and mate finding and choice (Alcock 2009; Bradbury and Vehrencamp 2011). Most bushcrickets (Orthoptera, Tettigonioidea) produce acoustic signals (calling song; see Glossary for definitions of

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10905-026-09901-9.

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terminology) for mate finding – either the females approach singing males or both males and females perform a duet, where either partner may perform phonotaxis (Korsunovskaya 2009). The production of these songs (in bushcrickets by stridulation; see Heller and von Helversen 1986; Gwynne 2001; Montealegre-Z 2012; Stumpner et al. 2013) typically induces vibrations in the substrate as a byproduct (Keuper et al. 1985; Hill and Shadley 2001; Stölting et al. 2002). Partners can use this vibratory signal when orienting towards a singer (Latimer and Schatral 1983; Weidemann and Keuper 1987), but the information is largely redundant for encoding the emitter's identity and quality and merely represents a functional "backup" to the song (Hebets and Papay 2005; Hebets and McGinley 2019). Moreover, the vibrational component is often detectable in close range only, for example when male and female sit on the same plant. Since most bushcricket species initiate communication over long distances (e.g. Römer and Lewald 1992; von Helversen et al. 2015), most of the approach relies on the airborne component of the song.

On the other hand, in many Neotropical bushcricket species, males call females by combining sound with tremulation, i.e. body shaking without impacting the substrate, emitting an exclusively substrate-borne vibration signal (Morris et al. 1994; Stumpner et al. 2013; ter Hofstede et al. 2017). Representatives of the Conocephalinae and Pseudophyllinae subfamilies are particularly well known for this type of multimodal signalling (which has otherwise only rarely been reported in other groups; Bradyporinae: Busnel 2019; Phylloporinae: Korsunovskaya et al. 2022). Acoustic communication in these species is often reduced and tremulation evolved secondarily in response to substrate-gleaning bats that eavesdrop on insect sounds (Belwood and Morris 1987; Morris et al. 1994; Römer et al. 2010). While they typically combine stridulation and tremulation when calling partners, *Onomarchus uninotatus* (Pseudophyllinae) females were found to produce tremulation as the sole response to a distant male singing (Rajaraman et al. 2015). Some species, however, may combine song with tremulation with no apparent reduction of acoustic signalling: in *Nesoecia nigrispina,* a pseudophylline, males complete their calling song cycle with a series of tremulations (Korsunovskaya and Zhantiev 2022). In most bushcrickets, females tremulate in response to male signalling in close range, and males may also initiate tremulation after detecting a potential partner on the same plant (Busnel et al. 2019; Morris 1980; Morris et al. 1994; de Luca and Morris 1998).

Since, in contrast to grasshoppers and crickets, bushcricket males do not produce a distinct courtship song when a pair has met, tremulation signals may compensate for its absence, facilitating mate choice. Given also the bushcrickets' elaborate and sensitive vibrosensory system (e.g. Rössler et al. 2006), one might expect tremulation (or other types of vibratory signals) as a complementary signal to occur more commonly among bushcrickets than in species with typical courtship songs. Alternatively, they may simply have been overlooked by researchers. Most known vibration signals in bushcrickets involve vigorous body shaking, which is conspicuous to humans. Yet, insect vibrational signalling – including examples from Orthoptera – may be more subtle and detectable with specialized vibration sensors only (e.g. Stritih and Čokl 2012; Stritih-Peljhan and Žunič, 2024).

Here we present an example of a well-studied bushcricket, *Ancistrura nigrovittata*. It is one of many phaneropterine bushcrickets, in which the male initiates acoustic communication with a calling song, while receptive females produce a stridulatory response, which is temporally strictly coupled to the male song (Heller and von Helversen 1986; Heller et al. 2015). In *A. nigrovittata*, the male song comprises a chirp (composed of about 8 syllables) and, after a delay of 250 to 350 ms, a so-called trigger syllable (Fig. 1). A receptive female responds with a short and constant delay of 30 to 40 ms to this trigger syllable (Heller and von Helversen 1986; Dobler et al. 1994b). Unique among studied Phaneropterinae is the difference in carrier frequency between male and female signals (Dobler et al. 1994a; Heller and Hemp 2015): male song peaks around 14–16 kHz, female reply peaks around 24–28 kHz (Fig. 1). The carrier frequencies as well as the temporal structure are necessary to initiate duetting and phonotaxis (Dobler et al. 1994a,b). Duetting may start in the laboratory at a distance of about 8 m between male and female (Stumpner, unpublished). When a female responds, the male immediately starts walking towards it (Dobler et al. 1994a). However, highly motivated females may start phonotaxis towards the male at any distance (Stumpner, unpublished). In

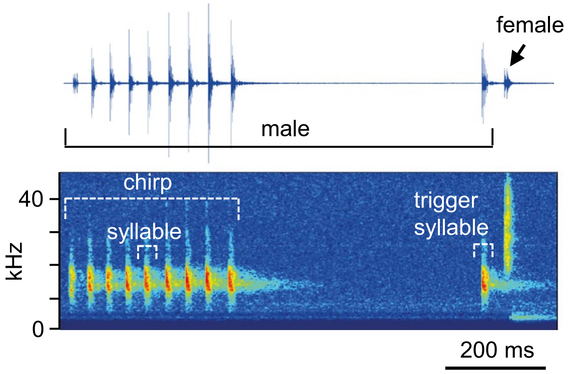

Fig. 1 A male–female acoustic duet. The male signal comprises a multiple-syllable chirp followed by a separate (single or double) trigger syllable eliciting a brief, one-syllable female response

the final approach, the male may switch from a song with chirps and trigger syllables to a song comprising only chirps with an increased chirp rate. We call this a courtship song, since its function is not to elicit female acoustic replies. However, chirps are also produced in contact with males (Heller 1988; Stumpner, unpublished). When the sexes come into physical contact, males may produce the courtship song or stop acoustic signalling and try to manoeuvre themselves under the female for initial coupling, which likely involves sperm removal as described for related species (von Helversen and von Helversen 1991). This behaviour, interrupted by long pauses, may occur repeatedly until the large spermatophore is transferred. Any other regular vibroacoustic behaviour was not observed so far.

Since there are no published data on close-range communication in *A. nigrovittata* – in contrast to the well-documented long-range acoustic behaviour – our aim was to study possibly overlooked vibratory signalling. We were motivated by occasional observations of whole-body shaking triggered by contact with other individuals (which turned out to have a repellent function) and the presence of multiple auditory and vibratory interneurons in the first level of sensory processing (Stumpner and Nowotny 2013; Cillov 2024); one of them responds to both the male song and low frequency vibration (Cillov 2024). In addition, the high degree of convergence of auditory and vibratory inputs onto common neurons in the ventral nerve cord in other bushcrickets (Rössler et al. 2006) further suggests an important role of vibratory signals in communication. After initial experiments confirmed the presence of vibratory signalling independent of stridulation, we set out to characterize the vibratory dynamics of pair-formation and its interplay with acoustic signalling in this species. We demonstrate that vibratory signalling is not merely a byproduct of acoustic signalling, but represents an additional communication channel based on independently produced signals used by both sexes during pairing.

Materials and Methods

Animals

We used adult *Ancistrura nigrovittata* (Phaneropterinae) originating from Greece, kept in a permanent colony in Göttingen, Germany, with periodic additions of wild-caught individuals (the most recent ones in the years 2008, 2013, 2021). The colony is held at a temperature of 25°C and under a partially reversed day/night cycle of ca. 14/10 h. Experimental animals were kept in cages (40×30×25 cm) separated by sex prior to their final molt. Fresh blackberry branches were provided for support and as food, along with cricket chow (Nekton, Keltern – IKG Dammfeld, Germany) and water.

Experiments

Experiments were conducted in an anechoic chamber on an anti-vibration table at a temperature of 24–26 °C during the animals' night phase under red illumination.

Animal Preparation: Males were brought to the laboratory individually in vials, while females were brought as a group in the same cage they were reared in. Each animal was marked with a unique combination of coloured dots (Edding 750, Edding, Germany) applied to the pronotum and abdomen for individual identification. Prior to the experiment, one or two active signallers along with one or two responsive females were selected (also see below Experimental Procedure).

