Ultrasonic reverse stridulation in the spider-like katydid Arachnoscelis (Orthoptera: Listroscelidinae)

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Published online: 23 Jul 2013.

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This paper illustrates the biomechanics of sound production in the neotropical predaceous katydid *Arachnoscelis arachnoides* (Insecta: Orthoptera: Tettigoniidae). Described and previously known from only one male specimen, this genus of predaceous katydids resembles spiders in their general body appearance. To call distant females, male katydids produce songs by stridulation where one forewing possessing a sclerotized file rubs against a row of teeth (scraper) on the other wing. In most katydid species, the songs are produced during the wing-closing phase of the stridulation. Morphological comparative studies of the stridulatory apparatus of the type specimen of *Arachnoscelis arachnoides* and males of other closely related species suggest that this insect sings with a frequency of ca. 80 kHz to attract conspecific females. We found an abundant population of *A. arachnoides* in Central Northeast of Colombia and undertook a complete analysis of the biomechanics of stridulation in this species. Using ultrasound-sensitive equipment and high-speed video, we determined that male *A. arachnoides* sing at ca. 74 kHz and use elastic energy and wing deformation to reach such ultrasonic frequencies. In contrast to most katydids, males of this species produce their calls during the opening phase of the wing; this form of stridulation is discussed.

Keywords: ultrasound; elastic energy; Colombia; stridulation; biomechanics

Introduction

Male katydids produce calls by stridulation, rubbing their forewings to call distant females. A plectrum or scraper on the anal margin of the right wing (RW) is passed across a file (a wing vein modified with teeth) on the left wing (LW) (Dumortier 1963). The wings open and close in a cyclic manner, but sounds are usually produced during the closing phase (Walker and Dew 1972; Walker 1975; Morris 1999). Essentially, this is a multiplication process by which the frequency of the slow motion of the wings (the 30–60 Hz during opening and closing) is multiplied by the high-frequency vibrations produced by scraper and file-teeth encounters. This step of frequency multiplication is necessary as muscles are far too slow to generate wing vibrations at high frequencies (Michelsen 1998). The vibrations produced by tooth strikes are subsequently amplified by wing membranes, the second step of sound production in these insects.

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The simplest form of a call is that in which each tooth strike generates a sinusoidal oscillation of the wing resonator, which can be sustained in time if subsequent tooth strikes occur at the correct time and phase (Bennet-Clark 2003). Therefore, this will create a continuous pulse made of sustained oscillations that correspond with the number of file teeth. For instance, if the file has 200 teeth properly organized, a hypothetical complete sweep of the scraper across all file teeth would end in a pulse with nearly 200 sustained oscillations, subject to the condition that tooth strike rate (TSR) matches wing resonance (Bennet-Clark 1999; Montealegre-Z 2005, 2012).

This suggests that the organization of file teeth and the speed of wing closure dictate the carrier frequency (f_c) of the call. For example, a fast wing closure can strike more teeth per second than a slow closure and therefore produce a high frequency of scraper-tooth encounters (i.e. more sound cycles per second). An elevated TSR can be achieved by accelerating the wings during the closing phase or increasing the file tooth density or both (Montealegre-Z 2005; Montealegre-Z et al. 2006). In any case, for efficient sound radiation, TSR should match the resonant properties of the wings (Prestwich and O'Sullivan 2005). But there is also a physiological limit on the acceleration of the wings during the closing phase in katydid species singing above 40 kHz (Montealegre-Z et al. 2006). These katydids usually exhibit small body sizes (Montealegre-Z 2009) and their muscular mass is so small that they might not be able to generate the necessary power to close the wings at elevated speeds. Therefore, these animals use scraper deformation to obtain an elevated high-frequency TSR that is otherwise hard to achieve with normal muscle twitches (Montealegre-Z et al. 2006). But to effect the scraper deformation during the closing phase, the wings should be paused each time when pushing the scraper behind a file tooth to store elastic energy by deformation. Consequently, the scraper is quickly released and strikes over one or a few teeth at elevated speeds, producing a TSR unusually high, which matches wing resonance. This mechanism does not produce a continuous pulse but rather a train of discrete pulses separated by silent intervals associated with the scraper pauses (Montealegre-Z et al. 2006).

