

## SONG ENERGETICS OF THE BLADDER CICADA, *CYSTOSOMA SAUNDERSII*.

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(Received 31 March 1980)

### SUMMARY

1. Males of *Cystosoma saundersii* produced their calling songs while tethered to holders.
2. Oxygen consumption during singing was  $0.136 \text{ ml min}^{-1}$ , equivalent to  $45.0 \text{ mW}$ , an increase of  $42.55 \text{ mW}$  over the resting metabolic rate.
3. Maximum sound output was  $90.6 \text{ dB}$  at  $20 \text{ cm}$ . The whole sound-field was measured and represents a power output of  $0.35 \text{ mW}$ . The efficiency of sound production is  $0.82\%$ .
4. Heat production, estimated from the weight of singing muscle, was  $28.7 \text{ mW}$ . This leaves  $13.5 \text{ mW}$  of output unaccounted for.
5. Comparison with other species of insects suggests that none are more than an order of magnitude more efficient than *C. saundersii*.

### INTRODUCTION

Many animals produce sounds which serve the function of intraspecific communication. Such sound production involves a certain cost in the form of increased metabolism to provide the necessary energy. Measurements of the components of this energy budget are pertinent to the study of both the mechanisms involved in sound production and the place of sound communication in the animal's overall energy budget. A reasonably complete energy budget for sound production should include estimates of the energy input in terms of oxygen used (i.e. metabolic rate) and of the energy output mainly as heat and sound. However, few animals will sing under the conditions required to obtain all these measurements. To circumvent this difficulty, the energy input may be estimated indirectly (e.g. Counter, 1977) or estimates of energetic efficiency may be limited to part only of the total energy transformation during sound production (e.g. Bennet-Clark, 1970; Brackenbury, 1978).

In this study, we have been able to measure directly both the energy input and sound output, and so to estimate the overall efficiency of sound production in the cicada, *Cystosoma saundersii*. Cicadas generate sound by means of a pair of tymbals, each of which is activated by a single, large tymbal muscle. Sound pulses are generated by twitch contractions of the tymbal muscle, which occur at a frequency of about  $\text{Hz}$  in *C. saundersii*. In this species, the heat produced by the tymbal muscles during singing has already been estimated by Josephson & Young (1979).

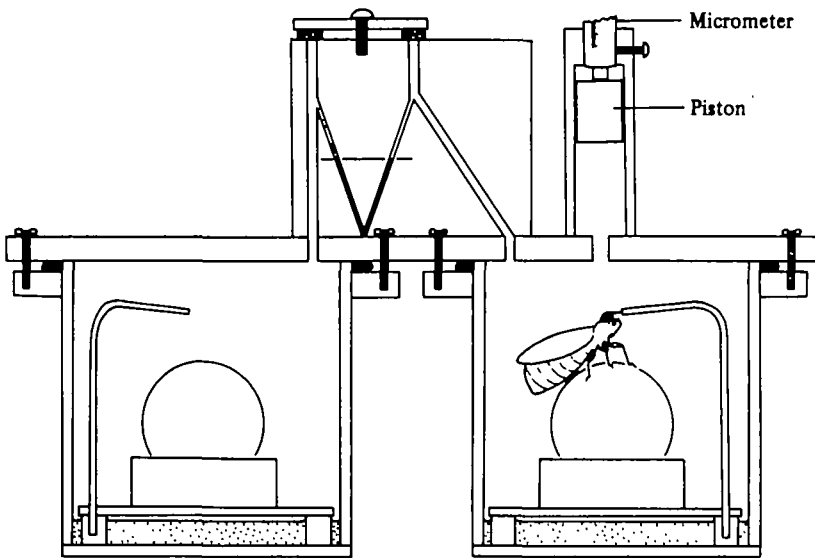


Fig. 1. The respirometer constructed to measure oxygen uptake in *C. saundersii*. The animal chamber is on the right and the compensation chamber on the left.

