

## THE ENERGETIC COSTS OF CALLING IN THE BUSHCRICKET *REQUENA VERTICALIS* (ORTHOPTERA: TETTIGONIIDAE: LISTROSCELIDINAE)

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### Summary

1. The metabolic costs of calling for male *Requena verticalis* Walker (Tettigoniidae: Listroscelidinae) were measured by direct recordings of oxygen consumption. The acoustic power output was measured by sound pressure levels around the calling bushcricket.

2. The average metabolic cost of calling was  $0.143 \text{ ml g}^{-1} \text{ h}^{-1}$  but depended on calling rate. The net metabolic cost of calling per unit call, the syllable, was calculated to be  $4.34 \times 10^{-6} \pm 8.3 \times 10^{-7} \text{ ml O}_2 \text{ syllable}^{-1} \text{ g}^{-1} \text{ bodymass}$  (S.E.) from the slope of the relationship between total  $\dot{V}_{\text{O}_2}$  and rate of syllable production. The resting  $\dot{V}_{\text{O}_2}$ , calculated as the intercept of the relationship, was  $0.248 \text{ ml O}_2 \text{ g}^{-1} \text{ bodymass h}^{-1}$ .

3. The energetic cost of calling for *R. verticalis* (average mass 0.37g) was estimated at  $31.85 \times 10^{-6} \text{ J syllable}^{-1}$ .

4. Sound pressure levels were measured around calling insects. The surface area of a sphere of uniform sound pressure level [83dB SPL root mean square (RMS) acoustic power] obtained by these measurements was used to calculate acoustic power. This was 0.20mW.

5. The metabolic efficiency of calling, based on total metabolic energy utilisation, was 6.4%. However, we propose that the mechanical efficiency for acoustic transmission is closer to 57%, since only about 10% of muscle metabolic energy is apparently available for sound production.

6. *R. verticalis* emits chirps formed of several syllables within which are discrete sound pulses. Wing stroke rates, when the insect is calling at its maximal rate, were approximately  $583 \text{ min}^{-1}$ . This is slow compared to the rates observed in conehead tettigoniids, the only other group of bushcrickets where metabolic costs have been measured. The thoracic temperatures of males that had been calling for 5min were not significantly different from those of non-calling males.

7. For *R. verticalis*, calling with relatively slow syllable rates may reduce the total cost of calling, and this may be a compensatory mechanism for their other high energetic cost of mating (a large spermatophylax).

### Introduction

Communication by acoustic signals is widespread throughout the animal kingdom.

Key words: energetics, acoustic efficiency, calling, bushcricket, *Requena verticalis*, Tettigoniidae.

Where signals are used in mate attraction, it is usually the male that calls and the female searches for the caller (Bailey, 1991a). Studies on the metabolic costs of calling have concentrated on animals that call more or less continuously, such as frogs, cicadas, crickets, mole crickets and conehead tettigoniids (Tettigoniidae: Copiphorini) (e.g. Ryan *et al.* 1983; MacNally and Young, 1981; Bennet-Clark, 1970; Kavanagh, 1987; Prestwich and Walker, 1981; Forrest, 1991; Stevens and Josephson, 1977; Counter, 1977), although not all animals call in this way. In nature, many animals have extremely short calling times and others break up the call into a series of temporally isolated call sequences. Perhaps of all acoustical animals, bushcrickets have the widest range of calling strategies in terms of the temporal structure of the song. Calls may be extremely brief sounds, such as in some phaneropterines (Heller, 1990), or nearly continuous and cicada-like, as in the calls of coneheads (Josephson, 1973; Counter, 1977).

In comparison to previous studies on the metabolic cost of insects that call almost continuously, such as crickets, mole crickets and bushcrickets, this paper examines the metabolic cost, acoustic output and efficiency of calling in a species of listroscelidine bushcricket, *Requena verticalis*, where the male's call is formed of discrete pulses of sound separated by intervals of silence. Furthermore, whereas most previous studies have measured metabolic cost manometrically over time, we measured, by a paramagnetic technique, the percentage utilisation of oxygen per syllable of emitted sound.

The cost of producing sound is additional to other costs of mating (Calow, 1979). In those animals where components of reproductive investment by the male comprise more than just the donation of its sperm, any metabolic cost of calling could energetically constrain the male's mating behaviour (Arak, 1983). Additionally, where there is variation among males in the use of metabolic energy for calling, perhaps resulting in a louder, longer or more complex call, females may prefer these more energy-requiring calls as an indicator of superior male quality (Rand and Ryan, 1982; Arak, 1988, in frogs; Forrest, 1983; Hedrick, 1986; Bailey *et al.* 1990, in ensiferan Orthoptera: although see Gerhardt, 1991, for a more moderate argument). If female preference can be demonstrated for those males investing more energy in their calls, it will be their genetic material that will spread through the population: they will be fitter. In the event of this assumption being true, it becomes important to provide a reliable measure of this cost and, in particular, the proportional cost of calling against other aspects of male courtship and mating. The experiments described in this paper were carried out in the context of those addressing broader questions germane to the relative costs of calling and mating within this species (Simmons *et al.* 1992).