Montealegre-Z (2009) demonstrated a significant interaction of f_c as function of mirror dimension and suggested the equation:

$$f_c = \exp^{(4-1.2\ln \mathrm{ML})}, \tag{1}$$

where ML is the mirror length (in mm). Therefore, in katydids with small body size wing resonance is regularly high, as f_c negatively scales with wing radiator size which, in turn, positively scales with body size (Montealegre-Z 2005, 2009).

In this paper, we study the biomechanics of sound production used by the neotropical katydid *Arachnoscelis arachnoides* (Insecta: Orthoptera: Tettigoniidae) and present an anatomical description of the stridulatory apparatus. *Arachnoscelis* is a monotypic genus of predaceous katydid that resembles spiders in their general body appearance. The genus is known only from the type species (Montealegre-Z et al. 2013). Males and females are brachypterous and exhibit sexual dimorphism in colouration, with females showing a highly mottled body pattern compared to males (Figure 1). However, due to body appearance, several species have been erroneously incorporated within the genus *Arachnoscelis* (see Montealegre-Z et al. 2013).

Species of phylogenetically related genera have been known to use extreme ultrasonic calls for communication (Montealegre-Z et al. 2006). For instance, Montealegre-Z et al. (2006) reported another spider-like species of katydid incorrectly identified as *Arachnoscelis* sp. from Colombia to describe the mechanism of elastic energy explained
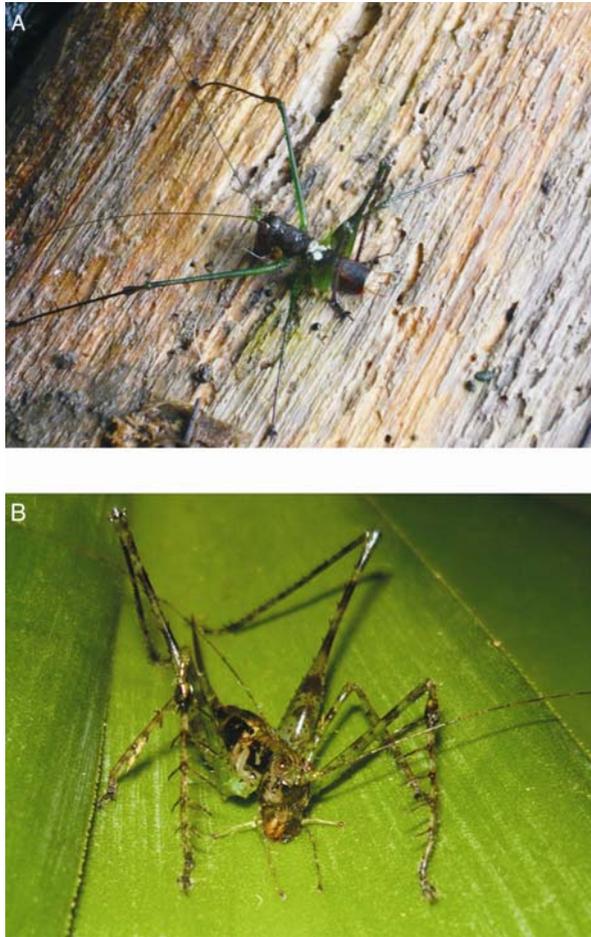
Figure 1.   *A. arachnoides*. (A) male and (B) female. To view a colour version of this figure, please see the online issue of the journal.

above. This species produces a very unusual ultrasonic call consisting of a tone peaking at ca. 130 kHz, the highest mating call ever recorded in nature.

FM-Z examined the holotype of *A. arachnoides* in the Museum of Zoology at the University of Michigan in 1999 (specimen borrowed by Dr Theodore Cohn from the type depository). Fitting the mirror dimension of this specimen (ca. 0.7 mm in diameter) into Equation (1) suggests that in life this animal should have produced songs with a frequency of ca. 83 kHz. Recently, the authors found a region in Colombia where individuals of *A. arachnoides* are relatively abundant, offering a unique opportunity to study these exotic creatures.

