



More than stridulation: signal interaction and constraint in the complex vibroacoustic courtship of a cricket

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Abstract

Field crickets (Gryllidae) produce sounds by tegminal stridulation, well-studied for its role in female attraction and choice. However, understanding female preferences for their courtship song remains elusive, despite considering additional chemical, visual, and thermal signals. Beyond stridulation, crickets also display vibrational courtship behaviours that remain largely unexplored. Using *Acheta domesticus* as a model, we conduct the first comprehensive analysis of the entirety of vibroacoustic courtship signals in crickets, including their interaction. Employing audio recording, laser vibrometry, and videorecording, we unveil a complex signal involving simultaneous wing stridulation, body tremulation, and leg drumming against the substrate in a prolonged display, unique among insects. We identify robust correlations, coupling, and coordination between these signal components. We show the tightest coupling between the two types of stridulation pulses, and between tremulation and drumming signals, while drumming-stridulation coupling is less consistent, revealing a constraint on drumming performance. This constraint in the expression of one signal component, without a trade-off, represents a specific case within complex dynamic signalling. In addition, we find no correlation between drumming rate and its accuracy relative to stridulation, challenging common expectations. Our findings indicate that the information conveyed by the complex courtship display in *A. domesticus* is not simply proportional to that in the song, shedding light on previous ambiguities surrounding its function. Spectral-intensity analysis indicates the closest perceptual connection between stridulation and drumming signals, likely commonly influencing female choice, while proposing another function for tremulation. Further research should delve deeper into the function of this intricate signal.

Significance Statement

Our study delves into the domain of vibroacoustic signals in insects, specifically crickets, exploring the information conveyed by their complex dynamic displays. While traditional acoustic signals in crickets have received the most attention, our pioneering study of the entire set of vibroacoustic signals during the courtship of a field cricket (*Acheta domesticus*) unveils a complex signal involving coordinated wing stridulation, body tremulation, and leg drumming against the substrate. Notably, we reveal a performance constraint specific to one signal component, which represents a unique case in complex dynamic signalling. Also, we find no correlation between the display vigour and skill, challenging common expectations. This study not only enhances our understanding of cricket courtship but also contributes to our knowledge of complex signalling in animals.

Keywords Male quality · Substrate vibration · Sound · Complex signal · Dynamic signal · Insect

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Introduction

Animals often communicate using complex signals with multiple components in the same or across sensory modalities. These multicomponent and multimodal signals play a crucial role in enhancing communication by increasing the information content, improving the effectiveness of signal transmission, and influencing receiver response through the

interaction between signal components (Candolin 2003; Hebets and Papaj 2005; Hebets and McGinley 2019). A particular challenge lies in understanding these interactions, both in terms of signal production and receiver perception (Partan and Marler 1999; Hebets and Papaj 2005; Halfwerk et al. 2019). Courtship is a prominent context where such complex signals are observed, where their primary function is to advertise the signaller's quality and expedite mating decisions (Bastock 1967; Mitoyen et al. 2019).

In insects and other arthropods, courtship relies crucially on mechanical signals transmitted via the substrate (as vibrations) and air (as sound; Strauß et al. 2021, Virant-Doberlet et al. 2023). These signals are functionally closely related at both the production and sensory detection sides (Caldwell 2014), providing a unique perspective on complex signalling. This system allows for dynamic communication employing various body parts, from the head to abdomen and appendages (Ewing 1989; Virant-Doberlet et al. 2023). The signals may not even require a specialised structure for their production, such as in case of vibration (tremulation) of body parts and their drumming on the substrate, and the same body part may be engaged in different signalling mechanisms (Virant-Doberlet et al. 2023). For example, an abdomen may be vibrating, drumming, or scraping the substrate, thereby emitting mechanical energy as an unimodal signal only in one medium or as a bimodal signal into both the substrate and air (Strauß et al. 2021; Virant-Doberlet et al. 2023; see also Caldwell 2014). Different signalling structures and mechanisms can be applied simultaneously or sequentially in various combinations (Elias et al. 2003, 2006; Stritih-Peljhan and Virant-Doberlet 2021; Virant-Doberlet et al. 2023). This versatility, from the complex unimodal to bimodal emissions, provides rich grounds for exploring complex signalling, which has so far been predominantly studied in spiders (e.g., Elias et al. 2006; Gibson and Uetz 2008; Hebets 2008; Girard et al. 2011, 2015; Choi et al. 2022).

Crickets (Grylloidea), and particularly field crickets (Gryllidae), offer an alternative venue to study the function, evolution, and sensory basis of complex dynamic signals in-depth. They are widely used as models for studying sexual behaviour, although with a strong focus on their acoustic communication (Huber et al. 1989; Zuk and Simmons 1997; Robinson and Hall 2002; Hedwig 2014; Schöneich 2020). Males produce sound by rubbing (stridulation) their tegmina, which is the primary means of attracting female from a distance and the most conspicuous signal during the close-range courtship, as well. Yet, accumulating evidence suggests that this final stage of partner choice is multimodal, as the song alone fails to explain it (reviewed in Stritih-Peljhan and Virant-Doberlet 2021; Kuriwada 2023). The courtship song does not reliably signal male attributes (e.g.,

Wagner and Reiser 2000; Gray and Eckard 2001; Reşk 2012; Harrison et al. 2013), although this is presumably its main function (Fitzpatrick and Gray 2001; Gray 2005; Zuk et al. 2008). Studying additional signals, such as contact mechanosensory, chemical, and even thermal cues (Erreger et al. 2018) has not yet clarified female preferences (reviewed in Stritih-Peljhan and Virant-Doberlet 2021).

However, the exploration into cricket communication reveals a broad spectrum of vibrational behaviours that accompany the traditional acoustic signals during courtship. These behaviours include antennal, wing, whole body, and abdominal vibrations, as well as drumming by the palpi, legs and abdomen on the substrate, which are often displayed in concert with the song (Stritih-Peljhan and Virant-Doberlet 2021). Despite these behaviours being well documented across cricket families (Alexander and Otte 1967; Mays 1971; Bell 1980; Evans 1988; Dambach and Beck 1990; de Mello and dos Reis 1994; Preston-Mafham 2000; deCarvalho and Shaw 2010), the characteristics of the emitted signals and their function remain largely unexplored.

Our recent work highlights the role of these dynamic cricket signals as functional complements to their song, indicating their potential to increase courtship significance both through increased energetic demands and display coordination (Stritih-Peljhan and Virant-Doberlet 2021). Simultaneously, in the pacific field cricket, *Teleogryllus oceanicus*, a previously unknown drumming signal was discovered accompanying the song (Broder et al. 2021), yet, its function remains unclear, as females preferred non-drumming individuals (Wikle et al. 2023). This underscores the challenge of understanding female choice for the complex signal without a thorough analysis of all its components and their interactions (see Mitoyen et al. 2019). Moreover, in dynamic courtship displays based on motor activity, the overall signal complexity (Mitoyen et al. 2019; Choi et al. 2022) and performance quality (Byers et al. 2010; Fusani et al. 2014) also provide useful information for females on male attributes.

Based on this foundation, we aimed to explore deeper into the male vibroacoustic courtship at the example of the house cricket, *Acheta domestica*, long known for its simultaneous body tremulation and stridulation (Alexander and Otte 1967; Hack 1998). Neither the characteristics of this combined signal nor those of the tremulation signal alone have ever been investigated. In this species, the ambiguity surrounding the song relates to the finding that the females receive and use the information about the costliness of male courtship, while this information is not reflected in the song parameters (Nelson and Nolen 1987; Reşk 2012). More specifically, the probability of song production and the proportion of time spent singing are condition dependent, and the females prefer the individuals with a higher duty cycle of

song (Nelson and Nolen 1987; Ręk 2012). Yet, the pulse rate as an energetically costly song parameter (Hack 1998) does not reflect male condition or influence female mating decisions (Nelson and Nolen 1987; Ręk 2012). We suggest that the ignorance of the male display complexity may be the primary cause of this discrepancy. Specifically, we anticipate that the expression of the complex signal, and thus the potential information it conveys, may not directly correlate with stridulation, so far considered as the sole non-contact mechanical signal relevant to females. The current disagreement between female preferences and the song may arise not only from such nonlinearities but also from the emergent information within the signal, such as the quality of coordination between its components, potentially underlying the disparity.