### Materials and methods

Male *Requena verticalis* (Listroscelidinae: Tettigoniidae) were collected from gardens around the campus of the University of Western Australia during late summer (January and February, 1991). Individual males were housed in plastic containers before being transferred to 60ml plastic syringes for metabolic experiments; insects seemed to be unaffected by this confined space and called as often as caged insects. Clearly, the acoustic conditions of the insect within such confined conditions could produce

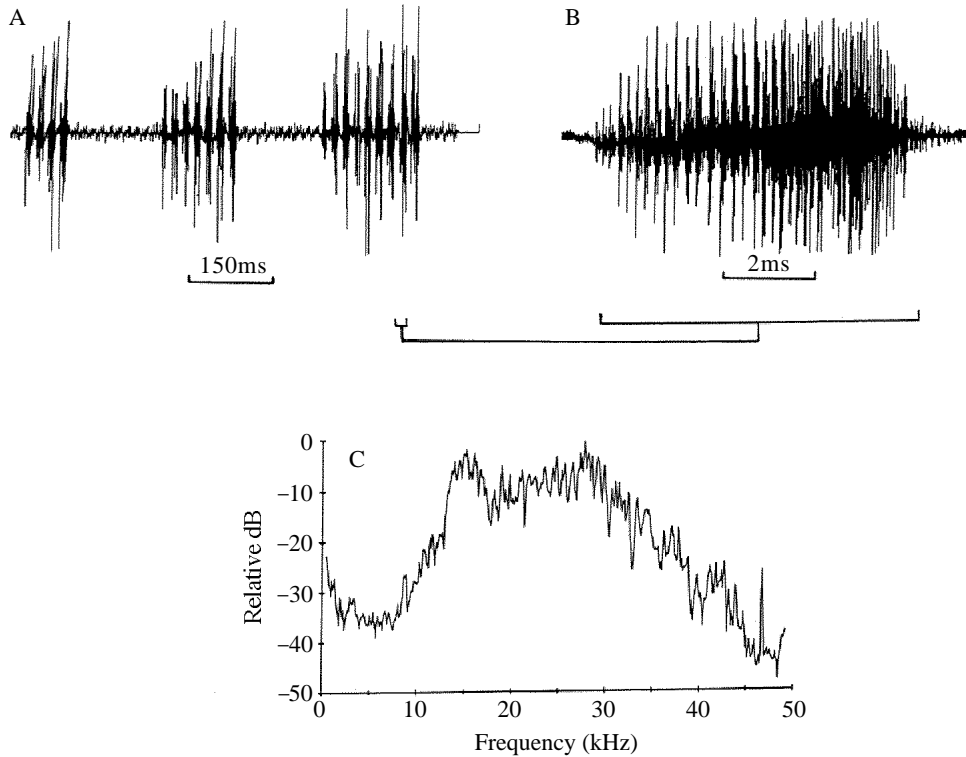


Fig. 1. The call of *Requena verticalis*. The temporal aspects of the call showing its division into 4–8 syllable chirps (A) and the discrete structure of the syllable into separate tooth impacts (B). (C) A typical frequency spectrum recorded with a Bruel and Kjaer 4135 microphone from one male with the two main peaks of acoustic power at 16 and 28kHz.

uncontrollable acoustic effects such as a coupling between the wings and the walls of the syringe by the presence of standing waves. These effects should be minimal over the time taken to measure metabolic costs as the animal could change its position within the tube, which would randomise any acoustic anomalies. The mean body mass of males was  $0.37 \pm 1.12$ g (s.e.,  $N=23$ ).

#### *The call*

The call of *R. verticalis* consists of a series of chirps (Fig. 1A) each comprising several syllables (Fig. 1B) produced at a rate of approximately  $40 \text{ syllables s}^{-1}$ . A chirp is the smallest call unit that can be resolved by the human ear (Broughton, 1963), whereas the syllable is formed by one closing movement of the wings where the edge of the right wing, the plectrum, engages on the teeth of the file of the left wing. The sounds produced by the impact of the plectrum against the teeth of the file form some  $40 \pm 7$  (s.e.,  $N=6$ ) discrete rapidly decaying pulses, which, unlike that of crickets and many conehead tettigoniids, is harsh and not resonant.

In this paper we take the duration of a syllable to be the time for the wings to produce the sound-emitting closing stroke, plus the period of silence, where the wings are moved

to the start of their stridulatory cycle. The period of sound production has a duration of approximately 15ms whereas the silent interval is approximately 10ms (Fig. 1). The power of the frequency spectrum is typical of many tettigoniids in that it covers a range from sonic (approx. 10kHz) to ultrasonic (approx. 50kHz). Although the call is broadband, there are two major peaks of sound power, one between 15 and 20kHz and the other close to 30kHz (Fig. 1C) (Bailey and Yeoh, 1988).

The number of syllables within each chirp varies between males (Schatral and Bailey, 1991). Some males produce an almost continuous call, where there are few breaks in the structure of the chirp, whereas other males break up chirp sequences into a series of discontinuous calls. For this study we did not differentiate between continuous and discontinuous callers. Rather, we counted the number of syllables each male produced over the duration of the metabolic measurements.

Syllables were counted electronically by gating a pulse triggered by the onset of the sound. A delay, set to the approximate length of the sound-on part of the syllable, ensured that only the onset of each syllable event was counted. Males tend to sing when in the presence of other calling males (Schatral and Bailey, 1991) and, in order to measure metabolic data at the insect's maximum calling rate, caged males were housed close to the experimental males (a technique employed by Taigen and Wells, 1985, who placed their experimental chambers within a chorus of frogs; *Hyla versicolor*).

The call was recorded using an ultrasonic detector (QMC bat detector), which is provided with an adjustable narrow band-pass filter that can be set to the call frequency of the song. A flared horn over the microphone provided high directionality, allowing us to count the syllables produced by only the experimental focal male.