In order to measure the other components of song energetics, we have taken advantage of the fact that *C. saundersii* will produce its calling song while tethered to a holder (Simmons & Young, 1978; Josephson & Young, 1979). Undisturbed males in the field produce their calling song only for about 30 min at dusk, the onset of the chorus being triggered by the falling light intensity (Hill & Hill, in prep.). Tethered males will often sing at the normal time, even if quite isolated from the natural chorus. The metabolic rate was measured in individuals which sang while tethered inside a respirometer. Sound output was measured from individuals which sang while tethered in the field. The calling songs produced by these tethered males and the songs of wild (non-tethered) males were recorded on tape for comparison. These songs have been subjected to a computer analysis (Young, 1980), which shows that tethering the cicada does not affect the physical characteristics of the calling song. Also it confirms that the sound frequency of the song is unusually low, having a mean peak frequency of 865 Hz.

#### MATERIALS AND METHODS

Specimens of the Australian bladder cicada, *Cystosoma saundersii* Westwood, were obtained at Port Macquarie on the coast of New South Wales. The animals were captured by hand while singing in the early evening. Most experiments were carried out at Port Macquarie but some of the respirometry measurements were made on animals air-freighted to Melbourne.

The oxygen consumption of singing males was measured using a compensating respirometer (Fig. 1) based upon the design of Davies (1966). Each chamber has a volume of 1.25 l. In this design, oxygen consumed by the animal is compensated for by advancing the micrometer bore. The maximum displacement using the bore alone is about 1 ml. We expected that this would be insufficient to compensate for the oxygen

used during an average singing period since the estimated heat production from the tymbal muscles alone would require some 2.6 ml O<sub>2</sub> (Josephson & Young, 1979). The capacity was increased by abutting the micrometer bore against a piston of radius 9.5 mm (Fig. 1), giving a displacement of up to 7.25 ml.

Experimental animals were tethered by waxing the pronotum to a holder which was secured to a base-plate. The tethered animals were able to walk on a styrofoam ball, 5 cm in diameter, which floated on water contained in a small cylindrical chamber mounted on the base-plate. The base-plate itself was mounted on four legs, 1 cm high, so that it stood clear of the concentrated NaOH placed at the bottom of the respirometer chamber (Fig. 1). The base-plate was a loose fit in the chamber and was drilled with holes around its periphery to permit free circulation of air above and below. This assembly, complete with animal, was sealed in the animal chamber and a replica assembly, without animal, was sealed in the compensation chamber. 40 ml of 5 M-NaOH was placed in each chamber. The respirometer was then immersed into a constant-temperature water bath at 23 °C, in which water was circulated by a stirrer, about 2 h before the normal chorus time (dusk) to allow thermal equilibration to occur. Upon commencement of singing the crossbar was closed. Oxygen consumption was measured from 5 minutes after onset until the termination of singing.

Following successful respirometry runs, and also following successful sound level readings (see below), the tymbal muscles of the co-operative animals were dissected out. These were either weighed at once or preserved in alcohol and subsequently rehydrated in locust saline, blotted and weighed.

The sound field of singing males was measured by moving a microphone round tethered individuals at a constant radius of 0.2 m by means of the apparatus shown in Fig. 2. The tethered male was mounted on an assembly essentially similar to that used for respirometry but rendered as small as possible so as not to interfere with the sound field. This assembly was secured to the top of a steel rod, 50 cm high, anchored in the centre of a steel frame (Fig. 2). The microphone was mounted on a semi-circular steel rod by means of a moveable clamp. The semi-circular rod could be rotated in a full circle around its bearings on the two support pylons and fixed at any angle by means of wing nuts. Thus, a complete sphere of readings could be obtained.

The microphone was Brüel & Kjaer type 4131 and was connected by a 3 m long cable to a Brüel & Kjaer type 2203 sound level meter, displaying root-mean-square pressure. Measurements were expressed in dB re 10<sup>-12</sup>Wm<sup>-2</sup>. The meter was recalibrated before each trial using a Noise Source, Brüel & Kjaer type 4240.