To explore these predictions, we examined characteristics of the entirety of male vibroacoustic signal components emitted into the substrate and air, using combined audio recording, vibration recording using laser vibrometry, and videorecording. We focused our attention on their temporal characteristics and their interactions to assess the potential information content of the complex signal. We also provide details on signal frequency and intensity features to enhance our understanding of its perception, as well as lay ground for future interspecific comparison. The study significantly advances our understanding of the cricket courtship, while also providing a novel example of a complex dynamic signal with distinctive constraints within insects and animals in general.

Materials and methods

Animals

The crickets, purchased as young to mid-sized larvae from Bugs International, Irsingen, Germany, were kept in glass containers (24×38×24 cm) with Vermiculite as substrate and egg cardboard cover at 24±1 °C, under a reversed 12 h/12 h light/dark cycle. Larvae were kept in groups of between 50 and 100 individuals, and adults of up to 20 individuals. Upon their imaginal molt, crickets were separated by sex and kept in groups with an age difference of 3 to 4 days. To reduce their aggression, the males were individually separated into plastic containers (17×7×5 cm) at least one day prior to an experiment. At all stages, the animals received food (fish food in flocks, zucchini, carrots and/or apples) and water *ad libitum*. Experiments were conducted with 2- to 5-weeks old adults.

Recording sound and vibration

We paired an unmated male with a female on a low-middle frequency loudspeaker (12.5 cm in diameter), surrounded by transparent foil to restrain the animals. Each experiment lasted until copulation, or maximally 30 min following courtship initiation. To capture all acoustic and vibrational components of the courtship signal, we simultaneously recorded sound and substrate vibration signals, from 55 courting males, using a portable laser vibrometer (PDV 100, Polytec, Waldbronn, Germany) and an omnidirectional microphone (ECM8000, Behringer, Germany) with a pre-amplifier (Tube Ultragain Mic 100, Behringer, Germany). A foil for laser beam reflectance at various spots on the loudspeaker membrane allowed recording adjacent to the signaller. We used a loudspeaker membrane as a nonresonant reference substrate, a method often employed in studies of insect vibrational communication (e.g., Čokl 2008). Sound and vibration were recorded using a Sound Blaster (Creative X-Fi Surround 5.1 pro, Singapore) in Raven Pro 1.6 (Cornell Laboratory of Ornithology, Ithaca, New York, USA) at 44 kHz sampling rate and 16-bit resolution. The vibration recording was calibrated using a vibration calibrator (type 4294, Brüel and Kjær, Denmark). A reference signal generated by the calibrator (at 10 mm/s) was recorded with the laser vibrometer into Raven Pro 1.6 under the same settings as in the experiments, allowed for a direct application of the calibration factor to all recordings. The absolute sound intensity was not analysed. All experiments were conducted under red illumination and a temperature of 24±1 °C, and were videorecorded (HC-VXF990, Panasonic).

Sound and vibration signal analysis

Signal analysis was conducted in Raven Pro 1.6. (Cornell, Ithaca, USA), following the selection and filtering of recordings in Audacity 3.1.3 (Audacity Team). During post-recording, we applied a 200 Hz high-pass filter to reduce background noise in the auditory channel. In the vibratory channel, we used a 200 Hz high-pass filter to remove tremulation before analysing stridulation and drumming signals, and a 250 Hz low-pass filter to remove stridulation and drumming before analysing tremulation signals. All signals were manually annotated, and Audacity was used to produce representative power spectra. Generally, no prior knowledge was considered when analyzing different signal types from the same individual or signals from different individuals, thereby minimizing observer bias.

Restless females frequently caused courting males to change position, interrupting their tremulation and drumming activity (Suppl. Figure 1). Therefore, only parts of recordings with minimal locomotion were analysed.

Additionally, the analysis excluded the short initial ‘warm-up’ period after courtship initiation, in which drumming and tremulation rates were still increasing to their representative values (Suppl. Figure 1).

Temporal analysis

To investigate the potential of the complex signal to provide different information to the female than stridulation alone, we assessed its energetic demands and coordination quality via a detailed analysis of the rates and temporal relations of its components. This was performed on recordings from 15 males, each with 55–65 phrases of courtship song (see Figs. 1 and 2) selected from 3 to 6 different sections of signalling under above criteria. In case of stridulation and drumming, this included hundreds of signals per male for the analysis. We chose to analyse such long sections due to noted variability in drumming performance, which limited the analysis to individuals courting at least somewhat reluctant females.

Stridulation

We measured the periods, and calculated rates, of high-frequency stridulation tick-pulses and low-frequency stridulation trill-pulses (from in-phrase periods of the latter) and counted the number of these pulses per phrase (Figs. 1 and 2). We measured durations for a subset of pulses, as explained in more detail below (see Spectral-intensity analysis).

Drumming, and its association to stridulation

We applied an amplitude threshold criterion set at 10% of the average vibrational amplitude (peak) of the most intense drums within each song phrase, which reliably distinguished drumming from other impact disturbances. We measured the in-phrase periods and calculated rates of drum signals and counted their number per phrase (Fig. 1). We calculated the ratio of drums to stridulation trill-pulses

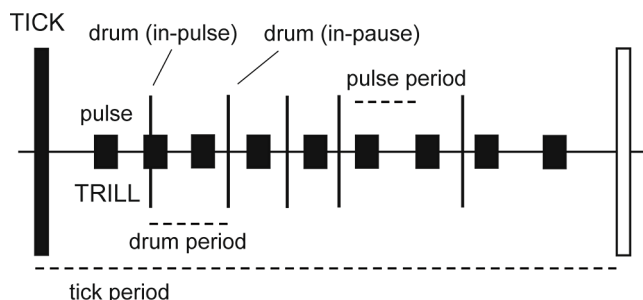


Fig. 1 Schematic representation of stridulation and drumming signals in a song phrase, depicting their evaluated temporal and association parameters

emitted per phrase (i.e., ‘‘drum-pulse ratio’’) and the proportion of drums emitted (by their peak amplitude) in the pauses between stridulation pulses. We also calculated the proportion of drums in individual pulse periods, and their proportion associated with different numbers of successive stridulation pulse periods. In the rare instances where two drums were emitted within the same pulse period (in less than 2% of drums overall), we treated them as a single event for the calculation of drum-pulse associations.

To assess the level of coordination between drumming and stridulation, we compared the observed distribution of drums relative to stridulation pulses with their expected random distribution in each individual. We calculated the mean relative duration of pauses between stridulation pulses in a phrase to represent the random probability of drum emission during pauses. We calculated the mean reciprocal stridulation pulse period value (also including tick to 1st pulse period) to represent the random probability of drums occurring in a specific period. Using combinatorics in Python, we calculated all possible configurations of placing n elements (all observed numbers of drums emitted per phrase) in m positions (the mean number of stridulation pulse periods per phrase). We then counted the number of configurations by types of grouping with successive stridulation pulses and calculated the proportion of drums in each grouping type to represent their random probability of occurrence. This and the previous approach assumed the possible occurrence of a single drum per pulse period (as observed in over 98% of cases).