#### *Metabolism*

Oxygen consumption was determined by placing the bushcricket in a sealed 60ml syringe for 6h. At the completion of this period, the percentage oxygen content of the gas in the syringe was analysed with a Servomex 574 oxygen analyser to  $\pm 0.01\%$ ; the final  $O_2$  content was generally 19–20%. (Oxygen exchange across the walls of the syringe, or through its seals, was negligible.) The gas was expelled from the syringe into the analyser using a Razel Scientific syringe injector through Ascarite and Drierite to remove  $CO_2$  and water respectively. In estimating percentage  $O_2$  it was only necessary to sample most of the air within the syringe. Thus, when calculating  $\dot{V}_{O_2}$  we used the total syringe air space (corrected for body mass assuming density=1) and not the volume of air expelled. All experiments were conducted within the temperature range  $21 \pm 1^\circ C$ . The rate of  $O_2$  consumption ( $\dot{V}_{O_2}$ ; ml STPD  $O_2$   $g^{-1} h^{-1}$ ) was calculated from the decreases in  $O_2$  content of air using standard equations (e.g. Seymour, 1973).

It was found that 6h was sufficient to enable us to measure oxygen consumption during calling, and over this period there was sufficient variation in the length of time each male called to allow us to calculate the metabolic cost of calling by regressing the total oxygen consumption against the number of syllables produced. The slope of this regression is the metabolic cost of calling per syllable, and the intercept is an estimate of the metabolic cost at rest. The volume of oxygen consumed per gram body mass per syllable was

converted to an equivalent work unit using the conversion factor  $19.796 \text{ J ml}^{-1} \text{ O}_2$  at STPD (Elliot and Davidson, 1975).

Measurements of thoracic temperature of 10 calling and 6 non-calling males were made using a Radio Spares type-K thermocouple meter and a chromel–alumel thermocouple insulated in a glass tube with a 1.0mm diameter tip. Males were allowed to call for 5min before thoracic temperature was measured. Calling males were immediately restrained within a gauze net, and the probe was plunged into the thorax. The time between the insect stopping its call and the probe being inserted was never more than 10s. Non-calling males had not called during the previous hour. Ambient temperatures ranged from 18 to 28°C.

#### *Acoustics – measuring the sound field*

The sound field was measured separately for two males in order to determine acoustic power. The least accurate way to do this is to measure the sound pressure level (SPL) at a fixed distance from the animal and assume that the sound field is close to spherical, or hemispherical in the case of a ground-calling animal (e.g. Brackenbury, 1977; Counter, 1977; Ryan, 1985*a*). However, recording in one plane around the body axis of an insect perched on a vertical stem illustrates the severe reduction of intensities on the ventral aspect created by the shielding of the body (for example, MacNally and Young, 1981; Bailey, 1985). Consequently, a more accurate approach is to measure sound pressures at a combination of angles and azimuth positions (see, for example, Bennet-Clark, 1970; MacNally and Young, 1981; Kavanagh, 1987; Prestwich *et al.* 1989). Such a polar plot of sound pressures can be measured with fixed intensities (MacNally and Young, 1981; Kavanagh, 1987), or by measuring them at a fixed distance and calculating the position of a predetermined isobar by assuming a reduction in SPL of 6dB for each doubling of distance from the source (Bennet-Clark, 1970; Prestwich *et al.* 1989). Both techniques arrive at a three-dimensional shape bounded by a fixed isobar.

In this study we used the direct measurement of dB SPL around the insect in three planes. We obviated any problems of response time, peak or RMS (root mean square) acoustic power, produced by conventional sound level meters, by calibrating the distance/intensity against a fixed voltage displayed on an oscilloscope (a technique recommended by Prestwich *et al.* 1989). The sound pressure level used to set the excursion of the signal on the oscilloscope had been previously calibrated by broadcast Gaussian white noise (speaker – Leaf Tweeter EAS-10TH400a) set to 83dB (re  $10^{-12} \text{ W}$ ) at 20cm using a Bruel and Kjaer 2209 SPL meter with a Bruel and Kjaer 4135 microphone. Stochastic amplitude fluctuations within white noise can lead to severe errors in measuring peak-to-peak values of SPL; however, these errors were avoided by measuring peak-to-peak volts over several seconds (the time base of the oscilloscope was set to 1s per division). This procedure provided us with the best estimates we could obtain with this apparatus of the RMS values for the sound period of the syllable in line with current convention.

A male was allowed to call unhindered from a thin vertical metal rod (diameter 5mm). The microphone, held on a mobile stand, was brought up to the insect until the signal,

amplified through the Bruel and Kjaer sound level meter, was at the predetermined peak-to-peak level as viewed on the monitoring oscilloscope. This distance was approximately 20cm and was independent of any near-field sound effects (c.f. MacNally and Young, 1981). The position was maintained for 15s to ensure that the observed signal remained constant (see above comments in relation to white noise), then the distance from the microphone to the insect was recorded. At each elevation, except anterior and posterior, distances were taken at four azimuth positions: dorsal, ventral, left and right of the animal. This resulted in 14 coordinates for each complete sample. Five replicates were taken at each position resulting in 70 measurements for each male. The mean difference for each coordinate around the calling male was used to construct a two-dimensional shape giving  $\pm$ s.e. distances for each coordinate.

All measurements were made within an anechoic room where the background noise levels were below 50dB SPL. Because the difference between background noise and the source level was greater than 10dB, background did not contribute significantly to the measured sound source (Beranek, 1971).