A major goal of this article is to test the hypothesis that males of *A. arachnoides* produce songs with an f_c of ca. 83 kHz as predicted by Equation (1) on the preserved type specimen. Such a frequency also suggests that the sound produced should not be a continuous pulse but a train of discrete short pulses separated by silent intervals, which reflect the scraper pauses required for scraper distortion and elastic energy storage.

Materials and methods

Specimens and locality

Locality: Colombia, Boyacá, Coper, Vereda Turtur, Sector San Ignacio. 5°25′32.51″N, 74°0′9.07″W, elevation 1561 m. Coper belongs to the west province of the Departamento de Boyacá and is located 133 km from Tunja (the capital of Boyacá). Elevation lies between 600 and 2600 m above sea level. Average temperature is 23°C and the annual rainfall is 3152 mm, therefore three different thermal floors are identified: warm 171 km^2, temperate 17 km^2 and cold 14 km^2. Coper has an area of 202 km^2. Specimens (five males and one female) were collected at night between 25 October 2009 and 30 October 2009 and transported to Palmira, Colombia, for acoustic recordings and experiments using a custom-built acoustic room.

Sound recordings and analysis

Sound recordings were obtained using a 1/8 in. Bruel & Kjaer Type 4138 condenser microphone, connected to a Brüel & Kjaer 2633 preamplifier (Brüel & Kjaer, Nærum, Denmark). Data were stored in a notebook computer using an NI USB-6259 M Series USB board (National Instruments, Austin, TX, USA) and LabVIEW version 9 (32 bit) 2009 software interface (National Instruments). The microphone's sensitivity was calibrated using a sound-level calibrator (Bruel & Kjaer, 4231) and a custom-built LabVIEW set-up. In the field, the acoustic room consisted of a normal concrete room of 2.0 m × 2.0 m × 2.4 m with all the walls and roof covered with professional acoustic sound treatment studio foam (Hyped up Acoustics, Hemel Hempstead, UK). Specimens were housed in individual cylindrical cages (5 cm diameter, 15 cm height) made of metallic screen. The cages were hung from the roof of the recording room using a thin 1.3-m thread. This arrangement allows the caged specimen to be suspended away from the walls, floor and roof of the room by more than 1 m, and therefore minimize sound reflections. The microphone was positioned posterior to the specimen, 10 cm away from the stridulatory apparatus using a long-range movable arm. Recordings were obtained at 512 k samples/s. Recorded signals were analysed using a signal processing tool in Matlab (Version 7.8.0347, R2009a; The MathWorks, Inc., Natick, MA, USA) and a custom-designed Matlab code.

Recordings of wing motion

Stridulatory movements were recorded at 1000 frames per second using a high-speed video camera NAC Hi-DCam II (Model A504kc, NAC Image Technology, Simi Valley, CA, USA). Video and sound data were edited and synchronized using VirtualDub V1.9.11 (http://www.virtualdub.org/) and Adobe Premiere Pro CS4 (Adobe Systems Incorporated, San Jose, CA, USA) and analysed frame by frame using the software ImageJ V1.42 (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA).

Anatomical measurements

For morphological measurements, specimens were preserved frozen (− 24°C) in individual vials; a small amount of formalin was injected in the body to stop *rigor mortis* and help to preserve colouration. The stridulatory file has been shown to have taxonomic and acoustic importance (Walker and Carlysle 1975; Montealegre-Z 2005), and we associate the organization of file teeth with the song produced. Stridulatory structures were measured from scanning electron microscope (SEM) pictures. The wings of two

specimens were dissected and placed directly in the microscope sample chamber without the need of gold or carbon coating. Measurement of inter-tooth spacing was carried out using the dimension tool of Corel Draw X4 (Corel Inc., Ottawa, ON, Canada) and SEM photographs as indicated by Montealegre-Z and Mason (2005) and Montealegre-Z et al. (2006). Wing venation nomenclature follows Bethoux (2012).

