Generation of extreme ultrasonics in rainforest katydids

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Summary

The calling song of an undescribed Meconematinae katydid (Tettigoniidae) from South America consists of trains of short, separated pure-tone sound pulses at 129 kHz (the highest calling note produced by an Arthropod). Paradoxically, these extremely high-frequency sound waves are produced by a low-velocity movement of the stridulatory forewings. Sound production during a wing stroke is pulsed, but the wings do not pause in their closing, requiring that the scraper, in its travel along the file, must do so to create the pulses. We hypothesize that during scraper pauses, the cuticle behind the scraper is bent by the ongoing relative displacement of the wings, storing deformation energy. When the scraper slips free it unbends while being carried along the file and its deformation energy contributes to a more powerful, higher-rate, one-tooth one-wave sound pulse, lasting no more than a few waves at 129 000 Hz. Some other katydid species make pure-tone ultrasonic pulses. Wing velocities and carriers among these pure-tone species fall into two groups: (1) species with ultrasonic carriers below 40 kHz that have higher calling frequencies correlated with higher wing-closing velocities and higher tooth densities: for these katydids the relationship between average tooth strike rate and song frequency approaches 1:1, as in cricket escapement mechanisms; (2) a group of species with ultrasonic carriers above 40 kHz (that includes the Meconematinae): for these katydids closing wing velocities are dramatically lower and they make short trains of pulses, with intervening periods of silence greater than the duration of the pulses they separate. This signal form may be the signature of scraper-stored elastic energy.

Key words: Orthoptera, Tettigoniidae, ultrasound, bioacoustics, elastic, stridulation, resilin, katydid.

Introduction

Arthropods produce sound by a diversity of mechanisms including: airstream modulation (Dumortier, 1963; Nelson, 1979); percussion (Stewart and Maketon, 1991); stick-and-slip (Patek, 2002); 'tymbalation' (Bennet-Clark, 1999), and the most common method: stridulation. The last three involve a frequency multiplier by which the slower oscillatory movements of body parts are converted into the much higher frequency oscillations of sound-radiating structures (Bennet-Clark, 1995; Michelsen, 1998). Here we present evidence that some katydids (Insecta: Orthoptera: Tettigoniidae), have evolved to produce signals at high ultrasonic frequencies by making use of a previously unrecognized form of tegmino-tegminal stridulation, one which incorporates something of the elasticity of a 'stick-and-slip' mechanism (Patek, 2002), to create a 'compound frequency multiplier'. This mechanism achieves dramatically higher song frequencies at, paradoxically, lower wing velocities than those of conventional stridulation.

Most Ensifera (crickets and katydids) generate their predominant sound components on the closing stroke of the forewings (Pasquinelly and Busnel, 1954; Morris and Pipher, 1967; Heller, 1988; Otte, 1992). Almost all cricket spp. call with nearly pure tones of 3–8 kHz (Leroy, 1966; Bennet-Clark, 1989; Otte, 1992). Many species of katydid also call with pure tones, but over a much wider range of carrier frequency (Heller, 1995; Morris et al., 1994). Many katydid carriers are ultrasonic (Pierce, 1948; Suga, 1966; Montealegre-Z and Morris, 1999) and some species utilize high, >40 kHz, pure-tone ultrasonics (Morris et al., 1994; Montealegre-Z and Mason, 2005).

Stridulation of crickets: escapement

Crickets employ resonant stridulation (Elsner and Popov, 1978). Each nearly symmetrical forewing has a tuned forewing radiator (Nocke, 1971). To avoid destructive interference, oscillation of the left wing radiator is brought into phase with that of the right by the 'push' of each tooth upon a special region behind the scraper (Bennet-Clark, 2003). The oscillation of the sound-radiating structures on the two wings then controls the advance of the scraper along the file in a manner similar to

the escapement mechanism of a clock (Elliot and Koch, 1985; Koch et al., 1988) and so gives a 1:1 relation between each radiated sound wave and each contacted file tooth (carrier frequency (f_c)=tooth impact rate).

Pure-tone stridulation of katydids: non-escapement

For katydids producing pure-tone calls, recent evidence points to important departures from the mechanism of cricket sound production (Montealegre-Z and Mason, 2005). These katydids generate sustained wavetrains or trains of short pure-tone pulses. (These pulses are 'sustained' in the sense that like the pulses of crickets they are kept from decaying by input of additional energy.) Unlike crickets, strongly asymmetric forewings are almost universal in katydids (Dumortier, 1963). Their left forewing appears damped and probably has a reduced role in sound radiation (Montealegre-Z and Mason, 2005). And advance of the scraper along the katydid file will not be regulated by sound-radiating oscillations of wing membranes (as in escapement). Rather the insect must maintain a wing velocity in relation to file tooth density, independent of the radiator, to achieve the pure tone. In other words, for a katydid to generate a pure-tone carrier, the wing (or the scraper) must either pass at constant velocity over uniformly spaced teeth, or the scraper must change velocity to offset changing tooth density: the time taken for the scraper to travel from one tooth to the next must be made constant (Montealegre-Z and Mason, 2005; Prestwich and O'Sullivan, 2005).

Several species of crickets studied to date, in addition to some katydids that use pure-tone sounds, have files whose tooth densities gradually decrease basad. These increments in intertooth distances combine with increments in the relative velocity of the closing tegmina, to yield a carrier dominated by one frequency (Montealegre-Z and Mason, 2005; Prestwich and O'Sullivan, 2005). Here we present data, from katydids producing such (tonal) calls at extremely high frequencies, indicating that the speed of wing movement alone cannot account for the tooth impact rate. Our data suggest a novel stridulatory mechanism in which tooth impact rate is uncoupled from the wing speed, to allow the production of high-frequency sound by brief intermittent bursts of high-speed scraper movement.

Scraper flexibility and velocity

The scraper of crickets and katydids is a flexible structure (Bennet-Clark and Bailey, 2002; Bennet-Clark, 2003; Montealegre-Z and Mason, 2005; Prestwich and O'Sullivan, 2005). During its catch and release from each file tooth, it experiences minor changes in speed (Prestwich and O'Sullivan, 2005), suggesting a brief bending then spring-back, moving relative to the rest of the wing. Hence, depending on the compliance and length of the scraper flexible area (see below), the scraper may move with velocities different from that of the tegmina (the scraper's driving force). The work described here concerns katydids that have evolved very high carrier frequencies whose scraper appears to have been elaborated for greater flexibility. In a manner comparable to the stick and slip mechanism of spiny lobsters (Patek, 2001), where packets of energy are stored by elastic tissue during a stick phase and later released to contribute to the sound production of a slip phase, we propose that the bending of the flexible scrapers of these katydid species store energy that, upon release, propels the scraper with elevated velocity across file teeth.

Materials and methods
Specimens

Fieldwork in lowland rainforests (Pacific and Amazon) in Colombia and Ecuador between 1996 and 2003 resulted in the collection of six adult (four males, two females) specimens of an undescribed species of *Arachnoscelis*. Only two males were recorded and are distinguished here by year as 96 and 03: one of them contributed to our high-speed video analysis (see below). One was taken at night from understorey vegetation on the Pacific coast of Colombia, in the rainy coastal lowlands in Western Valle del Cauca, the other from dense forest on the nearby island of Gorgona. This species belongs to the subfamily Meconematinae. The remarkable nature of this insect's high frequency pure-tone song led us to develop the model we suggest here.

A number of other species were chosen for study, all also exhibiting tonal carrier frequencies. They are intended to represent a wide range of carrier frequencies from the low audio to the high ultrasonic. Their localities and critical features of their stridulation are listed in Table 1. Some were chosen because of the availability of data on song structure, wing closing velocities, tooth density, etc. A few, *Phlugi*s from the Amazon basin of Colombia and an unnamed species of the pseudophylline *Myopophyllum* from Ecuador, were available as live specimens for high-speed video analysis. Some species were also selected for either their known high ultrasonic carriers or their known low-frequency carriers.

The unavoidably small sample of *Arachnoscelis* n. sp. may raise concern about how typical our measures are of the generating mechanism of this species. Observations of the generation features of *Arachnoscelis* n. sp. recur in the comparative analysis of other species (e.g. *Myopophyllum* n. sp.), and our two specimens match each other closely in their stridulatory behaviour, especially in physical song features relevant to the hypothesis of scraper-based energy, e.g. mean pulse period for one is 2.42 ms (*N*=9 calls) and for the other 2.00 ms (*N*=19 calls). Confidence is also increased where, in the absence of living specimens, similar patterns of stridulation show compatible parameters of wing movement (see Results); also by the fact that the measurements of the sound generator of both male individuals fit the curve of f_c *vs* mirror dimension at ~130 kHz (Montealegre-Z, 2005).

