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Simultaneous measurement of metabolic and acoustic power and the efficiency of sound production in two mole cricket species (Orthoptera: Gryllotalpidae)

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Summary

We here report the first simultaneous measurement of metabolic cost of calling, acoustic power and efficiency of sound production in animals – the mole crickets *Scapteriscus borellii* and *S. vicinus* (Gryllotalpidae). We measured O_2 consumption, CO_2 production and acoustic power as the crickets called from their burrows in an open room. We utilized their calling burrow as the functional equivalent of a mask. Both species had a respiratory quotient near 0.85, indicative of metabolism based on a mix of carbohydrates and fats. The metabolic rate was significantly higher in *S. borellii* (11.6 mW g^{-1}) than in *S. vicinus* (9.0 mW g^{-1}) and averaged about eight- to fivefold greater, respectively, than resting metabolism. In some individuals, metabolic rate decreased by 20% during calling bouts. Costs of refurbishing calling burrows in *S. borellii* were less than calling costs, due to the behavior's short duration (ca. 15 min) and its relatively low average metabolic rate (4 mW).

Acoustic power was on average sevenfold greater in *S. borellii* (21.2 *vs* 2.9 μW) and was more variable within individuals and across species than the metabolic rate. The efficiency of sound production was significantly higher in *S. borellii* (0.23 *vs* 0.03%). These values are below published estimates for other insects even though these mole crickets construct acoustic burrows that have the potential to increase efficiency. The cricket/burrow system in both species have an apparent $Q_{\text{ln decrement}}$ of about 6, indicative of significant internal damping caused by the airspaces in the sand that forms the burrow's walls. Damping is therefore an important cause of the low sound production efficiency. In field conditions where burrow walls are saturated with water and there is less internal damping, calls are louder and sound production efficiency is likely higher.

File tooth depths and file tooth-to-tooth distances correlated with interspecific differences in metabolism and acoustic power much better than with wing stroke rates and plectrum-to-file tooth strike rates. To further investigate these correlations, we constructed two models of energy input to the tegminal oscillator. A model based on transfer of kinetic energy based on differences in tegminal velocity and file tooth spacing showed the most promise. Related calculations suggest that if there are no elastic savings, the power costs to accelerate and decelerate the tegmina are greater than the predicted power input to the tegminal oscillator, and that they are similar in the two species even though *S. vicinus* has a nearly threefold higher wing stroke rate.

Key words: mole cricket, Gryllotalpidae, *Scapteriscus borellii*, *Scapteriscus vicinus*, acoustics, bioacoustics, energetics, respirometry, stridulation, morphology, efficiency.

Introduction

Crickets produce sound as their forewings (tegmina) close and specialized structures (the file teeth and the plectrum) engage each other. In this process, the plectrum (a sclerotized region at the medial terminus of the Cu2 vein) of the left tegmen is gathered and released by successive file teeth (triangular bumps on the lower surface of the Cu2 vein) of the right tegmen. The rate of this catch-and-release equals the frequency of the sound produced by the cricket, known as its carrier frequency, f_C). At some point the surfaces become disengaged and the tegmina reverse their movement. During this opening phase, these surfaces are not engaged and no sound is produced. Thus, one tegminal cycle results in a pulse of sound waves near the f_C followed by a silent period. The tegminal cycling rate is commonly termed the wing stroke rate (f_{WS}). For a detailed overview, please see Bennet-Clark (1989).

Trilling calls, where a large number of sound pulses are produced without extended pauses, are supported by high rates of metabolism (Prestwich and Walker, 1981; Kavanagh, 1987; Lee and Loher, 1993). Given the importance of loud signals, we expect that natural selection should favour mechanisms that efficiently convert energy stores into sound. However, we know very little about sound production efficiency (E) in insects. Moreover, the few estimates that exist (MacNally and Young, 1981; Kavanagh, 1987; Prestwich, 1988; Forrest, 1991; Bailey et al., 1993) were obtained by dividing each species' average value for acoustic power (P_{ac}) by the species'

average metabolic power for calling, P_{call}. These measures are useful in establishing general relationships but they do not permit rigorous tests of hypotheses relating to inter- and intra-specific differences in E. Another problem with previous studies is that all involved calculation of E using measurements of P_{call} and P_{ac} taken at different times. The use of respirometry (simultaneous determination of O_2 consumption and CO_2 production) to obtain accurate measurement of a cricket's P_{call} requires small respirometry chambers if there is to be good time resolution. However, these same vessels are unsuitable for the measurement of acoustic power (Prestwich et al., 1989; Prestwich, 1994).

Our purpose was to measure the energetics of calling, the sound production, and the E of sound production in two sibling species of mole crickets (Orthoptera: Gryllotalpidae) that produce songs with different f_{WS} and f_C. As with most mole crickets, these species employ specially constructed calling burrows (Fig. 1) that should allow them to produce loud calls at a lower f_C than would be expected for insects of their size (Bennet-Clark, 1970, 1987; Daws et al., 1996; Nickerson et al., 1979). We devised a technique that allowed for the concurrent determination of P_{call} and $P_{ac.}$ These data allowed us to test for intra- and inter-specific differences and to relate these results to factors associated with the cricket's burrows and the morphology of their stridulatory structures. We used these data to construct and evaluate two models designed to predict the energy input into the tegminal oscillator/acoustic radiators and to estimate the maximum costs associated with overcoming inertia during the opening and closing movements of the tegmina.

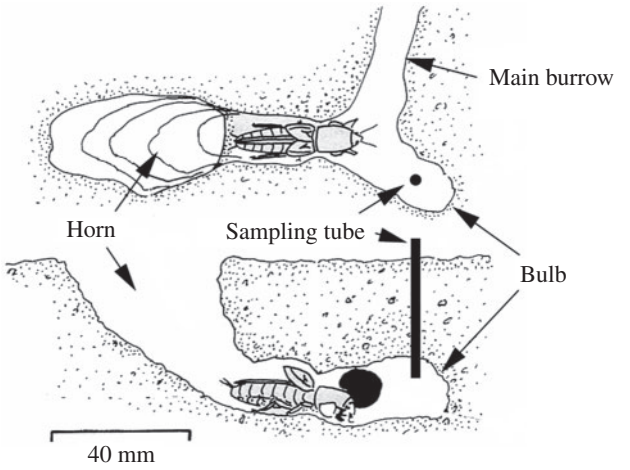

Fig. 1. Two views of the calling burrow of *Scapteriscus borellii* with the approximate location of the gas sampling tube. The single, oval-shaped opening acts as an approximately 1/3-wavelength radiator set in an infinite baffle. The horn matches the radiation impedance of the insect's acoustic radiator (tegminal harps) with that of the opening of the burrow. Males sing as shown from the constricted region with their heads facing into the burrow and their elevated tegmina largely filling the space above the cricket. The bulb is a straight or curved blind-ended burrow 1/4-wavelength in length with an opening to the main burrow in its side wall. The insect's harps are doublet sources and sound broadcast from their dorsal (anterior) surface into the bulb is reflected and then returns to the harps in phase with the sound emitted being emitted into the horn. Thus, the dimensions of the burrow, calling position of the insect, and acoustical properties of the burrow walls are all crucial to the system's performance (Bennet-Clark 1970, 1987; Daws et al., 1996). Figure modified from Bennet-Clark (1989) and used with permission.

Materials and methods

Animals and environmental conditions

We collected *Scapteriscus borellii* Giglio-Tos (formerly known as *S. acletus*; see Nickle, 1992) and *S. vicinus* Scudder (see Walker and Moore, 2004) in the vicinity of Gainesville, Alachua County, Florida, USA during May and June. Individuals were taken at sound traps or by digging them from their calling burrows. Late spring/early summer maturing individuals tend to be smaller than those that mature at other times and also show less interspecific size difference (Forrest 1987). We housed each individual in a separate screened 20 l plastic bucket (0.33 m×0.47 m diameter×height). We fed them Purina® Cricket Chow and apple slices and maintained them at 25±2°C on a light cycle that approximated the field. Each bucket was filled to within 0.02 m of the top with packed, moist 'play sand' (intended for sandboxes and the like). Play sand is courser, less compact, and contains less fine mineral and organic matter than the typical sandy soils that mole crickets inhabit in north-central Florida. We used play sand to avoid exposing the crickets to parasites, although in retrospect, it would have been better to use autoclaved sand from typical habitats (see Results).

Analysis of acoustic features of calls

We collected representative calls from inside a low reverberation room at 25°C. Recordings were made using a Sennheiser (Wedemark, Germany) shotgun microphone (model ME 66 back electret type capsule in conjunction with a K6 powering module) and Marantz (D&M Professional, Itasca, IL, USA) PMD 201 portable analog cassette tape recorder and type II high bias tape. Calls were digitized using a 16-bit National Instruments (Austin, TX, USA) A-2100 A/D board resident in a Macintosh (Cupertino, CA, USA) IIci computer. The A-2100 board was equipped with an anti-aliasing filter and sampled at 44.2 kHz. Except as noted, we analyzed calls using Canary© 1.2.4 software (Cornell Laboratory of Ornithology, Ithaca, NY, USA).

We estimated the period of a tegminal cycle as the mean time between the start of two successive sound pulses (Fig. 2); the inverse of these values gave the f_{WS}. Several 1 s waveform samples were analyzed for each individual. We measured the f_C in two ways. Cycle-to-cycle f_C was determined by a custom-made program developed using National Instrument's LabView. The program uses the zero-crossing (ZC) method to find each cycle's period and frequency (Simmons and Ritchie, 1996; Bennet-Clark, 1999). It is freely available from author K.N.P. (http://www.holycross.edu/departments/biology/kprestwi/ZC). Average f_C was estimated as the peak frequency

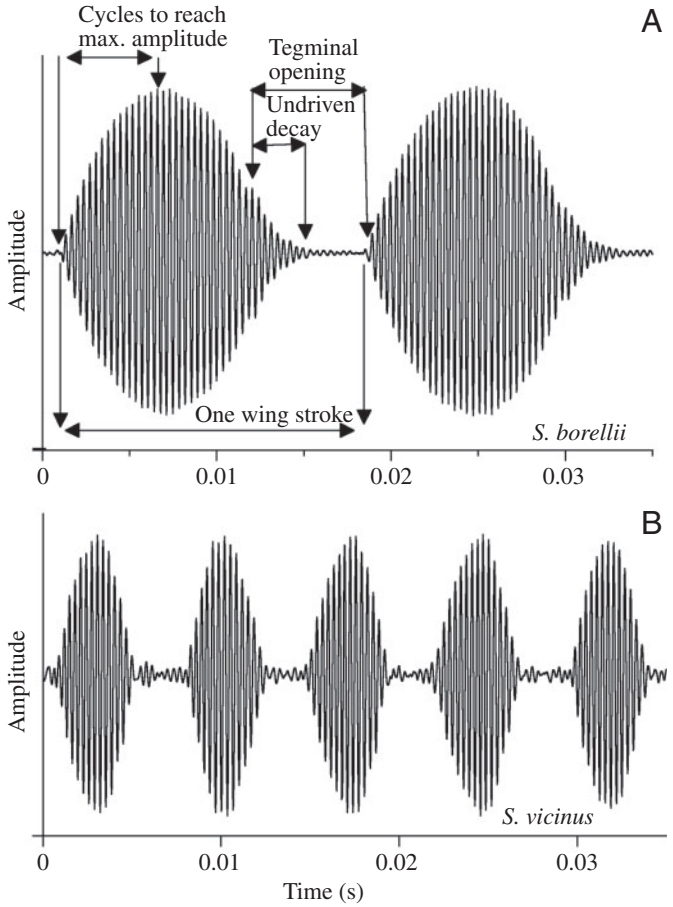

Fig. 2. (A) Sound pulses of *S. borellii* and our conventions for deducing the number of driven cycles and the duration of the closing and opening phases. (B) Sound pulse of *S. vicinus*.