Test Setup: We used a 50 cm blackberry (*Rubus sp.*) branch – one of the host plants – as a test substrate. The branch had three or four compound leaves, with one leaf pair in an upper and one in a lower position, each pair extending in opposite

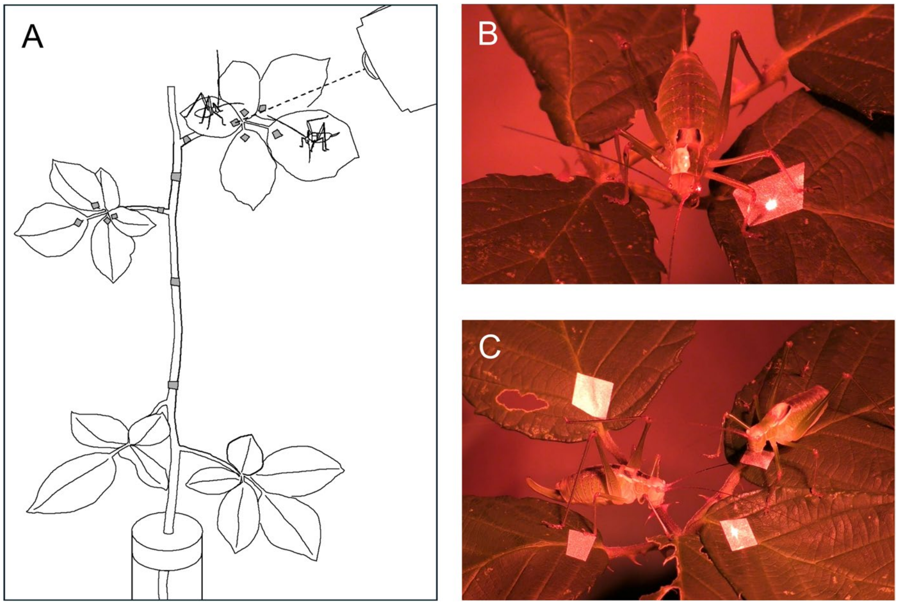

Fig. 2 Experimental setup for recording vibration signals of *A. nigrovittata* on a branch of *Rubus sp.* **A**) Schematic drawing of an experimental plant, with laser reflectance measurement points: on the main branch, at the base of the petiole supporting the compound leaves, and on the individual leaflets. The dashed line represents the laser beam. A female responding to calls from a distant male (**B**) and a pair during the close-range courtship (**C**) were typically positioned on one of the (upper) compound leaves

directions (Fig. 2). We used six plants of such geometry throughout the experiments. The lower 20 cm of the branch was inserted through thick foam into a glass jar filled with water and fixed to the table. Reflective foil was attached to the leaflet bases, petioles, and stem at 8 cm intervals for laser vibration recording (Fig. 2).

Experimental Procedure: All experiments were video-recorded with a Panasonic (HC-VXF990) camcorder. Simultaneous sound and substrate vibration recordings were conducted using a laser vibrometer PDV-100 (Polytec, Waldbronn, Germany) and a unidirectional microphone (4133, Brüel & Kjær, Denmark) with a preamplifier (2610, Brüel & Kjær). The microphone was positioned about 20 cm from the top of the plant. The two-channel sound and vibration input was digitised using a Sound Blaster (Creative X-Fi Surround 5.1 pro, Singapore) and recorded with the program Raven Pro 1.6 (Cornell Laboratory of Ornithology, Ithaca, New York, USA) at 44 kHz sampling rate and 16-bit resolution. Synchronisation between the video and audio-vibration recording was achieved by a loud clap at the beginning of each session, providing a clear synchronization mark. An ultrasound detector (D 120, Pettersson, Sweden), which converts ultrasonic signals into the audible range, was occasionally used to monitor sound signals in real time and aid their identification during video analysis. Vibration recordings were calibrated using a vibration calibrator (type 4294, Brüel & Kjær, Denmark), which provides a reference signal of 10 mm/s. Sound intensity was not analysed.

The selected females were placed individually onto one of the top leaves of the test plant, while individual males were kept in foam-covered boxes, allowing acoustic interaction before their release. To increase the chances of a successful start (male calling and sustained female responsiveness after placement on the plant), we often began the experiment with two male–female pairs. The females were placed on different plants (if two plants were in the setup simultaneously) or on different compound leaves of the same plant and the males in the boxes were put close to the plant. Then, only one duetting pair was kept (except for inactive females, which were sometimes left on the same plant to avoid disturbing the other). After recording a responding female on the plant, the male was either transferred to the bottom of the stem or placed next to the female if she was no longer responding acoustically. During short-range courtship, vibrations were primarily recorded from the bases of leaflets supporting the signaller or the immediately adjacent leaflet for 30–45 min, with the laser beam adjusted as needed. During male approach and in prolonged unsupervised recordings (e.g. overnight), data were also collected from the petiole of the compound leaf hosting the female. Some males called from the same position on a plant for extended periods, and the vibrational component of their song was recorded from various locations on the stem and leaves.

Signal Analysis

Recordings were analysed in Raven Pro 1.6 following filtering in Audacity 3.1.3 (Audacity Team). We applied a 10 Hz high-pass filter to all vibration recordings to reduce movement-related noise, while sound recordings were high-pass filtered at 1 kHz.

For males (n = 10), we analysed the first 30 tremulation pulse trains emitted after their initial contact with the female, measuring the pulse train period and the number of pulses per train. For individual tremulation pulses, we analysed the first 40 pulses for duration, in-train rate and duty cycle, and peak frequency (the latter only for those pulses emitted on a leaf surface). Pulse peak amplitude was analysed in relation to measurement location (i.e., on the same leaflet, on the neighbouring leaflet, or on the petiole of the compound leaf supporting the signaller). For females (n = 6), which were reluctant to respond vibrationally for prolonged periods, the set of emitted signals was more limited; we analysed 3–30 pulse trains with 15–40 individual pulses per female. The same parameters as for males were analysed. We further analysed the dominant frequency and peak amplitude of stridulatory vibrations from 8 males and 7 females that signalled on a leaf surface, taking 15 male chirps/female replies per individual. For spectral analysis, we applied a Fast Fourier Transformation with a size of 16,384 points.

Statistical analysis was first performed using the Mann–Whitney U test for male–female comparisons and the Kruskal–Wallis test to assess interindividual differences in the measured parameters. However, the large sample size led to many significant differences that appeared biologically irrelevant, prompting us to rely on a Linear Mixed-effects Model (LMM), which effectively accounts both for interindividual variability as a random effect (in the context of male–female comparisons) and for unequal sample sizes between males and females. We report results from both analyses, providing a robust and transparent assessment of the data.

Results

Ancistrura nigrovittata bushcrickets are known for their acoustic duetting prior to pair formation (see Introduction and Fig. 1). The stridulatory wing movements also produce low-frequency vibrations in the substrate (Fig. 3). In addition, we show that both sexes combine stridulation with abdominal tremulation, either simultaneously or in succession, producing additional prominent substrate-borne vibration signals. Tremulation is not easily visible to the naked eye but is clearly seen in close-ups of video recordings (Suppl. Video 1, Suppl. Video 2).

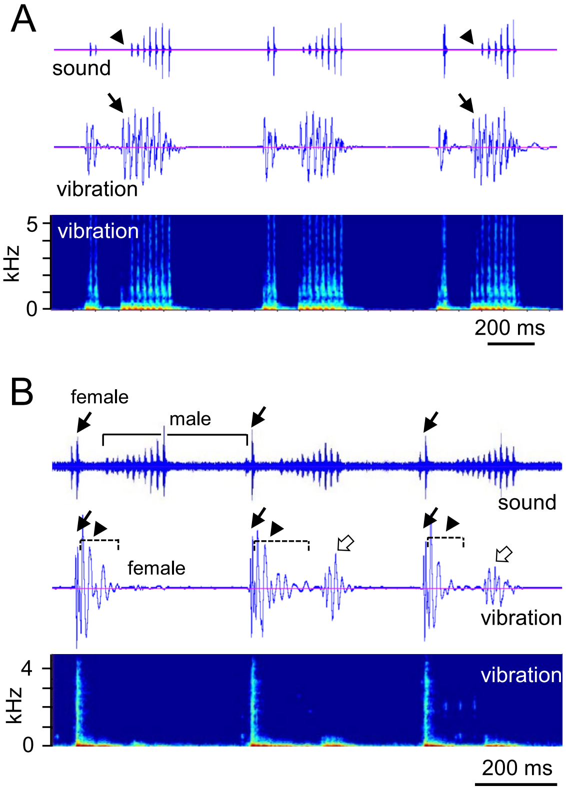

Fig. 3 Stridulation signals. **A**) Sound and vibration components of the male song emitted on a plant. Low-frequency vibrations induced in the substrate reflect large-scale (opening and closing) wing movements; an initial cycle of these movements may be silent (arrows show corresponding vibration waves, arrowheads indicate "missing" sound syllables). **B**) Sound and vibration components of a female response to a male singing from a separate substrate (i.e., male signals detectable on the sound trace). A transient bimodal stridulatory response (arrows) is prolonged with a lower-frequency vibration induced in the body, unique to females (sections indicated by an arrowhead and dashed line). This immediate response to the male trigger syllable may be followed by a secondary vibratory peak from a silent wing movement (empty arrow; see also Suppl. Video 1). Note that vibration components above 1 kHz (seen on spectrogram) are largely an artifact of sound-induced plant vibrations resulting from frequency conversion by the ultrasound detector