#### *Estimations of acoustic power*

The acoustic power radiated by a source must pass through any surface that encloses the source. For a simple non-directional source of sound, located at the centre of a spherical surface, the total sound power can be estimated as the product of intensity ( $W m^{-1}$ ) and area ( $m^2$ ) (Beranek, 1971). The acoustic power contained will be:

$$W = S \times 10^{(L_{p,iso} - 120)/10},$$

where  $W$  is power in watts,  $S$  is surface area ( $m^2$ ) of the isobar, and  $L_{p,iso}$  is SPL (dB: re  $20 \mu Pa$ ) of the isobar.

Bennet-Clark (1970) determined the surface area of an irregular 80dB isobar by the use of Pappus's theorem. Where SPL readings had been recorded at a fixed distance from the sound source (e.g. MacNally and Young, 1981; Kavanagh, 1987), the power output for each position (or coordinate) could be calculated by assuming a uniform sphere of a set radius (i.e. the fixed distance) at the intensity at that given coordinate. The total power output could then be taken as the average of all these values.

We estimated the surface area for the sound field of *R. verticalis* by two methods and then used the more conservative of the values so obtained. The first was by approximating the area with that of a sphere of similar size, with average radius equal to the mean radial distance for each coordinate. The second was to use Simpson's rule where we more precisely assumed the shape of the ovoid.

The power output through the surface area surrounding a sound source is given in watts ( $J s^{-1}$ ). A mean value for acoustic power output may be justified in those animals that produce a continuous call (for a minimum duration of at least 1s) but *R. verticalis* produces a chirp composed of several discrete syllables and each syllable is formed by transients of sound produced by the impact of the plectrum on the teeth of the file. We therefore calculated the acoustic power for the duration of sound emission for a single syllable. The average duration of sound emission for a syllable was taken from two counts of 120 chirps from two males recorded under identical conditions.

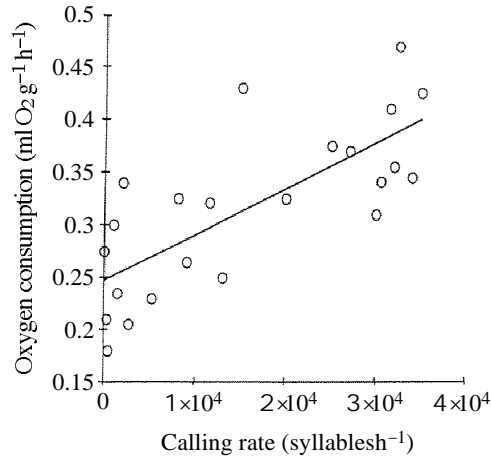


Fig. 2. The relationship between oxygen consumption and the number of syllables produced per hour. Each symbol represents one measurement for one male ( $y=4.337\times 10^{-6}x+0.248$ , where  $x$  is calling rate,  $r^2=0.563$ ,  $P<0.0001$ ).

## Results

### *Oxygen consumption and energetic cost for calling*

The total metabolic rate of male *R. verticalis* at 20°C was positively correlated with the total number of syllables emitted ( $r^2=0.563$ ;  $P<0.0001$ ;  $N=23$ ) (Fig. 2). There is clearly considerable scatter of the  $\dot{V}_{O_2}$  values, possibly reflecting random locomotor activity of the bushcrickets during metabolic measurements. This would overestimate the resting metabolic rate (intercept value) but would not bias the average metabolic cost per syllable (slope). The resting metabolic rate was  $0.248\text{ml O}_2\text{ g}^{-1}\text{ h}^{-1}$  (indicated by intercept  $\dot{V}_{O_2}$ ). The slope of the regression relationship between metabolic cost and the rate of syllable production was  $4.337\times 10^{-6}\pm 8.34\times 10^{-7}\text{ ml O}_2\text{ syllable}^{-1}\text{ g}^{-1}\text{ bodymass}$  (s.e.), which corresponds to a net metabolic energy consumption ( $0.371\times 19.796\times 4.337\times 10^{-6}$ ) of  $31.85\times 10^{-6}\text{ J syllable}^{-1}$  for a mean male mass of 0.371g.

The estimated total metabolic cost of calling for the maximum syllable count (approximately  $35000\text{ h}^{-1}$ ), where the male was calling for almost 100% of the time, was  $0.399\text{ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ ; this corresponds to a net cost for 100% calling of only  $0.151\text{ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ .

### *The sound field*

The sound field around *R. verticalis* is clearly asymmetrical, in both the horizontal and sagittal planes (Fig. 3). Distances to the isobar follow the trend of maximum values at 45° through to a minimum at 135°. Hence, as expected, most of the power is directed dorsally and more to the right than to the left of the insect, which is coincident with the opening of the tegmen. There was little variation in the shape of the sound fields between males tested.

The surface area of the spheroid was  $0.91\text{ m}^2$  estimated by Simpson's rule, and  $0.68\text{ m}^2$  from a sphere of similar radius based on a mean radius of  $0.23\pm 0.17\text{ m}$ . We consider that,