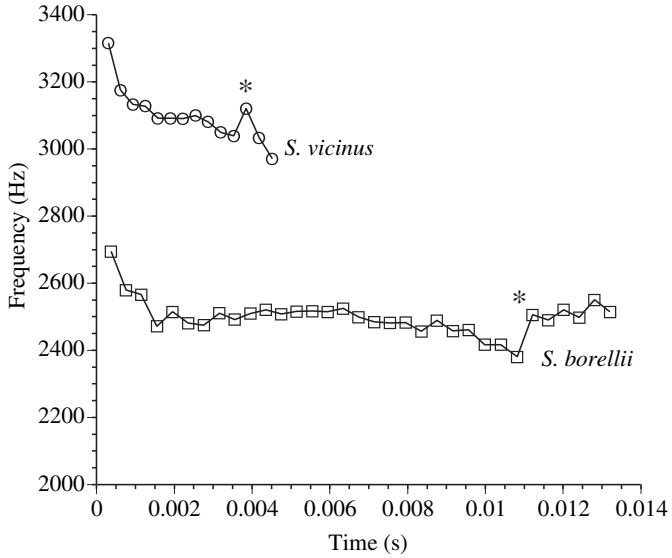

Fig. 3. Cycle-to-cycle frequencies (f_C) of single sound pulses for representative *S. borellii* and *S. vicinus* at 25° C. The f_C is not constant and decreases by 5–10% late in the call (especially so in this *S. vicinus* individual). The instantaneous jumps in frequency late in the pulses (asterisks) are believed to be associated with the disengagement of file and plectrum. This is followed by a period of undriven vibration, during which the sound amplitude drops exponentially. Although the patterns given in this figure are typical, a number of individuals of both species showed different degrees of f_C stability and sometimes lacked a noticeable change in frequency at the start of the sound amplitude's exponential decay.

of a Canary fast Fourier transform (FFT) spectrogram obtained from 1 s of normal calling. FFT estimates are weighted towards the most energetic frequencies in the analyzed pulse while averages of ZC measurements ignore amplitude.

Driven cycles and cycles to peak power

Driven cycles are sound cycles where sustaining energy is added *via* the stridulatory system to the tegmina's acoustic oscillator/radiator (the harp and file; see Bennet-Clark, 2003). We estimated the number of driven cycles per pulse as those from the start to the time when the sound pulse amplitude began to decay exponentially. This type of decay is indicative of an undriven oscillator (Fletcher, 1992). We emphasize that it is possible to miss the beginning of the undriven phase of a pulse by perhaps one or two cycles. Our data for *S vicinus* are more prone to error because their pulses are briefer than in *S. borellii* (see Figs 2 and 3). The number of tooth strikes needed to reach peak amplitude is the number of driven cycles from the start of a pulse to when peak amplitude is reached.

The quality factor, Q

This parameter measures a resonant system's internal to external damping and also the rate at which such a system reaches maximum amplitude or decays (Bennet-Clark, 1999). Q is given as:

$$Q = \frac{2\pi f_0 m}{R} = \frac{\pi}{\ln(decrement)}, \quad (1)$$

where f_0 is the resonant frequency (Hz), m is the system mass (kg), R is the damping (specific acoustic) resistance and ln(*decrement*) is the difference of the natural log of the peak amplitude successive waves produced by an undriven oscillator (Bennet-Clark 1989, 1999).

Ideally, Q is determined by exciting a resonant structure with a high-amplitude acoustic source. When the driving sound is abruptly stopped, the undriven decaying sound from the subject is recorded and Q is calculated from the ln(*decrement*) of successive peaks (Bennet-Clark 1989, 1999). We needed to know the Q of the cricket-burrow system. This system consists of two coupled resonances: the insect's tegmina and the burrow (Bennet-Clark, 1970, 1987). However, we could not find a satisfactory way to mount the tegmina in the normal singing position within a burrow and then perform the measurements. This forced us to use the decay of the sound at the end of cricket-produced sound pulses. The main pitfall to this approach is the inclusion of amplitude values that, although found during the decaying portion of the call, nevertheless were driven by tooth-plectrum impacts. Fig. 2 shows that towards the end of a sound pulse, the amplitude decreases over

a number of cycles. Initially the decay is non-exponential and is likely due to lower energy input to the vibrating system. The exact transition between this and a true exponential decay is difficult to identify by inspection and so we calculated '*Q*-like' values from the each successive pair of peaks during the pulse decay. Partially driven waves have large 'false-*Q* values' because their decay is less than what is seen with undriven waves. When the tegmina are finally no longer being mechanically driven, the calculated *Q* values stabilize around a lower, true *Q* value. For a given sound pulse, we averaged the cycle-to-cycle *Q* values for the true exponential decrease phase. We then replicated the measurement four times for each individual, calculated individual's means and then used these to find species averages. The point identified as the start of exponential decay usually coincides with an abrupt frequency shift (Bennet-Clark and Bailey, 2002).

Morphometric measurements

We froze males of both species, removed and weighed the tegmina, and measured the triangular-shaped harp along its two principal axes using the inside margins of the veins as boundaries. Then, we measured the pronotum medially and dissected out, blotted and weighed the tegminal musculature. Mass was measured using a Mettler (Columbus, OH, USA) Model AC100 balance that reads to 0.1 mg. Likely sources of errors include possible inclusion of connective tissue in addition to the muscle and a ±0.1 mg variance in weight found by repeatedly weighing the same sample. Dr Thomas J. Walker provided some of these data to us.

Scanning electron microscopy of stridulatory files

We dissected right and left files from the tegmina of dried males of both species, glued them to stubs, sputter-coated them using an Anatech (Alexandria, VA, USA) Hummer VI-A and examined them using a JEOL (Peabody, MA, USA) Model JEM-5400 Scanning Electron Microscope (SEM). Each specimen was rotated to ensure a side view that allowed for the accurate determination of file tooth depth. Typical magnification was 1000× or 1500×. Once we had obtained a complete set of images for each file, we measured the depth of each tooth as illustrated in Fig. 4 and the tooth-to-tooth distance (referred to as the 'pitch' by Bennet-Clark, 1970, 1987).

To estimate measurement variation, all specimens were placed in the SEM and photographed on at least two different days. Measurements of tooth depth from the photographs were done twice and were blind – the person doing the measuring did not know the sample number. Repeat measurements were always within 10% (and usually much less) of each other.

Respirometry

Respirometry consisted of simultaneous measurements of CO_2 production and O_2 consumption. We used two airstreams, one from the cricket's burrow or a respiratory chamber (for resting rates) and the other from the room. The samples were first pulled through a Drierite column to remove water and then passed through a CO_2 analyzer (LI-COR LI-6251, Lincoln, NE, USA) or Anarad AR 50 (Carrollton, TX, USA). Upon emerging from the CO_2 analyzer, both air streams were scrubbed free of CO_2 and water by soda lime and Drierite. Both samples then passed through a dual channel O_2 analyzer operated in the differential mode (Sable Systems Model 1 FC-2 'Oxzilla', Las Vegas, NV, USA or Ametek Applied Electrochemistry S-3A/II with N-37M sensor, Paoli, PA, USA). An Ametek Applied Electrochemistry R-2 pump was upstream from the O_2 analyser and the two flow rates were set to equal values using either two Sierra Instruments mass flow control values (150 ml min^{-1} capacity; Monterey, CA, USA) operated by a Sable Systems controller or by two Cole-Parmer Manostat Riteflow® 150mm Flowmeters (Vernon Hills, IL, USA). Flow rates were 60–75 ml min^{-1}. We read gas fraction data from the O_2 and CO_2 analyzer analog outputs using a 16-bit resolution National Instruments NB MIO–16X A/D board in the Mac computer. The A/D process was controlled by a custom program developed using National Instruments LabView® software. The program recorded data points that were the average of 100 readings taken over a 0.1 s period, each with a theoretical resolution of 76 μV. A new round of measurements was made every 2 s. The averaging procedure corrected for small, short-period, random fluctuations in the instrument and A/D converter outputs. At the conclusion of an experiment, the software saved the data in a spreadsheet format for later analysis.

There were a number of potential sources of error in our respirometry. The experimenter's presence and position in the room will change F_{O_2} and F_{CO_2} in the ambient air. To avoid this, whenever the observer (K.N.P.) was in the room, he breathed through an Otis valve that routed his expired breath into a Douglas bag. A more difficult set of problems related to

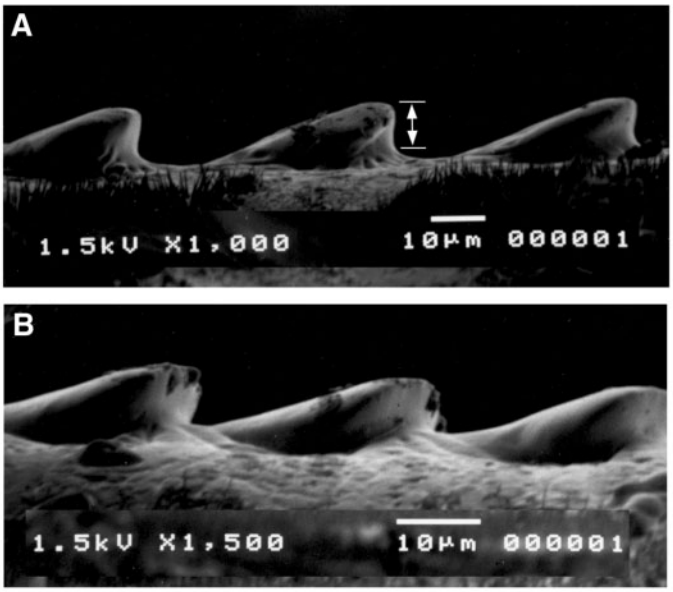

Fig. 4. Scanning electron micrographs in side view of the files of *S. borellii* (A) at 1000× magnification and *S. vicinus* (B) at 1500× magnification. Measurement of tooth depth is illustrated in A.

the conflict between gas sampling that gave good time resolution and the capabilities of the gas analyzers, especially the O_2 analyzers, to register consistent differences. Obtaining high precision oxygen fractions (F_{O_2}) is difficult because at sampling flow rates that give good time resolution, the differences in F_{O_2} caused by the cricket are relatively small compared to the background concentration of O_2. Additionally, O_2 analyzers are sensitive to changes in airflow rate such as occurs when sand from calling burrows entered the sampling tube. Finally, O_2 analyzers are also prone to significant drift. This problem is made worse by the fact that the two O_2 detectors in the instruments we used tended to drift independently of each other (although the FC-2 was considerably more stable).