Recordings of sound and wing motion
Sound recordings

The extreme ultrasonic nature of the calls of *Arachnoscelis* n. sp. were discovered at night in a hotel room in Cali Colombia, using a hetrodyning bat detector (U30, Ultra Sound

Table 1. *Morphological, physical and behavioural attributes of katydid males of several species that use pure-tone calling song*

Species	N	Locality	Body size (mm)	TS (μm)	TD Teeth (mm^{-1})	CWV (mm s^{-1}) Observed	CWV (mm s^{-1}) Estimated	SV (mm s^{-1})	TSR1 (TD×CWV)	TSR2 (TD×SV)	f_c (kHz)
1. *Panacanthus pallicornis*	8	Co: Bosque de Yotoco	38.4±2.8	24.0	35	120.0±1.8	112.0±2.6	122.3±1.5	4200.0	4280.5	5.0±0.3
2. *P. cuspidatus*	2	Ec: Napo, Jaguar	49.0±3.5	16.0	60	180.0±3.0	178.6±2.1	190.2±08	10800.0	11400.0	11.0±0.5
3. *Championica walkeri*	5	Ec: Tinalandia	28.6±3.1	10.0	54	170.7±2.2	170.0±1.8	162.7±2.7	9234.0	8785.8	13.3±0.2
4. *Copiphora rhinoceros**	3	CR: La Selva	42.5±3.0	13.6	58	NA	152.0±0.6	148.2±1.2	8584.0	8595.6	8.7±1.1
5. *Co. cf gracilis*	2	Co: Amazon Amacayacu	36.5±2.1	6.4	147	118.6±4.1	112.0±2.8	107.0±4.8	15895.0	15729.0	16.5±0.8
6. *Co. gracilis**	1	Ec: Napo, Primavera	33.7	6.0	105	NA	214.3	196.3	20265.0	20611.5	20.6
7. *Metrioptera sphagnorum* (LF mode)	2	Ca: ON, Upsala	20.1±1.5	14.9	67	59.1±2.8	50.0±1.3	256.3±2	3959.7	17172.1	17.2±0.7
8. *Eubliastes aethiops*	2	Co: Gorgona island	49.6±1.3	20.5	51	151.1±1.4	157.3±0.7	443.0±1.6	7701.0	22593.0	21.6±0.9
9. *Eu. chlorodictyon**	1	Co: Valle, Bajo Calima	38.1	14.7	75	NA	322.0	400.7	24150.0	30052.5	27.3
7. *Metrioptera sphagnorum* (HF mode)	2	Ca: ON, Upsala	20.1±1.5	7.9	125	78.6±3.8	65.1±3.2	264.0±2.8	5642.0	33000.0	34.0±1.2
10. '*nr. Loboscelis* sp. 1'	5	Ec: Tinalandia	24.2±1.7	8.0	110	237.1±2.4	344.0±1.8	324.0±0.9	26081	35640.0	35.0±2.3
11. '*nr. Loboscelis* sp. 2'	2	Co: Valle, Bajo Calima	27.1±1.6	8.6	117	298.0±12.1	332.0±2.2	344.0±1.1	34866.0	40248.0	40.7±1.1
12. *Uchuca halticos*	2	Ec: Napo, Jaguar	22.0±1.1	6.0	168	187.5±2.2	233.3±3.6	243.0±2	31584.0	40824.0	42.3±2.1
13. *Phlugis* sp.	1	Co: Valle, Cali, km 18	14.0	11.8	90	46.2	51.6	561.0	4140.0	50490.0	47.6
14. *Drepanoxiphus angustelaminatus**	1	Pa: Barro Colorado	20.0	11.0	90	NA	25.6	803.0	2340.0	72270.0	73.0
15. *H. ecuadorica**	1	Ec: Napo, Jaguar	28.0	10.0	117	NA	16.4	658.0	1918.8	76986.0	65.8
16. *Haenschiella* n. sp.*	1	Ec: Napo, Jaguar	27.0	16.0	64	NA	23.7	1680.0	1536.0	107520	105.5
17. *Myopophyllum* n. sp.	2	Ec: Napo, Cosanga	31.9±2.3	20.0	48	121.5±4.9	122.6±17.4	1310.0±10	5884.8	62880.0	65.5±7.7
18. *M. speciosum**	4	Ec: Napo, Baeza	33.3±1.5	24.0	41	NA	37.9±1.6	1992.0±18	1558.0	81672.0	83±4.8
19. *Arachnoscelis* n. sp.	2	Co: Gorgona Island	13.0±2.2	9.0	100	12.8±1.4	24.3±4.3	1161.0±18	1300.0	117400.0	128±6.2

Data organized by congeners. Average temperature 23.4±2.5°C.

TS, tooth spacing; TD, tooth density; f_c, carrier frequency; CWV, avarage closing wing velocity measured with high speed video (HSV); SV, scraper velocity; TSR, tooth strike rate calculated based on (1) CWV and (2) SV. Body measured as the midline from fastigium to last abdominal tergite.

*Data estimated from acoustic and anatomical measurements (no video). Co, Colombia; Ec, Ecuador; Pa, Panama; CR, Costa Rica; Ca, Canada.

NA, HSV recordings were not available to measure CWV.

M. sphagnorum has been included twice because this species uses two modes of stridulation: audio and ultrasonic (Morris and Pipher, 1972).

Advice, Wimbledon, London, UK) on the caged insect. This (1996) specimen was later lab-recorded in Canada, free field, with a 1/8″ Brüel & Kjær (B&K, Naerum, Denmark) condenser microphone (type 4138), clamped and directed vertically; microphone output went to a B&K 2606 amplifier, thence to a Racal (Store-4DS) instrumentation tape recorder (60″ s^{-1}). Recordings, slowed 8×, were transferred to a computer *via* a PCMCIA digitizing card (Ines i616) sampling at 200 kilosamples s^{-1}, high-pass filtered at 2 kHz. A power spectral density Fast Fourier Transform (FFT) obtained with Matlab (The Mathworks, Natick, MA, USA), was smoothed (Welch) and expressed in dB, relative to its most intense frequency peak.

For other species where acoustic recordings were available, the methods of recording and sound analysis are found in the respective literature: *Myopophyllum speciosum*, *Haenschiella* spp. and *Drepanoxiphus* (Morris et al., 1994); *Championica walkeri* and *Eubliastes chlorodictyon* (Montealegre-Z and Morris, 1999); *Copiphora rhinoceros* (Morris, 1980); *Panacanthus* spp. (Montealegre-Z. and Morris, 2004; Montealegre-Z and Mason, 2005); *Uchuca haltikos* (Montealegre-Z and Morris, 2003).

The remainder of mentioned species (*Metrioptera sphagnorum*, *Myopophyllum* n. sp., *Copiphora gracilis* and *C.* cf *gracilis*, *E. aethiops*, 'nr *Loboscelis* spp.' and *Phlugis* sp.) were recorded by the following procedure: the output of a 1/4″ microphone (B&K 4135) on a (B&K 2204) sound level meter was digitized (Tucker Davis, System II, Gainesville FL, USA) at 100 or 170 kilosamples s^{-1}. Analysis of acoustic data utilized DADISP 4.1 (DSP Development Corp., Newton, MA, USA) or Matlab software. The calling songs used in all these analyses were recorded in a sound-attenuating room at the University of Toronto (UT) at Mississauga; the average temperature of this room was 23.5°C.

Zero-crossing analysis

Songs were analysed with the Zero-crossing (ZC) module for Canary software (Laboratory of Ornithology, Cornell University). Zero-crossing (version 5) is freely available from Dr K. N. Prestwich (http://www.holycross.edu/departments/biology/kprestwi/ZC). Zero-crossing v.5 calculates the instantaneous frequency on a cycle-to-cycle basis. The software module starts counting waves at the first point in the record where the microphone voltage or sound pressure crosses zero. Two such crossings later is the start of the second cycle, and so on. Thus, the time separating three ZC events corresponds to the wave period (*P*). Since one cycle has two ZC events, the program calculates *P* for both half cycles and then an average *P* of the wave is calculated; therefore, 1/*P* is the average frequency of this wave. The ZC program then starts with the first zero-crossing event of the next cycle and continues its calculation process until the frequency of each wave has been measured. These features make the program appropriate for analyzing pure-tone signals (Bennet-Clark and Bailey, 2002; Bennet-Clark 2003; Prestwich and O'Sullivan, 2005). Other details of ZC analysis are provided in the ZC v.5

user's manual, from which the above description of the program's capabilities has been taken.

Wing motion

Recordings of wing movements were made using high-speed video (HSV) (Redlake Motionscope PCI1000s, San Diego, CA, USA). This system was synchronized with a computer data acquisition board (National Instruments BNC-2110, Austin, TX, USA; 16 bit) using MIDAS software (version 2.0 Xcitex Inc., Cambridge, MA, USA) for simultaneous recording of sound production. Recordings were acquired at 1000 frames s^{-1}, and acoustic data sampled at rates of 200 or 300 kilosamples s^{-1}. Insects were free on a wooden perch, the camera focused on either the stridulatory field or on the file and scraper (from posterior aspect). A microphone (B&K), directed at a specimen for sound recording, 1/8″ (4138) or 1/4″ (4939), fed either a B&K 2606 amplifier or B&K Nexus (Type 2690). Video recordings were analysed frame-by-frame, using MIDAS software. From these recordings we measured the closing wing velocity (*CWV*) and estimated the length of file traversed by the scraper during sound production. Only the 2003 specimen of *Arachnoscelis* n. sp. was examined by HSV.