Long-Range Signalling

Communication starts with the male emitting a long-distance calling song, which induces a female acoustic reply – a short click in response to the trigger syllable of the male song (Figs. 1, 4). In males, each stridulatory wing movement generates a corresponding low-frequency vibration wave in a simple one-to-one relationship (Fig. 3A). In contrast, the female's reply is accompanied by more complex body vibrations, highly prolonged over the acoustic component (Fig. 3B). Frame-to-frame video analysis, along with the independent combination of these vibrations with higher-amplitude tremulation signals (Fig. 4) suggest that, apart from the initial wave, these are passive after-vibrations of the female body induced by stridulation (Fig. 3B). These signals are often biphasic, with the second peak associated with a soundless

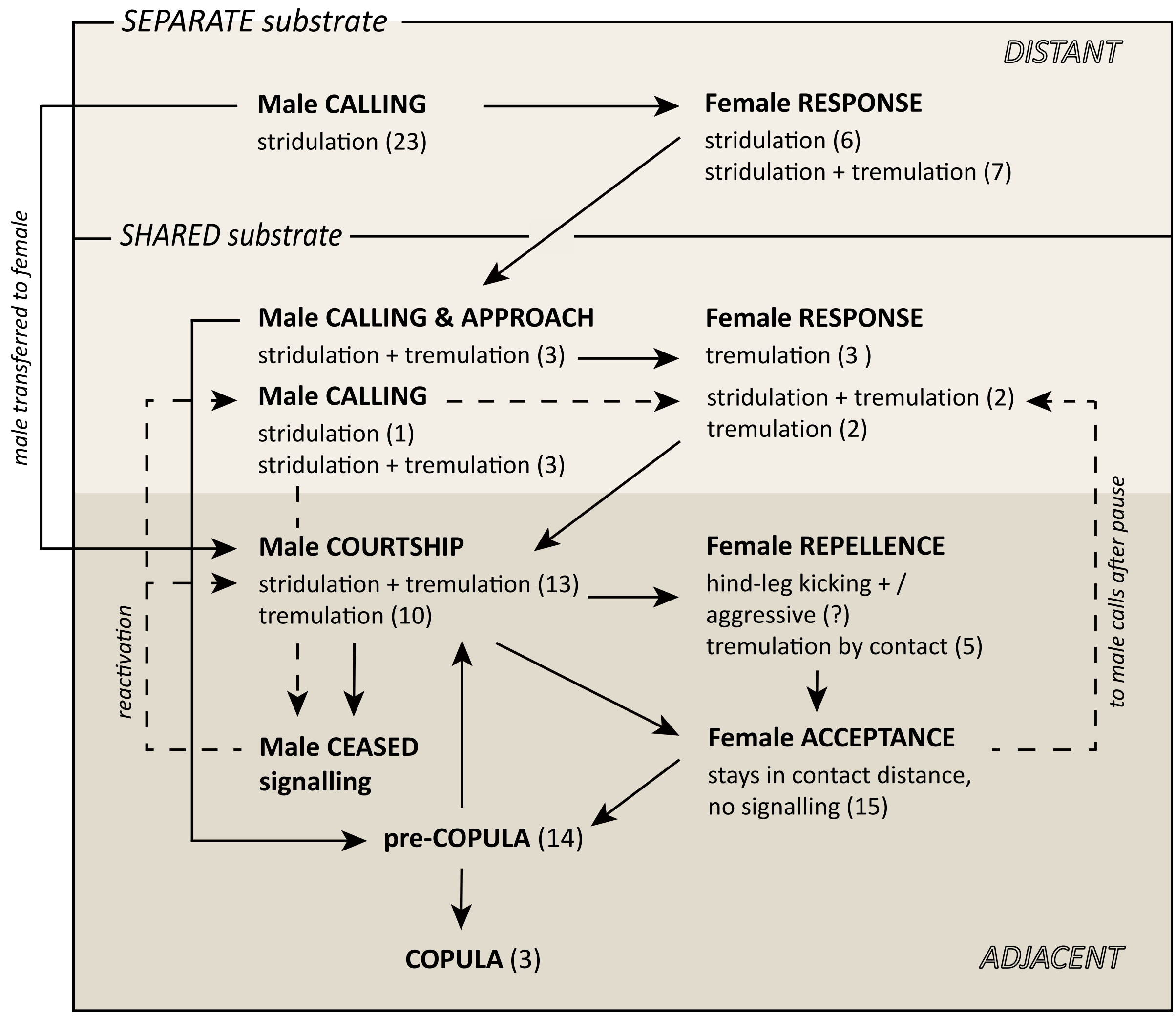

Fig. 4 Ethogram of pre-mating behaviour of *A. nigrovittata*. The data are based on 23 experiments. Each trial began with males calling on a separate substrate from the female in focus. In three experiments, the male located the responding female on the plant unaided; in the remaining 20, the male was transferred to the female's vicinity (on the shared plant substrate). Subsequently, males emitted signals within contact range of the female. Note that the frequency of different behavioural contexts does not necessarily reflect their actual probability of occurrence, as the mating sequence may have been terminated at various stages following the initiation of close-range courtship. However, within each specific context, the signal records do represent the probability of specific signal types being emitted, which was the primary focus of the study. The recordings included 19 male and 14 female individuals

wing movement immediately following the acoustic click (Fig. 3B; Suppl. Video 1).

In females regularly responding to the male song, series of such vibroacoustic responses combine in various ways, simultaneously or in succession, with intermittent groups of tremulation pulses that are no longer synchronized with the male song (Fig. 5A). Simultaneous stridulation and tremulation reveal no strict temporal relation between the two components, indicating independence of the two signalling mechanisms (Fig. 5B). While such complex female signals are typical for the initial calling phase of pair-formation, they can also be transiently expressed following periods of quiescence (resting or feeding) and partner separation, after the male has already located and courted the female on the same plant (Fig. 4).

Short-range Signalling

Male Signalling Attributes

Duetting males perform phonotaxis towards the responding female. To focus on the interaction on the same plant, we transferred a duetting male from the vial to the base of the plant. One male directly jumped from the opened vial to the plant. On the plant, the male seems to search for the source of the vibroacoustic signals (Figs. 4, 6). Already during the search, the males start emitting tremulation signals as single pulses and (more often) as pulse trains, characteristically combined with the song. They continue such signalling once they have located the potential mate (Figs. 4, 6A, 7A; Suppl. Video 2). In all situations and contexts, male tremulation pulses are accompanied by a tick with similar sonic carrier frequency as the song and a consistent latency around 30 ms following pulse onset, an association not characteristic for female tremulation. Similarly as in females, male tremulation pulses and stridulation can either occur simultaneously or in succession. If the male tremulated while producing a calling song, the ticks accompanying tremulation occur exactly at the time of the trigger syllables (Fig. 7B).

The signalling modes of males and females across different communication contexts are summarised in Table 1. This overview provides a framework for interpreting the sequential interactions illustrated in the ethogram (Fig. 4).

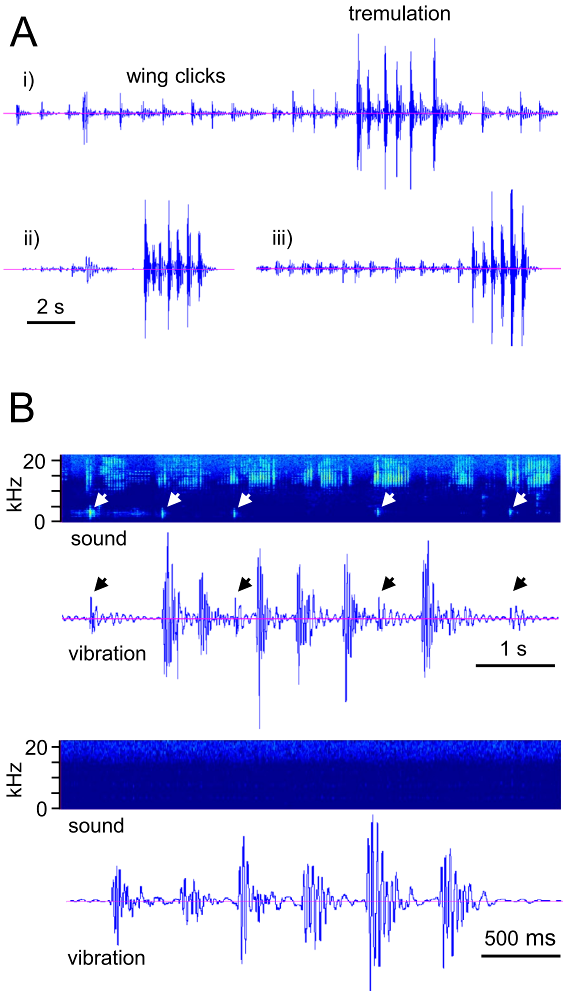

Fig. 5 Female vibroacoustic response to male song. **A**) Sample vibration traces demonstrating production of tremulation pulse trains in relation to series of wing clicks, which represent synchronised responses to the male song (seen as lower amplitude vibration signals). Tremulation can occur during acoustic responses (i), separately from these (ii; despite continuous male singing), or can directly terminate a series of stridulatory responses to male song (iii). **B**) Two sections of female tremulation emitted with (above) and without accompanying stridulation (below). In the upper example, arrowheads indicate female stridulatory signals in both channels (note that female sound is shifted to the sonic range by the ultrasound detector)