Tremulation

We assessed tremulation rates, often not evident from vibration recordings (see Results), through video analysis. Utilising frame-by-frame examination (in Filmora 11, Wondershare), we counted the cycles of body motion with 0.5 cycle resolution. The analysis focused on the same recording sections (rounded to the closest second) as with other signals, with subdivisions for sections longer than 7 s for statistical purposes. Tremulation rates were so determined from 6 to 9 sections per male, each lasting 4–7 s. On this basis, tremulation activity could not be quantitatively compared to that of drumming and stridulation beyond the comparison of signal rates.

Spectral-intensity analysis

To facilitate understanding of the perception of the complex signal, we measured the dominant (peak) frequency (from the power spectrum) and peak velocity of its components in both auditory and vibratory domains (where applicable) from 17 males. Measured was the first 30 stridulation ticks,

stridulation pulses, and drum signals (with no overlap) in the selections. In the same signals, we also measured signal duration. For tremulation (which did not produce discrete signals), the frequency and amplitude were measured in the periods of individual song phrases. Due to mechanical differences between the central and lateral sections of the loudspeaker membrane, we analysed the signal characteristics emitted on these sections separately.

Statistics

We report mean values (with SD) for normally distributed data and median values (with IQR) for non-normally distributed data, the latter including the dominant frequency measured as a discrete variable. We assessed the nature of data distribution using the Kolmogorov-Smirnov test. For tremulation rates, we applied weighted mean and SD values, considering the duration of the evaluated sections. We used a paired T-test to compare the observed and random distributions of drums in pauses between stridulation pulses (both normally distributed). We used the Mann-Whitney U test to compare the emission of pulses in the individual pulse periods with their hypothetical random distribution, and to compare the observed and hypothetical distribution of drum groupings with successive pulses (not normally distributed in all periods and groupings, respectively). We examined the relationships among signal temporal and association parameters using the curve estimation function (in Microsoft Excel). We assess their statistical significance using Pearson's correlation, as well as quadratic and cubic regression functions. In the case of significance in more regression models, we used the simpler one. We compared the frequency and intensity characteristics of signals between the lateral and central parts of the loudspeaker membrane using ANOVA and reported them separately in cases where

a significant difference was found. We conducted all statistical tests using SPSS 14.0 (Chicago, SPSS Inc.).

Results

The complex vibroacoustic signal

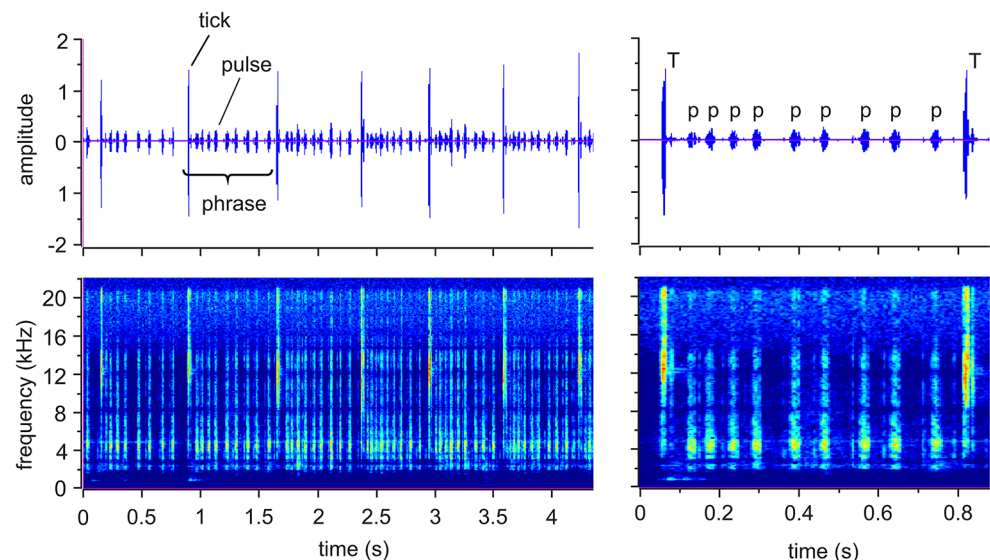
The stridulatory song of *A. domesticus* males (Fig. 2) represents only one component of a much more complex vibroacoustic courtship signal emitted by simultaneous action of wing stridulation, body tremulation and leg drumming against the substrate (Fig. 3, S1, Suppl. Video 1). Our experimental recordings, and many more observations of the males courting not in standardized conditions, affirm that this signal combination represents a consistent pattern of male courtship behaviour.

Drumming and tremulation occur in a close association during the display, with a short delay following song initiation. In the initial courtship bout, the median occurrence of the first leg drum was in the second song phrase (IQR 1.– 5. phrase), 1.24 s (IQR 0.43–2.94) after the initial stridulation tick ($n=27$). Afterwards, several additional seconds were typically required for drumming and tremulation to reach their representative expression, while stridulation assumes its typical pattern from the onset (Suppl. Figure 1). In this complex signal, the components emitted by stridulation, drumming, and tremulation occur in a pattern of regular exchange, described in more detail below.

Stridulation

The stridulatory courtship song is composed of repetitive elements, called phrases, each containing one high frequency pulse or 'tick', followed by a series of low frequency pulses

Fig. 2 The stridulatory courtship song of *A. domesticus*. The song consists of repetitive elements called 'phrases', each with a single high frequency pulse called the 'tick' (T), followed by a series of low frequency pulses (p) of lower amplitude, called the 'trill'. The phrase indicated on the left is shown at an expanded scale on the right. Presented is the recording immediately after the initiation of the song before the inclusion of drumming and tremulation. Signal amplitude is in arbitrary units