Stridulatory file and scraper

Files were sputter-coated with gold and viewed on a Hitachi Scanning Electronic Microscope at the Department of Zoology, UT. Measurements of file dimensions were obtained from digitized SEM photographs using the dimension tool of the drawing program Corel Draw (ver. 11, Corel Inc., Ottowa, ON, Canada). Inter-tooth distances were measured from the tip of one tooth to the tip of the next (see Montealegre-Z and Mason, 2005) and tooth density (TD) was calculated as the number of teeth divided by the length of the functional region of the file.

The functional scraper of tettigoniids is an acute upturned carina situated at "the hind margin of the right fore wing" (Ragge, 1955), shaped to insert between the file teeth of the left wing. This carina sits at the extreme margin of the region, posterior to the radial and cubital veins, modified in males for sound generation. Vein homologies are unclear (Jost and Shaw, 2006), but the first vein encountered behind the scraper, has been termed here the third Anal, following Desutter-Grandcolas (Desutter-Grandcolas, 2003) (see Results) and the cuticular region in between (from scraper to A3), is referred to here for convenience as the 'scraper shelf' to suggest its rather low mass as a projection relative to the sclerotized and thickened third Anal vein to which it attaches.

This scraper shelf region was examined for at least one specimen of each of the species listed in Table 1 using both microtome sectioning and electron microscopy. For the microtome, parts of the tegmina were dissected and then embedded in Spur's solution. Transverse sections were treated with dibasic staining (Di Sant' Agnese and De Mesy Jensen, 1984). Samples were mounted on slides, observed and then measured under a light transmission microscope. For scanning electron microscopic examination, the right tegmen of a fresh or liquid-preserved specimen was sectioned across the scraper

with a razor blade as indicated (Montealegre-Z and Mason, 2005) and prepared as above.

Wing and scraper velocities

Strain is created between scraper and file teeth by opposing muscle-generated shear forces (Josephson, 1985). During wing closure the scraper should move at velocities comparable to those of the wing, experiencing minor deceleration and acceleration each time a tooth is contacted and/or the scraper released. This condition is common in species with relatively short scrapers, which permit the teeth to be contacted in sequence (Montealegre-Z, 2005). However, in species where the scraper's width (see Results) and flexibility is greater, it may move at velocities higher or lower than that of the wing. We therefore distinguish scraper velocity (SV) from CWV, and argue below that for katydid species producing pure tones and extreme ultrasonic frequencies, a modified form of stridulation occurs in which scraper and wing velocities are intermittently uncoupled (in contrast to the escapement model). Our hypothesis predicts that SV should be higher than CWV during sound production in species using extreme ultrasonic frequencies.

Given tuned wings and continuous contact between file and scraper (basic assumptions of an escapement mechanism), the oscillation period of radiated sound corresponds exactly to the time the scraper spends between two teeth. If inter-tooth distances are known, one can estimate the scraper's instantaneous speed (the speed required for the scraper to travel between two teeth). We determined the time spent by the scraper travelling between two teeth ($=P$) using zero-crossing (ZC) analysis of recorded songs (Montealegre-Z, 2005), as the inverse of the instantaneous song frequency (see details above). These time values (oscillation periods) are converted to instantaneous scraper velocities by dividing by the inter-tooth distance for every pair of teeth. Instantaneous SV can be averaged over the entire song to give a measure that allows comparison with CWV. ZC analysis can also be used to relate events associated with scraper behaviour to the waveform (Prestwich and O'Sullivan, 2005).

We measured CWV from HSV recordings (observed CWV) and compared it with average scraper velocities estimated as described above. This procedure was conducted in those species for which measurements of CWV (based on HSV) were available: *P. pallicornis*, *P. cuspidatus*, *C. walkeri*, *Co.* cf. *gracilis*, *E. aethiops*, *M. sphagnorum*, 'nr *Loboscelis* spp.', *U. haltikos*, *Myopophyllum* n. sp., and *Arachnoscelis* n. sp. (only the 2003 specimen) (see Table 1).

To evaluate the mechanism of stridulation we compared the frequency of produced sound with the tooth-strike rate (TSR) of the scraper. In a conventional (escapement) stridulatory mechanism, the TSR matches the sound frequency and will be determined by the product of CWV and the number of teeth per unit distance of file (TD). Also, average SV and CWV should be similar and the TSR calculated using either of these should yield similar values that match the sound frequency, f_c.

A discrepancy between CWV and average SV may arise if wing movement during stridulation is discontinuous, as is known to be the case in many katydids producing nonresonant songs (Heller, 1988; Heller and von Helversen, 1993). In this case CWV would be underestimated as the measured wing-stroke duration would include pauses in wing movement. Alternatively, a difference in CWV and average SV could arise due to movement of the scraper relative to the wing, such that with continuous wing movement the scraper alternately bends, while remaining stationary as the wing moves, then releases to travel over a succession of file teeth at elevated velocity relative to the wing (Morris and Pipher, 1972). In this case, SV being calculated on the periods of successive cycles of sound production (excluding silent intervals), it would yield a higher value than CWV.

The songs of all (known) katydid species producing pure tones at high ultrasonic frequencies consist of trains of several pulses produced on a single wing stroke, but with the pulses very short and set apart from each other, typically by silent intervals much longer than the pulses themselves (see below). (For convenience these are referred to here as SSTP: short spaced tonal pulses.) Therefore, to analyse the relationship between TD, CWV, SV and f_c, we must (1) distinguish between continuous and discontinuous wing movement and (2) identify in song recordings which cycles of radiated sound correspond to tooth engagements rather than to free oscillation of sound radiating structures. Determining the nature of wing movement (1) will provide the correct time value for calculating wing velocity. Identifying driven oscillations in the recorded sound (2) will indicate the number of file teeth involved in sound production.

Identification of driven oscillations

For trains of pulses, we estimated how many teeth of the file are used (to make driven oscillations), by summing all the waves (rising and sustained) of all the pulses in a train. Oscillations, coinciding with the rising and sustained part of each wave train, are produced when the scraper is driven along the file to generate radiator oscillations. Free decay follows the driven portion of the waveform and might occur with both structures still in contact, or as both structures experience total disengagement (Bennet-Clark and Bailey, 2002; Prestwich and O'Sullivan, 2005). Incrementing and sustained regions were determined, based on ZC analysis of each pulse. For driven oscillations, the instantaneous frequency should be more or less constant, but when the scraper springs ahead from its maximum deflection, or stops, a sudden change in the instantaneous frequency is expected. Oscillations occurring after this change should form part of the free decay (Montealegre-Z, 2005; Prestwich and O'Sullivan, 2005).

A method for estimating CWV in the absence of living specimens

For some species of interest, living specimens were unavailable for HSV recordings (*Co. rhinoceros*, *Co. gracilis*, *E. chlorodyction*, *Haenschiella* spp., *Drepanoxiphus* sp., *M.*

speciosum, see Table 1). Unable to obtain direct measurements of their *CWV*, we derived an estimate of overall wing speed (estimated *CWV*, Table 1) under the assumptions of a conventional escapement mechanism as follows. The duration of sound production in a single wing stroke defined the total time of wing movement. For a one-to-one correspondence between radiated sound waves and tooth engagements by the scraper, the total number of driven oscillations produced on a single wing stroke [that is, the number of sound waves excluding the free decay at the end of within-closure pulses or of the song (Montealegre-Z, 2005; Prestwich and O'Sullivan, 2005)] is equivalent to the number of file teeth involved. Using anatomical data from preserved specimens to obtain the distance represented by this number of file teeth, we estimated *CWV* as this distance divided by the duration of sound production.

Statistical analysis

Including *Arachnoscelis* n. sp., we obtained body and generator measurements (body size, number of file teeth, intertooth distance, tooth density), together with closing wing velocity and song carrier for 19 species of katydid pure-tone singers (Table 1). The range of carrier frequencies used by these species extends from the low audio (<5 kHz) to the high ultrasonic (>100 kHz).

For the 19 species we analysed data on *CWV* and song frequency (f_c) by cluster analysis, using partitioning around medoids (PAM) (Kaufman and Rousseeuw, 1990; Struyf et al., 1997). We analysed the relationship between song frequency and closing wing velocity by ANCOVA with wing velocity as a continuous variable and group membership (high *vs* low frequency) as a categorical variable. In addition, a similar analysis was performed using the product of file tooth density and wing speed (=average *TSR*) as the continuous variable. The purpose of this analysis was not to address questions on the evolution of stridulatory mechanisms. Our goal, rather, was to identify species in which the relationship between wing velocity and sound frequency is inconsistent with a sustained-pulse mechanism. All statistical analyses were done using R software (v2.0.1, www.r-project.org).

Results

Carrier, wing velocity and tooth contact rate

Arachnoscelis n. sp.

Adults of *Arachnoscelis* n. sp. are small: male body length is 12–14 mm (Table 1). The insect's form, a short body set high upon long legs, gives it a spider-like appearance (Fig. 1A) and suggests a predatory lifestyle: in captivity it catches and eats *Drosophila*. The fore and middle limbs bear a series of elongate articulated spines (Rentz, 1995). The forewings are quite reduced and used only for calling (Fig. 1A, Fig. 2); brachyptery is characteristic of the genus *Arachnoscelis* (Nickle, 2002).