To minimize error from these sources, we (i) selected flow rates that provided the desired time resolution yet that are low enough so that the animal creates a reliably detectable difference in partial pressure between the sample and reference streams; (ii) used short measurement periods (seldom longer than 15 min), always followed by re-standardization of the two airstreams; (iii) carefully monitored air flow rates (see below); and (iv) performed many replications. The volumes of the acoustic burrows were 10–15 ml (Bennet-Clark, 1987) and we found that 60–75 ml min^{-1} flow rates were high enough to give good temporal resolution, low enough to give values of F_{O_2} that were distinguishable from environmental and instrumental fluctuations, and were low enough that sand was usually not aspirated into the system. A mathematical model that used burrow volume, flow, estimated metabolic rates, and initial gas concentrations, predicted that, under expected conditions, less than 3 min would be required to reach a steady state once sampling began. In order to err towards caution, we sampled air from the burrow of continuously calling crickets for at least 4 min before using the gas fractions in metabolism calculations. To evaluate the success of these procedures, we compared the magnitude of typical changes in F_{O_2} associated with calling metabolism to the largest fluctuations in F_{O_2} observed when monitoring room air over the same time interval. Changes in F_{O_2} in going from rest to calling were minimally 8 times this standard. We note that drift was never a problem with CO_2 readings. Changes in F_{CO_2} during calling were greater than 10% of the analyzer's full span and more than twice the background F_{CO_2}.

Calculations of the rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were according to Withers (1977):

$$\dot{V}_{O_2} = \dot{V}\left(\frac{F_{IO_2} - F_{EO_2}}{1 - F_{IO_2}}\right), \quad (2)$$

$$\dot{V}_{CO_2} = \frac{\dot{V}[(F_{ECO_2} - F_{ICO_2}) - F_{ICO_2}]\dot{V}_{O_2}}{1 - F_{ICO_2}}, \quad (3)$$

where $\dot{V}$ is the airflow at STPD, F_{IO_2} and F_{ICO_2} are the oxygen and CO_2 fractions for the air before it passed by the cricket (reference stream), and F_{EO_2} and F_{ECO_2} were the fractions after it had passed the cricket.

To facilitate comparison with previous studies, we calculated metabolic rates on both whole animal and mass-specific bases. Crickets were weighed when first placed in their sand-filled bucket and about every 10 days thereafter. The reason for not weighing more frequently was to avoid disruption of the burrow system. Typically crickets did not call for several days after extensive burrow disruption. Nevertheless, mass changes were small (about ±5% of total initial mass) and their direction was unpredictable.

All evidence suggests that calling crickets are completely aerobic (Prestwich, 1994). Accordingly, we found metabolic power (mW) from $\dot{V}_{CO_2}$ by finding the respiratory quotient ($RQ=\dot{V}_{CO_2}/\dot{V}_{O_2}$) and then using this to find energy equivalence of a volume of CO_2 from a standard conversion table.

Sampling air from the calling burrow

Several hours before 'lab sunset', we sprinkled water on the soil of each cricket's container. This packed the sand and increased the likelihood that the crickets would build or reopen an acoustic burrow and sing. Individuals began tuning their burrows shortly after the lab sunset. Calling began within half an hour and continued for up to 2 h.

We sampled gas from the bulb portion of the burrow (Fig. 1) using a Tygon tube (3 mm o.d., 2.5 mm i.d.). To place the sampling tube, we guessed the location of the bulb from the shape of the burrow opening and then gently punched through the overburden with a 3 mm diameter dowel (using a swirling motion that tended to pack sand into the burrow walls). Resistance to pushing the dowel decreased when the bulb was breached. We then gradually widened the hole to a final diameter of 4–5 mm. Finally, we inserted the sampling tube to a depth slightly greater than the sampling hole and then sealed the sampling tube in place by tamping moist soil around the tube and by adding small amounts of water with an eyedropper. As a result, air was drawn into the burrow opening, past the cricket and then to the sampling tube. The burrow became the functional equivalent of a mask.

The problems with this method are that (i) sand can enter the sampling tube, and (ii) air from sources besides the burrow entrance might be able to enter the sample air stream. Entry of sand resulted in increased resistance to airflow as compared to when the gas analyzers were standardized. Increased resistance leads to decreased air stream pressure, which results in spuriously lowered O_2 partial pressures and erroneously inflated metabolic rates. Fortunately, sand was easy to detect after the run by inspection and/or during a run by decreases in flow rate and F_{O_2}. Any time more than a few grains were present in the tube (about 30% of all measurements), the data were discarded.

We believe that contamination of the sampling air stream by gases not from the calling burrow (e.g. from the main burrow) was a minor problem. Although we knew that air from the main burrow and soil interstitial air contained more CO_2 and less O_2 than air entering the burrow, we also knew that both of these

were high-resistance pathways. To ensure that their resistance remained high, we watered and packed the surface as mentioned previously and made certain that the exponential horn (Fig. 1) was the only opening to the animal's burrow. We also ascertained that burrow and interstitial gases did not cause noticeable errors with the following procedure. Typically, when mole crickets stop calling, they fill the exponential horn with sand. During the day when the mole crickets were typically deep in the soil, we unplugged the horn and set up the sampling and recording apparatus as described above. However, we covered the opening of the horn with a cut-off top of a plastic soft drink bottle. The cut ends were buried in the soil and the bottle's top was connected *via* a tube to a Douglas bag filled with essentially pure N_2. We sampled O_2 and CO_2 from the covered burrow as if there were an animal calling and found that during the first 30 s to 1 min, F_{CO_2} was slightly elevated and thereafter it dropped to zero (as did O_2). These data indicated that some CO_2 (most likely from the calling burrow and the main tunnel) was sampled at the start of the measurement interval. However, the calling burrow gas was quickly replaced with N_2 and, by 3 min equilibrium, with the main burrow gas. Since our experimental measurements all relied on steady-state F_{O_2} and F_{CO_2} values taken over a 5–10 min interval, this transition period was not a problem.

There was no measurable effect on sound pressure level, f_C or f_{WS} as a result of inserting the sampling tube. We concluded that the energetics of calling was not altered by our sampling procedure.

Resting metabolic rates

We measured resting $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ by putting crickets in 25 ml flow-through respirometry chambers with a flow rate of 25 ml min^{-1}. Each chamber contained a folded, moistened piece of paper towel that simulated wet sand and allowed the animals to hide. Measurement periods typically lasted 30 min, during which time the crickets remained inactive. These are not standard metabolic rates because the animals had access to food up to the time of the measurements. It is unlikely that *S. borellii* and *S. vicinus* ever undergo periods of food deprivation and we wished our data to be as comparable as possible to natural conditions.

Acoustic power

We measured sound pressure levels (SPL) at the same time we measured the cricket's calling metabolism. We used a Larson-Davis (Provo, UT, USA) Model 812 sound pressure level meter (re: 20 μPa) set to the slow r.m.s. (0.5 s time constant) and 'C' scale settings (Peterson, 1980). The SPL meter was calibrated at least once a week, although it rarely required adjustment. Since both species' songs are continuous trills of nearly identical sound pulses, a true r.m.s. (average) SPL can be obtained by taking 2 s or more of continuous readings (Prestwich et al., 1989). The experimenter held the SPL meter's detachable microphone at a series of defined positions in the far field, 0.25 m from the burrow while using a thin metal rod and wire hemisphere as a distance gauges.

Forrest (1991) reported that the sound fields in both species are essentially hemispherical. We confirmed this by determining sound fields for four individuals of each species by measuring SPL at 33 regularly spaced points on a 0.25 m hemisphere (Prestwich et al., 1989; Forrest, 1991). SPL readings were usually within ±1 dB of the average SPL with occasional values up to 3 dB different from average (usually those taken near ground level). The fact that the sound fields were approximately hemispherical made us confident that we could determine the acoustic power output accurately and rapidly by using five positions (vertical, and 45° above ground level on lines running through the long axis of the burrow opening and its perpendicular). We repeated these measurements 3–4 times for each individual during the 10 min interval when respiration was also being measured. Each SPL value was then converted to intensity I using the equation:

$$I = 10^{\left(\frac{\mathrm{SPL}-120}{10}\right)}, \quad (4)$$

where I is in Wm^{-2} (see Fletcher, 1992, p. 95). The results were averaged to give an average I for the surface of a 0.25 m radius hemisphere sound field. The product of I and surface area (0.393 m^2) gives P_{ac} (acoustic power output) in W.

Since we knew that the sound fields are not exact hemispheres, we attempted to estimate the error inherent in our method. Accordingly, we measured ten 33-point sound fields and calculated their surface areas using a custom-made computer Excel spreadsheet that summed the areas of a surface determined by triangles whose vertices included all measurement points (see Forrest, 1991). We then took a five-point subset of the 33 values using the points that corresponded to those used in our sound field measurements. From this, we determined the average distance to the isobar as used with the 33-point set, and calculated the surface area of a hemisphere of that radius. The largest discrepancy between these methods was nearly 11%, but overall it averaged ca. ±3%.

Statistical analyses

Unless otherwise reported, all tests of significance used a two-tailed t-test that assumed unequal variance or one-way analyses of variance (ANOVA). Efficiency and other measures calculated from ratios were transformed by taking the arcsine of the square root of the data expressed prior to statistical analysis (Sokal and Rohlf, 1981, p. 427). In this paper, we consider the result of any statistical test where the chance of a null hypothesis being correct, P, was <0.05 as significant: P<0.01, was considered highly significant. We do not believe in following these cutoffs blindly and so we do discuss some cases where $0.15<H_0>0.05$. In all other cases we simply term the results non-significant.

Results

Sound production and stridulation

Figs 2 and 3 show typical sound pulses and cycle-to-cycle f_C for both species at 25°C. During the driven portion of a

Table 1. *Characteristics of the calls and stridulation of* S. borellii *and* S. vicinus *at 25°C*

Species	Mean f_C (kHz)	Q	f_{WS} (Hz)	Driven portion of a sound pulse	Tooth strikes (driven cycles) s^{-1}	Tooth strikes per sound pulse	Tooth strikes needed to reach peak amplitude	P_{ac} (mW)
S. borellii	2.66±0.13 (9)	7.1±1.3 (8)	55±2 (9)	0.90±0.02 (9)	1660±79 (9)	30.4±1.2 (9)	15.5±0.7 (9)	21.2±5.8 (7)
S. vicinus	3.17±0.18 (8)	5.6±1.0 (8)	150±8 (8)	0.78±0.06 (8)	1555±335 (8)	10.7±2.2 (8)	6.7±1.2 (8)	2.9±1.4 (5)
P	<0.001	0.002	<0.001	<0.001	NS	<0.001	<0.001	<0.001

Values are means ± S.D. (*N*).

f_C, carrier frequency; Q, quality factor; f_{WS}, wing stroke; P_{ac}, acoustic power.