Because of the short singing period (30 min) we took readings from one hemisphere only in the manner indicated in Fig. 3. Readings were taken in four vertical rings, which are termed  $\frac{1}{2}\pi$  (= saggital),  $\frac{3}{4}\pi$ ,  $\frac{1}{4}\pi$  and  $\frac{1}{8}\pi$  in order to distinguish them from the positions on each ring. Each vertical ring was sampled in eight positions, at the following angles: -45° anterior, anterior, +45° anterior, dorsal, +45° posterior, posterior, -45° posterior and ventral. A reading was taken at the lateral position also. These measurements were made in an open field on a farm, with the apparatus being more than 20 m from other males of *C. saundersii*. Readings were not commenced until 5 min after the onset of singing because the song increases in volume during the first few minutes (Simmons & Young, 1978; Josephson & Young, 1979).

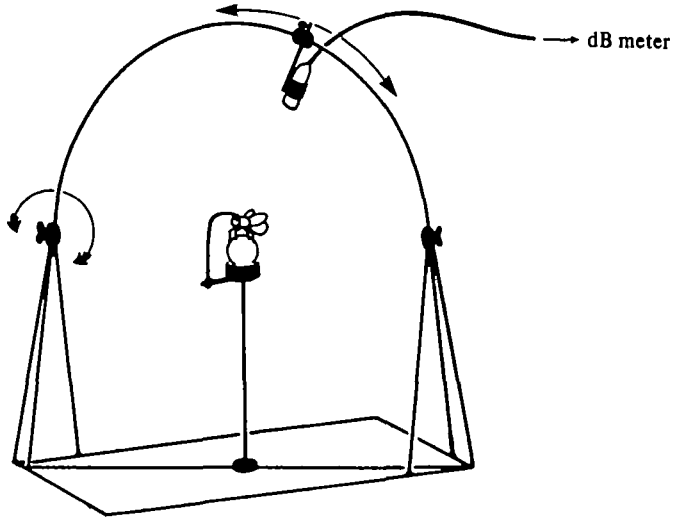


Fig. 2. The apparatus used to take sound-pressure level readings around a tethered, singing male. It is constructed of steel rod throughout. The clamp holding the microphone can slide along the semi-circular rod, which can itself be rotated through  $360^\circ$  as indicated by the arrows in each case. These movements are centred about the position of the insect.

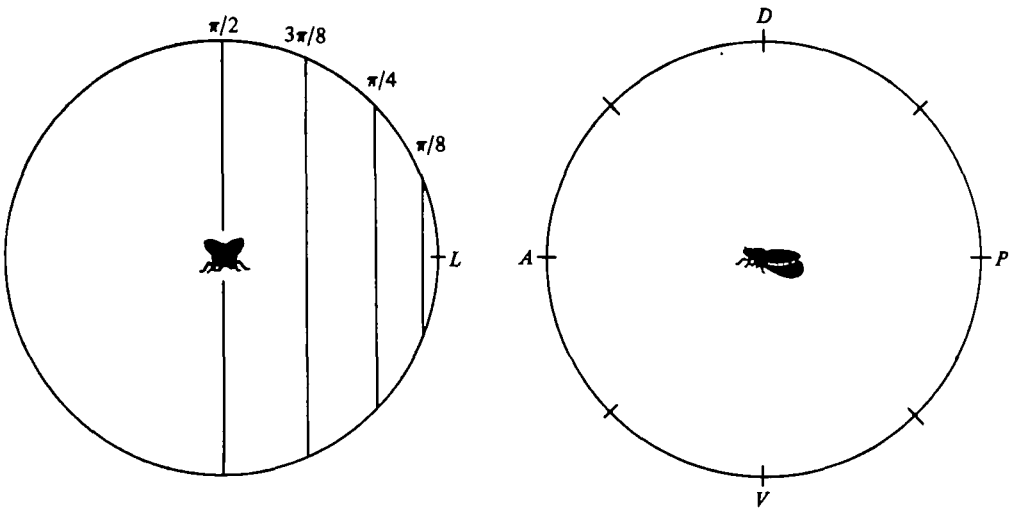


Fig. 3. Diagram showing the method of taking readings with the apparatus shown in Fig. 2. Readings were along 4 vertical rings, seen from the anterior aspect on the left. The sampling positions on each vertical ring are seen from the lateral aspect on the right. *A*, anterior; *D*, dorsal; *L*, lateral; *P*, posterior; *V*, ventral.