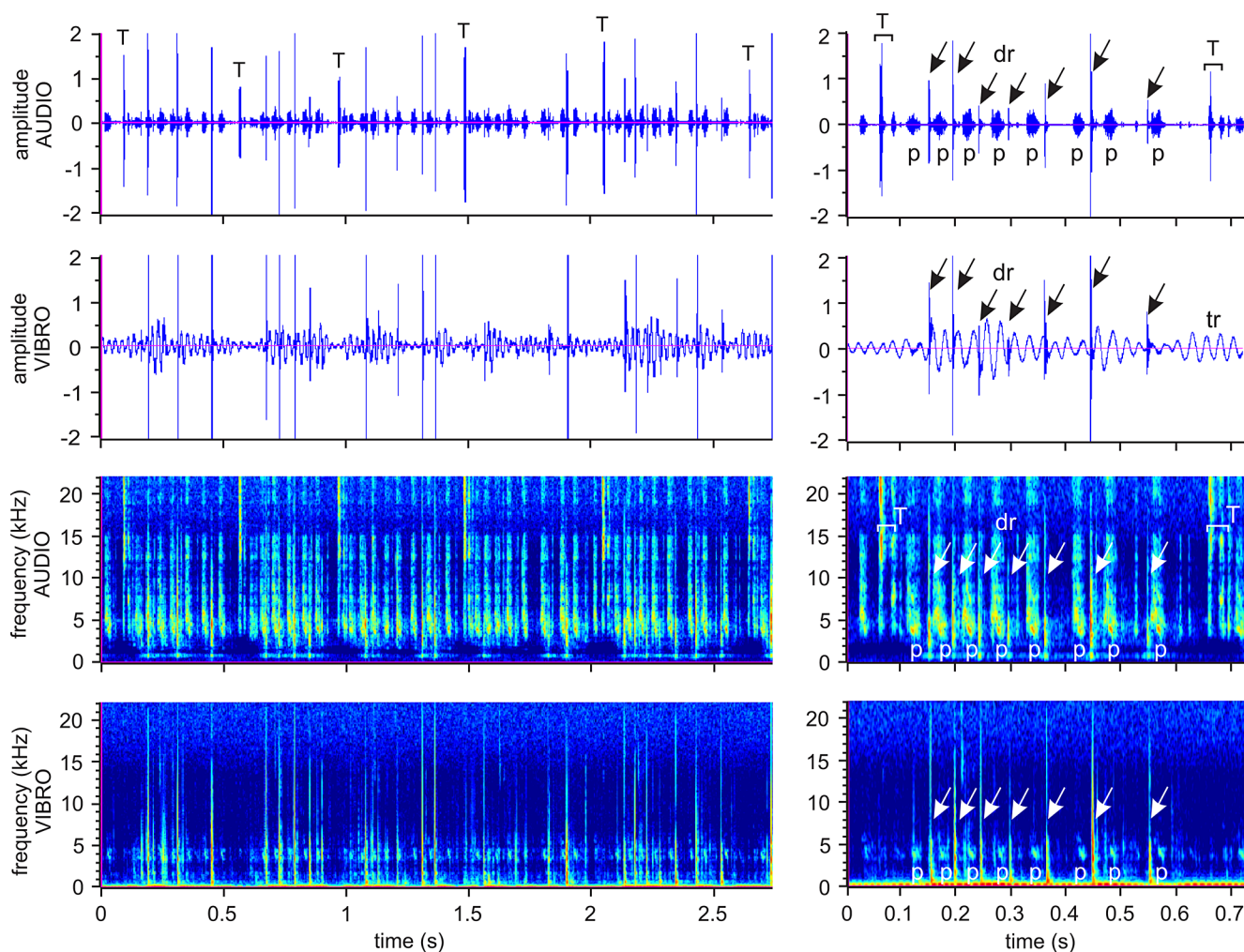


Fig. 3 The complex vibroacoustic signal emitted by stridulation, drumming and tremulation in *A. domesticus*. Presented is a two-channel recording of sound (audio) and substrate vibration (vibro), when the male was signaling on a loudspeaker membrane. T: stridulation ticks; p: stridulation pulses; arrows (dr): leg drumming against the substrate (each strike producing a transient signal); tr: body tremulation (pro-

ducing a continuous, amplitude modulated signal). Note the occurrence of drums in the pauses between stridulation pulses, along with the general increase in tremulation amplitude. Signal amplitude is shown in arbitrary units, with 1 corresponding to 0.579 mm/s in the vibration channel

in the ‘trill’ (Fig. 2); the latter with considerable components both in the substrate and air (Figs. 3 and 4). On average, a phrase contained 9.30 (SD 2.10; $n=929$, $N=15$) trill pulses (called ‘pulses’ in the following manuscript). The pulses occurred at a mean rate of 18.48 Hz (SD 5.45; Table 1), with the variation between 14.66 Hz (SD 3.70, $n=623$) and 22.59 Hz (SD 6.44, $n=523$) among males. The ticks occurred at a mean rate of 1.66 Hz (SD 0.42 Hz; Table 1), with the variation between 1.13 Hz (SD 0.25, $n=64$), and 2.05 Hz (SD 0.36, $n=65$) among males. The rates of ticks and pulses were linearly correlated (Pearson’s correlation, $r=0.722$, $P=0.002$; Fig. 6a), maintaining a stereotyped phrase structure across rates.

ducing a continuous, amplitude modulated signal). Note the occurrence of drums in the pauses between stridulation pulses, along with the general increase in tremulation amplitude. Signal amplitude is shown in arbitrary units, with 1 corresponding to 0.579 mm/s in the vibration channel

Drumming

Drumming is performed mostly by forelegs, and to a lesser extent also by midlegs, each leg typically producing several consecutive drums. Yet, attributing these signals to individual leg movements was in most cases not possible due to the limited 24-frame rate of video recordings. However, in a sequence where the count of identified drum signals aligned between video and audio recordings, the forelegs accounted for 82% and midlegs to 18% of the signals ($n=43$). Each foreleg produced up to four and each midleg up to two consecutive signals.

The impact of each leg against the substrate produced a transient pulse with the amplitude peak in the first few milliseconds and a progressive decay. These signals had a

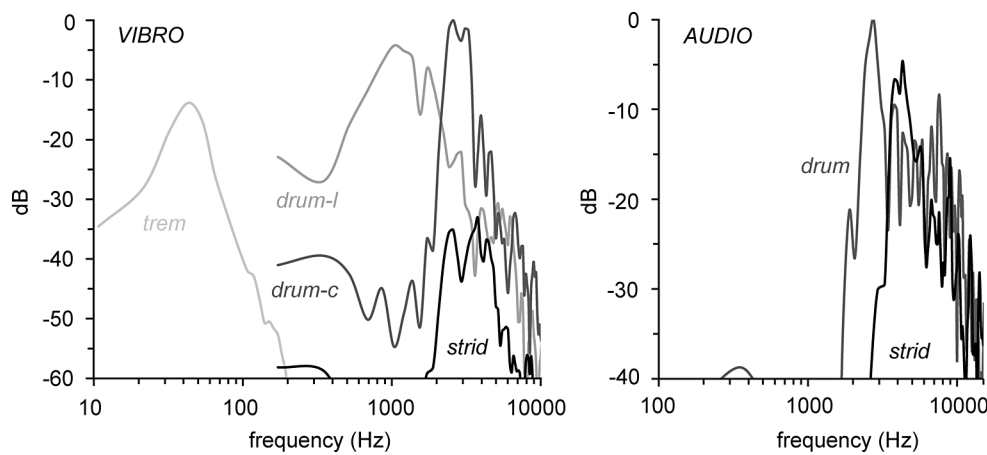


Fig. 4 Sample spectra of the various signal components in the substrate and air. The left side illustrates the vibratory and the right side the auditory components of tremulation, drumming, and stridulation (trill) pulse signals. The spectral peaks of these examples align with the median dominant frequency of the sample. Their relative intensi-

ties illustrate differences between the median values of the vibration velocity / sound intensity of the signals (normalised with $\text{dB} = 20 \cdot \log(S/S_{\text{max}})$; for the absolute values, see Table 1). trem: tremulation; drum-l: drumming on the lateral section of the loudspeaker, drum-c: drumming on the central section of the loudspeaker; strid - stridulation pulse

Table 1 Spectral, intensity and temporal parameters of courtship stridulation, drumming, and tremulation signal components in the auditory and vibratory channels

	Frequency (kHz)		Amplitude		Duration (ms)		Rate (Hz)	
	Vibro	Audio	Vibro mm/s	Audio m/s ²	Vibro normalized*	Audio	Vibro	Audio
Stridulation - ticks	n.a.	18.26 (13.44–20.33)	n.a.	n.a.	7.31 (6,31–10,53)	n.a.	24 (10)	1.66 (0.42)
- pulses	3.79 (2.92–4.31)	4.31 (3.96–5.17)	0.025 (0.016–0.034)	0.56 (0.35–0.78)	1	/	22 (5)	18.48 (5.45)
Drumming	Cen: 2.41 (2.41–2.76) Lat: 1.03 (0.69–2.07)	2.76 (2.41–4.13)	0.787 (0.429–1.476)	Cen: 17.78 (9.92–33.09) Lat: 5.12 (2.09–10.52)	1.70 (1.31–2.15)	Cen: 6 7 (2) Lat: 14 (9–20)	6 (2)	11.31 (7.52–17.24)
Tremulation	0.043 (0.038–0.043)	n.a.	0.230 (0.160–0.345)	0.061 (0.040–0.092)	n.a.	n.a.	n.a.	3.77 (0.43)

Values represent mean (with SD) and median (with interquartile ranges) for normally and non-normally distributed data, respectively. Dominant frequency, peak amplitude, and duration were measured for $n=510$ drumming and stridulation signals/pulses, and $n=340$ tremulation intervals in 17 males. Rate was measured for $n=2536$ drums, $n=7709$ stridulation (trill) pulses, $n=913$ stridulation ticks (all from 55–65 song phrases per male), and $n=112$ videorecorded intervals in 15 males. Cen: central section of the loudspeaker membrane ($n=150$), Lat: lateral section of the loudspeaker membrane ($n=360$); the separation indicates significant influence of location on the measured parameter. *Amplitude of audio signal components relative to that of stridulation pulses in the same individual (median values). / - not evaluated (for stridulation pulses, which were of similar duration in both channels), n.a. - not applicable