Results

The calling song of five males was recorded in lab conditions using ultrasound-sensitive equipment. The call of one male elicits singing in others but no particular synchrony was noticed. The following acoustic measurements are the mean averages taken from five males (recorded at 24°C and six calls per individual). Each call of *A. arachnoides* is a train of 30–42 discrete pulses, lasting 47.3 ± 6.1 ms (Figure 2(A)). In a bout of singing lasting several minutes, single pulse trains are repeated irregularly every 6–28 s, with the mean centred at 10.7 ± 6.2 s. Pulse amplitudes gradually increase reaching a maximum towards the end of the last 1/3 and decrease during the last 1/4 (Figure 2(A)). Each discrete pulse lasts 64.6 ± 27.8 µs (Figure 2(B)), with a pulse period of 1.81 ± 0.85 ms, pulses recur at an average rate of 737 ± 174 pulses per second. The number of cycles in each discrete pulse varies between 4 and 6 (Figure 2(B)). Output energy is centred at 74.2 ± 7.7 kHz (Figure 2(C)), with no significant energy below 50 kHz. The quality factor ($Q_{3\,dB}$) measured from the spectrum was relatively low; 3.42 ± 0.58 across all males recorded. Sound level measured at 10 cm ranges between 65 and 115.5 dB (SPL re 20 µPa).
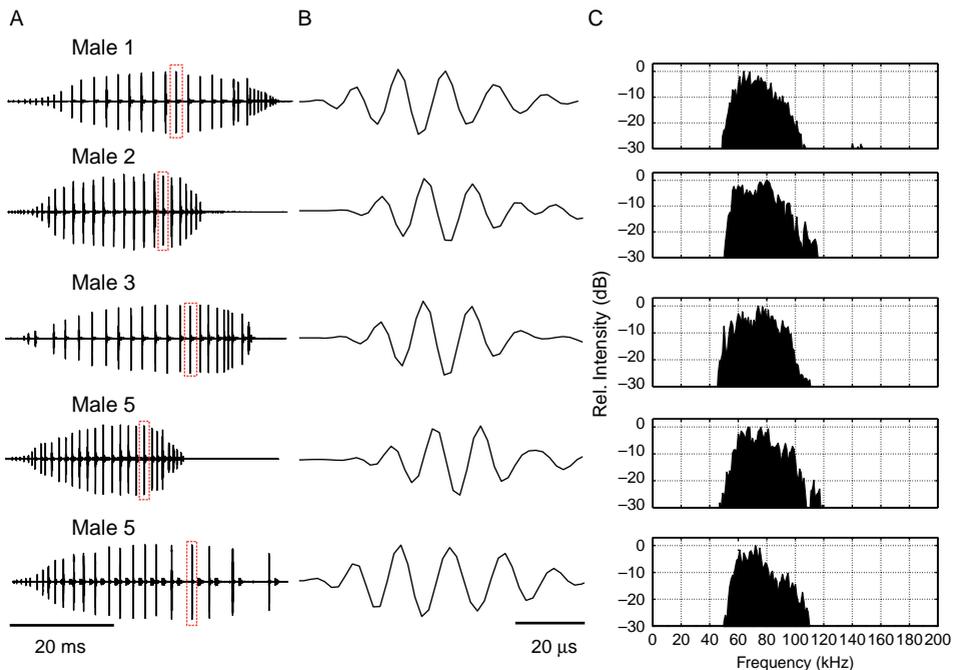

Figure 2.   Acoustic analysis of call parameters measured from five males. Column (A): complete call or train of pulses. Column (B): close-up of a discrete pulse (for each specimen the pulse encircled in the dashed box). Column (C): power spectra of the calls in A.