Table 1. *Oxygen uptake and heat production in C. saundersii males*

(Means and 95% confidence intervals)

	Oxygen uptake (ml O <sub>2</sub> min <sup>-1</sup> g muscle <sup>-1</sup> )	Energy equivalent (mW)	Tymbal muscle weight (mg)	Estimated heat production (mW)
Singing ( $n = 10$ )	1.63 ± 0.27	45.0 ± 7.26	85.1 ± 11.15	28.70 ± 3.76
Resting ( $n = 3$ )	0.007 ± 0.002	2.45 ± 1.26	—	—

## RESULTS

1. *Respirometry*

Out of 20 respirometry experiments, males sang in only ten but these seemed unaffected by their confinement in the respirometer. At the normal chorus time (dusk), they walked on the styrofoam ball, adopted the singing posture and sang continuously for 20–30 min. The average rate of oxygen consumption by these ten males during singing was 0.136 ml min<sup>-1</sup> (S.E. = 0.010). Thus males which sang for a full 30 min used 4.1 ml of oxygen, which is approximately 1.5% of the available oxygen in the respirometer chamber. Hence there was little likelihood of low oxygen stress occurring during singing. The amount of energy used during singing (Table 1) was calculated from the oxygen depletion data by using an oxycaloric conversion value of 19.796 J ml O<sub>2</sub><sup>-1</sup> (Elliot & Davison, 1975). A series of determinations was also carried out on non-singing males in the respirometers. However, at this temperature (23 °C), only three males were sufficiently quiescent to qualify as resting males and so provide an estimate of resting metabolic rates (Table 1).

The heat generated by the sound-producing tymbal muscles has been estimated in *C. saundersii* by Josephson & Young (1979). Heat production in our respirometry experiments (Table 1) was estimated by substituting the weights of the tymbal muscles of the experimental animals into equation (7) of Josephson & Young (1979). Muscle weights were measured only for the singing males.

2. *The sound-field and acoustic power*

Eight attempts were made to measure the sound-field, of which five were successful, resulting in the measurement of two right and three left hemispheres. The sound-fields were symmetrical about the saggital plane so that henceforth no distinction is made between left and right hemispheres. The tethered males sang continuously for 20–30 min. In only two trials, when the males sang for the longer period, was it possible to complete measurements for the  $\frac{3}{4}\pi$  and  $\frac{1}{4}\pi$  rings. The background sound-pressure level was approximately 63 dB. The ambient temperature during these experiments was 20–24 °C ( $\bar{x} = 21.5$ ; S.E. = 1.0).

The average maximum sound-pressure level recorded from the five tethered males was 90.6 dB (S.E. = 0.64). In four of these, the maximum value was recorded at the

Table 2. *Sound levels recorded around singing males*

(dB below the maximum value for each specimen.)

	$\frac{1}{2}\pi^*$		$\frac{3}{8}\pi\dagger$		$\frac{1}{2}\pi^*$		$\frac{3}{8}\pi\dagger$	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Ventral	3.80	0.49	3.00	0.32	3.45	0.30	3.75	0.47
-45° Post.	2.10	0.36	1.38	0.39	1.95	0.35	2.63	0.55
Posterior	0.45	0.18	0.0	0.0	0.30	0.30	1.00	0.32
+45° Post.	0.50	0.18	0.38	0.24	0.55	0.15	1.50	0.0
Dorsal	1.40	0.17	1.63	0.08	1.90	0.19	1.88	0.24
+45° Ant.	3.15	0.13	3.13	0.24	3.05	0.05	2.63	0.24
Anterior	4.25	0.29	4.00	0.32	3.75	0.08	3.50	0.32
-45° Ant.	4.65	0.35	4.38	0.39	4.45	0.17	4.50	0.63
Lateral*	2.25	0.21						

\*  $n = 5$ . †  $n = 2$ .

$\frac{1}{2}\pi$  posterior position but in one of the cases where the  $\frac{3}{8}\pi$  ring was included the maximum was found at the  $\frac{3}{8}\pi$  posterior position. The sound-pressure level at each position on each ring was converted into dB below the maximum level for each male. The means and standard errors for each position are given in Table 2. Note that the smaller the value, the louder is the song at that particular co-ordinate.

