

SOUND RADIATION BY THE BLADDER CICADA *CYSTOSOMA SAUNDERSII*

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Summary

Male *Cystosoma saundersii* have a distended thin-walled abdomen which is driven by the paired tymbals during sound production. The insect extends the abdomen from a rest length of 32–34 mm to a length of 39–42 mm while singing. This is accomplished through specialised apodemes at the anterior ends of abdominal segments 4–7, which cause each of these intersegmental membranes to unfold by approximately 2 mm.

The calling song frequency is approximately 850 Hz. The song pulses have a bimodal envelope and a duration of approximately 25 ms; they are produced by the asynchronous but overlapping action of the paired tymbals. The quality factor Q of the decay of the song pulses is approximately 17.

The abdomen was driven experimentally by an internal sound source attached to a hole in the front of the abdomen. This allowed the sound-radiating regions to be mapped. The loudest sound-radiating areas are on both sides of tergites 3–5, approximately 10 mm from the ventral surface. A subsidiary sound-radiating region is found mid-ventrally on sternites 4–6. Sound is radiated in the same phase from all these regions. As the abdomen was extended experimentally from its resting length to its maximum length, the amplitude of the radiated sound doubled and the Q of the resonance increased from 4 to 9. This resonance and effect are similar at both tergite 4 and sternite 5.

Increasing the effective volume of the abdominal air sac reduced its resonant frequency. The resonant frequency was proportional to $1/\sqrt{(\text{total volume})}$, suggesting that the

air sac volume was the major compliant element in the resonant system. Increasing the mass of tergite 4 and sternites 4–6 also reduced the resonant frequency of the abdomen. By extrapolation, it was shown that the effective mass of tergites 3–5 was between 13 and 30 mg and that the resonant frequency was proportional to $1/\sqrt{(\text{total mass})}$, suggesting that the masses of the tergal sound-radiating areas were major elements in the resonant system.

The tymbal ribs buckle in sequence from posterior (rib 1) to anterior, producing a series of sound pulses. The frequency of the pulse decreases with the buckling of successive ribs: rib 1 produces approximately 1050 Hz, rib 2 approximately 870 Hz and rib 3 approximately 830 Hz. The sound pulse produced as the tymbal buckles outwards is between 1.6 and 1.9 kHz. Simultaneous recordings from close to the tymbal and from tergite 4 suggest that the song pulse is initiated by the pulses produced by ribs 2 and 3 of the leading tymbal and sustained by the pulses from ribs 2 and 3 of the second tymbal.

An earlier model suggested that the reactive elements of the abdominal resonance were the compliance of the abdominal air sac volume and the mass of the abdomen undergoing lengthwise telescoping. The present work confirms these suggestions for the role of the air sac but ascribes the mass element to the in–out vibrations of the lateral regions of tergites 3–5 and the central part of sternites 4–6.

Key words: cicada, *Cystosoma saundersii*, resonance, bioacoustics, sound radiation, frequency control.

Introduction

Sound is produced in male cicadas by the rapid buckling of paired tymbals situated on the first abdominal tergite (Pringle, 1954). The ribbed tymbals produce a train of clicks, which may occur rapidly and merge into a single sound pulse or occur more slowly and produce a train of separate sound pulses (see, for example, Young and Josephson, 1983; Fonseca, 1994; Bennet-Clark and Young, 1992; Bennet-Clark, 1997). In many cicadas, the pulses produced by the tymbal buckling provide high-pressure sound impulses to the interior of the large air-

filled abdomen. These high-pressure pulses may then excite sympathetic vibrations or resonances which are radiated as sound.

Various types of abdominal sound radiators have been described in cicadas: a common form, exemplified by the large Australian cicadas *Cyclochila australasiae* or *Macrotristria angularis*, is that the air sac and large thin ventral tympana or eardrums form the components of a Helmholtz resonator (Young, 1990; Bennet-Clark and Young, 1992) and the sound

is radiated through the large tympana. In other cicadas, such as the small Portuguese cicada *Tympanistalna gastrica*, certain components of the sound produced by the tymbals excite vibrations of the walls of the abdomen (Fonseca and Popov, 1994; Fonseca and Bennet-Clark, 1998), which radiate a low-frequency component of a complex song. Other components of the song in *T. gastrica* are radiated via the tympana or directly from the outer surfaces of the tymbals. In all cases, some part of the abdomen, driven by the tymbals, acts as a secondary resonator from which sound is radiated.