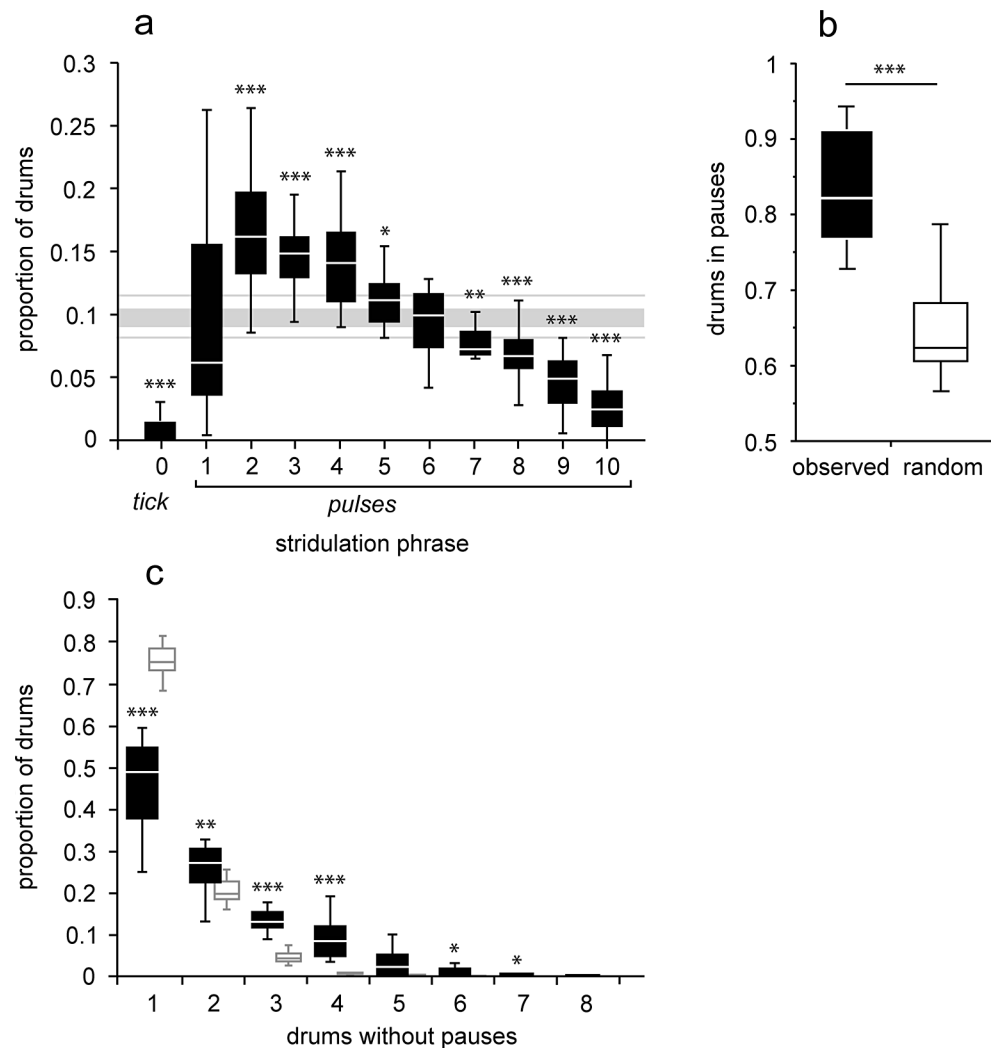
broadband frequency structure in both auditory and vibratory domain (Figs. 3 and 4). Their rate was highly variable, both within and between individuals. The median (in-phrase) drum rate of the entire sample was 11.31 Hz (IQR 7.52–17.24; $n=2536$, $N=15$) and ranged from 6.42 Hz (IQR 4.15–8.82, $n=130$) to 16.18 Hz (IQR 10.45–22.73, $n=243$) among males (see also Fig. 6c).

Association of drumming with stridulation

The temporal association of drumming and stridulation components in the complex signal is illustrated in Fig. 5. Drumming predominantly occurs during the trill periods

of the song (Figs. 3 and 5a). The vast majority of drums (98.5%) were emitted individually (once) per pulse period, predominantly in the pauses following the stridulation pulses. The proportion of drums in the pauses was 0.84 ($n=3408$, $N=15$) overall and ranged from 0.73 ($n=308$) to 0.94 ($n=220$) between the males (Fig. 5b; see also Fig. 6g). Such occurrence of drums significantly differs from their expected random distribution in pauses (paired T-test, $t=9.88587$, $P<0.001$, $n=15$; Fig. 5b). A drum was very rarely emitted immediately following the tick, significantly below random expectation (Fig. 5a). Drum occurrence was the highest in the first half of the trill in all males, and during the second pulse period overall, and progressively

Fig. 5 (a) Temporal association of drumming and stridulation components of the complex signal. In all insets, the y-axis shows the proportion of drums emitted by individual males ($n = 119\text{--}314$, $N = 15$) in boxplots with interquartile ranges, excluding outliers, compared to their hypothetical random distribution. (a) Drum association with each successive stridulation pulse period per phrase. The x-axis represents the phrase structure with a tick and the mean (+1) number of pulses in the trill. The gray area represents the interquartile range and the gray lines the span of the random distribution. The indicated significance levels are based on the Mann-Whitney U test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. (b) Drums emitted in pauses between stridulation pulses, with indicated significance level based on the Wilcoxon Signed-Rank test ($P < 0.001$). (c) Drums in the associations with different numbers of successive stridulation pulses, without an intercalated pause of one pulse interval; black bars—observed distribution, empty grey bars—hypothetical random distribution. The indicated significance levels are based on the Mann-Whitney U test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)