High-speed video reveals that, in contrast to most katydids, the major amplitude components of the call are produced during the opening stroke of the wings (Figure 3, see Supplementary Material). During the opening phase, the scraper strikes the file teeth with an average speed of 14.24 mm/s to produce the call in a reverse manner. This opening movement is discontinuous because the wings briefly pause after the production of each discrete pulse in the call, that is during the silent intervals of the call (Figure 3). The observed sequence of small amplitude pulses occurring at the start of the syllable (Figure 3) is
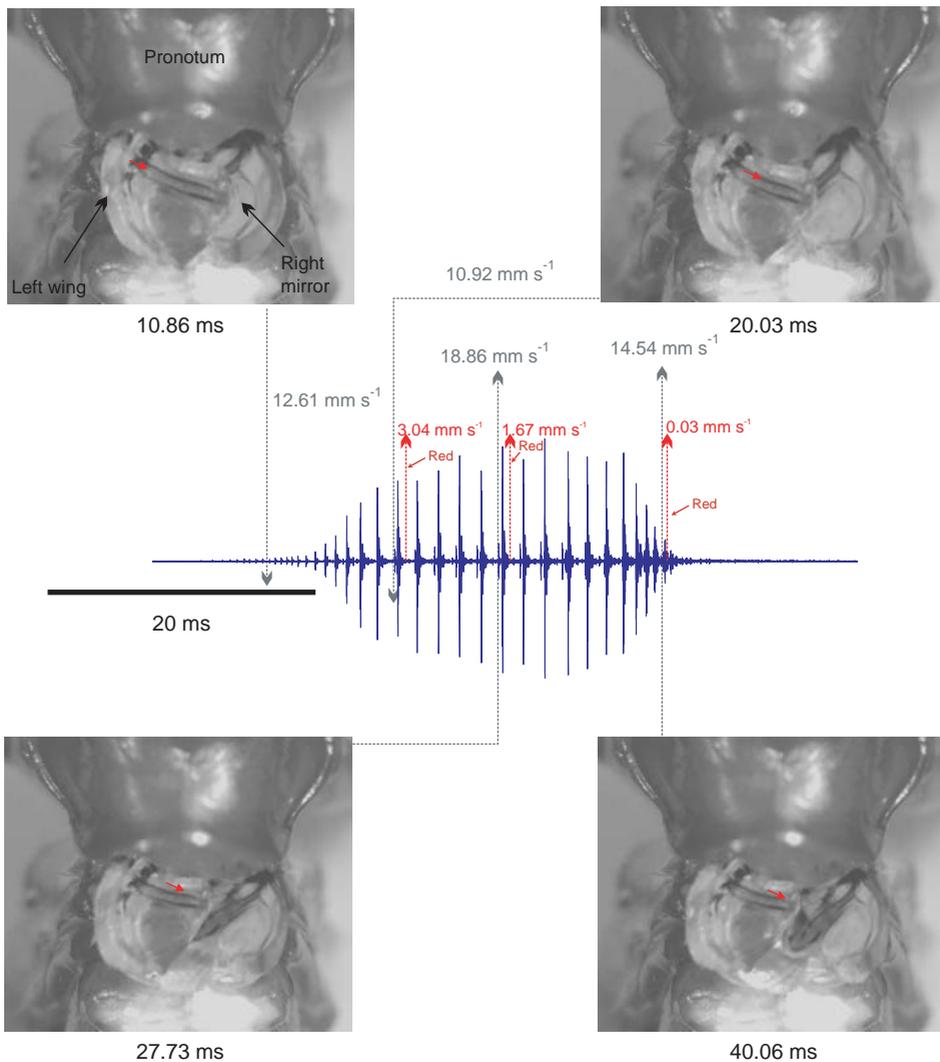
Figure 3. Four successive frames from high-speed video correlate opening wing positions with the pulse train of *A. arachnoides*. Insect faces to the top. The red arrow on the left wing depicts scraper position observed through transparency of the left tegmen. Broken lines match picture and wing velocities to the oscillogram. The wings develop a velocity before each production of a pulse (grey dashed lines) and then become almost still over the interval of pulse generation (red dashed arrow). The time of each frame is indicated below the pictures. To view a colour version of this figure, please see the online issue of the journal.