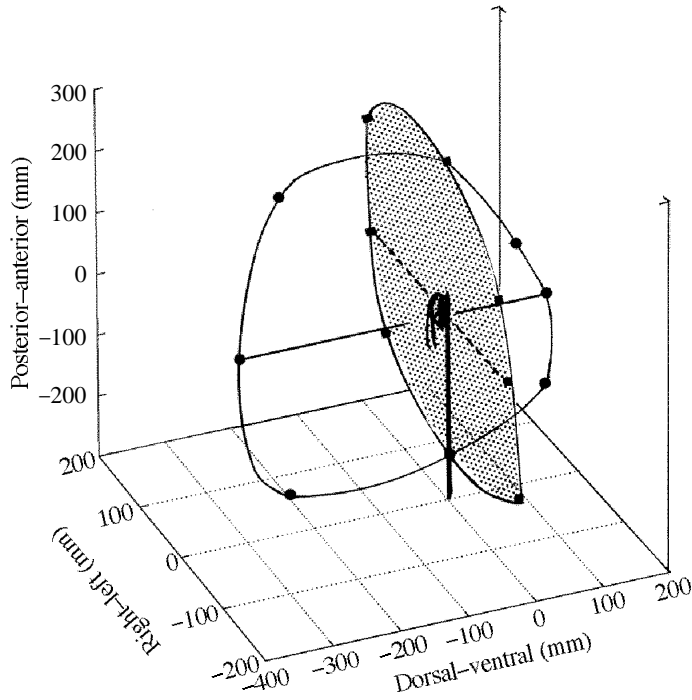


Fig. 3. A plot of mean distances ( $N=5$ ) to the 83dB (SPL) isobar in two planes around a calling male *Requena verticalis*. Stippled area indicates the right-to-left sagittal plane while the clear area is in the dorsal-to-ventral plane.

because of the severe distortion in the sound field due to the position and opening of the tegmina, the value represented by Simpson's rule is an overestimate. We therefore determined the area of the sound field to approximate a sphere, radius  $r$ , where  $r$  is the mean distance to all coordinates.

Prestwich *et al.* (1989) maintain that RMS acoustic power should be used to measure acoustic efficiency since it and the metabolic power input ( $\dot{V}O_2$ ) are time-averaged: the oxygen consumption during calling represents the sum of the energy expended, not the instantaneous peak power developed by the muscles during call production (see also discussion by Bennet-Clark, 1970; MacNally and Young, 1981; Kavanagh, 1987). The isobar at 83dB was used to calculate the surface area of the spheroid around the insect and hence the acoustic output. This resulted in a value of  $1.357 \times 10^{-4} W$  (calculated as  $W = \text{area of sphere} \times 10^{(\text{SPL of isobar} - 120)/10}$  after Prestwich *et al.* 1989:  $0.68 \times 10^{(83-120)/10} = 1.357 \times 10^{-4} W$ ).

#### *Thoracic temperatures*

There were no significant differences between air temperature and thoracic temperatures for non-calling and calling males over a range of ambient temperatures from 19 to 27°C. For non-calling males,  $T = +0.18 \pm 0.49^\circ C$  (s.e.,  $N=6$ ); for calling males,  $T = +0.37 \pm 0.41^\circ C$  (s.e.,  $N=10$ ).



*Acoustic efficiency*

The measurement of metabolic energy expended per syllable allows for a realistic measure of acoustic efficiency for *R. verticalis* (cf. Prestwich and Walker, 1981), even though only a proportion of the calling time has an acoustic output. The average duration of a single chirp (see above) was  $107.2 \pm 1.3$  ms, and an average chirp consists of four syllables, giving an average duration for the syllable of about 25 ms (see Schatral and Bailey, 1991). Since the sound-producing wing movement takes 15 ms, the acoustic energy output for each syllable is  $2.036 \times 10^{-6}$  J (acoustic power  $\times$  duration of sound emission of syllable). The conversion of metabolic to acoustic energy is therefore achieved at an efficiency of 6.4% (i.e.  $100 \times 2.036 \times 10^{-6} / 31.85 \times 10^{-6}$ ). This calculation makes no assumptions concerning when O<sub>2</sub> is used during the syllable; both the acoustic energy output and O<sub>2</sub> energy input are expressed per syllable event.

**Discussion**

Arriving at reasonable estimates of the energetic and acoustic costs of calling, and further being able to make comparisons between taxa, requires a degree of methodological conformity. Prestwich *et al.* (1989) provide critical comment on techniques for both anurans and insects and, in regard to the measurement of sound, this paper follows as much as possible their procedures. The central theme of our study was to document the energetic costs of calling in a bushcricket, which uses discrete tooth impacts within each syllable and calls with a wing stroke rate far slower than that of the coneheaded tettigoniids, the only other group of Tettigoniidae that have been subject to investigation. The results of this paper provide additional insight into the partitioning of metabolic costs between calling and mating to those described in Simmons *et al.* (1992). This is of particular interest because male *R. verticalis* not only expend energy in acoustically signalling their intent to mate, but also provide the female with an energy-rich spermatophylax during copulation. The energy used in the production of this nuptial gift is a metabolic cost and, under certain nutritional conditions, males will channel energy into the production of the spermatophylax rather than into calling (Simmons *et al.* 1992).

*Differing methodologies*

The metabolic cost to insects of calling is usually calculated as the difference between metabolic rate during calling and at rest. There are two problems with this approach. First, it is usual to measure both resting and calling metabolic rates manometrically, but there are potentially serious artefacts in using such a technique for the measurement of activity metabolism, partly as a result of non-steady-state thermal gradients arising from a high rate of metabolic heat production (Hillman *et al.* 1979). This would especially affect the measurement of metabolic rate for insects that warm up and call at elevated temperatures (e.g. genera such as *Euconocephalus* and *Neoconocephalus*; Stevens and Josephson, 1977).