Each call of *Arachnoscelis* n. sp. is a train, 10–24 ms in duration, of 5–13 very brief sinusoidal pulses (Fig. 1B). In a bout of singing lasting several minutes, single pulse trains
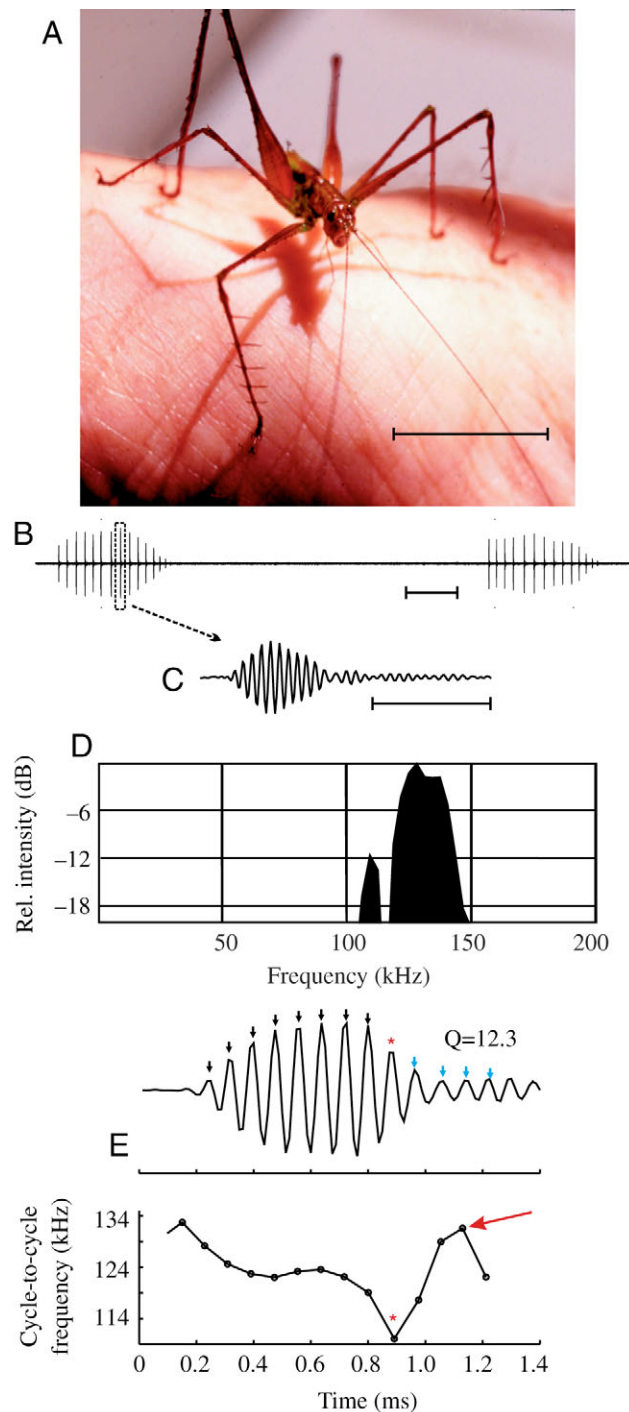

Fig. 1. Features of *Arachnoscelis* n. sp. (A) Male adult insect on human arm (photo by D. E. Klimas); scale bar, ~15 mm. (B) One calling song of two pulse trains, more typically one train; scale bar, 20 μs. (C) High resolution of a mid-train pulse; scale bar, 100 μs. (D) Smoothed power spectrum of calling song. (E) ZC analysis of the pulse in D. Note how the frequency drops for the driven cycles (black arrows), indicating a decrease in velocity, then increases during decay (red arrow), suggesting that the scraper has disengaged from the file (event indicated by red asterisks); note that the file's resonant frequency is normally higher than that of the calling song. Blue arrows show the free decay of the pulse. Q, quality factor.

(rarely two in quick succession as in the figure) are repeated every 1.7 s (at 20–22°C). The average number of pulses in the train was consistently higher (12.7) for the 1996 specimen than for the one (6.7) collected in 2003.

Peak amplitudes achieved in early pulses increment, diminishing in later ones (Fig. 1B), and in mid-train a number of pulses in succession may peak uniformly. Each pulse lasts about 120 μs (Fig. 1C); pulse period was 2.42 ms for the 1996 specimen, 2.00 ms for the 2003 specimen. There are about 7 waves in each pulse (driven oscillations) before decay begins. Pulses recur at an average rate of 588 s^{-1}. Output energy in the 1996 specimen was centred at 122.9 kHz, and for the 2003 specimen it was 128.6 kHz (Fig. 1D). There was no energy below 100 kHz in the spectrum of either specimen.

As determined using ZC analysis (Fig. 1E) for *Arachnoscelis* n. sp., near pulse onset there was a slight increment in the instantaneous frequency coincident with the first few waves. Instantaneous frequency then decreases as the pulse progresses until it jumps up rapidly again as (presumably) scraper disengagement occurs (Prestwich and O'Sullivan, 2005).

Songs of the 2003 specimen, recorded by HSV, gave a *CWV* of 12.8 mm s^{-1}. This is an average velocity over the whole closing interval; one that assumes continuous wing movement. The frame rate of the HSV (1 frame ms^{-1}) is too slow relative to the duration of the sound pulses (120 μs) to reveal wing behaviour during pulses, but the silent interpulse intervals (2.15 ms and 1.83 ms, means for 1996 and 2003 specimens, respectively) were long enough to allow detection of wing movement in these intervals. Comparing wing velocities measured between successive frames, those intervals that included sound outputs gave a lower *CWV* (Fig. 2); only intervals without pulse production (silent intervals) over the course of a single wing stroke, gave maximal wing velocities. These results suggest that wing displacement in this species only occurs when pulses are not being generated. In some cases, sound pulses occurred with no detectable displacement of the tegmina (Fig. 2B).

The file of *Arachnoscelis* n. sp. bears approximately 70 teeth within a 0.70 mm length a TD=100 teeth mm^{-1} (Table 1, Fig. 3). The total distance moved by the scraper along the file during a single wingstroke was 0.35–0.40 mm (for the 2003 specimen), but there is evidence that the complete file might
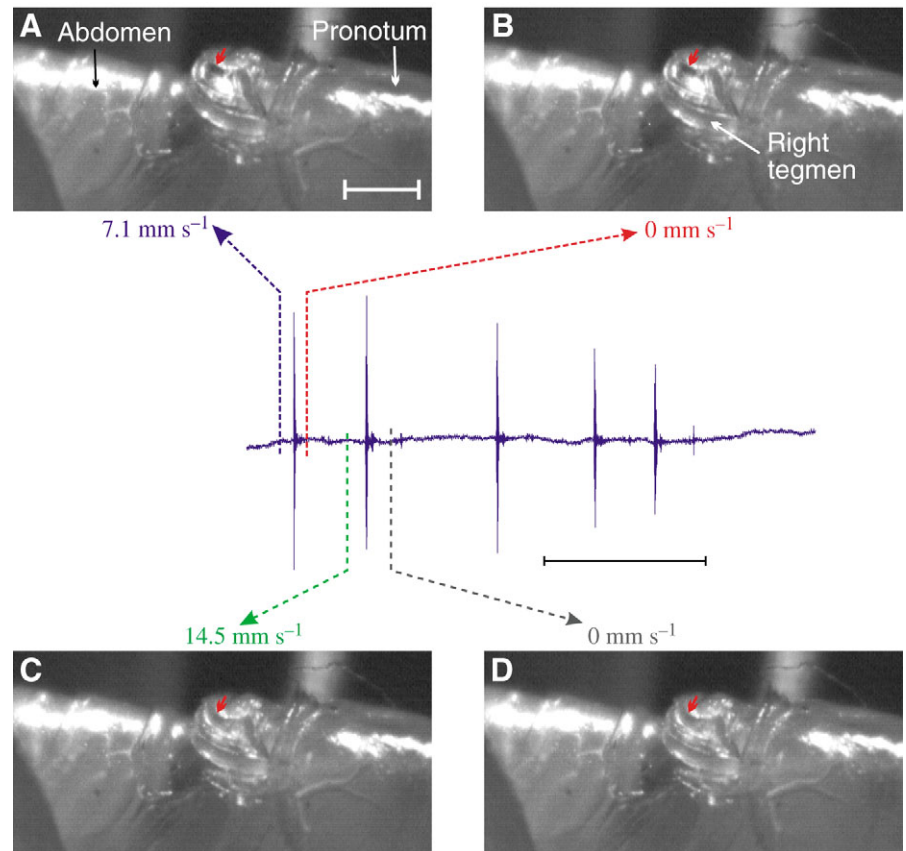

Fig. 2. Four successive frames from high-speed video relate closing wing positions to the pulse train of *Arachnoscelis* n. sp. Insect faces to the right. The anal margin of the overlying (file-bearing) left wing is marked by a red arrow; coloured broken lines match picture and wing velocities to the oscillogram. The wings develop a velocity before each production of a pulse (calculated *CWV* below frame) and then become almost still over the interval of pulse generation; scale bar, 5 ms. (A) *CWV* is at 7.1 mm s^{-1}; scale bar, 0.5 mm. (B) During the production of the first pulse (compare A and B) there is no detectable movement of the wings and the *CWV* drops to zero. (C) The wings close further, giving a *CWV* of ~14.5 mm s^{-1}. (D) Next pulse is produced, again without measurable displacement of the wings. Association of motionless wing intervals with sound pulses implies scraper movement.