produced when the scraper strikes some of the small and closely spaced teeth located in the basal end of the file (Figure 4(B)). Note that this group of teeth also shows lower variance in spacing than the larger teeth (Figure 4(C)). The number of functional teeth in the file (nearly 35–40, see file description below) suggests that each discrete pulse results from a single tooth strike, and that the oscillation produced by it decays before the next tooth is struck.
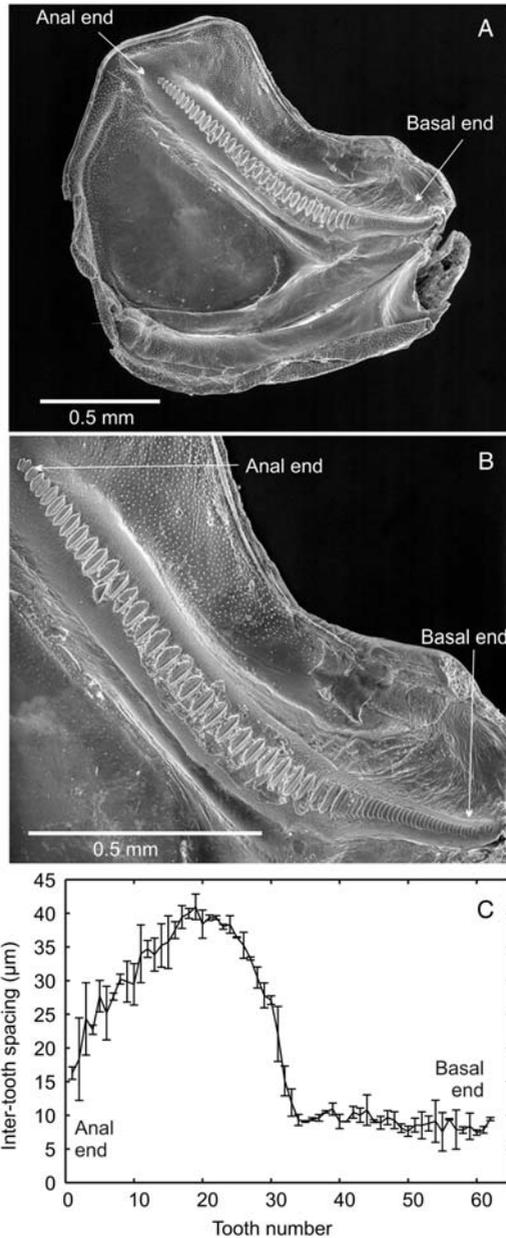

Figure 4. The stridulatory file of *A. arachnoides*. (A) The entire left tegmen in ventral view showing the stridulatory file and mirror; (B) a close-up view of the file; (C) average inter-tooth spacing measured from two males. Error bars indicate one standard error.

Discussion

Our acoustic analysis supports the hypothesis that the type specimen of *A. arachnoides* in life produced a calling song in the ultrasonic range. As predicted from equation (1) (ca. 83 kHz): we measured f_c values between 66.5 and 81.5 kHz in the population recorded. We also confirm that at such extreme frequencies, the call envelope consists of a train of discrete pulses separated by silent intervals (opposite to a continuous pulse, which is highly associated with low frequencies and moderate ultrasounds < 40 kHz).

The call of *A. arachnoides* is produced unusually during the opening phase of the wings, a case of reverse stridulation (Montealegre-Z 2012). The wings are opened in a discontinuous way causing the scraper to pause behind each file tooth, which results in the silent intervals observed between discrete pulses. Such scraper pauses are also well documented in other katydids singing at extreme ultrasonic frequencies but producing the call in a conventional way during the closing phase (Montealegre-Z et al. 2006). Scraper pauses are believed to be essential to produce the most favourable scraper deformation required to accumulate potential mechanical energy (elastic energy). Once the scraper has reached maximum deformation, it is released from a tooth and springs forwards at elevated speeds, contacting the next available teeth at elevated strike rates (ca. 66,000–81,000 teeth/s, in *A. arachnoides*, but deformation occurs during the opening phase). The observed discontinuous scraper motion of *A. arachnoides* does not require the systematic organization of file teeth observed by several authors in other species, producing sustained pure tone pulses by contacting all file teeth in sequence (Bennet-Clark 2003; Montealegre-Z and Mason 2005; Prestwich and O'Sullivan 2005; Gu et al. 2012; Montealegre-Z 2012). Instead, the file in these insects shows an unusual increment and decrement in inter-tooth spacing (Figure 4(C)), which indicates that file arrangement is not adapted for a continuous sweep and that the systematic organization of file teeth is not as important when scraper deformation is used to produce discrete pulses.