The shape of the sound-field in the horizontal and saggital planes is illustrated in Fig. 4. It can be seen that the region of highest intensity is three times louder than the lowest on a linear scale. The sound-field is clearly asymmetrical. Most of the power is directed posteriorly and more is directed dorsally than ventrally. Least power passes through the anterior-ventral region, where the leg musculature and dense coxal and thoracic cuticle are located.

From the measurements of sound-pressure level we calculated the amount of acoustic power passing through a spherical shell of 0.2 m radius, using the relationship

$$P = 4\pi r^2 (\text{antilog } [SPL - 120]/10),$$

where  $P$  is power;  $r$ , is the radius of the sphere in metres;  $SPL$ , the sound-pressure level in dB (Olson, 1957). Since the song consists of a relatively pure tone (Young, 1980), the sound-pressure levels yield an accurate estimate of power output. For each male, the power was calculated for each position on each ring on the assumption of a uniform sphere of 0.2 m radius at that intensity. The total power output was then taken as the average of all these values. The mean total power output of the five males was 0.35 mW (S.E. = 0.05).

In order to obtain a basis for comparison with wild (non-tethered) males, we performed a least-squares regression of the sound-pressure level at the saggital ( $\frac{1}{2}\pi$ ) posterior position (dB, abscissa) against the total power output (mW, ordinate) for these five tethered males. The average reading in dB at the saggital posterior position for the five males was 90.1 dB (S.E. = 0.41). The resultant equation is

$$\log_e P = 0.203 SPL - 19.428,$$

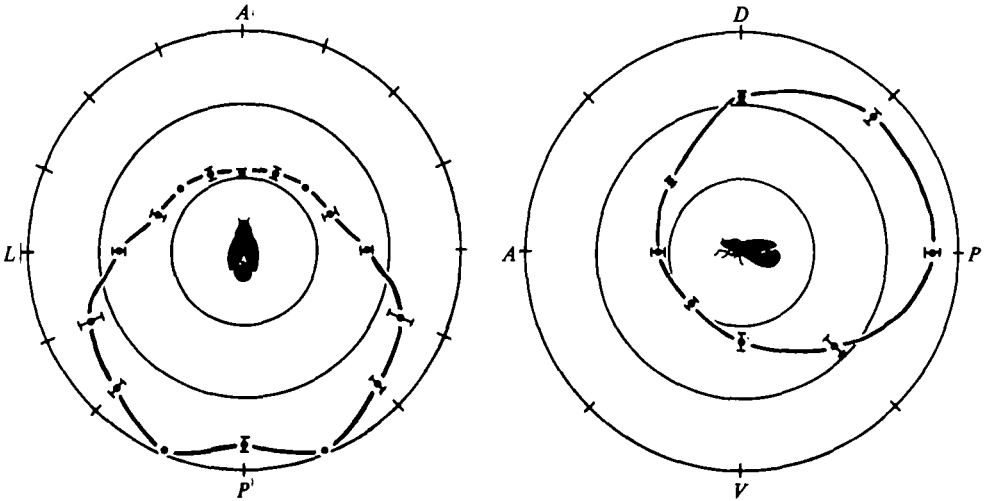


Fig. 4. The sound-field around a singing male of *C. saundersii*. *Left*, the horizontal plane (seen from dorsal aspect); *Right*, the saggital plane (seen from lateral aspect). The concentric rings represent sound intensity on a linear scale with respect to the lowest value recorded ( $-45^{\circ}$  Anterior in saggital plane). The solid circles are the means of sound-pressure level readings and the bars are one standard error on either side. For some positions the standard errors are too small to be illustrated. Abbreviations are as in Fig. 3.

where  $P$  = estimated power output ( $r^2 = 0.978$ ,  $p < 0.01$ ,  $n = 5$ ). The sound-pressure level was measured in 17 wild males at 0.2 m from the saggital posterior position during their calling song. The power output of each of these males was then estimated using equation (1). The means and 95% confidence intervals of these quantities are respectively  $90.25 \pm 0.75$  dB and  $0.35 \pm 0.05$  mW.