For P_{ac} and Q, each individual was measured a minimum of four times; for all other parameters, each individual was measured a minimum of ten times. These values were then averaged for each individual and the averages were pooled to compute species statistics. Statistical inferences were from two-tailed *t*-tests assuming unequal variance; closing time percentages were arc-sine transformed before performing the *t*-test. NS, not significant.

sound pulse, f_C typically either remains approximately constant (~20% of individuals) or decreases by less than 10%. These figures also show the abrupt increases in frequency at the end of the sound pulse that are believed to coincide with disengagement of the stridulatory surfaces (Bennet-Clark and Bailey, 2002; Bennet-Clark, 2003).

Table 1 summarizes species averages for call parameters related to energetics. The f_{WS} is nearly threefold greater in *S. vicinus* and its mean f_C is about 20% higher, as reported previously by Ulagaraj (1976). The percentage of the tegminal cycle when there is contact between the stridulatory surfaces is significantly greater in *S. borellii* (64% *vs* 52%). Moreover, *S. borellii* strikes significantly more teeth per wing stroke (30.4 *vs* 10.7), and a significantly greater number of teeth before maximum sound amplitude is reached (about 16 *vs* 7) than *S. vicinus*. There were no significant differences in the numbers of teeth struck per second, about 1600 in both species at 25°C. The Q values of the cricket-burrow systems were about 6–7. These Q values lie between Bennet-Clark's measurements for the burrows and tegmina in *S. borellii* (Bennet-Clark, 1987).

There were highly significant interspecific differences in P_{ac}. Table 1 shows that on average *S. borellii* produced about 7 times (~8.6 dB) more acoustic energy than did typical *S. vicinus*. There was no overlap in P_{ac} values between the species. Among *S. vicinus* there was an 18-fold difference in individuals' mean P_{ac}, and there were statistically significant differences in P_{ac} (P=0.02). By contrast, P_{ac} in *S. borellii* varied by only a factor of three among individuals and this difference was not statistically significant. We note that Forrest (1991) measured SPL and P_{ac} for both species as individuals called from containers identical to the ones we used. Our analysis of Forrest's published data does not reveal significant differences in P_{ac} between the two species (P=0.25, 20 d.f., *t*-test). The means we report for each species (Table 1) fall within the ranges of P_{ac} reported by Forrest, but the mean P_{ac} we measured for *S. borellii* is about 3.1-fold or 5 dB greater (P=0.001, 20 d.f., *t*-test) than that obtained by Forrest (1991). On the other hand, the mean P_{ac} that we measured for *S vicinus* is about one-third the value measured by Forrest (1991). This is a significant difference (P=0.04).

The differences between our data and published P_{ac} values led us to re-measure P_{ac} on 3 subsequent years using the same conditions as in the original experiments. Later results agreed with our earlier measurements. We also took field measurements on unconfined individuals. These showed that *S. borellii* was louder (typically ~2–3 dB SPL) than its congener and that both species had approximately the same shape sound field as we measured in the laboratory and as was found by Forrest (1991). The reasons for the discrepancies remain unclear. In any case, our results reinforce earlier measurements showing that the amount of acoustic energy that leaves the burrow of these species is highly variable and that *S. borellii* usually produces more sound (Ulagaraj, 1976; Forrest, 1991).

File morphology

The length of the file is similar in both species (Table 2). In *S. vicinus,* tooth spacing was approximately constant along the lengths of both the left and right files (Fig. 5). By contrast, in *S. borellii* there was marked variation in tooth-to-tooth distance along both the left and right files. Fig. 5 shows that, moving from the plectrum, tooth spacing begins to increase at about tooth number 5 and reaches a maximum spacing between numbers 25 to 30. Thereafter, the spacing gradually decreases.

Besides differences in the pattern of tooth spacing, there are 30% more teeth per file in *S. vicinus* and the teeth are 50%

Table 2. *Morphometric measurements of the files of* S. borellii *and* S. vicinus

Species	File length (mm)	Total teeth	Teeth mm^{-1}
S. borellii	2.53±0.39	64.3±5.1	25.6±3.7
S. vicinus	2.18±0.12	84.0±9.6	38.5±1.8
P	0.27	0.05	0.012

Values are means ± S.D. (N=6 individuals for all measurements).

Statistical analysis was a *t*-test assuming unequal variance (two-tailed).

Data kindly provided by T. J. Walker.

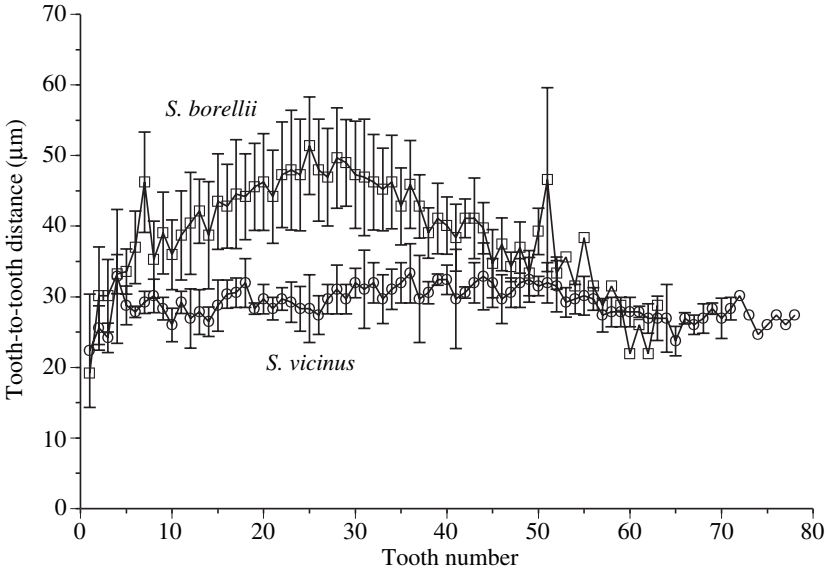

Fig. 5. Mean tooth-to-tooth distances as a function of tooth number for the right files of *S. borellii* (squares) and *S. vicinus* (circles). Teeth are numbered starting with the most medial (plectrum end of file). Similar results are obtained for the files of the left forewings. Values are means ± 95% CI, *N*=6 for most points.

more densely packed (Table 2). Part of the difference in tooth density is explained by the 1.2-fold greater average distance between file teeth in *S. borellii*, especially mid-file (Fig. 5). Moreover, in the region of the file most likely used for stridulation (tooth numbers 5–45) the inter-tooth distances average about 1.5-fold greater in *S. borellii* (maximum of about 1.7-fold difference). All of these ratios are highly significant statistically, as are the ratios for left side files. We note that our measurements of tooth-to-tooth distance are twofold greater than those reported by Bennet-Clark (1987) for *S. borellii.* We believe that his measurements (of what he called the file pitch) are of the 'tooth interval' – the distance between the end of one tooth and start of the next, instead of the distance between tooth 'peaks' that we used (see Fig. 4). If we use this definition, we find distances similar to Bennet-Clark's.

The average tegminal closing velocity is greater in *S. borellii*, even though it has the lower f_C. The tooth strike rate equals the f_C, and so teeth are hit about 1.2 times as frequently in *S. vicinus* (Table 1). However, the average distance between teeth in the sections of the file likely used for stridulation average are 1.5 times greater in *S. borellii.*

Each species' file teeth have similar shapes (Fig. 4) but the teeth are decidedly larger in *S. borellii.* For right tegmina, the *S. borellii* to *S. vicinus* ratio of tooth depth is 1.33 (Fig. 6) and for the left it is 1.24. In *S. borellii*, the right file teeth were deeper than the left, a highly significant difference, although this traced entirely to the first 20 teeth, which tended to be shallower on the left tegmen ($P<<0.001$ for all comparisons; *t*-tests). By contrast, we found no significant difference in left and right side tooth depths for *S. vicinus* (P=0.12, 156 d.f.; *t*-test). We note that our measurements of file tooth depth for *S. borellii* average 30% less than those reported by Bennet-Clark (1987). We believe the difference is explained by the fact we were able to obtain higher magnification images.

Tegminal and thoracic morphology

Morphometric measurements of the tegmina and associated musculature for similarly sized individuals of both species are given on Table 3. Correlations between pronotal length and tegminal muscle masses, although all positive, were not statistically significant. The lack of significance may trace to the small size range of the crickets we measured. Although *S. borellii* is louder than *S. vicinus* (Table 1), we found no significant differences in their tegminal muscle masses, an observation that seems inconsistent with our measurements of a higher mass-specific calling metabolism (see below). Nor were the apparent left *vs* right side asymmetries in muscle mass statistically significant. Lack of statistical significance is not the same thing as identity and we view these results with caution, given the difficulty of repeatably excising small muscles.

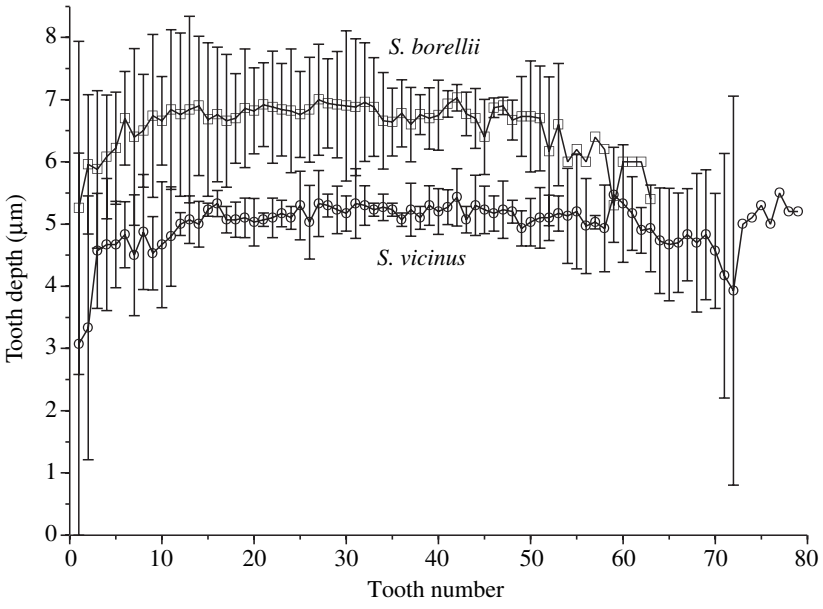

Fig. 6. Mean file tooth depths as a function of tooth number for the right files of *S. borellii* (squares) and *S. vicinus* (circles). Teeth are numbered starting with the most medial. Similar results are obtained for the files of the left forewings. Values are means ± 95% CI, *N*=5 for most points.