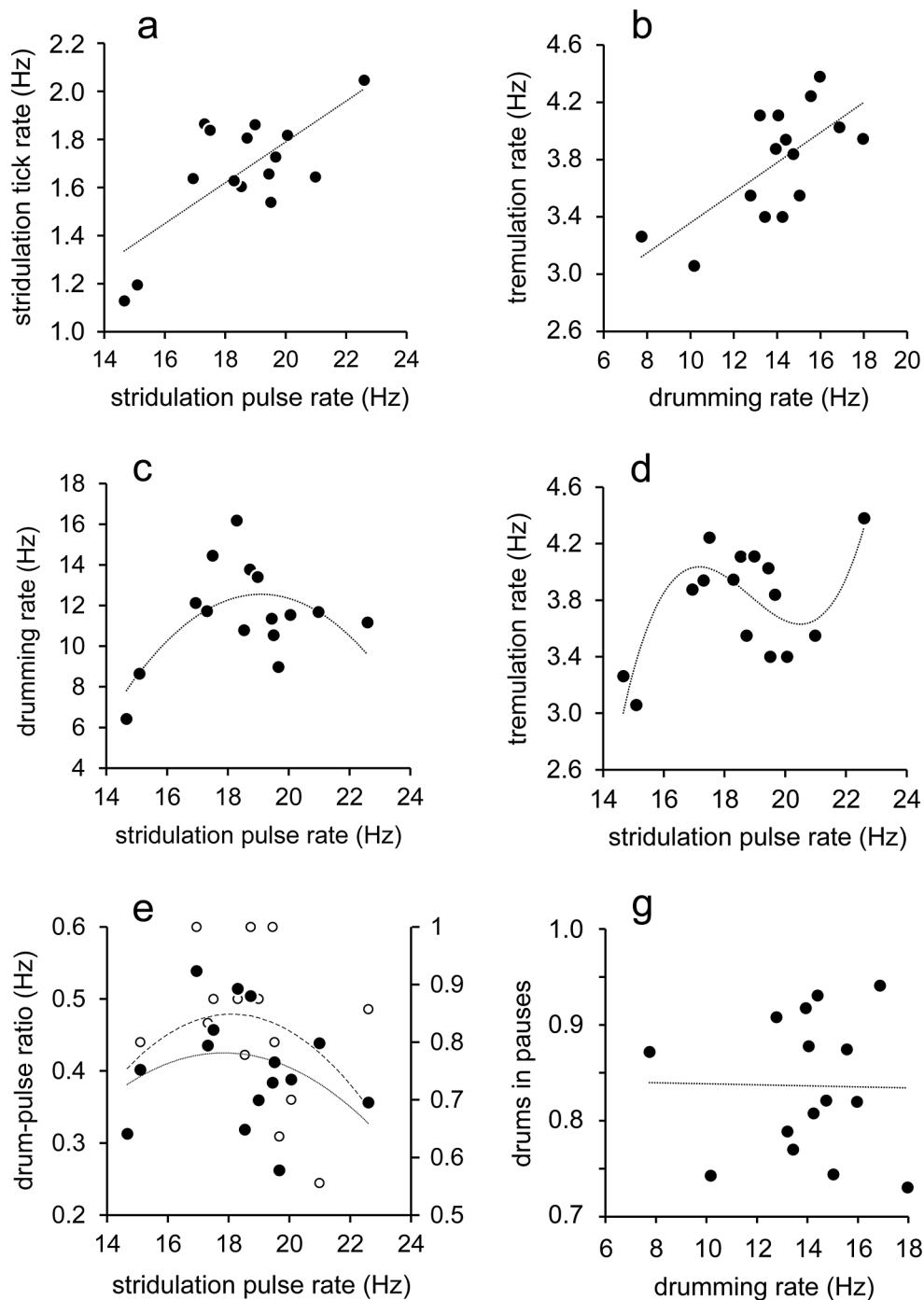
decreased with each subsequent pulse in the trill (Fig. 5a). Drums occurred significantly more often in the periods from the second to fifth pulse and significantly less often than expected by chance after the sixth pulse (Mann-Whitney U test; for test values, see legend to Fig. 5a). Most drums were separated by a pause of at least one pulse period, and the likelihood of drum occurrence in association with successive pulses decreased exponentially with their number in such a series (Fig. 5c). This pattern significantly differs from random occurrence: grouped drums occurred significantly more often in most associations, while single drums occurred significantly less often than expected by chance (Mann-Whitney U test; for test values, see Fig. 5c).

The drum-pulse ratio was generally low and variable from phrase to phrase, with an average of 0.40 (SD 0.17, $n = 929$), ranging from 0.26 (SD 0.16, $n = 55$) to 0.54 (SD 0.18, $n = 65$) among males (see also Fig. 6e). A substantial part of its variability within individuals was related to its fluctuation between directly subsequent phrases (Suppl. Figure 2). A drum-pulse ratio of 1 was achieved extremely

rarely; only three males emitted a drum after each pulse in just one of their phrases analysed (i.e., in 0.3% of the total, $n = 929$; see also Fig. 6e). The association between drumming and stridulation rates shows the best and statistically significant fit when modelled as a quadratic function (with pulses: $F(2, 12) = 8.158$, $P = 0.006$ / $F(2, 12) = 4.042$, $P = 0.045$ for mean / median drumming rates, Fig. 6c; with ticks: $F(2, 12) = 13.520$, $P < 0.001$ / $F(2, 12) = 5.955$, $P = 0.016$ for mean / median drumming rates). The peak drumming rate occurs when the stridulation rate approximates the sample median (Fig. 6c; see also Table 1).

The dependence of the drum-pulse ratio on stridulation rate exhibits an initial brief rise followed by a consistent decline of its upper-bound values (for method, see Podos 1997). This negative trend is statistically significant (Pearson's correlation, $r = -0.8579$, $P = 0.028$; Fig. 6e). While the complete set of values shows the best fit to quadratic function, this fit is not statistically significant ($F(2, 12) = 0.734$, $P = 0.5$; Fig. 6e). The proportion of drums emitted in pauses exhibits no dependence on drumming rate or drum-pulse

Fig. 6 The relationships between the temporal and association parameters of the complex signal. Presented are means from individual males, and medians in (d) (due to non-normal data distribution), together with regression lines of best fit by the least-square analysis. In (e), maximal values (white circles, right scale) are also depicted along with their regression line (dashed). $R^2 = 0.5217$ (a), 0.465 (b), 0.4033 (c), 0.6365 (d), 0.1120 (e), 0.1266 (f), 0.0011 (g)



ratio (Pearson’s correlation, $r=0.018-0.089$, $P=0.752-0.946$; Fig. 6g).

Tremulation

Body tremulation occurs with rhythmic lateral movements or “swinging” of the body at a low rate, clearly noticeable to an observer (Suppl. Video 1). Produced was a continuous, amplitude modulated signal confined to the substrate,

with most spectral energy below 100 Hz (Figs. 3 and 4A; Table 1). For the most part, the amplitude peaks did not clearly correspond to the individual phases of body movement. However, in some instances, particularly with slower signallers, this correspondence was more evident (Fig. 7). The mean rate of tremulation movement was 3.77 Hz (SD 0.43 Hz; $n=112$, $N=15$), varying from 3.06 Hz (SD 0.16 Hz, $n=7$) to 4.38 Hz (SD 0.23 Hz, $n=6$) among males (see also Fig. 6b).

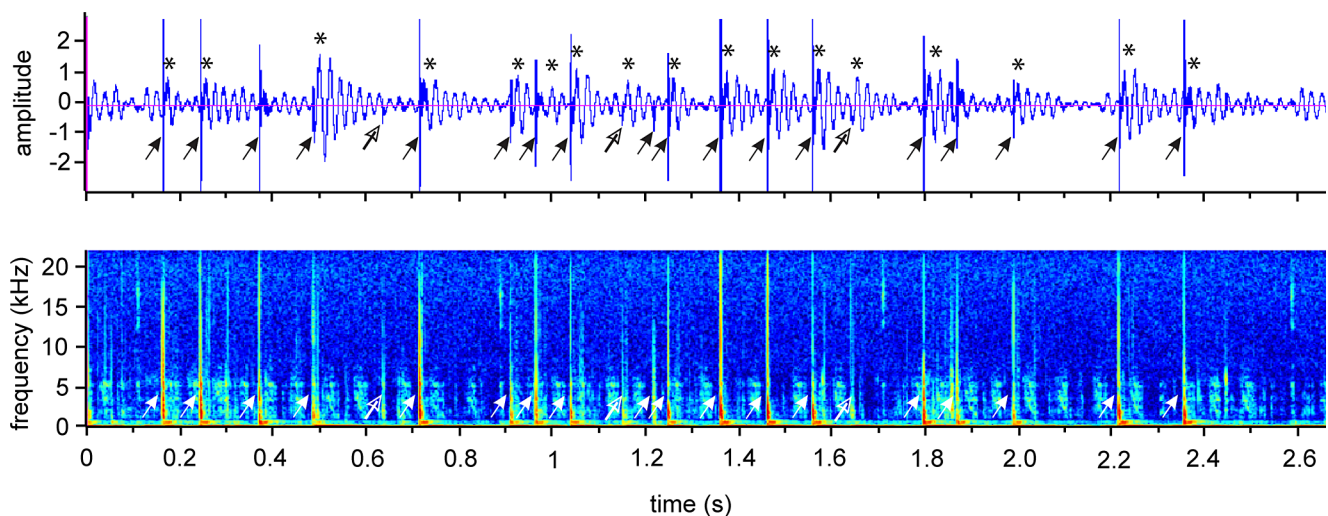


Fig. 7 Temporal association of tremulation and drumming components of the complex signal. An example vibration recording with a more strongly pronounced amplitude modulation in the tremulation signal. The tremulation rate, calculated from the peaks (indicated by asterisks), matches the one determined from the video of the same section.