The second methodological problem involves the calculation of the net metabolic costs

Table 1. Summary of body mass, call type, resting and calling oxygen consumption rate ( $\dot{V}O_2$ ), factorial and absolute metabolic scope, wing stroke rate, acoustic power emission and acoustic calling efficiency for a range of insects

Species	Mass (g)	Call type	Resting $\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )	Total $\dot{V}O_2$ when calling (ml g <sup>-1</sup> h <sup>-1</sup> )	Factorial metabolic scope <sup>a</sup> (ml g <sup>-1</sup> h <sup>-1</sup> )	Absolute metabolic scope <sup>b</sup> (ml g <sup>-1</sup> h <sup>-1</sup> )	Wing stroke rate (min <sup>-1</sup> )	Total $\dot{V}O_2$ per wing stroke <sup>c</sup> (ml O <sub>2</sub> WS <sup>-1</sup> g <sup>-1</sup> )	Acoustic power (mW)	Acoustic efficiency (%)	Method	Reference
<b>Tettigoniidae</b>												
<i>Requena verticalis</i>	0.37	Chirp	0.248	0.399 <sup>d</sup>	1.61	0.151	583 <sup>d</sup>	1.14×10 <sup>-5</sup>	0.1357 <sup>e</sup>	6.4 <sup>h</sup>	Paramagnetic	1
<i>Neoconocephalus robustus</i>	0.88	Continuous	0.76–1.92	2.05–15.8	13.2	≈1–14	10220	0.33×10 <sup>-5</sup> – 2.6×10 <sup>-5</sup>	1.8	≈2.1 <sup>g</sup>	Manometric	2, 3, 7, 8
<b>Grylloidea</b>												
<i>Teleogryllus commoictus</i>	0.60	Chirp	0.309	1.209	3.91	0.90	–	–	1.51×10 <sup>-3</sup>	0.05 <sup>h</sup>	Manometric	4
<i>Anurogryllus arboreus</i>	0.31	Continuous	0.315	3.891	12.4	3.576	4419	1.47×10 <sup>-5</sup>	6.58×10 <sup>-3</sup>	0.093 <sup>g</sup>	Manometric	5, 6
<i>Oecanthus quadripunctatus</i>	0.05	Continuous	0.476	3.818	8.0	3.342	2296	2.77×10 <sup>-5</sup>	0.010×10 <sup>-3</sup>	1.81 <sup>g</sup>	Manometric	6, 9
<i>Gryllotalpa australis</i>	0.87	Continuous	0.420	5.303	12.6	4.88	4200	2.10×10 <sup>-5</sup>	0.27	1.05 <sup>g</sup>	Manometric	4
<b>Cicadidae</b>												
<i>Cystosoma saundersii</i>	1.30	Continuous	0.301	6.281	20.9	5.98	2520 <sup>f</sup>	4.15×10 <sup>-5</sup>	0.35	0.82 <sup>g</sup>	Manometric	7, 4

1. Present study; 2. Stevens and Josephson, 1977; 3. Counter, 1977; 4. Kavanagh, 1987; 5. Prestwich, 1988; 6. Prestwich and Walker, 1981; 7. MacNally and Young, 1981; 8. Josephson and Halverson, 1971; 9. Forrest, 1991.

<sup>a</sup> $\dot{V}O_{2,calling}/\dot{V}O_{2,rest}$ .

<sup>b</sup> $\dot{V}O_{2,calling}-\dot{V}O_{2,rest}$ .

<sup>c</sup>Total  $\dot{V}O_2$  when calling/(60×wing strokes per minute); WS, wingstroke.

<sup>d</sup>At maximal calling rate.

<sup>e</sup>RMS syllable.

<sup>f</sup>Tymbal contraction rate.

<sup>g</sup>Continuous callers:

$$\text{Percentage} = \frac{100 \times \text{acoustic power (W)}}{\text{net metabolic cost of call (W)}}$$

$$= \frac{100 \times (\text{acoustic power, mW}) \times 3600}{(\text{absolute metabolic scope, ml O}_2 \text{ g}^{-1} \text{ h}^{-1}) \times (\text{mass, g}) \times (19.796) \times (1000)}$$

<sup>h</sup>Chirpers (see text):

$$\text{Percentage} = \frac{100 \times \text{acoustic power (W)}}{\text{net metabolic cost of call (W)}}$$

$$= \frac{100 \times (\text{acoustic power, mW}) \times (\text{duration of sound within syllable, ms})}{(\text{absolute metabolic scope, ml O}_2 \text{ g}^{-1} \text{ h}^{-1}) \times (19.769) \times (1000) \times (\text{wing stroke rate} \times 60)}$$

of calling as the total metabolic rate during calling minus the metabolic rate at rest, if there is an increase in thoracic temperature during calling. Some of the increment in metabolic rate will be due to a  $Q_{10}$  effect of thermal elevation on the resting metabolism and not due to calling *per se*. The potential significance of thoracic warming on the calculated cost of calling seems to have been ignored in many studies.

#### *Metabolic rates for calling*

The resting metabolic rate reported in this study for *R. verticalis* ( $0.248 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at about  $20\text{--}25^\circ\text{C}$ ) is similar to that of most other insects ( $0.30\text{--}0.48 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ; Table 1). Resting metabolic rates reported for *Neoconocephalus* are much higher ( $0.76\text{--}1.92 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ). The predicted resting metabolic rate for insects at  $25^\circ\text{C}$  (Withers, 1992) corresponds to between  $0.21$  and  $0.53 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the insects listed in Table 1 (mass  $0.05\text{--}2.0 \text{ g}$ ).