Interaction Dynamics on the Shared Plant

In our setup, the male reached the female within 15 to 30 cm from where it entered the plant in all three recorded cases in 30 to 75 s. On branching points or when the female does not respond to several consecutive songs, the male often makes

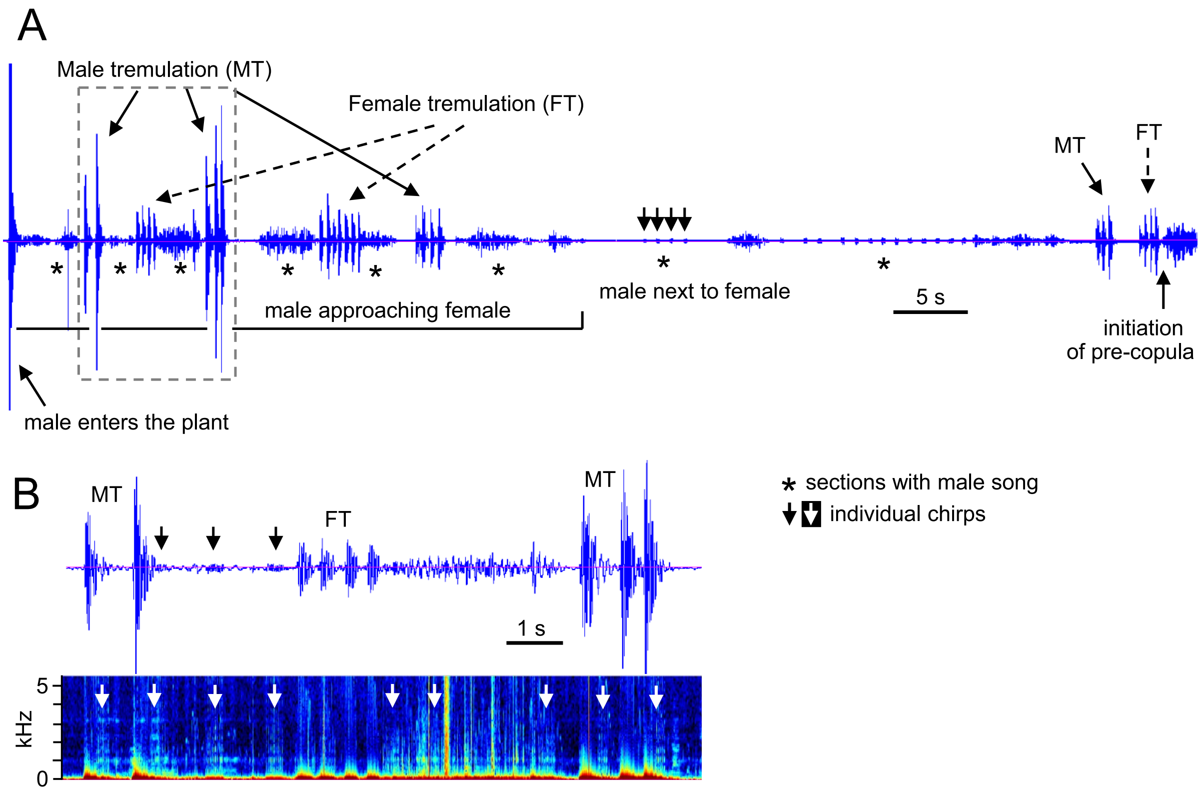

Fig. 6 Male–female vibroacoustic duet on a plant. **A**) Sample vibration trace from the moment of male's approach to the plant following female acoustic response, until contact between the partners occurs. Asterisks mark sections containing male song, and black or white arrows point to a few individual chirps (only visible since no other movements occur). **B**) Expanded view of the section marked by a dashed frame in (**A**), with the corresponding vibration spectrogram in the lower trace. Note the occurrence of female tremulation either during 'silent gaps' or transiently inhibiting male approach and singing

tilting movements of the body typical for 3-D sound localisation (Rheinlaender et al. 2007) with the forelegs contacting both paths on branching points, which also provides information about the source of vibration elicited by female tremulation. In all three cases, the male located the female after three or fewer tremulation responses. In this phase, male and female exchange tremulations in a loose duet, during which male tremulation and the female tremulation in response are often interspersed by calling songs and movement of the male (Fig. 6). Moreover, the females do not respond acoustically to the male signals as regularly as before. Once the male locates the female (or after being introduced to her vicinity), female vibroacoustic signalling typically ceases while the male continues with tremulation as the primary signal in the contact range, which can be combined with singing (Figs. 4, 7). However, female tremulatory or combined acoustic-tremulatory response to male signals can occur transiently following longer periods of quiescence, after the partners have already come into contact and separated again (Fig. 4). Female tremulation is never triggered by male tremulation alone; it always follows male signalling including the song. Often, tremulation signals coincide with a transient inhibition of the partner's activity (for example walking) or occur immediately after its cessation (Figs. 6, 7A; see Table 2 for sample sizes across contexts). In addition, irregular high-amplitude body tremulation of the female, not producing a pulsed signal, was occasionally observed after contact—alone or together with kicking of the male—apparently serving a repellent function (Fig. 4).

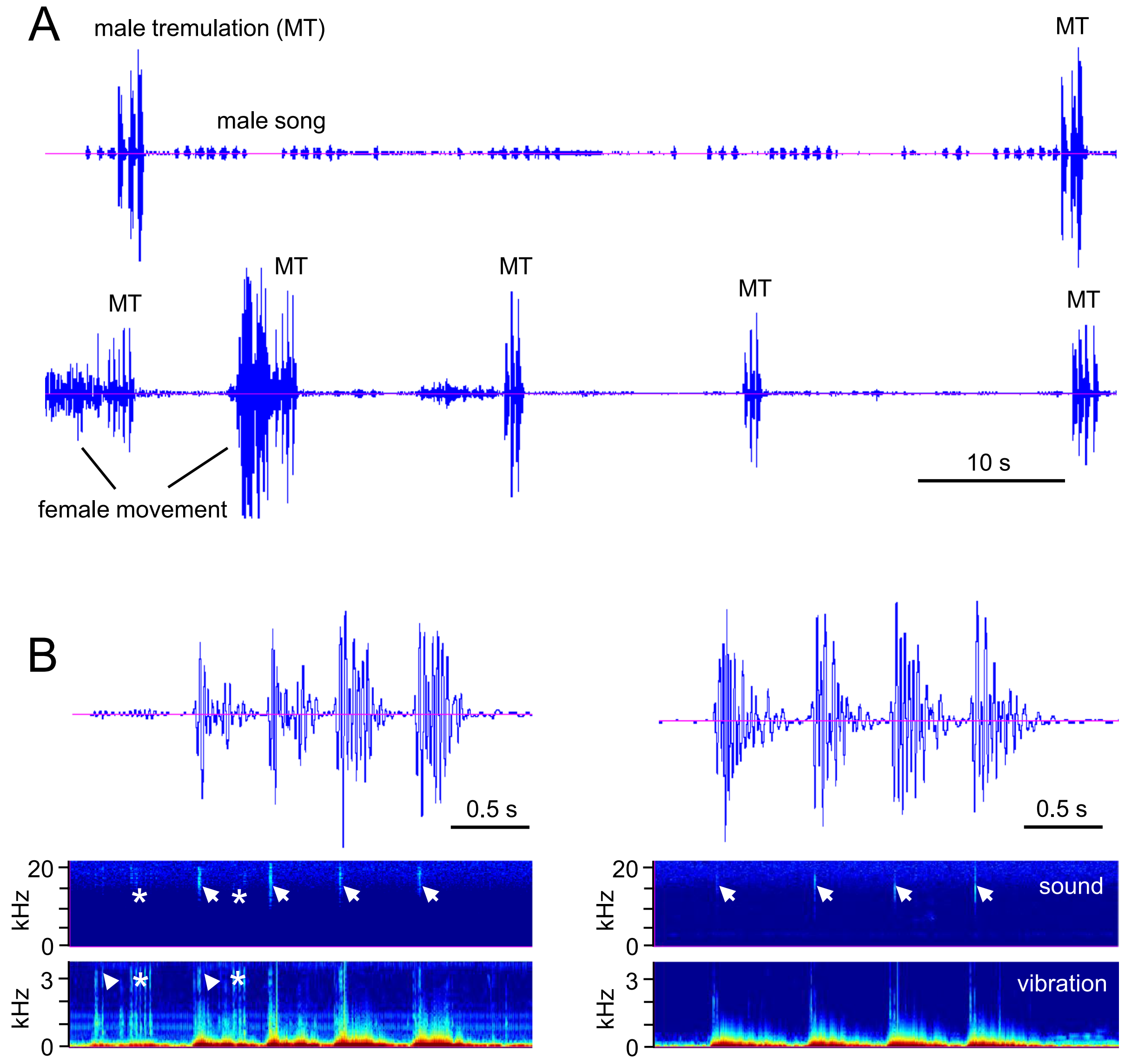

Fig. 7 Male close-range vibroacoustic courtship. **A**) Vibration recordings demonstrating tremulation in the presence (above) and absence of song (below). In case of female movement, male tremulation is often seen immediately following cessation of female activity. **B**). Close up of male tremulation pulse trains, in the presence and absence of song, revealing the occurrence of a short acoustic tick at each tremulation pulse onset (white arrows in the sound spectrogram). With simultaneous stridulation and tremulation, the tick at the pulse onset is much louder than the chirp and appears to replace the trigger syllable in the song (arrowheads in the vibration spectrogram – lower trace). The chirps of the song are marked by asterisks in the spectrograms