also be used for sound production, allowing longer pulse trains (see below). If this insect used a grylloid escapement mechanism, i.e. with a 1:1 relationship between tegminal oscillator and tooth contact rate, then to produce a 129 kHz sound pulse, the scraper would have had to contact teeth at the rate of 129 000 s^{-1} at a velocity of ~1161 mm s^{-1} (see Table 1 for tooth spacing, TS). But in fact the HSV-measured (overall) *CWV*, however, was only 12.8 mm s^{-1}. If the scraper and right tegmen moved as a single unit (i.e. no relative movement of scraper and *SV*=*CWV*), this is an order of magnitude slower than the necessary *SV* to meet teeth at a rate of 129 000 s^{-1}. In one specimen of *Arachnoscelis* n. sp. the total number of driven oscillations in the song was nearly equal to the number of file teeth (64 waves *vs* 67 file teeth). In songs from the specimen recorded with HSV, the scraper of *Arachnoscelis* n. sp. contacted no more than 35–40 teeth, all in the basal half of the file (Figs 2, 3).
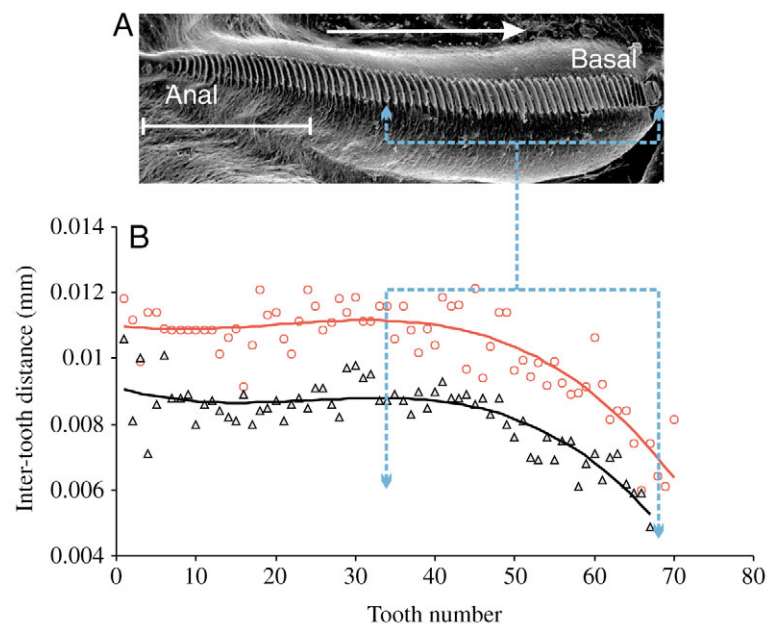
Fig. 3. File morphology of *Arachnoscelis* n. sp. (A) Scanning electron microphotograph shows the stridulatory file atop its transverse swollen vein. The long white arrow gives direction of scraper travel. Scale bar, 0.2 mm. (B) Inter-tooth distances for two specimens, the smaller animal below. Broken blue lines show the functional region (basal half) of the file as determined from HSV recordings of the 2003 specimen, which makes 4–5 pulses song[-1]. Sound recordings of the 1966 specimen suggest that some specimens use a larger file region, which implies the production of a larger pulse train (more pulses), as shown in Fig. 1B.

Other SSTP species

We obtained video recordings of wing movements during sound production for males of three additional SSTP species: *Myopophyllum* n. sp., *Phlugis* sp. and *Eubliastes aethiops*. Two specimens of *Myopophyllum* n. sp. sang with a carrier (average) of 65.5 kHz (Table 1). For both specimens, and unlike *Arachnoscelis* n. sp., there was detectable tegminal displacement in all frames within the closure pulse train, consistent with an absence of any pause in wing advance (i.e. this is apparently not a stepwise wing closure). *CWV* values calculated over all frame intervals that incorporated a pulse, always increased: see e.g. Fig. 4, pulse 1 from 94.9 to 141.7 mm s^{-1}. *CWV* values measured over a frame interval where no pulse occurred, consistently decreased. This observed feature is consistent with augmented velocity during scraper advance (pulse generation) and depressed velocity during (putative) scraper bending (Fig. 4). Overall *CWV* was 122.6±17.4 mm s^{-1}.

Stridulation by a single specimen of *Phlugis* sp. was analysed by HSV. Each of this specimen's calls was composed of a train of just two discrete pulses (Montealegre-Z, 2005). A pattern of forewing movement was observed very like that of *Arachnoscelis* n. sp. To generate its 48-kHz pulses on the basis of a driven resonant mechanism would require a tooth contact rate of ~48 000 s^{-1}, but by the measured *CWV* the rate of tooth contact would be ~4140 s^{-1} (Table 1). There was an obvious acceleration of this insect's wings, increasing *CWV* to ~40 mm s^{-1} before the first pulse was produced. During the production of the first pulse, *CWV* decreased dramatically to almost zero, then
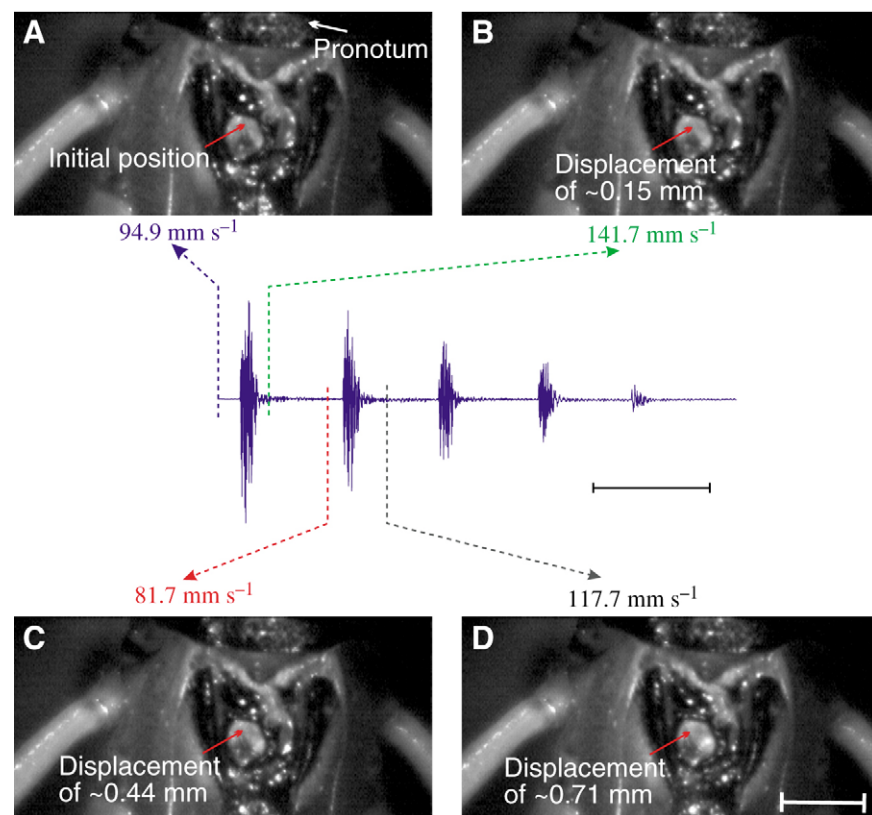
Fig. 4. Four successive frames from high-speed video (scale bar 3 mm) showing tegminal positions within the time course of the (closing) AM pulse pattern in *Myopophyllum* n. sp. The insect is oriented upward. The position of the right wing scraper region, visible through semitransparent wing cells of the left, is marked by a red arrow; coloured broken lines show where in the oscillogram time course the frame was obtained. (A) CW velocities are associated with each frame: the wings lose velocity before the production of a pulse. Scale bar, 2 ms. (B) There is a conspicuous displacement of the wings during the production of a pulse and the *CWV* increases to ~142 mm s^{-1}. (C) The wings close again more slowly during the silent interpulse interval and *CWV* drops to ~82 mm s^{-1}; during this time interval the scraper is relocated. (D) The new pulse is produced with a conspicuous displacement of the wings; *CWV* increases to ~118 mm s^{-1}.
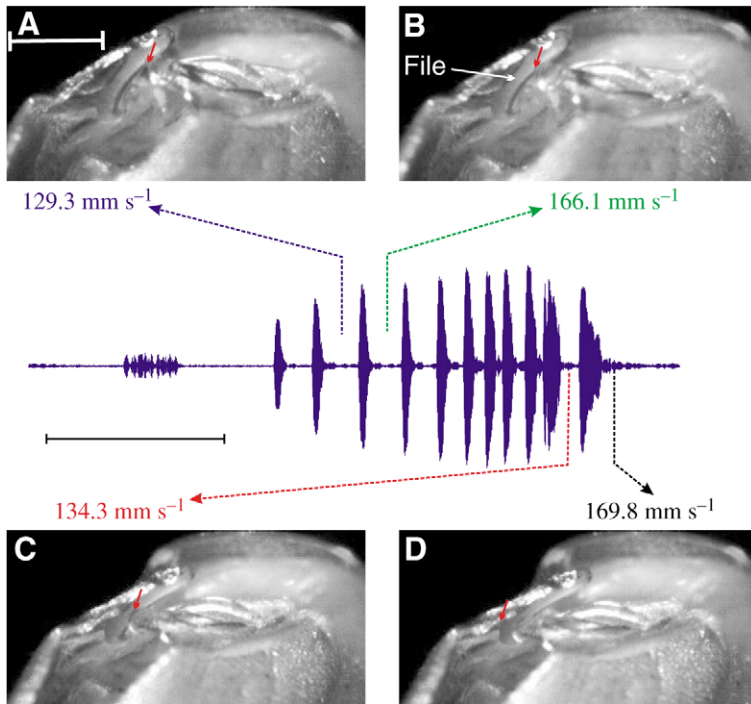
Fig. 5. Four successive frames from high-speed video (scale bar 3 mm) showing tegminal positions within the time course of the (closing) AM pulse pattern in *Eubliastes aethiops*. Latero-posterior view (right side of the insect). The position of the scraper over the file is marked by a red arrow; coloured broken lines show where in the oscillogram time course the frame was obtained. (A) *CWV* values are associated with each frame: the wings lose velocity before the production of a pulse. Scale bar, 10 ms. (B) As for *Myopophyllum* sp. n., there was a conspicuous displacement of the wings during the production of a pulse and the *CWV* increases to ~166.1 mm s^{-1}. (C) For the final pulse of the train, the wings close again more slowly during the silent interpulse interval and *CWV* drops to ~134.3 mm s^{-1}, and increases again during the pulse to 169.8 mm s^{-1} (D). The movement of the scraper ends close to the basal part of the file.