Table 3 also presents average dimensions of the harps for the right side tegmina. Note that these measurements are for different insects than those given in Table 2. Regressions of pronotal lengths with harp's linear dimensions and areas (not given) were highly significant in both species: larger animals generally possessed larger harps. Harp area is about 7.5% greater for *S. vicinus*. The orthodox view is that the acoustic inertance of the harp should vary directly with area, especially in closely related species (Nocke, 1971). If we assume that the spring constant of the tegminal acoustic resonance is the same in both species and is independent of harp area and body size, then we predict the f_C to be about 3.5% lower in *S. vicinus*, when in fact it averages 20% higher (Table 1). This suggests that either harp area does not strictly predict inertance or/and that harp stiffness is greater in *S. vicinus*. Bennet-Clark (2003) showed that in *Teleogryllus*, the most important resonant structure is the file. If this were the case in *Scapteriscus*, harp area would not necessarily be a good predictor of f_C.

Metabolism

Figs 7–9 show $\dot{V}_{CO_2}$ and/or $\dot{V}_{O_2}$ during calling in *S. borellii*. Results for *S. vicinus* were similar. Fig. 7 is typical of 60% of our records. This individual called continuously except for brief 12–24 s stops at time =5 and 7 min. Otherwise, $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ were approximately constant, consistent with a constant P_{ac}. This individual's respiratory quotient (RQ) was steady at about 0.89, similar to the values for all individuals of both species (Table 4) and indicative of mixed fat/carbohydrate metabolism.

In contrast to Fig. 7, about 40% of our measurements of metabolism during continuous calling showed that the metabolic rate gradually decreased between 5 and 20%. Fig. 8 is the record for a cricket that called continuously for 6 min. Its metabolic rate increased and then slowly dropped by nearly 20% while maintaining a constant value RQ. Fig. 9 shows $\dot{V}_{CO_2}$ for another *S. borellii* over an 18.5 min period, containing seven distinct calling bouts ranging in duration from 90 s to nearly 5 min. Peak and average $\dot{V}_{CO_2}$ differs between many of the calling periods.

We suspected that decreases in metabolism during continuous trilling were artifacts due, for example, to a lack of equilibration of the burrow air with the cricket's expired respiratory gases (see Materials and methods). Yet Fig. 9 depicts a result where the burrow was sampled continuously and where the highest metabolic rates were measured during the shorter calling bouts. If crickets had a constant calling metabolic rate, then short calling bouts would have the greatest chance to produce underestimates. Nor could the decreases be explained as the metabolic reflection of decreased body movements; unlike many other crickets, mole crickets do not move about when calling. During four long calling bouts in two individual *S. borellii*, we observed P_{ac} decreases of 10–15% (about –0.4 to –0.7 dB) over a time when respiratory rates decreased by an average 15%. Although detectable using a SPL meter, this decrease in P_{ac} is difficult for human observers to discern. Recently, one of us (K.N.P.) obtained similar results in

Table 3. *Morphological traits associated with sound production in* S. borellii *and* S. vicinus

Species	Body mass† (g)	Pronotal length† (mm)	Total tegminal mass (g)	Tegminal muscle mass (mg)			Right harp dimensions (mm or mm^2)		
				Right	Left	Total	Width	Length	Area
S. borellii	0.952±0.203 (7)	8.9±0.9 (8)	0.0053±0.0001 (7)	4.4±1.0 (6)	4.0±0.6 (6)	8.4±0.8 (6)	3.2±0.3 (5)	4.2±0.2 (5)	6.7±0.7 (5)
r‡	0.91 (*P*<0.001)	–	0.86 (*P*=0.013)	0.29 (*P*=0.58)	0.18 (*P*=0.73)	0.51 (*P*=0.30)			
S. vicinus	0.955±0.162 (8)	8.2±0.5 (8)	0.0064±0.0001 (8)	4.4±1.6 (8)	4.1±1.4 (8)	8.6±2.9 (8)	3.2±0.2 (5)	4.5±0.2 (5)	7.2±0.6 (5)
r‡	0.93 (*P*<0.001)	–	0.37 (*P*=0.39)	0.67 (*P*=0.19)	0.62 (*P*=0.38)	0.67 (*P*=0.25)			

Values are means ± S.D. (*N*).
†Regression of body mass (*M*) on pronotal length (*L*): *S. borellii*: *M*=189*L*–740; r^2=0.83; *P*=0.004; 1,6 d.f., ANOVA; *S vicinus*: *M*=322*L*–1687; r^2=0.87; *P*<<0.001; 1,7 d.f., ANOVA.
‡All Pearson–product correlations (*r*) are with pronotal length. Correlations were tested for significant differences from zero using one-way ANOVA.

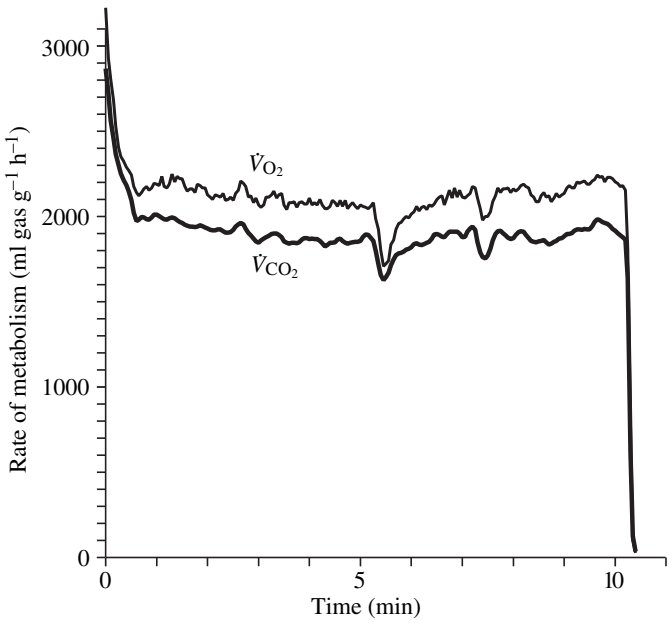

Fig. 7. Simultaneous measurements of $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ in a calling *S. borellii*. The initial drop is associated with washout of gases in the burrow prior to the start of an airflow and sampling. The two dips coincide with brief periods when the cricket stopped calling. Average RQ≈0.91. This figure shows the most commonly observed respiratory measurement in both species – one or two minutes of equilibration followed by steady rates of metabolism at a constant RQ.

a gryllid (*Anurogryllus arboreus*) under highly controlled conditions. We conclude that an individual's calling metabolic rate can vary although the mechanism is not clear.

Table 4 makes several interspecific comparisons of metabolic rates. At rest, there were no significant interspecific differences in either whole-animal or mass-specific measures of respiration and the RQ values suggested carbohydrate metabolism. All individuals used for resting rates were approximately the same size. By contrast, the interpretation of the data for calling individuals was complicated by size biases. Although similar variation in body size and mass is seen in field collections, the mass of *S. borellii* that called in our study averaged over 20% less, with smaller pronota, than the *S. vicinus* used in the calling study. Given this difference, we preferred to use mass-specific $\dot{V}_{CO_2}$ for interspecific comparisons of calling costs. By this measure, *S. borellii* averaged 40% higher metabolic rate. On the other hand, whole-cricket metabolic rates during calling were not significantly different.

We note an apparent conflict between results in Tables 3 and 4. Table 3 suggests that similarly sized individuals of the two species have nearly identical tegminal muscle mass. Assuming that calling metabolism mostly reflects the activity of tegminal muscles and since we expect smaller muscles in smaller individuals, then we expected lower whole-animal rates of metabolism in the smaller *S. borellii*. Yet their calling metabolic rates were nearly the same as the larger *S. vicinus*. In retrospect, it would be far more useful to have obtained muscle masses and

Table 4. *Calling and resting metabolism in* S. borellii *and* S. vicinus

Condition	Species	Mass (g)	$\dot{V}_{O_2}$ (μl O_2 g^{-1} h^{-1})	$\dot{V}_{CO_2}$ (μl CO_2 g h^{-1})	RQ	Metabolic power (mW g^{-1})	Metabolic power (mW)	Net cost (P_{call}–P_{rest})	Metabolic scope (P_{call}/P_{rest})	Acoustic power (mW)	Efficiency (%) (P_{ac}/P_{call})	Efficiency (%) (P_{ac}/$P_{call-net}$)
Rest	*S. borellii* (*N*=6)	0.863±0.120	241±20	227±37	0.96±0.14	1.4±0.1	1.2±0.1	–	–			
	S. vicinus (*N*=6)	0.978±0.008	288±37	290±22	1.05±0.10	1.7±0.2	1.6±0.1	–	–			
P		0.39	0.26	0.16	0.72	0.66	0.04	–	–			
Calling	*S. borellii* (*N*=7)	0.826±0.071	2098±156	1804±72	0.84±0.07	11.6±0.8	9.4±0.5	10.2 (8.3×P_{rest})	8.2 (7.8×P_{rest})	0.0212±0.0024	0.23±0.02	0.026±0.02
	S. vicinus (*N*=5)	1.075±0.006	1387±162	1297±80	0.86±0.11	9.0±0.5	9.6±0.6	7.3 (5.3×P_{rest})	7.0 (6.0×P_{rest})	0.0029±0.0014	0.03±0.01	0.04±0.02
P		0.02	0.01	0.01	0.96	0.02	0.91	–	–	<0.001	<0.001	<0.001

Metabolic power was calculated from $\dot{V}_{CO_2}$. The net cost of calling was estimated as P_{call}–P_{rest}.

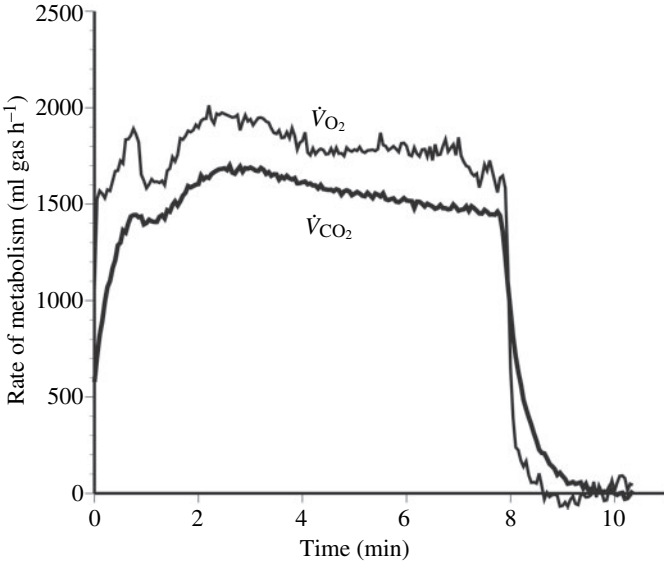

Fig. 8. Simultaneous measurements of $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ in a continuously calling *S. borellii*. Sampling was underway when the cricket began calling. This record shows that continuously calling crickets do not necessarily have constant metabolic rates. Note that O_2 records sometimes can spike and drift independently of the more reliable CO_2 data (see start and middle of record). Near the end of the record the sampling tube was removed from the burrow and both measures of metabolism fell to essentially zero.