Note the consistent occurrence of leg drums shortly after the onset, and occasionally just before the offset, of tremulation amplitude increases. Full and empty arrows indicate leg drums above and below the amplitude threshold, respectively. The signal amplitude is shown in arbitrary units, with 1 corresponding to 0.157 mm/s

Association of tremulation with drumming and stridulation

The timing and rate of tremulation were most closely associated with those of drumming (Figs. 3 and 6b). At times, the signal's amplitude modulation accurately represented tremulation movements; these recordings revealed the emission of drums shortly after onset, and with more efficient drummers also shortly before offset of tremulation amplitude increase (Fig. 7). Accordingly, we found significant linear correlation between tremulation and drumming rates (Pearson's correlation, $r=0.682$, $P=0.005$, and $r=0.5123$, $P=0.05$, for mean and median drumming rates, respectively), with an approximate 1:2 to 1:4 relationship (Fig. 6b). The rate of tremulation movements was significantly linearly correlated with that of stridulation ticks (Pearson's correlation, $r=0.724$, $P=0.002$). In contrast, the relationship between stridulation pulse and tremulation rates was found to be more complex, with the best and statistically significant fit to a cubic function ($F(2,12)=6.4211$, $P=0.009$; Fig. 6d).

Signal frequency, amplitude, and duration

The median dominant frequency of stridulation (trill) pulses was 4.3 kHz in the air and 3.79 kHz in the substrate (Fig. 4; for the IQR, see Table 1). Frequency composition of the substrate component was similar for the ticks (but weak and not formally analysed), with the median dominant frequency at 18.26 kHz in the air (Table 1). In the substrate, the median dominant frequency of drums was 1.03 kHz on the lateral and over twice as high on the central section of the loudspeaker membrane (the shift influencing both the

fundamental and harmonic frequencies), while in the air it was 2.76 kHz with no location-related difference (Table 1). The dominant frequency peak of tremulation signals was almost invariably at 43 Hz.

In the air, the stridulatory ticks were over seven times more intense than pulses (Table 1), while the substrate component was strongest for pulses (median at 0.025 mm/s, Table 1). The median peak amplitude of the auditory drumming component was 1.7 times higher than that of stridulation pulses. In the substrate, drumming was by far the most intense of all signals (Table 1). Tremulation signals had the median peak velocity at 0.23 mm/s (Table 1).

The mean signal duration was 24 ms for the ticks and 22 ms for the pulses. Drumming signals were much shorter, and similar between the air and substrate when emitted on the central membrane (around 6 and 7 ms, respectively), while on the lateral membrane the substrate signal was approximately twice as long (Table 1).

Discussion

Complexity of cricket courtship display

In field crickets and other cricket taxa, the characteristics and function of vibrational signals, which are not only a by-product of stridulation but often complement it in a complex courtship display, have remained largely unexplored or even primarily overlooked (Stritih-Peljhan and Virant-Doberlet 2021). This holds true even for model cricket species, such

as *A. domesticus*, which has been studied behaviourally for decades (see Horch et al. 2017).

We present the first comprehensive study of the entirety of vibroacoustic signals emitted during cricket courtship, analysing their characteristics and interactions as potential targets of female choice. We demonstrate that in addition to body tremulation (Alexander and Otte 1967; Hack 1998), males also drum with the legs against the substrate while singing; a behaviour observed in other crickets but not in conjunction with tremulation (de Mello and dos Reis 1994; Wikle et al. 2023).

The complex vibroacoustic signalling of *A. domesticus*, which utilises three different mechanisms requiring prolonged simultaneous movement and coordination of different body parts, is unique not only among crickets but also compared to katydids and other Orthoptera, despite the diverse sound and vibration production mechanisms seen in these groups (e.g., Morris et al. 1994; de Luca and Morris 1998; Stumpner et al. 2013; Korsunovskaya et al. 2020; for other examples see Virant-Doberlet et al. 2023). *A. domesticus* represents an exceptional case of dynamic signalling known within insects in general, as most species combining multiple vibroacoustic mechanisms produce serial signals that do not overlap in time, or transiently combine at most two to produce a composite signal (e.g., Asopinae stink bugs, Žunič et al. 2008; Philloporinae bushcrickets, Korsunovskaya et al. 2020; Drosophilinae fruit flies, Mazzoni et al. 2013; for a comprehensive review, see Virant-Doberlet et al. 2023). Thus, alongside the intricate visual-vibratory courtship of spiders (e.g., Kozak and Uetz 2016) and the combined song and dance performances of birds (e.g., Miles and Fuxjager 2018), crickets may provide another example of complex dynamic signalling that merits examination of signalling effort, complexity, and coordination as potential factors influencing female choice.

Quantity and quality aspects of the complex signal

Traditionally, the components of the complex signals have been either viewed as redundant signals providing a functional backup or as signals conveying multiple messages to the receiver (Møller and Pomiankowski 1993; Johnstone 1996; Candolin 2003). This view changed when also considering the perceptual mechanisms of receivers (Rowe 1999; Hebets and Papaj 2005; Starnberger et al. 2014; Halfwerk et al. 2019), the interaction between signal components (Partan and Marler 1999; Hebets and Papaj 2005; Hebets et al. 2016), and the complexity and quality of (dynamic) displays (Byers et al. 2010; Fusani et al. 2014; Mitoyen et al. 2019) to gain insight into signal function and evolution. We apply these perspectives to the complex signal of *A. domesticus*,

discussing its communicative potential beyond that of the stridulatory song.

Signal costs

Earlier studies on *A. domesticus* revealed that the females receive reliable information about male condition from the courtship display and select traits based on their costs, such as the time spent singing, while this information is not reflected in song parameters (Nelson and Nolen 1987; Reş 2012). Specifically, the energetically costly pulse rate (Hack 1998) neither reflects male condition nor influences female mating decisions (Nelson and Nolen 1987; Reş 2012). Our study sheds light on this discrepancy, demonstrating that stridulation is only one of three components of the complex signal, whose joint costs do not appear to be simply proportional to that of stridulation. This is indicated through the non-linear correlation between stridulation vs. drumming and tremulation rates, suggesting that females would not be able to assess the quality of males solely from one signal parameter (as per the redundant signal hypothesis; Candolin 2003). This is a relevant argument since drumming and body tremulation are known as energetically demanding behaviours, the latter significantly costlier than stridulation (data from *A. domesticus*, Hack 1997; bushcrickets, Römer et al. 2010; spiders, Kotiaho et al. 1998). Tremulation serves as a reliable indicator of male condition in scaly crickets when emitted as a primary signal during courtship interruption (Andrade and Mason 2000) and also communicates size during courtship and aggressive behaviour in katydids (de Luca and Morris 1998; de Souza et al. 2011). All this indicates that the complex signal of *A. domesticus* could serve as a much more honest indicator of male condition than courtship stridulation alone, which generally lacks condition dependence in crickets (Wagner and Reiser 2000; Gray and Eckhardt 2001; Reş 2012). Our study, however, was not designed to identify which signal components, or their combinations, serve as primary indicators of male condition. We will address this issue in the future, along with testing which combinations of signal traits the females select.