The metabolic rate of calling insects is elevated to very variable extents. In *R. verticalis*, this elevation is only to about 1.6 times resting, while for most other insects the elevation may be 3.9–10 times, and for *N. robustus* in excess of this (Table 1). Such a marked variation in the factorial metabolic scope ( $\dot{V}_{\text{O}_2\text{calling}}/\dot{V}_{\text{O}_2\text{rest}}$ ) during calling undoubtedly reflects the nature of the call, and in particular the different wing stroke rates of the species investigated. While some insects call incessantly, with a seemingly constant action of either tymbal or wing muscles [e.g. *Cystosoma saundersii*; MacNally and Young (1981) and *Euconocephalus nasutus*, Stevens and Josephson (1977)], others, such as the cricket *Teleogryllus commodus* (Kavanagh, 1987), produce sound in short bursts of repeated syllables called chirps. Such a calling action is prevalent in many tettigoniids, but even so, estimates of the metabolic costs of sound production in terms of net  $\text{O}_2$  consumption per gram body mass for *T. commodus* are high with respect to *R. verticalis*. However, the calculated oxygen consumption per wing stroke (WS) for *R. verticalis* is about  $0.43 \times 10^{-5} \text{ ml O}_2 \text{ WS}^{-1} \text{ g}^{-1}$ . This is similar to values for most trilling species ( $1 \times 10^{-5}$  to  $4 \times 10^{-5} \text{ ml O}_2 \text{ WS}^{-1} \text{ g}^{-1}$ ) (Table 1).

Thoracic temperatures may be elevated by the heat production during calling. This is especially true for trilling species, where sound is produced almost continuously and wing stroke rates are often high. In chirping species, such as *R. verticalis*, heat production is low and will be dissipated after each chirp and so thoracic temperatures should remain at ambient and there would be no  $Q_{10}$  contribution to an increase in power output. Supporting this argument, we found that thoracic temperatures of *R. verticalis* were unaffected by calling activity despite the relatively high power output per syllable ( $0.20 \text{ mW}$ ). Similarly, in the cricket *Anurogryllus arboreus*, which has an extremely low acoustic power output, ( $6.6 \times 10^{-3} \text{ mW}$ , Prestwich and Walker, 1981;  $5.86 \times 10^{-2} \text{ mW}$ , Forrest, 1991), the body temperatures rose by no more than  $2^\circ\text{C}$  (Prestwich and Walker, 1981). In comparison, *Neoconocephalus robustus* has a differential of  $18^\circ\text{C}$  between ambient and muscle temperatures (Heath and Josephson, 1970). Changes in thoracic temperature during calling affect metabolic energy expenditure. Thus, an elevation of muscle temperature increases contraction rate as well as power output per contraction (Josephson, 1973; Stevenson and Josephson, 1990). However, although raising muscle

temperature will increase acoustic power output, this may not necessarily be translated into increased efficiency.

#### *Acoustic power and efficiency*

We have estimated an acoustic efficiency based on emitted acoustic power as calculated by SPL measured against a standard of white noise, so avoiding any requirement to take into account the time constant of the sound level meter (an important requirement when estimating SPL of the type of transient repeated signals; Prestwich *et al.* 1989). The efficiency of calling measured in this way was 6.4%, which is high compared to that of other singing insects (Table 1). Although Counter (1977) estimated efficiencies for *Neoconocephalus robustus* at 26%, MacNally and Young (1981) point out a number of anomalies in the calculations and recalculated a more conservative value of 2.1%. Similarly, Bennet-Clark (1970) reported the efficiency of conversion of muscular to acoustic power for a sound pulse of *Gryllotalpa vineae* as 35%. This too was recalculated by both MacNally and Young (1981) and Kavanagh (1987) to values less than 5%. These values are still high compared to most values for most insects, which are about 1%. Such acoustic inefficiency is surprising when one considers the central position of calling within the life of the animal. But published values for acoustic efficiency vary markedly for closely related taxa and more remarkably for species with similar sound-producing mechanisms. In addition, there is, in some cases, considerable between-male variation, particularly when sound fields are measured in nature (Forrest, 1991). In our laboratory measurements, where posture and calling position were carefully controlled, there was extremely low between-male variation.

Low acoustic efficiencies for calling in those insects studied so far could be explained by two related factors. First, errors in calculation of metabolic cost or acoustic power output could result in incorrect efficiency values. Second, a high proportion of the metabolic energy used for muscle contraction is not available for mechanical work. As stated earlier, calculating calling efficiencies and making interspecific comparisons relies on the accuracy of each of the methods used to determine metabolic power input and acoustic power output.

When calculating acoustic efficiencies, we can account for the biochemical inefficiency of the muscle's metabolic machinery; i.e. use *available* biochemical energy (i.e. ATP) rather than the oxygen consumption rate to calculate efficiency. When making acoustic efficiency calculations, other workers have ignored the obligate biochemical inefficiency of the muscle and its obligate heat production in converting metabolic energy into ATP. For example, muscle cells are often considered to be about 25% efficient in converting total energy used into biochemical available energy. If this were so, then the overall acoustic efficiency of *R. verticalis* of 6.4% would correspond to an acoustic efficiency from available energy of about 23% ( $6.4 \times 100/25$ ). However, the efficiency of insect flight muscle may be even lower than 25%, with some estimates as low as 10% (Ellington, 1984, 1985; Mizisin and Josephson, 1987; Stevenson and Josephson, 1990). Similar low efficiencies have been calculated for some invertebrate and vertebrate muscles (Heglund *et al.* 1982; Stokes and Josephson, 1988). Consequently, if muscle biochemical inefficiency is taken into account, the acoustical efficiency of *R. verticalis*

may be as high as 57%. Similarly, although not reaching as high a value as this, acoustic efficiencies for crickets and coneheaded tettigoniids would be raised by at least the same order of magnitude (tenfold).

Increases in acoustic power output can be achieved through the more efficient conversion of mechanical to acoustic energy by improved sound radiation (Bennet-Clark, 1989). Here limits will be applied by the morphology of the sound-producing structures and the environment into which the sound is projected (see Forrest, 1982; Bailey, 1991*b*). Optimising sound radiation can only be achieved by coupling the impedance of a cuticular wing to the less dense air mass and also by ensuring that the radiator is sufficiently large to avoid any acoustic short-circuiting (see Bennet-Clark, 1989). The size of this radiator determines the system's cut-off frequency.