The energy input required specifically for sound production may be estimated as the metabolic power during singing less the resting metabolic power. From Table 1 this quantity is  $45.0 - 2.45 = 42.55$  mW. Therefore, the overall efficiency of the conversion of metabolic power into power output as sound is  $0.35 \times 100 / 42.55 = 0.82\%$ . Not all sources of output have been identified since the sum of heat plus sound ( $28.7 + 0.35 = 29.05$  mW) falls short of the input (42.55 mW) by 13.5 mW. Possible, additional routes of output are considered in the Discussion.

#### DISCUSSION

Sound production in *C. saundersii* is obviously not a very efficient process. That our estimate is reasonably accurate is suggested both by the internal consistency of the values measured and by their agreement with corresponding values obtained in other insects. Thus the rate of oxygen uptake ( $1.63 \text{ ml O}_2 \text{ min}^{-1} \text{ g muscle}^{-1}$ ) agrees well with rates obtained from other insects during vigorous activities such as flight or stridulation (see Table 3 of Stevens & Josephson, 1977). The maximum sound output (90 dB at 20 cm) is comparable to that of other medium to large insects (e.g. Bennet-

Table 3. *Estimated power output during singing in various species.*

	Weight of singing muscle (mg)	Sound output (mW)	Sound power per unit muscle ( $\text{Wkg}^{-1}$ )	Source of data
<i>Cystosoma saundersii</i>	85	0.35	4.11	This paper
<i>Psaltoda argentata</i>	80.6	2.27	28.2	This paper
<i>Gryllotalpa vinnae</i>	58.6	1.2	20.5	Bennet-Clark (1970)
<i>Gryllus campestris</i>	19.8	0.06	3.0	Bennet-Clark (1970)
<i>Neoconocephalus robustus</i>	78*	1.8	23.0	Counter (1977) Stevens & Josephson (1977)

\* Weight assumed by Stevens & Josephson (1977) on the basis of figures for the locust (Weis-Fogh, 1952).

Clark, 1970; Dumortier, 1963; Nocke, 1971), as is the rate of warming and temperature excess of the active tymbal muscle (Josephson & Young, 1979).

Tethering males does not appear to affect their power output since the values obtained from tethered and from wild males are very similar. Moreover, Young (1980) has reported that the physical characteristics of the songs of these tethered males show no significant difference from those of wild males. Hence it is unlikely that tethering the cicadas has introduced any significant error.

A shortfall on the output side of the energy budget for singing was to be expected since not all sources of heat have been measured and heat and sound probably do not account for the total energy output. During the calling song, several small muscles contract tonically (Simmons & Young, 1978): the tensor muscle, the muscles extending the abdomen and the muscles raising the wings. The heat output of these muscles has not been estimated. Friction in the cuticle during vibration of the tymbals and the abdomen may be suggested as an additional route of energy dissipation. Such extra sources might reasonably account for the shortfall of 13.5 mW.

#### 1. *Comparison with efficiency of other species*

The estimate of efficiency obtained for *C. saundersii* may not be representative of other large cicadas, many of which sound far louder to the human ear. An approximate yardstick for comparison between species may be obtained by estimating the power output (in mW) from the observed sound-pressure levels during singing and dividing this by the unit weight of muscle employed in sound production (Table 3). In the Australian cicada, *Psaltoda argentata*, the sound-pressure level during the calling song, measured from the posterior aspect, is close to 100 dB at 20 cm ( $\bar{x} = 99.8$ ; S.D. = 1.5;  $n = 4$ ). Assuming a similar sound distribution pattern to *C. saundersii*, equation (1) was used to calculate the power output, which is 2.27 mW. Expressed per unit weight of muscle (Table 3), the power output of *P. argentata* is 6.86 times greater than that of *C. saundersii*. If this comparative figure indicates that *P. argentata*



energetically about seven times as efficient as *C. saundersii*, then the overall energetic efficiency for the song of *P. argentata* would be between 5 and 6%.