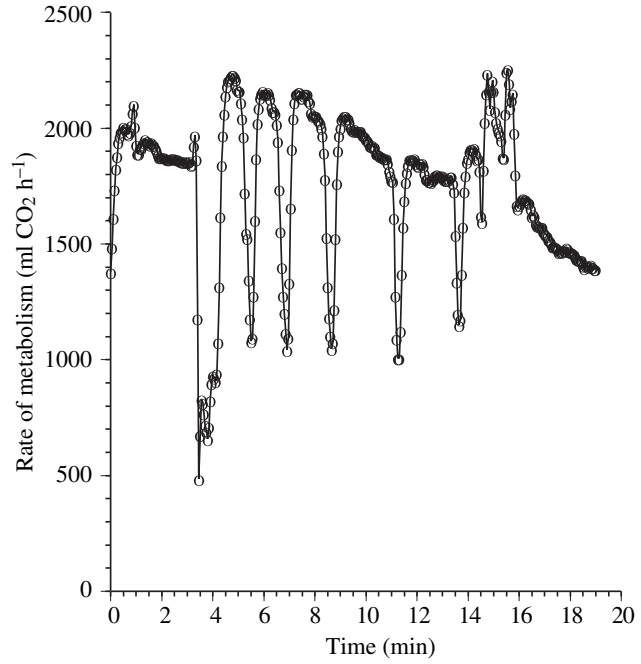

Fig. 9. $\dot{V}_{CO_2}$ in a *S. borellii* that frequently stopped and restarted calling. Air stream sampling was continuous. The metabolic rate decreased during each brief calling bout only to increase again when the cricket resumed calling. Overall, respiratory rate decreased by approximately 25%.

tegminal measurements for the same crickets used in the metabolism study. Nevertheless, the discrepancy illustrates the dangers inherent in comparisons involving related but different measures on different individuals.

We found intraspecific differences in whole-animal P_{call} in *S. vicinus*. In *S. borellii*, differences were suggested but were not statistically significant (one-way ANOVA, P=0.12; 6,36 d.f.). Regressions of P_{call} on mass were not statistically significant for either species. However, the sample sizes were small, as were the ranges of mass. Moreover, although mass is the most commonly used measure of size when normalizing metabolism, perhaps there are better indices less susceptible to recent feeding, drinking or evacuation. The usefulness of other size metrics needs to be investigated in more tractable and better-known species.

We obtained three measurements of the energetics of refurbishing and tuning burrows in *S. borellii* (for a detailed discussion of burrow building, see Bennet-Clark, 1987). Loose sand used to plug the burrow was moved about mostly in the first half of this period. Later, less sand was moved, although the animal continued moving about steadily except when it made brief (<5 s) calls to check on the progress of tuning its burrow. We were not able to separate satisfactorily the cost of digging from the cost of these brief calls. On average, a 0.83 g *S. borellii* needed about 14 min to complete the process, at a cost of between about 2.2 and 3.4 J. Average power consumption was slightly less than 4.0 mW, approximately 2.5 times resting but only 40% of the typical P_{call} (Table 4). For comparison, the net cost of calling in *S. borellii* for 14 min is about 7.7 J and calling bouts commonly last 2 h for a total calling cost of about 65 J.

Covariation of acoustic and metabolic power and the efficiency of sound production

We found little evidence for relationships between P_{call} and P_{ac}. Although individual's metabolic rates and loudness varied on different evenings, only one of six *S. borellii* and one out of four *S. vicinus* had statistically significant regressions of P_{ac} on P_{call}. Within these individuals, P_{ac} was generally more variable than P_{call}. Values often differed from the individual's mean by more than ±50%. Likewise, we did not find statistically significant linear regressions between individuals' mean P_{ac} *vs* their mean P_{call} (see Fig. 10, *S. borellii*, r^2=0.37, P=0.19, ANOVA, 1,5 d.f.; for *S. vicinus,* r^2=0.32, P=0.27; 1,3 d.f.). Thus, with our samples, P_{ac} is not a reliable indicator of a signaler's metabolic power. We caution that this conclusion is based on a small sample size with a small range of body sizes when compared to what can be found in the field.

Efficiency of sound production E is defined as the ratio of acoustic (output) to metabolic (input) power. Table 4 gives species averages and error terms computed using both total metabolism and net metabolism for calling. Our data are unique for animal sound production measurements because they allowed us not only to estimate E for individuals, but also to obtain error terms and test for differences. Calculated values of E based on total metabolism averaged 0.23% in *S. borellii*

(N=7) and 0.03% in *S. vicinus* (N=5), an approximately eightfold difference. The difference between species averages was statistically highly significant. Means and error terms for individuals are shown in Fig. 11. For *S. borellii*, coefficients of variation for E average 64% (range: 10–131%) and there were no statistically significant differences among individuals. By contrast, individuals' coefficients of variation for E were less in *S. vicinus* (mean 41%, range 25–78%) and there were statistically highly significant individual differences (P=0.002; 3, 21 d.f.; ANOVA).

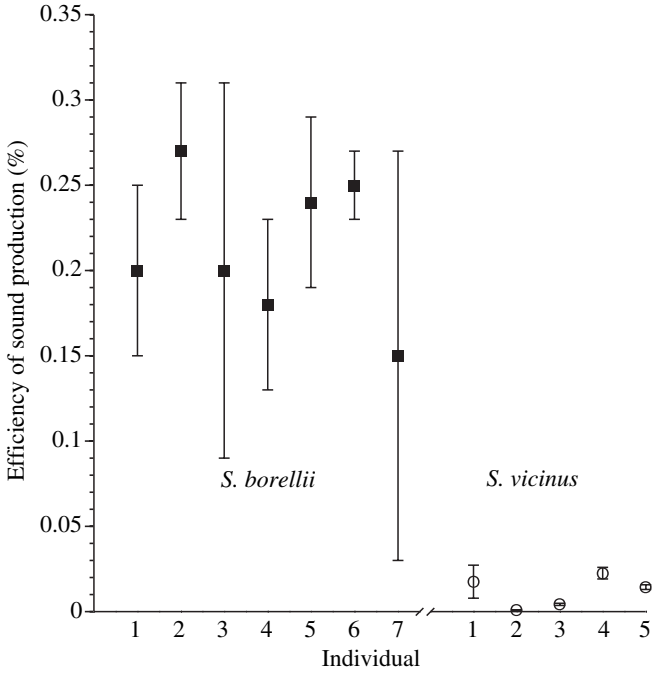

Fig. 11. Mean efficiency of sound production E for individuals of each species. There were no statistically significant differences in E between individual *S. borellii*. One *S. vicinus* had a mean E significantly lower than the others. In both species the major cause of variation in E was that P_{ac} was generally more variable than P_{call}. Overall E was significantly greater in *S. borellii* than in its congener. Values are means ± 95% CI.

Discussion

It is widely accepted that signals may evolve under sexual selection to reveal the underlying condition of the signaler. By one version of this scenario, only individuals in the best condition are capable of expending energy at high rates and over long periods of time. Signals are useful to the extent that there is a high degree of correlation between metabolic effort and a signal's energy-related attributes. In acoustic signals these attributes include the signal's power (P_{ac}) and time measures: (i) the calling effort (defined as the product of the signal's duration and repetition rate by Taigen and Wells, 1985) and (ii) duration of the calling bout. Hypotheses regarding the significance of the time components of acoustic signalling are easily tested because these measures enjoy straightforward relationships to metabolic effort. The power of the signal, on the other hand, is related to both metabolic power (P_{call}) and also strongly related to the energy transduction process, starting with the breakdown of fuel molecules and ending with the acoustic coupling between the signaller and its environment (Bennet-Clark 1970, 1989, 1995; Prestwich, 1994). Efficiency of sound production, E, can be viewed as the proportionality constant that relates P_{call} and P_{ac} and that quantifies transduction. We now examine these factors in *Scapteriscus* from mechanistic and evolutionary perspectives.

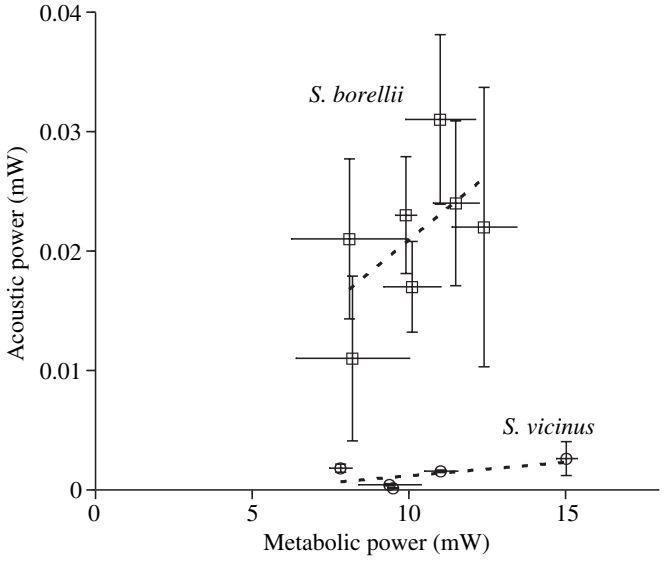

Fig. 10. Mean acoustic and metabolic power for individuals of both species. There was no statistically significant relationship between P_{ac} and P_{call} in either species. Values are means ± 95% CI.

Metabolism and calling

If a signal's energy attributes provide accurate information about the condition of the signaler, then we expect to see individual differences in whole-animal P_{call}. Moreover, call parameters that determine P_{ac} should reliably correlate with P_{call}. The causes of differences in P_{call} may be classified as size-dependent (larger crickets are expected to have larger muscles) and size-independent (general condition or calling strategy without respect to size). We found significant differences in P_{call} among individual *S. vicinus*, and our data suggest the same in *S. borellii* using samples consisting of similarly sized individuals (all masses within 15% of the species' sample mean). This supports the presence of size-independent differences in P_{call} in both species. This conclusion is also supported by evening-to-evening variation in some individuals' P_{call}. The average coefficient of variation (s.d./mean) in $\dot{V}_{CO_2}$ within individuals of both species over time was about 10% (maximum=15%), and our controls suggest that <20% of this variation was experimental artifact. Although we did not demonstrate them, we believe it likely that size-dependent differences in P_{call} will be found with a

sample that incorporated the full range of body masses seen in the field (mass varies in both species by a factor of 2–3).