*R. verticalis* differs from coneheads and gryllids in that its syllables are formed of pulses of sound caused by the impact of the plectrum of one wing on the teeth of the file of the other. The plectrum produces transients of sound at each tooth impact with the elasticity of the cuticular plectrum dissipating energy at each impact. In all other tettigoniids tested so far sound is produced by resonance between the natural vibration frequency of the mirror or harp area of the wing – the sound radiator – and the tooth impact rate (approx. 15kHz) (Bailey, 1970). Here, plectrum elasticity contributes to the generation of the following sound wave, and resonance may increase efficiency of sound production over that produced by discrete tooth impacts. The rapid wing stroke rate (100–200Hz) required by coneheads to generate their resonant calls at about 15kHz may, however, result in a decreased mechanical efficiency between mechanical and acoustic power through hypertrophy of the sarcoplasmic reticulum and T-tubules. There is also an effective reduction in muscle power per unit mass at high muscle contraction frequencies (Josephson and Young, 1985). Hence, the relatively high acoustic efficiencies described for *R. verticalis* may be due, at least indirectly, to its low stridulation rate, with more metabolic energy being available for sound production.

#### *Carrier frequency*

Finally, as the attenuation of sound is frequency-dependent, low frequencies travel further through vegetation than do high frequencies (Wiley and Richards, 1978). One way of increasing the efficiency of sound production is to use low- rather than high-frequency signals: the propagation of high frequencies demands higher metabolic energy to maintain an equivalent intensity over several metres. However, the propagation of low frequencies by small insects presents acoustical problems due mainly to the size of the animal's sound-generating structures (Bennet-Clark, 1970; Forrest, 1983; Ryan, 1985*a*); larger structures are required to produce lower frequencies. The lower size limit is the cut-off frequency.

Ryan (1985*b*) employed an equation, derived from that of an exponential horn (see also Bennet-Clark, 1989), to determine the cut-off frequency for the call of the frog *Physalaemus pustulosus*. Recognising the limitations of applying theory relating to exponential horns to a different acoustic system, we are nevertheless still able to arrive at a reasonable estimate of the lower optimal frequencies that *R. verticalis* could reasonably be expected to emit. Thus, using the same equation and assuming that the wing of *R.*

*verticalis* is both the main radiator of sound and is capable of acting as a baffle surrounding the smaller 'mirror' region of the wing, we calculate an approximate cut-off frequency of about 16kHz. In practice the radiation resistance of an acoustic source in a baffle increases to that of the surrounding air as the source radius rises to  $1/2\pi$  wavelength. Source to air impedance-matching efficiency will be optimal with sources larger than this critical radius. As the mean length of the ovoid wing (which because it is attached to the body might be considered an upper value for the source radius) is  $4.9 \pm 0.08$  mm (S.E.,  $N=5$ ), sounds with wavelengths below 30mm, corresponding to frequencies above 11kHz, are likely to be radiated with higher efficiency and hence to be louder than lower-frequency components of the call. Hence, the effective source radius of the wing, so attached to the body, will be smaller than this, and the frequencies the insect can radiate efficiently will be higher than 11kHz. The call has a broad power spectrum with upper frequencies above the secondary peak at 28kHz (Bailey, 1985; Bailey and Yeoh, 1988) and, because of the size of the radiator, there is a steady decline in sound energy beneath 15kHz (see Fig. 1C). The resulting call frequencies can be considered to be a compromise between those advantages gained in using the lowest possible frequency for sound transmission and those frequencies imposed by the size of the sound-radiating tegmina.

#### *Calling, metabolism and spermatophylax production*

Reducing the amount of calling time should reduce the male's metabolic requirements and these can be diverted to other activities. Prestwich and Walker (1981) calculated by manometry the portion of the daily metabolic budget used for singing by two crickets, *Anurogryllus arboreus* and *Oecanthus celerinctus*, to be 26–56% and 2.5–25% respectively. Although there was no indication of the energy reserves of crickets, starvation over several days led to no diminution of singing, and so the authors assumed that metabolic reserves were not depleted. However, germane to this study of the energetics of calling in *R. verticalis*, Simmons *et al.* (1992) clearly demonstrate that sound production is a metabolic cost that affects the energy expended for the production of the spermatophylax – a protein gift for the coupled female. Recently mated males, fed on a low-nutrient diet, took the same time to replenish their accessory glands as did males fed a high-nutrient diet, but had a reduced time spent in calling. Therefore, a speculative hypothesis from both these studies is that those tettigoniids that produce a large energy-rich spermatophylax may be under strong selection to reduce the costs of calling. *R. verticalis* produces a spermatophylax equivalent to about 20% of its body mass (Davies and Dadour, 1989) and has a very low metabolic cost of calling. By comparison, coneheads, which produce a minute spermatophylax (Gwynne, 1990), may be expected to invest more in calling.

In *R. verticalis*, there appears to be a trade-off between the metabolic cost of spermatophylax production and that of acoustically attracting a mate. However, there are undoubtedly other reasons for reducing time spent calling. One may be to reduce conspicuousness to predators (see Morris, 1980; Belwood and Morris, 1987; Belwood, 1990, for a discussion of calling strategies and bat predation). In other species, calling time is extremely short because the call of the male merely evokes an acoustical response

by the female towards which the male will move in search of a mate (Zimmermann *et al.* 1989).

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