Timing of Copulatory Contacts

Male close-range courtship typically occurs in bouts of varying duration, interrupted with periods of resting or feeding. During this stage, the pair repeatedly establishes copulatory contacts without actual spermatophore transfer (called pre-copula; Fig. 4). Males are generally more active in this respect, though females occasionally approach and mount the male for genital coupling as well. During uninterrupted courtship, the first pre-copula occurs in the first few minutes (median 131 s, IQR 40–221 s;

Table 1 Acoustic and vibrational signalling of males and females of *A. nigrovittata* during different communication phases (dominant, most frequent modes listed first)

Communication context	Male signalling	Female signalling
Long-range (separate substrate)	Stridulation	Stridulation, Tremulation
Long range (shared substrate)	Stridulation, Tremulation*	Tremulation, Stridulation
Close-range (contact distance)	Tremulation*, Stridulation	–

*Each male tremulation pulse is obligatorily accompanied by a single stridulatory tick at its onset, which is not listed separately in the table. Male stridulation refers exclusively to the male calling or courtship song

Table 2 Number of experiments and individuals of *A. nigrovittata* showing specific vibroacoustic behaviours in different interaction contexts. Included are counts reflecting defined thresholds for the analysis of behaviour and signals (detailed in footnotes)

Context	Number of experiments / individuals
Male calling	23 /19
Male courtship – at least shortly (few tremulations)	23 /19
Male courtship – at least 10 minutes (8 tremulation trains)*	15 / 14
Male courtship – at least 25 tremulation trains**	10 / 10
Female response – separate substrate	14 / 7
Female response – during male approach	3 / 3
Female response – after courtship reactivation	4 / 3
Female response – at least 3 tremulation trains†	6 / 6

*Considered the minimum period to assign and evaluate female behaviour under "acceptance" (see Fig. 4). **†Used for formal signal analysis

N = 12), and subsequent pre-copulas at around 10 min (median 738 s, IQR 653–11,346 s; N = 5), 25 min (median 1446 s, IQR 1308–1815s, N = 3), and 35 min (1666 and 2474 s; N = 2) following the initial contact between partners. In line with the decreasing frequency of these interactions, only three out of ten males successfully copulated with receptive females within the 30–45-min period of observation. In the two pairs recorded overnight for 8 and 13 h following courtship initiation, spermatophore transfer did not occur.

Tremulation Signal Characteristics

Temporal Parameters

Pulse trains: Males exhibit a median of 3 (IQR 2–4) pulses per train and females exhibit a median of 4 (IQR 3–6) pulses per train (see also Table 3 for an overview of signal parameters). This parameter shows no significant variability between individuals within either sex (Kruskal–Wallis tests; males: H = 3.8010, p = 0.578; females: H = 3.8010, p = 0.578), while the sex difference is significant (Mann–Whitney U = 14,212, $p < 0.001$; Mixed Linear Model: Coef = −1.469, $p < 0.001$; Fig. 8). The median pulse train period is 20.9 (IQR 13.4–42.7) seconds for males and 26.2 (IQR 10.7–55.2) seconds for females. Despite a significant interindividual variability within each sex (Kruskal–Wallis tests; males: H = 63.4556, $p < 0.001$; females: H = 9.6389, p = 0.047), and no significant sex difference shown by the Mann–Whitney U test (U = 9138, p = 0.605), the Mixed Linear Model indicates significantly shorter pulse train periods in males than females (Coef = −33.766, p = 0.045; Fig. 8).

Pulses: Male tremulations have a median pulse duration of 0.344 (IQR 0.284–0.389) seconds, a pulse rate of 2.51 (IQR 2.12–2.95) Hz, and a pulse duty cycle of 0.85 (IQR 0.74–0.94). These values are slightly lower in females, which have a median pulse duration of 0.332 s, a pulse rate of 2.41 Hz, and a pulse duty cycle of 0.81 (Fig. 8). According to the Mann–Whitney U test, there is no significant

Table 3 Overview of vibrational signal parameters and sample sizes for males and females

Signal	Parameter	MALE Median (IQR)	n (n_{min}-n_{max}) / N	FEMALE Median (IQR)	n (n_{min}-n_{max}) / N
TREMULATION					
pulse	duration (s)	0.344 (0.284 – 0.389)	400 (40) /10	0.332 (0.282– 0.395)	191(15 – 40) / 6
	rate (Hz)	2.51 (2.12 – 2.95)	400 (40) /10	2.41 (2.03 – 2.76)	165 (12 – 40) /6
	duty cycle	0.85 (0.74 – 0.94)	400 (40) /10	0.81 (0.68 – 0.93)	165 (12 – 40) / 6
	dominant frequency (Hz)	38 (27 – 43)	400 (40) /10	32 (26 – 38)	160 (24 – 40) /5
	peak amplitude (mm/s) same leaf	5.52 (4.67 – 6.81)	125 (10 – 40) / 4	4.01 (3.06 – 4.67)	31 (31) / 1
	peak amplitude (mm/s) next leaf	3.55 (2.18 – 5.42)	160 (40) / 4	2.19 (1.15 – 3.07)	89 (24 – 40) / 3
	peak amplitude (mm/s) petiolus	0.58 (0.37 – 0.96)	160 (40) / 4	0.32 (0.22 – 0.38)	47 (7 – 40) / 2
train	period (s)	20.9 (13.4 – 42.7)	284 (24 – 30) /10	26.2 (10.7 – 55.2)	65 (2 – 30) /6
	number of pulses per train	3 (2 – 4)	284 (25–30) /10	4 (3 – 6)	72 (3 – 30) /6
STRIDULATION	dominant frequency (Hz)	32 (27 – 38)	120 (15) / 8	16 (11 – 21)	105 (15) / 7
	peak amplitude (mm/s) same leaf	0.48 (0.22 – 0.69)	45 (15) / 3	0.54 (0.42 – 0.70)	60 (15) / 4
	peak amplitude (mm/s) next leaf	0.18 (0.15 – 0.31)	15 / 1	/	
	peak amplitude (mm/s) petiolus	0.09 (0.08 – 0.15)	60 (15) / 4	0.11 (0.08 – 0.18)	30 (15) / 2

n total number of analysed signals (range per individual in parentheses, min-max); *N* number of individuals

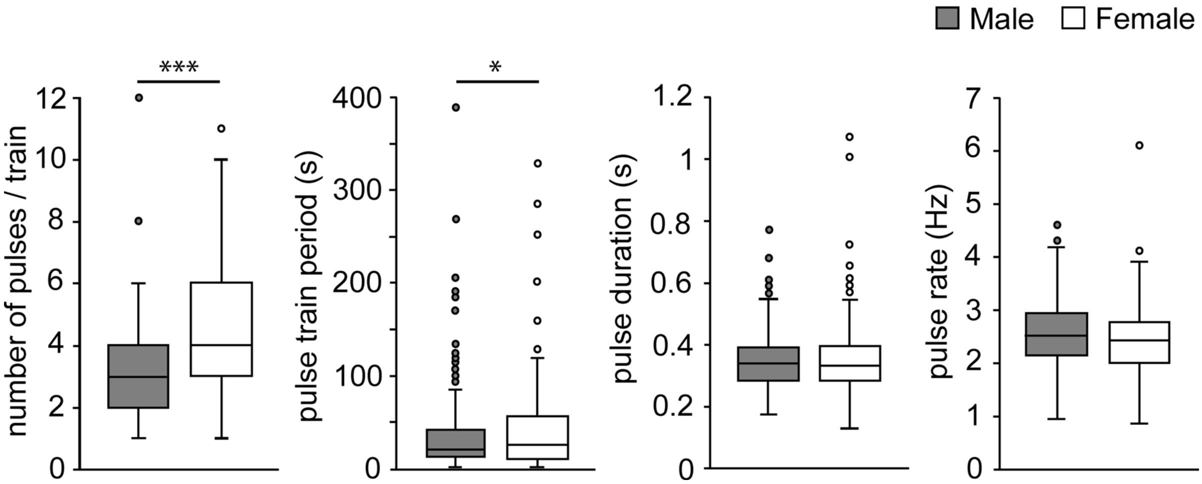

Fig. 8 Temporal parameters of male and female tremulation signals. Asterisks indicate the degree of significant differences in the Mixed Linear Model (* $p < 0.05$, *** $p < 0.001$)

difference between the sexes for pulse duration (U = 38,321, p = 0.950) and a low level of significance for pulse rate (U = 29,287.5, p = 0.035) and duty cycle (U = 29,405, p = 0.042). These differences, however, are not confirmed by the Mixed Linear Model (pulse duration: Coef = −0.021,