there was a short wing displacement elevating *CWV* to 52 mm s^{-1} in the next (silent) interval. The second pulse was produced and *CWV* decreased again to almost zero. It is possible that during the production of a pulse in both *Arachnoscelis* n. sp. and *Phlugis* n. sp. a short displacement of the wing occurs, but due to the small size of specimens and resolution of our HSV system, these were imperceptible.

Pure tone calling songs comprised of trains of discrete tonal pulses may also occur among species with quite low carriers, such as *Eubliastes aethiops* (Fig. 5) at ~22 kHz. Calls of this pseudophylline involve 11–12 regularly repeated sinusoidal pulses at each tegminal closure. *CWV* measured for the frame interval just before the fourth pulse of the train was 129.3 mm s^{-1}, increasing in the subsequent frame, which incorporates the third pulse, to 166.1 mm s^{-1} (Fig. 5); the same relative velocity changes are shown occurring in conjunction with the last pulse of the train. Just as with *Myopophyllum* n. sp., *E. aethiops* shows an increased speed of tegminal movement as there is an emission of each pulse and a depressed speed when no pulse is involved in the pair of frames that form the basis of a velocity measure.

During a closure, the average velocity of the wing of *E. aethiops* is 151 mm s^{-1} (Table 1). If this velocity were maintained throughout closure, given the insect's observed tooth density, a carrier would be produced of ~7701 Hz, only about one-third the ~22 000 Hz carrier observed. The observed carrier can be achieved only by a scraper velocity of about 440 mm s^{-1}, occurring within each of the pulses to augment the lower speed of the wing.

It was possible to obtain a direct measure of wing velocity for the four species (above): *Arachnoscelis* n. sp., *Myopophyllum* n. sp., *Phlugis* n. sp. and *E. aethiops*, plus
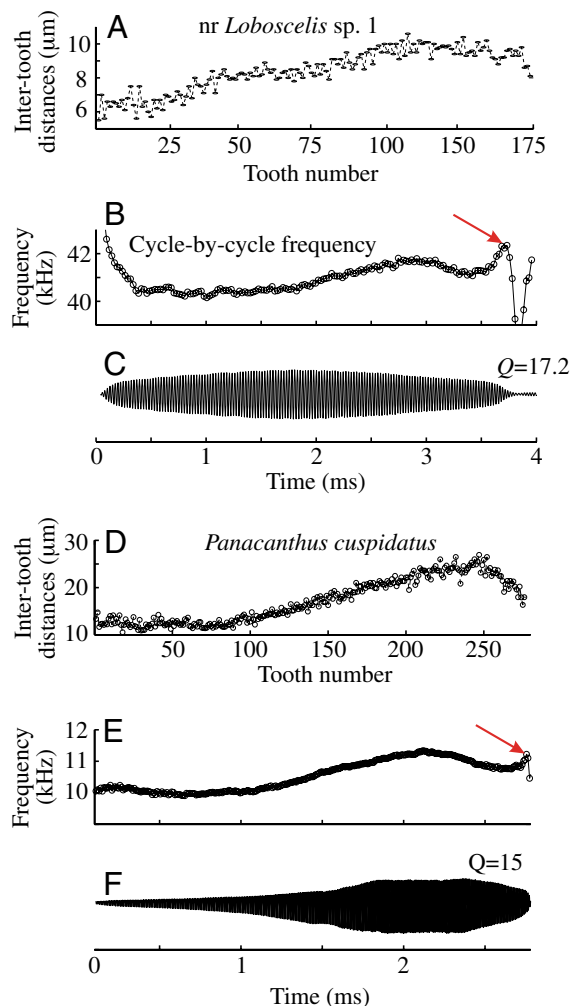

Fig. 6. File morphology and sound quality of two species of katydid using sustained pure tones. (A,D) Intertooth intervals plotted in their natural sequence on the file. (B,E) Zero-Crossing analysis of the pulse shown in C and F; red arrows indicate increments in frequency associated with scraper-file disengagement. (C,F) Sound pulse waveform.
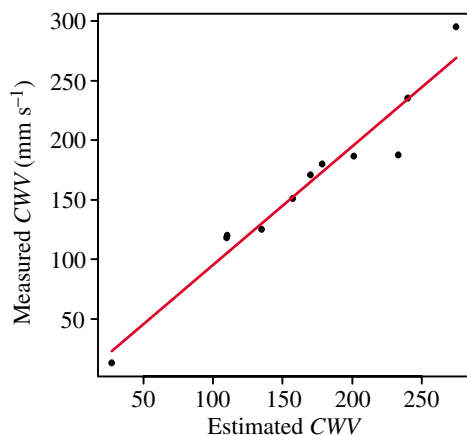
Fig. 7. Verification of our method of estimating closing wing velocity from oscillograms (especially for species where specimens were not available for HSV). Regression of known on estimated values indicates good agreement (see text).
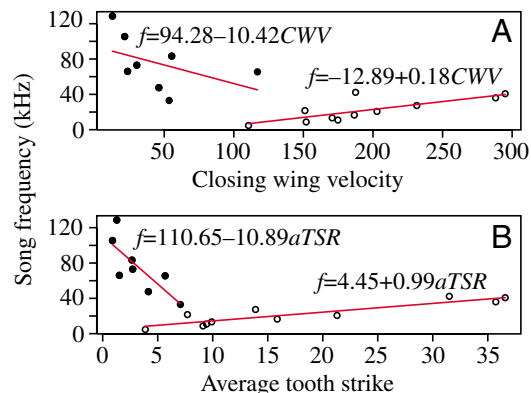

Fig. 8. (A) Analysis of relationship between song frequency and wing speed by ANCOVA with wing speed as the continuous variable and group membership (high *vs* low frequency). Closed symbols represent high-frequency singers (>40 kHz); open symbols, low-frequency singers (<40 kHz). (B) Same analysis using average *TSR* as independent variable.

another eight species singing in the low audio and ultrasonic range (see Table 1). But for the remaining seven species (Table 1, asterisks), only preserved specimens and previously recorded songs were available. In these cases direct measurement of *CWV* was not possible and the value was calculated from anatomical data and song recording (see Materials and methods). Examples of songs, measures of intertooth spacing and ZC analysis, as used to calculate *CWV* for several species, are shown in Fig. 6.

We verified that our method of estimating *CWV* was accurate by making the same calculations on the species for which direct measurements of *CWV* were available from high-speed video by calculating a regression of observed *CWV* on calculated *CWV* (slope=0.99, r^2=0.94, *P*<0.0001, Fig. 7). For all species, there was good agreement between estimates of the number of file teeth used in sound production and the number of teeth actually available on the file. In some cases not all of the file is used (Montealegre-Z and Mason, 2005), but in no instance did the number of driven oscillations exceed the number of available teeth.

Cluster analysis

Cluster analysis assigned each species to one of two groups based on the relationship between *CWV* and f_c. The procedure generated two groups, corresponding to species with song frequencies above and below roughly 35 kHz. ANCOVA analysis with frequency group as categorical and *CWV* as continuous variables showed significant effects of both group membership and *CWV*, as well as a significant interaction (Fig. 8A). In the low-frequency group there was a significant positive relationship between song frequency and *CWV* (*F*=13.8, *P*=0.005), whereas in the high-frequency group, *CWV* decreased with increasing song frequency, though this relationship was not significant (*F*=1.55, *P*=0.259).

Because *TSR* depends on both *CWV* and tooth spacing (density), we also repeated the ANCOVA using the product of

CWV and TD as the continuous variable. Overall results were similar to the previous analysis, with significant main effects and interaction (Fig. 8B). In this analysis, however, linear regression of song frequency with average *TSR* was significant in both groups, with a slope of unity for the low-frequency group (*F*=39.36, *P*≤0.001) consistent with the conventional model of resonant stridulation. In the high-frequency group, average *TSR* (product of *CWV* and TD) decreased steeply with increasing song frequency (*F*=9.81, *P*=0.02).