P_{call}, P_{ac}, E and calling parameters in crickets that trill are compared in Table 5. In comparison to the other species, both *Scapteriscus* species have low mass-specific P_{call}. The most relevant comparison is with an Australian mole cricket *Gryllotalpa australis*, which has a value of P_{call} about 2.6-fold greater than *S. borellii*. Prestwich and Walker (1981) proposed that f_{WS} might be of paramount importance in determining P_{call}. However, the data on Table 5 refute this hypothesis, at least as far as its being strongly determinative in all species. For instance, *G. australis* is roughly the same size and has a value for f_{WS} that is about half that of *S. vicinus*. Yet *G. australis*' cost of calling is 2.6-fold higher. The same holds when *S. borellii* and *S. vicinus* are compared: *S. vicinus* has the higher f_{WS} and the lower mass-specific P_{call}. Nor are the differences in P_{call} shown in Table 5 fully explainable by differences in calling effort. In crickets, calling effort is closely related to the total number of plectrum-to-tooth strikes per unit time. Using *Scapteriscus* as an example, the total number of teeth struck per second is the same in both species although there are significant interspecific differences in mass-specific P_{call} (Tables 1 and 4).

The data in Table 5 suggest call amplitude as a central correlate with P_{call}. *G. australis* has a greater SPL (Kavanagh, 1987) than either of the *Scapteriscus* (Table 1) and a higher mass-specific P_{call}. *Anurogryllus muticus* has a P_{call} about 2.5-fold greater than its congener, *A. arboreus* and a small data set (K.N.P., unpublished data) suggests that its average SPL is several dB greater. However, any correlation is complicated because f_{WS} in *A. muticus* is about twice that of *A. arboreus* (Table 5). Moreover, we found that P_{ac} in *S. borellii* was about sevenfold greater than *S. vicinus* even though its mass-specific P_{call} was only 30% greater.

In summary, it is evident and not surprising that energy is partitioned differently between f_{WS}, calling effort and signal amplitude in different species. The relationships between these variables need to be more systematically and rigorously investigated than in the past (Prestwich and Walker, 1981; Prestwich, 1994). It is especially important that individual differences in these parameters should be documented when they exist.

The acoustic burrow and the efficiency of sound production

In mole crickets, E is determined by (i) the characteristics of the acoustic burrow and (ii) the biochemical and mechanical processes that operate as energy is transferred from fuel molecules to the cricket's immediate acoustic environment (Bennet-Clark, 1970, 1989, 1995; Prestwich, 1994).

The burrow's effect on E is determined by its construction, the animal's calling position, and the porosity of the burrow walls (Bennet-Clark, 1970, 1987; Daws et al., 1996). If the soil is porous and filled with air, sound will penetrate the burrow walls and dissipate (Daws et al., 1996). This increases internal damping and lowers the Q (Eq. 1) of the cricket-burrow system (Bennet-Clark, 1989; Fletcher, 1992). The Q values we measured for individuals of both species calling within burrows are generally less than one-half those of isolated tegmina or crickets calling in the open (Nocke, 1970; Bennet-Clark, 1970, 1975, 1987, 2003; Prestwich et al., 2000).

Others have reported that mole cricket calls issuing from wetter burrows are louder (*Scapteriscus*; Ulagaraj, 1976; Forrest, 1979, 1983, 1989, 1999; *Gryllotalpa*; Bennet-Clark, 1970). In our study, two *S. borellii* whose singing burrows were located at the edges of ponds produced songs with mean SPL re: 20 μPa of 82–85 dB at 0.25 m, corresponding to P_{ac} of 62–124 μW. These values were three- to sixfold larger than we typically measured in the laboratory (Table 1). Several nights after capture, these same individuals called in the laboratory from moist (but not saturated) burrows and their SPL re: 20 μPa had decreased to approximately 75 dB at 0.25 m (P_{ac}≈12 μW). Heavy watering of the soil in the

Table 5. *Energetics of calling in trilling crickets at temperatures near 25°C*

Species	Mass (g)	f_{WS} (s^{-1})	Estimated P_{call}		P_{call}/P_{rest}	P_{ac} (mW)	E (%)	Reference(s)
			mW g^{-1}	mW				
Anurogryllus arboreus	0.42	70	20.5	8.6	11	0.059	0.69	Prestwich and Walker, 1981; Forrest, 1991
A. muticus[a]	0.40	132	51.5	20.6	16	na	–	Lee and Loher, 1993
Gryllotalpa australis	1.14	70	30.1	34.3	12	0.27	0.79	Kavanagh, 1987
Oecanthus celerinictus[a]	0.06	55	16.4	0.9	7	0.012	1.3	Prestwich and Walker, 1981; K.N.P., unpublished data
O. quadripunctatus[a]	0.06	38	21.8	1.2	7	0.010–0.042	0.83 (3.5)[b]	Prestwich and Walker, 1981; Forrest, 1991
Scapteriscus borellii	0.83	55	11.6	9.4	8	0.021 (0.124)[c]	0.23 (1.3)	This study
S. vicinus	1.1	150	9.0	9.6	5	0.0029	0.03	This study

Whole animal total metabolism is used in all estimates of P_{call}.

[a]Calling RQ has not been measured in these species. Forrest (1991) assumed RQ=0.85.

[b]Efficiency values in parentheses for *O. quadripunctatus* are based on the maximum P_{ac} values measured by Forrest (1991) in individuals calling from a leaf baffle and by assuming P_{call} from Prestwich and Walker (1981) for crickets not calling in a baffle.

[c]This power output corresponds to the highest value typically observed in the field in burrows whose walls are saturated with water.

cricket's buckets on subsequent days was accompanied by an increase in loudness of several dB without any consistent change in P_{call}. Regrettably, we failed to measure the burrow/cricket Q as a function of watering. Nevertheless, day-to-day differences within individuals' P_{ac} were greater in both species than was the variation in P_{call}. As has been suspected since the earliest field studies, reversible changes in P_{ac} are due to changes in burrow damping and therefore in E. Variation in P_{call} plays a comparatively minor role.

The E for both *Scapteriscus* species are several-fold lower than other trilling crickets, at least with the soil conditions prevailing during our measurements. Bennet-Clark (1970, 1987) and Daws et al. (1996) have shown that mole cricket burrows have the potential to confer exceptionally high E: certainly greater than 1% and perhaps much higher. In *Gryllotalpa australis, E* is about 1% (Kavanagh, 1987). Our data suggest that in *S. borellii* and perhaps its congener, E might be as high as 0.6–1.3% if the burrow walls are saturated with water. We predict similarly high E in species that live in non-porous, clay soils. However, in Florida few burrows are built in conditions where the walls are consistently saturated and we believe that E is commonly low if there has not been a recent rain. Bennet-Clark (1987, 1989) suggested that an important function of the acoustic burrow is to allow production of reasonably loud sounds at a lower f_C than could be radiated efficiently without the burrow. In many environments, lower frequencies attenuate less rapidly (Marten and Marler, 1977). Thus, for a given initial signal intensity, a lower f_C increases the potential number of females that might be attracted to a calling male (Bennet-Clark, 1987, 1989; Forrest, 1979; Forrest and Raspet, 1994). However, since intensity varies with soil conditions, the usefulness of the signal to conspecific females would seem restricted to species identity, caller location and habitat quality (Forrest, 1989; Forrest and Raspet, 1994), although it remains possible that information about the signaller's condition might be encoded in f_C and/or frequency stability (Simmons and Ritchie, 1996) or pulse duration.

Efficiency of sound production and the operation of the stridulatory apparatus

Discussions and analyses of energy transfers have centered on estimating E for the entire process and/or have focused on the coupling of the radiator to acoustic environment (Bennet-Clark, 1970, 1975, 1987, 1989, 1995; Kavanagh, 1987; Prestwich, 1994; Forrest, 1991; Bailey et al., 1993). What follows is our attempt to provide quantitative analyses of the energetics of stridulation proper. By this, we mean the power associated with: (i) contact between stridulatory surfaces that ultimately drive the vibrations of the tegminal oscillator; and (ii) accelerating and decelerating the tegmina when the stridulatory surfaces are not engaged (the entire opening stroke plus the closing stroke's initial and final accelerations). We first present two models of power transfer to the tegminal oscillator. They differ in how they calculate the energy transferred from the closing tegmina to the vibrating wing surface during each tooth strike.

The spring model

This model centers on finding the energy required to bend the file enough so that the plectrum disengages and moves on to the next tooth. The model assumes that the minimum bending required to unlock the file and plectrum would equal the file tooth depth. For both tegmina:

$$P = 2f_{WS}\beta \sum_{n=1}^{i} x_i^2 \approx 2nf_{WS}\beta\bar{x}_i^2, \quad (5)$$

where β is the file's spring constant (kg s^{-2}), assumed to be constant with length, n is the number of teeth struck during one tegminal closure, x_i refers to the depth of each file tooth, or, $\bar{x}$ is the average depth of the file teeth struck by the plectrum during a wing closure. The spring constant is estimated using the familiar resonance equation, the sound pulse's average f_C, and an estimate of the effective mass of the resonator. The other parameters required by Eq. 5 are found in Table 1 and Fig. 6 and give the number of plectrum to file impacts per second. The spring model views the plectrum as a rigid pick (see Fletcher, 1992) with its elastic properties being included in those of the file. It is likely that the model is too simple. For example, we have not explicitly included the elastic properties of the plectrum and its contributions to the catch-and-release process. Nor does the model take into account any bending of the file in excess of what is required to release the plectrum (Bennet-Clark and Bailey, 2002; Bennet-Clark, 2003). We simply have no measurements of the bending and that the plectrum is not fully understood.

The kinetic energy (KE) transfer model

Bennet-Clark (1970, 1987) found that the peak amplitude of each cycle during a sound pulse was directly related to the 'tooth pitch' (tooth-to-tooth distance) profile of the mid-section of the files in *Gryllotalpa vineae* and in *S. borellii*. Although Bennet-Clark did not write it, the implication of this relationship is that tooth spacing helps to determine the relative velocities of the tegmina at plectrum–tooth impact. Assuming a constant applied muscular force, a greater inter-tooth distance results in a greater tegminal velocity at tooth–plectrum contact since the time required to skip from one tooth to the next is constant due to the operation of an escapement-like mechanism (Nocke, 1971; Elliott and Koch, 1985; Koch et al., 1988).

The energy transfer that occurs while the plectrum is captured by the file may be conceived as having two immediate sources. The closing muscles are continuously active and therefore, when the stridulatory surfaces are engaged, energy that would otherwise accelerate the tegmina is directly transferred to the tegminal oscillator. The tegmina also lose velocity and therefore some of their kinetic energy

(KE) to the oscillator. When the plectrum is released, the tegmina again accelerate and gain KE that will be lost on the next tooth capture. We assume that the amounts of energy transferred by these two pathways, taken as an average over all capture and release cycles, are approximately equal. We base this assumption on what is known of the stridulatory mechanics of *Gryllus campestris* (Elliott and Koch, 1985; Koch et al., 1988). In this species, accelerations that are consistent with an approximately constant applied force occur when teeth are removed from the file. Moreover, EMG data suggest constant muscle fiber activation during much of the closing stroke.