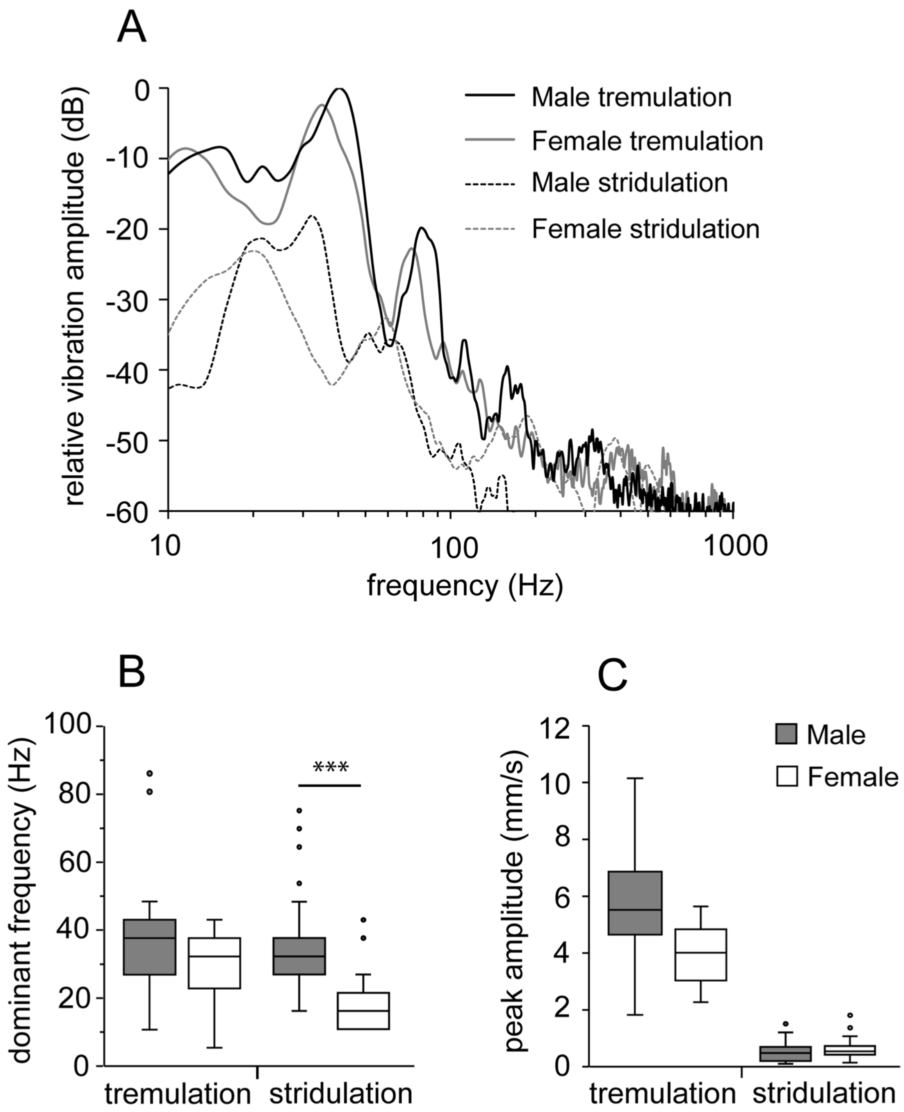

Fig. 9 Spectral and intensity characteristics of stridulatory vibration and tremulation signals produced by males and females. **A**) Representative signal spectra (normalized with $\mathrm{dB} = 20 \times \log_{10}$ [amplitude/maximum amplitude]). Distribution of dominant frequencies (**B**) and peak amplitudes (**C**) of vibrational signals recorded from the leaflet supporting the emitter. Asterisks indicate the degree of significant differences in the Mixed Linear Model (*** $p < 0.001$)

p = 0.490, pulse rate: Coef = 0.139, p = 0.459, pulse duty cycle: Coef = 0.019, p = 0.533), which suggests individual differences in these parameters to be a more significant source of variability than sex-based differences. In the Kruskal–Wallis tests, interindividual variability is highly significant for pulse duration (males: H = 133.4750, $p < 0.001$; females: H = 77.8108, $p < 0.001$), pulse rate (males: H = 144.2260; $p < 0.001$: females: H = 26.1701, $p < 0.001$) and pulse duty cycle (males: H = 64.7507, $p < 0.001$; females: H = 27.7189, $p < 0.001$).

Spectral and Amplitude Parameters

Median peak frequency for tremulation pulses is 38 (IQR 27–42) Hz for males, and 32 (IQR 26–38) Hz for females (Fig. 9A, B). The difference between sexes is highly significant in Mann–Whitney U test (U = 21,589.5, $p < 0.001$), while in the Mixed Linear Model, the fixed effect of sex is only marginally significant (Coef = 4.736, p = 0.064). In the Kruskal–Wallis test, peak frequency varies highly significantly between individuals of either sex (females – H = 23.0576, $p < 0.001$; males:

H = 117.4638, $p < 0.001$), as confirmed by a high random effect variance in the model (19.599). Amplitude varies with the distance to the point of measurement, with higher values measured closer to the signaller. When measured on the leaflet supporting the signaller, the signals' median peak velocity was 5.52 (IQR 4.67–6.81) mm/s for males and 4.01 (IQR 3.06–4.67) mm/s for females (Fig. 9C). When measured on the leaflet adjacent to the signaller, it was 3.55 (IQR 2.18–5.42) mm/s for males and 2.19 (IQR 1.15–3.07) mm/s for females. When emitted on the leaflets and measured on the petiole of the compound leaf, it was 0.58 (IQR 0.37–0.96) mm/s for males and 0.32 (IQR 0.22–0.38) mm/s for females. This corresponds to around 4–5 dB amplitude decrease from the leaflet carrying the signaller to other leaflets and to 20–22 dB decrease to the base of the petiole of the compound leaf. Overall, the amplitude is consistently higher in males than in females, but no statistical comparison has been made, because such a comparison would require more standardised settings with greater control over the signaller's location.

Vibratory Song Component

In males, the median dominant frequency of the vibratory song component is 32 (27–38) Hz (Fig. 9A, B), directly reflecting the rate of large-scale wing movements during stridulation (which may be silent in the syllable/chirp onset; Fig. 3). These signals are spectrally similar to those induced by tremulation but have a broader spectral peak (Fig. 9A). Their amplitude is about 20 dB lower than in tremulation (Fig. 9C), with the median peak velocity of 0.48 (IQR 0.22–0.69) mm/s on the leaflet supporting the signaller, 0.18 (IQR 0.15–0.31) mm/s on the neighbouring leaflet, and 0.09 (0.08–0.15) mm/s at the base of the compound leaf petiole. In females, the dominant frequency of stridulatory vibrations is about half of that in males and this difference is highly significant (Mann–Whitney U = 1119, $p < 0.001$; Mixed Linear Model Coef = 15.073, $p < 0.001$; Fig. 9B). The dominant frequency of stridulatory vibration is significantly different also between the individuals within sexes, especially in males (Kruskal Wallis H = 81.8756, $p < 0.001$ for males; H = 18.7238, p = 0.005 for females; Mixed Linear Model Group Var = 20.197). In females, the vibratory amplitude is similar to that in males (Fig. 9C), with a median of 0.535 (IQR 0.422–0.697) mm/s on the supporting leaflet and of 0.107 (IQR 0.08–0.177) mm/s on the compound leaf petiole.

Discussion

Acoustic communication in bushcrickets has been extensively studied across many species, including *A. nigrovittata*. For this and other species of Phaneropterinae, there has been no prior evidence of vibration signals emitted through mechanisms other than stridulation. The present study uncovers novel aspects of communication in *A. nigrovittata*, with a particular focus on the vibrational signal component. In addition to their well-known acoustic signals (e.g. Heller and von Helversen 1986; Dobler et al. 1994a, b), we found that both sexes also employ tremulation signals, which has previously gone unnoticed. These signals are produced during key stages of mating behaviour such as long-range calling and close-range courtship, and complement acoustic signals while being produced independently.

Several bushcricket species are known to emit both acoustic and tremulation signals during advertisement, including Neotropical examples with reduced auditory signalling (Belwood and Morris 1987; Römer et al. 2010; ter Hofstede et al. 2017), as well as others that add tremulation to a typical acoustic repertoire (Korsunovskaya and Zhantiev 2022). We recorded similar long-range advertisement signals in duetting *A. nigrovittata*, here emitted by stationary females, primarily in the absence of male cues on the same plant. We found that their tremulation and stridulation are produced with independent rhythms but may also occur simultaneously. In bushcrickets, only *Nesonotus reticulatus* (Pseudophyllinae) has been found to exhibit such a signalling pattern, with the two mechanisms showing no strict temporal coupling (Stumpner et al. 2013).