The nearest equivalent study to ours on other families of insects is that of Counter (1977) on the tettigoniid *Neoconocephalus robustus*. He estimates an overall energetic efficiency of 26%. This estimate is based on a sound-pressure level of 110 dB at 10 cm from the animal, and assumes this level is radiated uniformly all round the singing insect (Counter, 1977, p. 1006). However, there is some uncertainty about this figure. Firstly, it is unlikely that 110 dB is maintained uniformly round the animal since a uniform sound-field has not been found in other insects when adequately measured (Bennet-Clark, 1970; Nocke, 1971; and the present study). Secondly, Counter (1977, p. 996) gives a different figure in his results, of 116 dB at about 1 cm, a mean of 24 readings. From his Fig. 3D, it can be seen that the distribution of readings is somewhat skewed so that the mode is higher than the mean, being about 118 dB. Assuming that the insect is about 1 cm in diameter, and thus 1 cm from its surface corresponds to a sphere of radius 1.5 cm, we obtain a value of 118 dB over a sphere of radius 1.5 cm. This represents a far lower sound output than 110 dB at 10 cm, namely 1.8 mW rather than 12.6 mW (assuming a uniform sound-field in each case).

The energy input, as oxygen uptake, has been measured directly in *N. robustus* by Stevens & Josephson (1977). They found an average maximum oxygen uptake during singing of 15.8 ml O<sub>2</sub> h<sup>-1</sup>. By subtracting the resting metabolic rate of 1.92 ml O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> (Stevens & Josephson, 1977, Table 1), we obtain a figure of nearly 14 ml O<sub>2</sub> h<sup>-1</sup> g<sup>-1</sup> for the oxygen required for sound production. This represents an energy input of 87.8 mW. Thus a sound output of 12.6 mW gives an efficiency of 14.4% while the lower figure of 1.8 mW gives an efficiency of 2.1%. Counter (1977) estimated the energetic efficiency of singing in *N. robustus* from the ratio of sound production to heat production (values for the latter being taken from Heath & Josephson, 1970), assuming that heat and sound account for the total power output during singing (which must be equal to the total input). The value of 35.6 mW, which he obtained, represents only 40% of the total energy input measured by Stevens & Josephson (1977). Evidently, in *N. robustus*, a significant fraction of the energy is being dissipated by routes other than sound production or muscle heat loss. In view of the uncertainty about the level of sound output in this species, it is desirable that this be re-investigated so that a more accurate estimate of energetic efficiency can be made.

In the mole cricket, *Gryllotalpa vinnae*, Bennet-Clark (1970) has estimated the efficiency of conversion of the mechanical energy generated by muscle contraction into the acoustical energy in the sound-field round the animal during the calling song. A value of 35% was obtained for the most vigorous songs of this species. This value was based on the plausible assumption that the mechanical power available from the flight muscles, which move the wings to produce sound, is likely to be about 70 W kg<sup>-1</sup> (cf. Jensen, 1956; Weis-Fogh, 1977). He took the weight of the wing levators only, 50 mg, which should thus deliver 3.5 mW, of which only 1.2 mW appears as sound. If a value is to be obtained for the song as a whole, rather than for a single muscle contraction, then the wing depressors should also be included in the estimate. This makes total of 58.6 mg of flight muscle (Bennet-Clark, 1970, Table 2), which should

deliver close to 4 mW, giving an efficiency of 30% for the conversion of mechanical into acoustic energy. Assuming further that striated muscle converts metabolic into mechanical energy with an efficiency of 20% (Weis-Fogh, 1972; Weis-Fogh & Alexander, 1977), the overall efficiency of sound production in *G. vinae* is 6%.

Approaching the matter another way, we may compare the sound power output per unit weight of muscle (Table 3) in *G. vinae* and *C. saundersii*, in which case the power output of *G. vinae* is 4.98 times greater than that of *C. saundersii*. If this indicates that *G. vinae* is energetically about five times as efficient as *C. saundersii*, then on the basis of the present results, the efficiency in *G. vinae* would be  $4.98 \times 0.82$ , = 4%. Averaging these two approaches gives 5% as an estimate for the overall energetic efficiency of the calling song in *G. vinae*.