Performance constraint

Our study reveals that stridulation serves as the primary component of the complex signal, to which tremulation and drumming are added secondarily. All components occur in a pattern of regular exchange (i.e., periodic coupling), which is particularly consistent between stridulation ticks and pulses, on one hand, and between tremulation movements and drumming signals, on the other, as evidenced also from the linear correlation of their rates. Stridulation sets the 'template' to be matched one-to-one (in the trill) by drumming,

and at a lower rate by tremulation. However, this matching is achieved with low efficiency and high variability, and the occurrence of one drum per pulse is extremely rare, indicating significant performance challenges. The nonlinear correlations observed with stridulation rates indicate a specific constraint on drumming performance, with an upper limit at rates around 16 Hz and a drum-pulse ratio of 0.55. The latter reflects the lack of persistent drumming throughout the trill, despite its maximal (in-phrase) rate almost matching that of stridulation. This constraint does not seem to affect tremulation, whose complex dependence on the stridulation pulse, but not tick rate—to which tremulation is linearly correlated, may be considered a mere consequence of its tight coupling with drumming.

Similar performance constraints are found in songbirds and grey treefrogs, where trade-offs occur between vocal signal rate and bandwidth in birds (Podos 1997; Goller et al. 2022) and between male call rate and duration in frogs (Reichert and Gerhardt 2012; Ward et al. 2013). The mutual constraints in these examples, encompassing mechanical, energetic and temporal factors, pertain to intrinsically linked signal parameters that are difficult to produce simultaneously. The mutual relationship among these parameters is evident through a negative correlation across the entire range of their expression. By contrast, the constraint in *A. domesticus* is specific to an independently produced signal component and only manifests after reaching a specific effort threshold. To our knowledge, this represents a novel case of performance constraints in animal signalling.

This drumming constraint in the cricket may be partly mechanistic, as the leg's neuromuscular apparatus also serves body support and tremulation. Drumming may further be constrained by the lack of physiological adaptations in leg muscles for rapid repetitive contractions. In this context, the frequent pauses in the drumming rhythm dictated by stridulation (i.e., primarily occurring with isolated drums despite their grouping beyond random), along with the involvement of both forelegs and midlegs in drumming, indicate the necessity for frequent rest periods that avoid anaerobic metabolism (see Mowles 2014). The lack of such specialisation may be further seen in the generally low and variable occurrence of drums in the first trill-pulse period, just before reaching its transient maximum. This pattern can be interpreted as the activation phase following the 'allowed' pause during the tick period, similar to the gross drumming activation period during courtship initiation.

Performance quality through signal interaction

In complex signalling involving locomotor activities, the signaller's quality is conveyed not just through the vigour of performance, but also through the skill of coordinating

challenging motor actions (Byers et al. 2010; Fusani et al. 2014). In *A. domesticus*, we observed precise timing in the alternation of signal components reliant on the activity of distinct body parts—specifically the wings and the legs—requiring coordination. We evaluated the proportion of drums emitted in pauses between stridulation pulses as an emergent signal trait indicating coordination quality. Despite this parameter generally demonstrating high performance, it varied significantly between individuals, thus providing a putative basis for female choice. Interestingly, the proportion of drumming in pauses did not correlate with drumming rate or drum-pulse ratio, contrary to the expectation of trade-offs between quality and quantity of motor performance as demonstrated in acrobatic mating displays of a songbird (Manica et al. 2017). Hence, if female preferences in crickets rely on both courtship display vigour and skill, they might be even less evident when considering stridulation as its only relevant component.

Functional insights through spectral-intensity analysis

Analysing complex multimodal signals from the view of detection and integration facilitates understanding of their function and evolution (Halfwerk et al. 2019).

Stridulation and drumming as one percept

We have demonstrated that stridulation and drumming produce similar, higher frequency signals with simultaneous components both in the substrate and air. Crickets have specialised sensory organs detecting such signals; the leg subgenual organ for vibrations (with peak sensitivity at 0.5–1.5 kHz; Kühne et al. 1984) and the foreleg tympanal organ for sound (sensitive above 2 kHz; Imaizumi and Pollack 2001). In our recordings, drumming vibrations were at least 25 dB above threshold of the cricket subgenual organ (Kühne et al. 1984), indicating their effectiveness in various environments (see also Elias and Mason 2014). Part of this input will converge with the auditory stridulation input already at the cricket's subgenual organ sensilla, some of which exhibit bimodal sensitivity (Kühne et al. 1984), and next at the ventral nerve cord interneurons integrating auditory and vibratory information (Wiese 1981; Kühne et al. 1984). Besides, the vibrational component of stridulation may enhance signal detection on substrates like soil through simultaneous bimodal inputs (see Wiese 1981; Kühne et al. 1984). Similarly, the enhanced detection of drumming through its acoustic component, which was even louder than stridulation in our experiments, may be particularly effective on the stiff natural substrates like leaves (see de Mello and dos Reis 1994). All this suggests a strong functional

connection between drumming and stridulation, being either perceived as same modality signals or integrated into a common bimodal percept already at the low level of sensory processing in crickets.

Tremulation

We showed that, due to mainly horizontal body movements of the male, the rate of tremulation signal is not easily discernible in the vertical component of substrate motion (detected by the laser vibrometer), crucial in vibration detection. Although insects can detect horizontal substrate vibrations (Strauß et al. 2019), they may not effectively generate such signals on massive substrates, relevant for ground living crickets. Because *A. domesticus* is nocturnal (Yamano et al. 2001), tremulation movement also cannot be visually perceived by females.

Moreover, the signal's energy content below 100 Hz, typical of insect tremulation (Žunič et al. 2008; Stritih and Čokl 2012, 2014), indicates detection by proprioceptive sensilla mediating reflex responses in insects (Stritih and Čokl 2014; Strauß et al. 2021) alongside the inputs for complex vibration processing (Stritih et al. 2019). The primary function of tremulation may thus not be in signalling male quality but in inducing female immobility, commonly observed with male tremulation during courtship interruption and mate guarding of crickets (Evans 1988; Sakaluk 1991; Brown 1999; Su and Rentz 2000). Spectral and intensity properties of vibratory tremulation signal in our study (around 0.5 m/s² at 50 Hz) support this function, exceeding the threshold of cricket freezing response but remaining below the threshold of a startle response induced by vibration (Dambach 1989; Stritih and Čokl 2014). Yet, the continuous tremulation during courtship of *A. domesticus* may not be optimised for silencing females due to response habituation, leaving the function of this complex signal component ambiguous.

Conclusions

We provide the first comprehensive description of the complete set of vibroacoustic signals constituting courtship display in a species of Gryllidae. This reveals the complexity and synchronisation between multiple signalling mechanisms, including a drumming signal that went completely unnoticed despite decades of study of this model species. Our data calls for revisiting cricket courtship behaviour with a specific focus on vibrational signals that may complement stridulation. Given the strong research bias towards airborne sound, there is a need to re-evaluate the entire Orthoptera in this respect to improve our understanding of their vibroacoustic communication.

The courtship behaviour of *A. domesticus* represents a unique example of complex dynamic signalling in insects, utilising three different vibroacoustic mechanisms simultaneously. We demonstrate that the potential information conveyed to the female through this complex signal extends well beyond that provided by stridulation alone. This encompasses a performance constraint that may have played a crucial role in shaping the signal's function. Exploring the fitness-related value of different parameters of this signal and associated female preferences remain obvious next steps in future research.

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Data availability All data generated and analysed during this study have been uploaded to Zenodo with the DOI: <https://doi.org/10.5281/zenodo.10143458> (Zenodo.org).

Declarations

Ethics approval The study did not require ethics review and approval according to Slovenian (Invertebrates; Animal Protection Act, Official Journal of the Republic Slovenia, No 38/13, 21/18-ZNORG, 92/20 and 159/21) and EU legislation (Directive 2010/63/EU of the European Parliament and of the Council on the protection of animals used for scientific purposes) requirements. The experimental procedures used did not include manipulation associated with pain. The males used in experiments were euthanised by freezing at -20 °C and stored in ethanol. All other animals in the stock were provided with food and water until they died naturally.

Competing interests The authors declare no competing interests.

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