Female tremulation signals emitted together with the acoustic response to the male song may enhance the male's ability to localise the female on a shared substrate. A similar effect has been previously demonstrated for the vibratory component of the song (Latimer and Schatral 1983). In this context, tremulation may facilitate vibrotaxis by increasing the effective vibratory signalling range beyond that of stridulation. In our study, tremulation signal amplitude exceeded that of stridulatory vibrations by about 20 dB. With the peak velocity around 4 to 5 mm/s next to the signaller, these signals exceed the threshold of the most sensitive low-frequency tuned (< 100 Hz) receptor neurons recorded in bushcrickets by about 25 dB (Kalmring et al. 1978; at 50 Hz, their peak acceleration threshold is at ca. 8 cm/s^2, corresponding to 0.3 mm/s velocity). Tremulation signals are thus more likely to be transmitted across the entire host plant (e.g. Römer et al. 2010), between plants connected through soil and roots (Čokl et al. 2021), and even across air gaps between them. Vibratory signals propagating through a vibration-sound-vibration conversion across air gaps as large as up to 10 cm between appositioned leaves have been demonstrated even for much weaker planthopper vibrational signals (Eriksson et al. 2012; Gordon et al. 2019). This may help to explain why tremulation in *A. nigrovittata* is also characteristic for female responses to males signalling from a separate substrate. Once a responding female detects an approaching male on the same plant, the acoustic response to the male call is reduced, suggesting taxis guided by tremulation signals may be more efficient in the close range than song alone. The use of only one signal may also help conserve energy during localisation interactions. A similar pattern is observed in other bushcrickets such as *Copiphora rhinoceros*, where a calling male reduces his song while continuing tremulation after the female reaches his perch (Morris 1980). In this reversed call-search role scenario, such behaviour is thought to minimize signal exploitation by rivals.

As we did not record substrate vibrations from remotely calling males, we cannot rule out that they also produce tremulation signals in this context, as observed in females. However, these males did not emit acoustic ticks, which we found to be associated with tremulation in close range. Male tremulation thus appears to be elicited only upon detecting female vibration signals on the plant and may stimulate responses until localisation is successful. In addition, male tremulation is expressed as the primary close-range signal, often in the absence of song (and largely also in the absence of intense antennation) following partner contact. It thus appears to be a key component of extended courtship, which in our experiments mostly did not result in spermatophore transfer within about an hour – the typical observation time – nor in cases recorded overnight. The lengthy signalling periods, interspersed with regular abdominal contact (likely for sperm removal; von Helversen and von Helversen 1991), reflect the males' reluctance to mate without increasing their chance of paternity. Thus, the ultimate role of male tremulation in close range may be to keep the female involved, delay her withdrawal, or even synchronise the partners' behaviours to initiate copulation. In this context, tremulation signals may also advertise male quality, as seen in the bushcricket *Conocephalus nigropleurum*, where the rate of male close-range tremulation signals reflects the emitter's mass – indicative of a larger nuptial gift to the female (de Luca and Morris 1998). Similarly, in agonistic interactions of *Gnathoclita sodalis*, the number of tremulations and male size predict the contest outcome, while song parameters do not (de Souza et al. 2011). In *A. nigrovittata*, such information may be encoded in the temporal parameters showing significant interindividual variability, i.e. pulse train period, pulse duration, rate and duty cycle. However, experimental evidence does not yet exist.

Generally, carrier frequency of tremulation signals can indicate energetic effort of the signaller, as it may directly reflect the rate of muscle contractions generating body movements (Čokl et al. 2006). In our study, the signals' dominant (also fundamental) frequency largely varied between individuals (from 27 to 46 Hz), with no clear relation to either recording or the signaller location. However, more systematic recording of stridulatory vibrations from different points of the plant revealed some location-related effect. Since the dominant frequency of tremulation signals is substrate dependent as well (e.g., de Luca and Morris 1998; de Souza et al. 2011; Stritih and Čokl 2012), its information potential is low for *A. nigrovittata,* which inhabits a variety of host plants.

During duetting, the exchange of the complex vibroacoustic signals between partners may facilitate species and sex recognition. The temporal parameters of male and female tremulation signals are similar; however, the carrier frequency and pulse number differ significantly, albeit with a wide range of overlap. Additionally, the sound ticks coupled with male tremulation pulses may enhance sex differentiation; potentially relevant in situations where multiple individuals share the same communication space. At least in the centre of populations, several males and females often share the same branch (Cillov and Stumpner, personal observation).

Conclusions

Our findings suggest that vibratory signalling is an important and previously unnoticed element in *A. nigrovittata* communication, playing a role in both mate finding and courtship. In bushcrickets and other Orthoptera, tremulation signals are often considered evolutionarily derived relative to the songs (e.g., ter Hofstede et al. 2015, 2017). However, in insects, and specifically in Ensifera, vibrational signalling likely predated acoustic communication (Stumpner and von Helversen 2001; Stritih and Čokl 2012; Stritih-Peljhan and Virant-Doberlet 2021). Thus, vibrational signalling may also represent a remnant behavioural character in bushcrickets and be more prevalent than generally assumed. Our results prompt a re-evaluation of bushcricket communication – at least in close range – challenging the general perception that sound is the only non-contact mechanical signal in their sexual behaviour.

Acknowledgements We thank the reviewers for their detailed, constructive, and insightful comments, which helped us prepare a clearer and more accessible version of the manuscript.

Author Contribution All authors (NSP, AC and AS) contributed to the conception and design of the study. NSP collected and analyzed the data and prepared the figures. AS and NSP drafted the initial manuscript. All authors (NSP, AC and AS) contributed to revising the manuscript and approved the final version for submission.

Funding NSP received financial support from the Slovenian Research and Innovation Agency (Research Core Funding P1–0255).

Data availability All data generated and analysed during this study have been uploaded to Zenodo with the DOI: 10.5281/zenodo.14603608 (Zenodo.org).

Declarations

Competing interests The authors declare no competing interests.

Glossary

The glossary is partly following Hill and Wessel (2016). Since terminology is consistent neither in the bioacoustic nor in the biotremology (vibrational) literature, we explain our own usage of terms rather than attempting to create generalised definitions.

- **sound:** mechanical energy transmitted over the air (airborne) with particle movement in the same direction as the energy propagation
- **vibration:** mechanical energy transmitted over the surface of a solid substrate (substrate-borne) with particle movement perpendicular to the direction of energy propagation
- **acoustic signal:** information transmitted primarily via airborne waves, where any associated vibrational component is induced by the acoustic signal generation
- **vibrational signal:** information transmitted primarily via substrate-borne waves
- **stridulation:** friction between two specialised body parts (in bushcrickets, the forewings), which generates acoustic and vibrational signals; in hearing insects like orthopterans or cicadas, the acoustic component represents the primary communication signal
- **tremulation:** movement of the body without impacting the substrate, which generates vibrational signals without an acoustic component
- **song:** series of acoustic signals with a species-specific temporal and spectral pattern used in reproductive contexts

    calling song: song emitted in the absence of a nearby conspecific used for long-distance localisation, either triggering a reply or phonotaxis in conspecifics
    courtship song: song emitted in the presence of a nearby female used to initiate mating

- **syllable:** short acoustic signal produced during one full cycle of wing movement

    trigger syllable: single syllable emitted following a longer pause after the chirp in the calling song of *A. nigrovittata* and typically triggering female reply
    tick: very short syllable emitted by males at the onset of each tremulation pulse, with the same frequency spectrum as the calling song
    click: very short syllable emitted by females in reply to male song, often with broad spectral content

- **chirp:** longer acoustic signal consisting of a rapid series of syllables
- **pulse:** a short burst of vibration, consisting of only a few oscillatory cycles, and functioning as the smallest temporal unit of a signal
- **pulse train:** a sequence of vibration pulses delivered one after another with regular spacing, forming a distinct temporal group within a signal

References

Alcock J (2009) Animal behavior: an evolutionary approach. Sinauer Associates, Sunderland, MA

Belwood JJ, Morris GK (1987) Bat predation and its influence on calling behavior in neotropical katydids. Science 238:64–67. https://doi.org/10.1126/science.238.4823.64

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication. Sinauer Associates, Sunderland, MA

Busnel RG, Pasquinelly F, Dumortier B (2019). Body tremulations and their transmission as vibrations for short distance information transfer between *Ephippiger* male and female. In: Hill PSM, Lakes-Harlan R, Mazzoni V, Narins PM, Virant-Doberlet M, Wessel A (eds). *Biotremology: Studying vibrational behavior*. Springer Nature, pp 123–130

Cillov A (2024). Auditory descending neurons in the prothoracic network of the bush cricket *Ancistrura nigrovittata*. Georg-August-Universität Göttingen, doctoral thesis. https://doi.org/10.53846/goediss-10555

Čokl A, Virant-Doberlet M, Zorović M (2006) Sense organs involved in the vibratory communication of bugs. In: Drosopolous S, Claridge MF (eds) Insect sounds and communication: Physiology, behavior, ecology, and evolution. CRC Taylor & Francis, Boca Raton, pp 567–585