Consideration of their *CWV*, TD and f_c indicates that for all eight species in the high frequency group (all species exhibiting SSTP), a 1:1 relationship between tegminal oscillator and tooth-contact rate, the relationship essential for an sustained pure tone pulse, is not achievable with the observed or estimated closing wing velocity (Table 1, Fig. 8). All these species are closing their wings at speeds far below that necessary to account for the *SV* inherent in their high frequency carriers. To account for the high carrier and its short wavelength on a tooth per wave basis requires some other mechanism. We believe the likely basis, one consistent with the SSTP form of all these calls, involves a special mechanical contribution from the scraper.

Comparisons of scraper morphology

Certain morphological characteristics are peculiar to the scrapers of species in the high frequency group. Males producing these extremely high carriers with relatively low *CWV*s had a more extensively developed region of thin cuticle ('scraper shelf') between the scraper proper and the third anal vein. The vein itself was greatly thickened and relatively more massive than in species of the lower frequency group.

Scraper sections for *Panacanthus pallicornis* and nr *Loboscelis* sp. 1 are illustrated (Fig. 9A); they show a lesser development of their scraper shelf area, suggesting a lesser deformability of the scraper shelf relative to that of the two high frequency group species (Fig. 9B). For both *Arachnoscelis* n. sp.
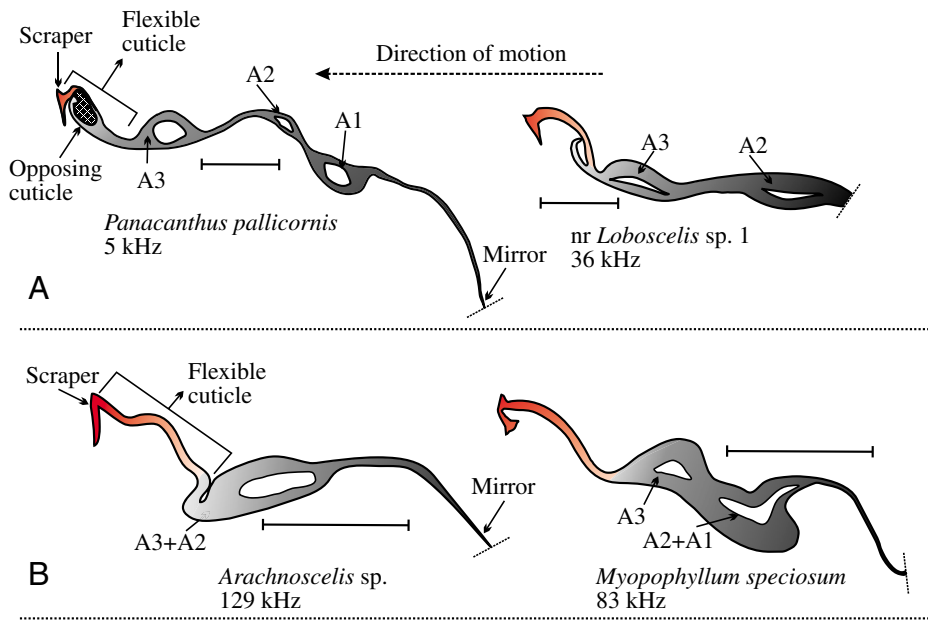
Fig. 9. Scraper profiles and their association with two types of resonant stridulatory mechanism: long-pulse and short-pulse. Each transverse section is taken normal to the scraper edge. (A) Two species producing pure-tone pulses below 40 kHz. (B) Two species producing extreme ultrasonics (>60 kHz) as short-spaced pulse trains. Note the distinctive morphology proximad of the scraper (red areas): the very modest extent of thinner (presumably more flexible) wing areas in A compared with their elaboration relative to increasingly massive veins in B. A1, A2, A3 indicate anal veins.

and *Myopophyllum* n. sp. transverse sections of the scraper shelf (Fig. 9B) show this region to be extremely thin and much more extensive, appearing to constitute a highly deformable region.

Discussion

Analysis of stridulation in Arachnoscelis and some other SSTP singers

On the basis of their sinusoidal nature, the SSTP ultrasonic pulses suggest a cricket-like generating mechanism involving one-wave per tooth. Available file teeth in these species roughly match the number of rising and maximal waves summed across the closing pulse train, consistent with driven resonance: there is approximately one tooth for each rising or maximal wave. But the wavelengths and the rates of tooth contact and the wing velocities necessitated by such a frequency multiplying mechanism in the SSTP songs, would appear to be beyond the speed of contraction of ensiferan wing muscles (Michelsen, 1998). These observations lead us to propose a role for 'uncoupled' scraper behaviour and elasticity to achieve high ultrasonic rates of pure-tone generation: the proposed mechanism is illustrated in Fig. 10 for *Arachnoscelis* sp. n. [That elastic energy residing in the scraper might contribute to stridulation was first suggested (Morris and Pipher, 1972) to explain ultrasonic pure-tone pulses made by the katydid *Metrioptera sphagnorum* in its ultrasonic mode.]

The scraper need not follow in lock-step the same changes in velocity, acceleration and displacement experienced by the rest

of the tegmen. Scraper and wing can be 'uncoupled' to some degree and move at different speeds as the forewings close. Periodically scraper velocity would drop to zero as its carina lodges behind a file tooth (e.g. tooth 22 of Fig. 10). The wings continue to move steadily by each other, bending the flexible (thin and produced) cuticular region between the carina and the third anal vein. This bending will store elastic (deformation) energy, which can then enhance scraper velocity when the scraper slips free. In Fig. 10B it is shown slipping free (of tooth 22) and driving forward over a series of eight file teeth, extending itself along the file until lodging again behind tooth 29. Driving at this speed, which is higher than the tegminal movement, it will create eight waves of incrementing amplitude (Fig. 10B).

This interpretation of how *Arachnoscelis* n. sp. sings is supported by observed variation in the instantaneous frequency of its single pulses (Fig. 1E). During the pulse onset, there is an increment in the instantaneous frequency for the first few waves (Fig. 1E), which suggests a higher velocity of the scraper at its release. Instantaneous frequency decreases as the pulse progresses and the scraper loses velocity. If the total number of driven oscillations involved in one closing stroke are added, one obtains a number of cycles represented in individual tooth contacts. The region of the file actually used holds ~40 teeth (specimen 2003); thus teeth are likely not skipped and all teeth over the functional file region are struck by the successive movements of the scraper. But this technique might vary and perhaps few teeth might be skipped when the wing moves during the silent interval.

Applying a lock-step (coupled) view of wing and scraper movement to the mechanism involved in SSTP singers, the wing (and the scraper) must stop, and remain so over the silent interpulse interval. Sound can only occur when there is wing displacement. Our HSV analyses of *Arachnoscelis* n. sp. show changes in wing position in two successive frames within a silent interval in the song: so something other than wing movement must be responsible for the generated sound, the scraper being the only feasible candidate.

In a decoupled view, for SSTP species the scraper would move, 'atop' the wing movement, to make each pulse of the train. The bending scraper should also have an effect on the general closing velocity of the wing: during the interval when it is lodged and bending, storing deformation energy, it should cause the wing velocity to drop. Then during the emission of the pulse, when the scraper pushes ahead along the file at a velocity (necessary to achieve the high tooth contact rate of the ultrasonic

carrier) higher than that of the overall wing movement, the scraper should contribute to an increase in wing velocity.

A decoupled mechanism predicts that for species where the wing moves continuously during closure, its velocity, established by two consecutive frames in advance of a pulse, should decline (the wings being slowed by having to bend the scraper) and then increase between two frames that bracket (include) the making of a pulse (because some of the deformation energy is given back to the wing speed). Exactly these velocity changes are shown in Fig. 4 (*Myopophyllum* n. sp.): 94.9 mm s^{-1} at a point just before a pulse begins, increases to 141.7 as the pulse is over, that is, the velocity of the wing is increased coincident with the making of the pulse; 141.7 then drops to 81.7 mm s^{-1} during the time taken to make the next frame that includes no sound, that is, the velocity of the wing decreases under the effect of bending the scraper lobe. A similar mechanism is used by *E. aethiops* (Fig. 5).

Though consistent with the decoupling of the scraper and wing these arguments about velocity do not apply in the same way to *Arachnoscelis* n. sp. In this species the HVR indicates the wings are brought to a complete halt, not just a slowing, after storing the energy for the 129 kHz pulse. In fact it is possible that at these slow speeds the insect triggers the dislodgement of the scraper as an independent motor act by slightly changing the shear forces between the wings that are keeping the scraper bent.

Stridulation in other high frequency SSTP singers

In our comparison of the songs of 19 species of katydids, the ANCOVA separates out a group of very high carrier frequency singers, all making forewing closures by SSTP and all showing very low tegminal closing velocities.