The implementation of silent intervals is seen as an adaptation to enlarge the ideal continuous pulse of very short duration that otherwise would have been produced if the file teeth were struck in a continuous and sustained manner at elevated speed (Montealegre-Z et al. 2006). Silent intervals are therefore artefacts that produce longer calls, but cause the spectrum to widen. In order to produce a continuous pulse at 74 kHz, the scraper should move with a speed of ca. 2310 mm/s (assuming an average inter-tooth spacing of ca. 31 μm), an unobtainable wing speed that would theoretically result in a pulse of only 0.8 ms in duration, not suitable to attract distant females. Therefore, the scraper pauses and the ensuing silent intervals 'artificially' produce a larger call.

Although most katydids produce the main amplitude components of their calls during the closing phase of the wings, a few species do the opposite. Reverse stridulation has been reported in a few European species of the genera *Phaneroptera* (Phaneropterinae) and *Uromenus* (Bradyporinae) (Heller 1988), and in all species of the neotropical genus *Ischnomela* (Montealegre-Z 2012). Montealegre-Z (2012) discussed the mechanical advantages of producing sound during the closing phase of the wings (the mechanism used by most katydid species) and contrasted these with those of reverse stridulation. A working hypothesis is that a scraper moving basally on the file offers an even control of stridulation, as the file's basal end provides an obligatory stop at the body. The silent phase (the opening), on the other hand, offers no such obligatory halt; wing halt on opening must be controlled by sensory feedback or by some mechanical stopper. Most of the species producing the call during the opening phase exhibit a scraper stopper or another file modification in the anal margin of the file (Heller 1988; Montealegre-Z 2012), but these are not observed in *A. arachnoides*.

The closing phase of the wings during stridulation is produced by lowering the tergum (indirect muscles), whereas the opening phase depends on pulling against the subalar and basilar sclerites in the wing hinges while rotating the tergopleural arm on each side (Kutsch and Huber 1989). Because during flight most of the aerodynamic forces are produced during the down stroke (Alexander 2002), it is expected that major sound output is produced by contraction of the muscles causing the down stroke (direct muscles) of the wing during flight, as those generate more output power than the upstroke muscles. But surprisingly, during stridulation of most katydids, these powerful direct muscles do not control the closing, but the opening phase. In *A. arachnoides*, the output power produced by the direct muscles during the opening phase seems to be as effective as that produced by the indirect muscles in other related species (producing sound during the closing phase). In *A. arachnoides*, the direct muscles controlling the opening phase enhance scraper deformation, scraper-tooth impacts and loudness.

As sound attenuation scales positively with increasing frequency, the emitted male call at 74 kHz should be loud enough in order to attract distant females. Ultrasound suffers large excess attenuation in rainforest environments (Griffin 1971; Marten and Marler 1977; Richards and Wiley 1980; Lawrence and Simmons 1982; Römer and Lewald 1992; Römer 1993). Such communication signals are therefore theoretically not suited to long-range attraction (Römer 1993). It is then expected that, in order to defeat the problem of excess attenuation, the emitted signal amplitude should be high and/or the female receptors should be ultrasensitive to detect vanishing ultrasonic energy. An alternative hypothesis is that some ultrasonic species use short-range communication in habitats favourable to the transmission of their signals, which might reduce the risk of detection by distant eavesdropping predators. However, field observations suggest that male *A. arachnoides* sing from trees (2–3 m elevation), and that females can detect the call from the ground, climb the tree and locate the singing male.

Here, we have evidence that ultrasonic signalling in *Arachnoscelis* involves sound levels above 110 dB (10 cm dorsal from the animal) which are considered unusually loud for such a small insect (Bennet-Clark 1998: Sueur et al. 2011). The mechanism of scraper distortion is therefore a good candidate to be responsible for the high sound intensity observed in the calls, as elastic deformation is associated with strong impacts and high-energy dissipation.

Supplemental movie caption

A stridulating male of *Arachnoscelis arachnoides* recorded at 1000 fps. The camera was focused on the stridulatory area of the insect. Video frames are synchronized with sound data recorded at 512 k-samples per second. Supplemental material for this article is available via the supplemental tab on the article's online page at http://dx.doi.org/10.1080/09524622.2013.816639.

Acknowledgements

Note

1. These authors contributed equally to this paper.

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