Thus, the power input is twice that associated with KE changes that occur during file–plectrum capture and release. Remembering this, then using the familiar equation for KE and finally incorporating variables for the tooth strike rate, we can write the power transfer for both tegmina as:

$$P = 2f_{WS}m\sum_{n=1}^{i}(v_{C,i}^2 - v_{R,i}^2) \cong 2nf_{WS}m(\bar{v}_C^2 - \bar{v}_R^2)\,, \qquad (6)$$

where m is the tegminal mass. The rightmost expression uses mean velocities for each tegmen's center of mass at the time the plectrum is captured ($\bar{v}_C$) and released ($\bar{v}_R$). We assume that $\bar{v}_C$ and $\bar{v}_R$ are roughly constant for most tooth strikes and that they differ from each other by perhaps 20% of the average closing velocity. This velocity range was obtained from magnified images of Elliott and Koch's data for closing velocity in *G. campestris* (Elliott and Koch, 1985). These plots show the velocity 'ripples' to be approximately triangular, and so:

$$\bar{v}_{Close} \cong 0.33(\bar{v}_C - \bar{v}_R) + \bar{v}_R \cong 0.33(\delta\bar{v}_R - \bar{v}_R) + \bar{v}_R\,, \qquad (7)$$

where $\bar{v}_{Close}$ is the average closing velocity at the tegminal center of mass, δ (assumed to be 1.2) is the proportion by which $\bar{v}_C$ exceeds $\bar{v}_R$.

Comparison of models

The predictions of the two models are compared in Table 6. The KE transfer model predicts a sevenfold greater energy transfer in both species than does the spring model. Crucially, when the calculated energy transfers are compared to measured P_{ac} for each species, the spring model fails to predict enough energy to account for the sound produced in *S. borellii* and although it does predict sufficient energy in *S. vicinus*, it implies an extraordinarily high E. Nevertheless, we are inclined to believe that Eq. 5 is correct and its inability to give reasonable values traces from two factors. First, there is considerable uncertainty associated with the spring constant's value. Second, using file tooth depth, the bending value is almost certainly an underestimate. Bennet-Clark and Bailey (2002) suggest that when relatively high amplitude vibrations occur, usually mid-way through a sound pulse, the Cu2 veins bend much more than the file tooth depth.

The KE transfer model yields predictions that are more consistent with our energetics measurements. It suggests that

Table 6. *Two models of energy input to the tegminal oscillator during stridulation*

			Spring model					Kinetic energy transfer model				
Species	f_{WS} (s^{-1})	Teeth struck per wing stroke	Vibrating mass[1] (μg)	Spring constant[2] (β) (kg s^{-2})	File tooth depth (mean; μm)	Power transfer[3] (μW)	P_{ac}÷power transfer	Power transfer÷P_{Call}	$\bar{v}_{Close}$ at COM[4] (m s^{-1})	Mass (mg)	Est. P[5] (μW)	P_{ac}÷est. P	Power transfer/P_{Call}
S. borellii	55	30.4	65	25	9.13	6.9	310%	0.07%	0.116	5.3	49	43%	0.5%
S. vicinus	150	10.7	65	25	7.11	3.9	70%	0.05%	0.080	6.4	27	11%	0.4%
S. borellii÷ *S. vicinus*	0.36	2.8	—	—	1.3	1.8	4.4	1.4	1.4	0.8	1.8	4	1.25

[1]Estimated for one tegmen as the product of the ratio of the average harp area for both species to the harp area for *G. campestris* times the estimated vibrating mass for *G. campestris* (Nocke, 1970).
[2]β for one tegmen was calculated using estimated vibrating mass (see 1) and f_C of each species (Table 1).
[3]'Spring model' power was calculated using Eq. 5.
[4]Mass is for both tegmina (Table 3). COM, centre of mass.
[5]The 'KE transfer model' calculation assumes that the change in velocity during a tooth capture cycle is 20% of the mean closing speed. The capture and release velocities were calculated with Eq. 7 and power transfer using Eq. 6.

Table 7. *Estimated maximum power requirements to overcome inertia during stridulation in* S. borellii *and* S. vicinus

Species	Mass[1] (mg)	f_{WS} (s^{-1})	Opening time[2] (ms)	Closing time[3] (ms)	Distance the COM moves[4] (mm)	Mean opening velocity of tegmen COM[5] $\bar{v}_O$ (m s^{-1})	Est. power to overcome inertia during opening[6] (μW)	Mean closing velocity of tegmen COM[7], $\bar{v}_C$ (m s^{-1})	Est. power to overcome inertia during closing[8] (μW)	Est. max. power to overcome inertia[9] (μW)	Est. KE power + Strid. power[10] (μW)	Percent. P lost to inertia÷(KE + Strid. P[11])
S. borellii	5.3	55	6.4	11.4	2.70	0.424	105	0.116	8	113	162	70%
S. vicinus	6.4	150	2.7	3.7	0.64	0.237	108	0.080	12	120	147	82%
S. borellii÷ *S. vicinus*	0.83	0.4	2.4	3.1	4.2	1.8	1.0	1.45	0.67	0.9	1.3	0.7

[1]The mass of both tegmina (from Table 1).

[2]The time between the end of the sound pulse and the start of the next pulse.

[3]The difference between the average period and the opening time (see 2).

[4]Twice the estimated length of the file that was stridulated. The length of the file that was stridulated was determined from the number of teeth struck during the closing stroke (Table 1) and from inter-tooth distances starting at the portion of the file just prior to where the maximum tooth depth is reached (Fig. 5). This distance was multiplied by 2 to give the displacement of the tegmen's center of mass (COM). The distance from the attachment of the tegmen to the thorax to the center of mass is about twice the distance from the attachment to the center of the file.

[5]The average velocity of the COM during either the acceleration or the deceleration of opening ($\bar{v}_O$). Assuming tegminal opening operates as in *Gryllus campestris*, the tegmina use about half of the opening stroke to accelerate to peak velocity and the second half to decelerate to rest (Elliott and Koch, 1985). Thus, we conservatively (under)estimated the peak opening velocity as the movement of the center of mass (previous column) divided by the closing time.

[6]Calculated as $4f_{WS}(0.5m\bar{v}_O^2)$. The constant 4 is used because there are two wings and each closing stroke has an acceleration and deceleration.

[7]The average velocity of the center of mass during closing ($\bar{v}_C$). The closing stroke contains brief periods of acceleration and deceleration at its beginning and finish. Most of stroke is occupied with stridulation where velocity is roughly constant. The energy required to overcome inertia at the start and end of the closure can be calculated using the mean velocity since it essentially equals the velocity changes at the start and finish of the closing cycle.

[8]Calculated as $4f_{WS}(0.5m\bar{v}_C^2)$. See 6 and 7.

[9]The sum of the estimated maximum opening and closing power requirements for overcoming tegminal inertia.

[10]The sum of estimated power requirements for overcoming inertia (see 9) and the KE transfer model power estimates (Table 6).

[11]The ratio of the two previous columns; it is an estimate of the percentage of the energy requirement for stridulation that is used to overcome inertia.

about 0.4% (*S. vicinus*) and 0.5% (*S. borellii*) of net mass-specific P_{call} (Table 4) is used to drive the tegminal oscillator. The majority of the energy would be lost in metabolism, in the contractile fibers, and in the elastic and skeletal systems (Bennet-Clark, 1995). The KE model also predicts that 11% (*S. vicinus*) and 43% (*S. borellii*) of the energy inputted to the oscillator is ultimately radiated as sound from the burrow. Although these numbers seem reasonable, when this calculation is repeated using the highest P_{ac} observed for *S. borellii* in the field, 125–250% of the energy input to the oscillator is predicted to convert into sound! Thus, energy inputs to the tegminal oscillator must be larger than calculated on Table 6. The suspect variables are v_C and v_R, which were estimated (see Eq. 7), not measured.

Efficiency and the inertial costs of stridulation

Stridulation requires the tegmina to be accelerated and decelerated during both halves of the tegminal cycle. In the absence of elastic storage mechanisms, inertial losses might be high, especially in species with high f_{WS}. However, Table 7 presents the results of calculations that suggest both *Scapteriscus* potentially require similar amounts of power to overcome inertia, even though *S. vicinus* has a wing stroke rate that is nearly threefold greater than *S. borellii*. This surprising prediction traces to *S. vicinus*' lower opening and closing tegminal velocities (related to the smaller file teeth and the shorter length of the file that is stridulated). Table 7 also predicts that, in the absence of thoracic resonance, (i) power requirements to overcome inertia are much greater in the opening than closing stroke due to higher velocities, and (ii) overcoming inertia is predicted to be a greater power sink than is the input to the tegminal oscillators (using the KE model; Table 6).

We want to emphasize the tentative nature of the predictions on Tables 6 and 7. These models are built on assumptions about thoracic skeletal/muscular resonance, file stiffness and bending, and tegminal velocities that may not be correct. Nevertheless, we include them as a first step in a more quantitative analysis of the energetics of stridulation in the hope that they will suggest future areas of investigation.

List of symbols and abbreviations

COM	centre of mass
E	sound production efficieny
f_0	resonant frequency of an oscillator
f_C	carrier frequency, the most energetic frequency from a spectrogram
F_{ECO_2}	fraction of CO_2 in air removed from the burrow sampling tube
F_{EO_2}	fraction of O_2 in air removed from the burrow sampling tube
F_{ICO_2}	fraction of CO_2 in air entering the calling burrow
F_{IO_2}	fraction of O_2 in air entering the calling burrow
f_{WS}	wing stroke, sound pulse, or syllable rate
H_0	null hypothesis
I	acoustic intensity (W m^{-2})
KE	kinetic energy
M	mass
n	number of teeth struck during one tegminal closure
N	sample size
P_{ac}	acoustic power
P_{call}	total metabolic power during calling
Q	quality factor
r	Pearson product–-moment correlation coefficient
R	the damping (specific acoustic) resistance
r^2	linear regression coefficient of determination
RQ	respiratory quotient, taken as equal to the respiratory exchange ratio
S	cross-sectional area
SPL	sound pressure level, re: 20 μPa
$\dot{V}$	gas flow rate
$\bar{v}_C$	average velocity of the center of mass of the tegmen when the plectrum is captured by a tooth
v_C	velocity of the center of mass of one tegmen at the capture of the plectrum by a file tooth
$\bar{v}_{Close}$	average velocity of one tegmen's center of mass during a closing stroke
v_O	opening velocity of tegmen COM
$\dot{V}_{CO_2}$	rate of carbon dioxide production
$\dot{V}_{O_2}$	rate of oxygen consumption
$\bar{v}_R$	average velocity of the center of mass of the tegmen when the plectrum is released by a tooth
v_R	velocity of the center of mass of one tegmen at the release of the plectrum by a file tooth
x	displacement
$\bar{x}$	average depth of the file teeth struck during a wing closure
x_i	the depth of each file tooth
β	spring (stiffness) constant
δ	proportion by which $\bar{v}_C$ exceeds $\bar{v}_R$ (assumed to be 1.2)

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