If the above comparisons are basically correct, it seems unlikely that even the loudest of insects is more than 10% efficient in energy conversion during singing. This is an order of magnitude better than the performance of *C. saundersii*. Where insect songs are generated by rapidly contracting, striated muscles, the limiting performance of the muscles might be expected to be similar in different species. Differences in overall efficiency would then be accounted for by differences in the efficiency of conversion of mechanical into acoustic energy. The process of sound radiation from the insect's surface into the environment is a critical link in the sequence of energy conversion. In order to transmit vibration efficiently from a solid, such an insect cuticle, to air, the radiating surface should have a diameter which is a substantial fraction of the wavelength of the sound produced so as to achieve good impedance matching (see Bennet-Clark, 1971; Michelsen & Nocke, 1974). *C. saundersii* has an enlarged abdomen, about 3 cm long, which acts as a resonant sound radiator (Fletcher & Hill, 1978; Simmons & Young, 1978) but this is still small in comparison with the wavelength of 865 Hz sound, which is about 40 cm. If these values are entered on standard plots of frequency against acoustic impedance (Bennet-Clark, 1971, Fig. 1; Michelsen & Nocke, 1974, Fig. 2), it can be seen that the abdomen of *C. saundersii* will fall below maximal efficiency as a sound radiator by between one and two orders of magnitude if it is likened to a disc set in a baffle and between three and four orders of magnitude if it is likened to a free disc. In practice, its performance is probably not as poor as this. The above comparisons indicate that *C. saundersii* is between five and seven times less efficient than *G. vinae*, which, by virtue of its specially constructed burrow, does operate close to maximal efficiency (Bennet-Clark, 1970, 1971). Therefore, the efficiency of the conversion of mechanical to acoustic energy in *C. saundersii* is probably about 5%.

## 2. Possible advantages of low frequency communication.

Although sound production in *C. saundersii* is a relatively inefficient and energetically costly process, there are a number of compensating biological advantages. One obvious advantage is lack of competition on this species' communication wavelength. There is no other animal in the same locality that we know of, which shares the frequency of *C. saundersii*'s calling song. The nearest competitors in this respect are closely related cicadas of the genus *Chlorocysta*, which often occur in the same locality and sing at the same time as *C. saundersii*. However, the largest of the species of *Chlorocysta* has a calling song with a frequency about twice that of *C. saundersii* so

There should be little interference in view of the sharply tuned hearing of *C. saundersii* (Young & Hill, 1977). There is another species of *Cystosoma*, *C. schmeltzi*, but this has a higher frequency calling song and is largely allopatric. Other diurnal cicadas often sing briefly at dusk during the calling period of *C. saundersii* but the frequencies of their songs are much higher, e.g. *Cyclochila australasiae*, with a song frequency around 4 kHz (Josephson & Young, in prep.). Similarly, several species of orthopterans call in the evenings in similar localities but all operate at much higher frequencies.

Another advantage of using 865 Hz sound for communication is that low frequencies are less liable to absorption and attenuation than high ones and so transmit over greater distances. This has been confirmed by a number of studies of outdoor acoustics, which are reviewed by Michelsen (1978) and Wiley & Richards (1978). Field studies by Marten & Marler (1977) and Marten, Quine & Marler (1977) suggest that sounds below 1 or 2 kHz are greatly attenuated very close to the ground but at 1 or 2 m above the ground low frequency sounds (1–3 kHz) are least attenuated (the sound 'window' of Morton, 1975). These effects vary with habitat and the "window" effect for low frequency sounds appears to be most marked in dense shrubbery of the forest edge (Marten, Quine & Marler, 1977, Figs. 2 & 3; Morton, 1975, Fig. 3). From their data, one may predict that, for maximum transmission, an animal should call from a site just over 1 m above the ground at a frequency of about 1 kHz. This prescription fits *C. saundersii* almost perfectly. This species is found in habitats where shrubs are rather thickly set and the male song perches are sharply concentrated at a height of 1.4 m above the ground (Doolan & Mac Nally, in prep.). Thus the calling song of *C. saundersii* is well suited to maximize transmission and so be an efficient means of communication between males and females.

We are specially indebted to Mr W. Arthur, who made the apparatus (Figs. 1, 2) and to the Cordell family, whose farm was used for the field studies. Dr M. J. Littlejohn kindly lent us the sound level meter and Ms J. Doolan assisted with the experiments.

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