Čokl A, Žunič-Kosi A, Moraes MCB, Borges M, Laumann RA (2021) Stink bug inter-plant communication with signals produced by vibration of lifted wings. J Insect Behav 34:194–210. https://doi.org/10.1007/s10905-021-09780-2

de Luca PA, Morris GK (1998) Courtship communication in meadow katydids: female preference for large male vibrations. Behaviour 135:777–794. https://doi.org/10.1163/156853998792640422

de Souza LR, Kasumovic MM, Judge KA, Morris GK (2011) Communicating male size by tremulatory vibration in a Columbian rainforest katydid, *Gnathoclita sodalis* (Orthoptera, Tettigoniidae). Behaviour 1:341–357. https://doi.org/10.1163/000579511X559418

Dobler S, Stumpner A, Heller KG (1994a) Sex-specific spectral tuning for the partner's song in the duetting bushcricket *Ancistrura nigrovittata* (Orthoptera: Phaneropteridae). J Comp Physiol A 175:303–310. https://doi.org/10.1007/BF00192989

Dobler S, Heller KG, von Helversen O (1994b) Song pattern recognition and an auditory time window in the female bushcricket *Ancistrura nigrovittata* (Orthoptera: Phaneropteridae). J Comp Physiol A 175:67–74. https://doi.org/10.1007/BF00217437

Eriksson A, Anfora G, Lucchi A, Lanzo F, Virant-Doberlet M, Mazzoni V (2012) Exploitation of insect vibrational signals reveals a new method of pest management. PLoS ONE 7:e32954. https://doi.org/10.1371/journal.pone.0032954

Gordon SD, Tiller B, Windmill JFC, Krugner R, Narins PM (2019) Transmission of the frequency components of the vibrational signal of the glassy winged sharpshooter, *Homalodisca vitripennis*, within and between grapevines. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 205:783–791. https://doi.org/10.1007/s00359-019-01366-w

Gwynne DT (2001) Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae. Cornell University Press, USA

Hebets EA, McGinley RH (2019) Multimodal signaling. In: Choe JC (ed) Encyclopedia of animal behavior. Elsevier, pp 487–499

Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57:197–214. https://doi.org/10.1007/s00265-004-0865-7

Heller KG (1988) Bioakustik der europäischen Laubheuschrecken. Verlag Josef Margraf, Germany

Heller KG, von Helversen D (1986) Acoustic communication in phaneropterid bushcrickets: species-specific delay of female stridulatory response and matching male sensory time window. Behav Ecol Sociobiol 18:189–198. https://doi.org/10.1007/BF00290822

Heller KG, Hemp C, Ingrisch S, Liu C (2015) Acoustic communication in Phaneropterinae (Tettigonioidea) - a global review with some new data. JOR 24:7–18. https://doi.org/10.1665/034.024.0103

Hill PS, Shadley JR (2001) Talking back: sending soil vibration signals to lekking prairie mole cricket males. Integr Comp Biol 41:1200–1214. https://doi.org/10.1093/icb/41.5.1200

Hill PS, Wessel A (2016) Biotremology. Curr Biol 26:R187–R191. https://doi.org/10.1016/j.cub.2016.01.054

Kalmring K, Lewis B, Eichendorf A (1978) The physiological characteristics of the primary sensory neurons of the complex tibial organ of Decticus verrucivorus L. (Orthoptera, Tettigonioidae). J Comp Physiol 127:109–121. https://doi.org/10.1007/BF01352295

Keuper A, Otto, C., Latimer W, & Schatral A (1985). Airborne sound and vibration signals of bushcrickets and locusts: Their importance for the behaviour in the biotope. In: Kalmring K, N Elsner (eds). *Acoustic and vibrational communication in insects: proceedings from the XVII. International Congress of Entomology*. P. Parey, Berlin, pp 135–142

Korsunovskaya OS (2009) Acoustic signals in katydids (Orthoptera, Tettigonidae). Communication 2. Entomol Rev 89:16–20. https://doi.org/10.1134/S0013873809010035

Korsunovskaya OS, Zhantiev RD (2022) Acoustic and vibrational signaling in true katydid *Nesoecia nigrispina*: three means of sound production in one species. PeerJ 9:e13749. https://doi.org/10.7717/peerj.13749

Latimer W, Schatral A (1983) The acoustic behaviour of the bushcricket *Tettigonia cantans*. I. Behavioural responses to sound and vibration. Behav Process 8:113–124. https://doi.org/10.1016/0376-6357(83)90001-3

Montealegre-Z F (2012) Reverse stridulatory wing motion produces highly resonant calls in a neotropical katydid (Orthoptera: Tettigoniidae: Pseudophyllinae). J Insect Physiol 58(1):116–124

Morris GK (1980) Calling display and mating behaviour of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). Anim Behav 28:42–51. https://doi.org/10.1016/S0003-3472(80)80006-6

Morris GK, Mason AC, Wall P, Belwood JJ (1994) High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). J Zool 233:129–163. https://doi.org/10.1111/j.1469-7998.1994.tb05266.x

Rajaraman K, Godthi V, Pratap R, Balakrishnan R (2015) A novel acoustic-vibratory multimodal duet. J Exp Biol 218:3042–3050. https://doi.org/10.1242/jeb.122911

Rheinlaender J, Hartbauer M, Römer H (2007) Spatial orientation in the bushcricket *Leptophyes punctatissima* (Phaneropterinae; Orthoptera): I. Phonotaxis to elevated and depressed sound sources. J Comp Physiol A 193:313–320. https://doi.org/10.1007/s00359-006-0186-6

Römer H, Lewald J (1992) High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. Behav Ecol Sociobiol 29:437–444. https://doi.org/10.1007/BF00170174

Römer H, Lang A, Hartbauer M (2010) The signaller's dilemma: a cost–benefit analysis of public and private communication. PLoS ONE 5:e13325. https://doi.org/10.1371/journal.pone.0013325

Rössler W, Jatho M, Kalmring K (2006) The auditory-vibratory sensory system in bushcrickets. In: Drosopoulus S, Claridge MF (eds) Insect sounds and communication: Physiology, behaviour, ecology and evolution. CRC Taylor & Francis, Boca Raton, pp 35–69

Stölting H, Moore TE, Lakes-Harlan R (2002) Substrate vibrations during acoustic signalling in the cicada *Okanagana rimosa*. J Insect Sci 2:2. https://doi.org/10.1093/jis/2.1.2

Stritih N, Čokl A (2012) Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive communication of Ensifera. PLoS ONE 7:e47646. https://doi.org/10.1371/journal.pone.0047646

Stritih-Peljhan N, Virant-Doberlet M (2021) Vibrational signalling, an underappreciated mode in cricket communication. Sci Nat 108:41. https://doi.org/10.1007/s00114-021-01749-7

Stritih-Peljhan N, Žunič-Kosi A (2024) More than stridulation: signal interaction and constraint in the complex vibroacoustic courtship of a cricket. Behav Ecol Sociobiol 78:122. https://doi.org/10.1007/s00265-024-03530-y

Stumpner A, Nowotny M (2013) Neural processing in the bushcricket auditory pathway. In: Hedwig B (ed) Insect hearing and acoustic communication. Springer, pp 143–166

Stumpner A, von Helversen D (2001) Evolution and function of auditory systems in insects. Naturwissenschaften 88:159–170. https://doi.org/10.1007/s001140100223

Stumpner A, Dann A, Schink M, Gubert S, Hugel S (2013) True katydids (Pseudophyllinae) from Guadeloupe: acoustic signals and functional considerations of song production. J Insect Sci 13:157. https://doi.org/10.1673/031.013.15701

ter Hofstede HM, Schöneich S, Robillard T, Hedwig B (2015) Evolution of a communication system by sensory exploitation of startle behaviour. Curr Biol 25:3245–3252. https://doi.org/10.1016/j.cub.2015.10.064

ter Hofstede H, Voigt-Heucke S, Lang A, Römer H, Page R, Faure P, Dechmann D (2017) Revisiting adaptations of neotropical katydids (Orthoptera: Tettigoniidae) to gleaning bat predation. Neotrop Biodivers 3:41–49. https://doi.org/10.1080/23766808.2016.1272314

von Helversen D, von Helversen O (1991) Pre-mating sperm removal in the bushcricket *Metaplastes ornatus* Ramme 1931 (Orthoptera, Tettigonoidea, Phaneropteridae). Behav Ecol Sociobiol 28:391–396. https://doi.org/10.1007/BF00164120

von Helversen O, von Helversen D, Rohrseitz K, Koopmann I, Stumpner A, Heller KG (2015) Signals and sex-specific active space in a duetting insect (Orthoptera: Phaneropteridae: *Poecilimon affinis*). J Orthopt Res 24:19–28. https://doi.org/10.1665/034.024.0104

Weidemann S, Keuper A (1987) Influence of vibratory signals on the phonotaxis of the gryllid *Gryllus bimaculatus* DeGeer (Ensifera: Gryllidae). Oecologia 74:316–318. https://doi.org/10.1007/BF00379376