Males of the first 12 species listed in Table 1 sing in the range of 5–45 kHz and exhibit *CWV* of ~120–300 mm s^{-1} (excluding *M. sphagnorum* and *E. aethiops*, see below). Among these species, *CWV* and *SV* are equal and the scraper makes an uninterrupted passage along the file, contacting consecutive teeth in a long series. For the remaining seven species, carriers range upward from 48 (*Phlugis*) to 129 kHz (*Arachnoscelis* n. sp.) but closing wing velocity is lower, in some cases dramatically: 13–140 mm s^{-1}. In these latter species, *CWV* no longer equates to *SV*. Lower *CWV* is least in evidence in the two species of *Myopophyllum*, probably because these two largest species have more muscular mass, allowing them to achieve higher velocities.

The seven high-frequency species of Table 1 share the production of a train of relatively short sound pulses, corresponding to a single closing file-run. As explained above, this pulse train is likely the signature of scraper-stored elastic energy. The scraper is apparently making a series of tooth lodgements along the file, each associated with scraper bending, and a succession of increased scraper velocities is achieved over very short durations. The work done by the scraper during each pulse occurs in a shorter time than could be managed by wing muscle alone and so will be at a higher power. In these species, scraper movement by wing muscle contraction is no longer the limiting determinant of scraper kinetic energy. The additional elastic energy brings us up to the necessary tooth-impact rates for the high ultrasonic frequencies. Slower overall closing wing velocities can maximise *SV* and so the distances travelled by the scraper for each elastic energy input, thus making lengthened pulses.

The occurrence of trains of pulses within single wing closures is not limited to these extreme high-frequency singers. Some species, e.g. *Metrioptera sphagnorum* and *E. aethiops*, present cases where elastic energy and low *CWV* are used to generate moderately high puretone ultrasonic frequencies. Shorter transient pulses can also be produced during wing closures, e.g. Cocconotini
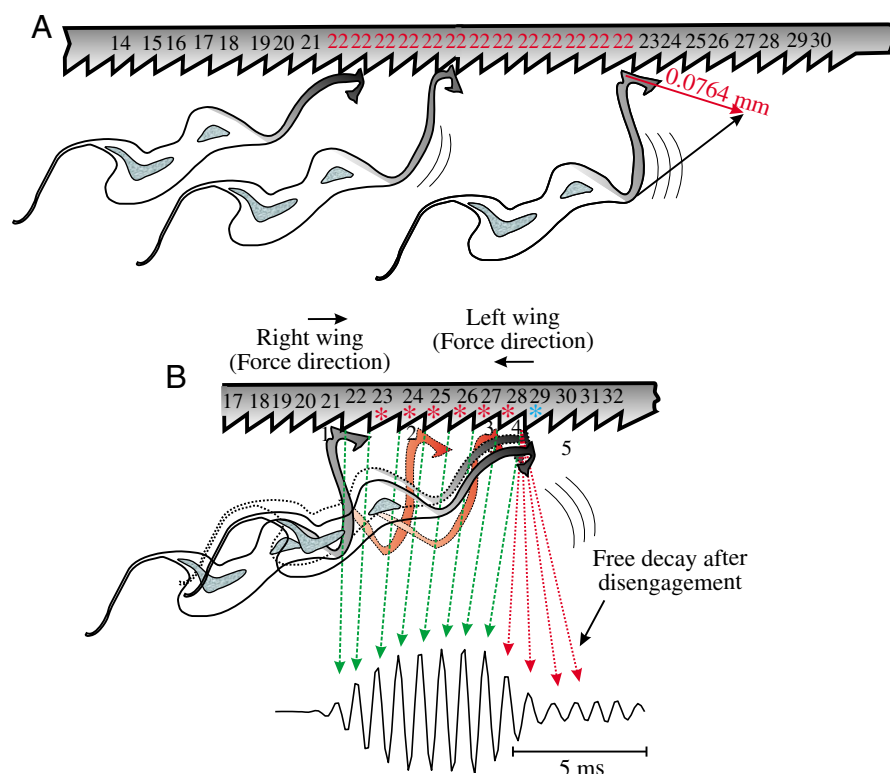

Fig. 10. Schematic cross-section of stridulatory file and scraper (based on anatomy of *Arachnoscelis* n. sp.) showing hypothetical mechanism of stridulation in extreme-frequency singers. (A) Different degrees of deformation the scraper may undergo while pausing behind a tooth in advance of pulse production. (B) With enough bending, the scraper's shape allows release, and it springs forward along a series of teeth lodging at the last tooth of the series (blue asterisk). Pulse-driven oscillations (one per tooth) indicated with broken lines, contacted teeth with red asterisks. Decay oscillations indicated by dotted red arrows.

(Monteleagre-Z and Morris, 1999). Other species with non-resonant, broadband spectra, e.g. *Pterophylla camellifolia* (Montealegre-Z and Morris, 1999), stridulate with a scraper–file mechanism differing from the one presented here, but also yielding pulse trains of short, rapid-decay, transient pulses).

The distinctive post-scraper morphology of the high frequency species group might help to predict SSTP structure for species with unknown songs. It is also possible that this region will prove to be specialized in terms of its elastic properties. For example, that it might incorporate resilin (Andersen and Weis-Fogh, 1964; Neff et al., 2000; Vincent and Wegst, 2004; Elvin et al., 2005). This needs to be examined in future work.

Selective forces for extreme ultrasonics

The song of *Arachnoscelis* n. sp. is the highest pure-tone call carrier presently known, surpassing the previous highest, that of another katydid, *Haenschiella* spp., at 106 kHz (Morris et al., 1994). [Another extreme carrier, but not a pure tone, is that of the pyralid moth *Corcyra cephalonica*: the dominant peak in the moth's broad-band spectrum is 125 kHz (Spangler, 1987).]

What selective forces might have favoured the evolution of these very high-frequency generators? Because ultrasonics lose energy more rapidly with distance, especially in humid air (Griffin, 1971; Römer and Lewald, 1992; Römer, 1993), it seems questionable they would aid in enticing distant females. Using such frequencies a caller limits his reach and (possibly) increases his cost. Two other hypotheses seem more plausible. (1) Enhanced directionality. At such short wavelengths body diffraction (normally not of importance) may become significant even for a very small insect and so enhance close-range localization mechanisms. For instance, the wavelength of the *Arachnoscelis* n. sp. song is ~2.7 mm, while this insect's body diameter is ~3.5 mm; this disparity is sufficient to cause scattering of sound by body diffraction (Mason et al., 1991; Morris et al., 1994; Mason and Bailey, 1998). (2) Eavesdropping avoidance. The heightened attenuation of these frequencies may in itself be adaptive in confining male to female transmission to a more intimate range, avoiding the attention of ultrasound-detecting insectivorous bats (Belwood and Morris, 1987; Belwood, 1990).

The extreme short wavelengths of these tropical katydids might also be an adaptation to improve radiation efficiency. Sound radiation efficiency is nearly zero at very low frequencies, when the wavelength is long compared with radiator diameter, rises to a maximum when the sound wavelength is comparable with the diameter, and then declines again more slowly (Fletcher, 1992). In practice the radiation resistance of a dipole acoustic source in a baffle increases to that of the surrounding air as the source radius rises to 1/4 wavelength (Fletcher, 1992; Bennet-Clark, 1998). The quarter wavelengths involved here approximate the diameters of their radiators (Montealegre-Z, 2005). A benefit of evolving in this fashion may have been improved sound radiation through reduced short-circuiting and better coupling of the impedance of the mirror membranes to the surrounding air mass (Bennet-Clark, 1989; Bennet-Clark, 1998).

Conclusion

In evolving to a higher carrier, some tettigoniid species have increased either TD or *CWV*, or both, while still contacting one tooth per sound radiating cycle (Montealegre-Z, 2005). In these species, *SV* and *CWV* remain equivalent as the scraper moves exactly in tandem with the wing. A few other species have to some degree separated *SV* from *CWV* and incorporated elastic energy into the generating process. Measuring *CWV*, file morphology and instantaneous frequency of pulse oscillations allows one to distinguish between these two species groups and to make predictions about the stridulatory mechanism a katydid, cricket or grig is using.

The rate at which an animal can do work (apply force through a distance) is normally limited by how fast muscles can contract. But deformed cuticle can return the work that went into its deformation much faster than a working muscle. Elastic energy is used by some arthropods to achieve powerful movement in this way. So for example, in the jump of a leafhopper or flea (Bennet-Clark and Lucey, 1967; Burrows, 2003; Krasnov et al., 2004), deformed cuticle provides power. In *Arachnoscelis* n. sp. and other species using extreme ultrasonic means, the paradox of high-frequency output by low-velocity wing movement can be resolved by invoking a mechanism that utilizes the power capability of elastic energy stored in cuticle.

List of symbols and abbreviations

A1	first anal vein
A2	second anal vein
A3	third anal vein
CWV	closing wing velocity
f_c	carrier frequency
FFT	Discrete Fourier transform
HSV	high-speed video
P	wave period
Q	quality factor. It measures a resonant system's internal-to-external damping and also the rate at which such a system reaches maximum amplitude or decays (Prestwich and O'Sullivan, 2005)
SSTP	short spaced tonal pulses. These are trains of several pulses produced on a single wing-stroke, the pulses are short and separated from each other by silent intervals
SV	scraper velocity
TD	tooth density
TS	tooth spacing
TSR	tooth-strike rate or tooth-contact rate
ZC	zero crossing

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