An unusual group of cicada species is the Australian bladder cicadas (see Moulds, 1990) such as *Cystosoma saundersii* and *Chlorocysta viridis*. As their names imply, the males in both these species have enormously expanded air-filled abdomens. The tympana, however, are relatively small (Young and Hill, 1977). The tymbals appear to act in a similar manner to that in other cicadas (Simmons and Young, 1978). In both these species, the song frequency is unusually low; it is close to 850 Hz in *C. saundersii* (Young, 1980), which is a far lower frequency than that predicted by the scaling of song frequency with the inverse of body length shown by many more typical cicadas (Bennet-Clark and Young, 1994).

Previous experiments with *C. saundersii* (Young, 1972) highlighted the importance of the abdominal bladder in sound production: its removal rendered the protest song 8–10 dB quieter than that of the intact insect. Also, the decay seen at the end of each song pulse suggests that the abdomen acts as a resonator.

Simple vibrating systems resonate by the interaction of two terms: a mass and a compliance (or in an electrical circuit, an inductance and a capacitance). In the Helmholtz resonators of typical cicadas that radiate sound through the tympana, the mass-like component is the inertance of the air moving through the tympanal apertures, and the compliant component is the volume of air in the abdominal air sac.

The acoustic principles underlying sound production by a flexible-walled resonator of this type have been discussed by Fletcher and Hill (1978), who also provided a model of the system. This model is considered in more detail below.

We describe experiments designed to explore the nature of the abdominal resonator, to test the model of Fletcher and Hill (1978) and to determine how the tymbals are involved in the excitation of sound production by the abdomen.

Materials and methods

The experiments reported here were carried out in a rented flat in Port Macquarie using apparatus brought to Port Macquarie by car. As a consequence, we did not have immediate access to various pieces of standard laboratory apparatus. Histological and anatomical observations were made using fixed material at either Melbourne or Oxford.

Insects

Males of *Cystosoma saundersii* Westwood were caught while singing in shrubs at dusk at Port Macquarie, New South

Wales, Australia. They were maintained on small shrubs at ambient temperatures of between 20 and 28 °C until required for experiments. Insects survived well in this regime and sang freely at dusk after capture. Experiments were normally performed within 2 days of capture.

Insect preparations

Insects were fastened by the pro- and mesonotum to 4 mm diameter brass rods using insect wax (Fig. 1). The insect then could be mounted in a variety of positions on a micromanipulator.

The songs of *C. saundersii* have been described by Simmons and Young (1978). Calling song (see Fig. 4A), which is produced spontaneously, consists of a long modulated trill of bimodal pulses, each of 20–23 ms duration, with peak power centred at 850 Hz. Protest song, produced when the insect is handled, is similar but the pulse structure is less regular and the song frequency is somewhat more variable (Simmons and Young, 1978).

Measurements of sound production during calling song were made with the intact insect fastened as above but free to walk on an expanded polystyrene ball floating in a bowl of water. Calling song production started at dusk and thereafter only continued if the insects were kept in the dark or in dim light; they stopped singing if touched.

Measurements of sound production during protest song were made after removal of the wings and all legs at the coxo-trochanteral articulation. Similar experiments, but using headless insects, were performed with the sound driven by an internal sound source. In both cases, manipulations of abdomen length were made by waxing the tip of a 4 mm diameter rod to the posterior end of the last abdominal segment (Fig. 1A,B); abdominal extension or shortening was controlled by mounting this rod in another micromanipulator.

The effective volume of the abdomen was increased by attaching the cap of a 12 ml screw-top plastic bottle to a thin ring of cardboard waxed to the last segment of the insect's body (Fig. 1C). After attachment, the tip of the insect's abdomen was cut away to open the air sac, and the bottle was then screwed onto the cap. After removal of the cap, the effective volume of the system was adjusted by adding water to or removing water from the bottle. The bottle was held open-end upwards in a micromanipulator and care was taken to prevent water from getting into the experimental insect. Measurements at close to the original volume of the insect's abdomen were performed after placing a cardboard disc across the inside of the cap of the bottle. After measurements of the sound had been completed, the volume of the insect's abdominal air sac was measured by filling it with water while it was supported open-end up.

The effective mass of parts of the abdominal cuticle was increased by attaching short lengths of 0.7 mm or 1.2 mm diameter solder wire to the cuticle using cellulose nail varnish (Fig. 1D). These weights were easy to remove and were weighed, together with attached nail varnish, after removal.

All preparations survived well over a series of experiments

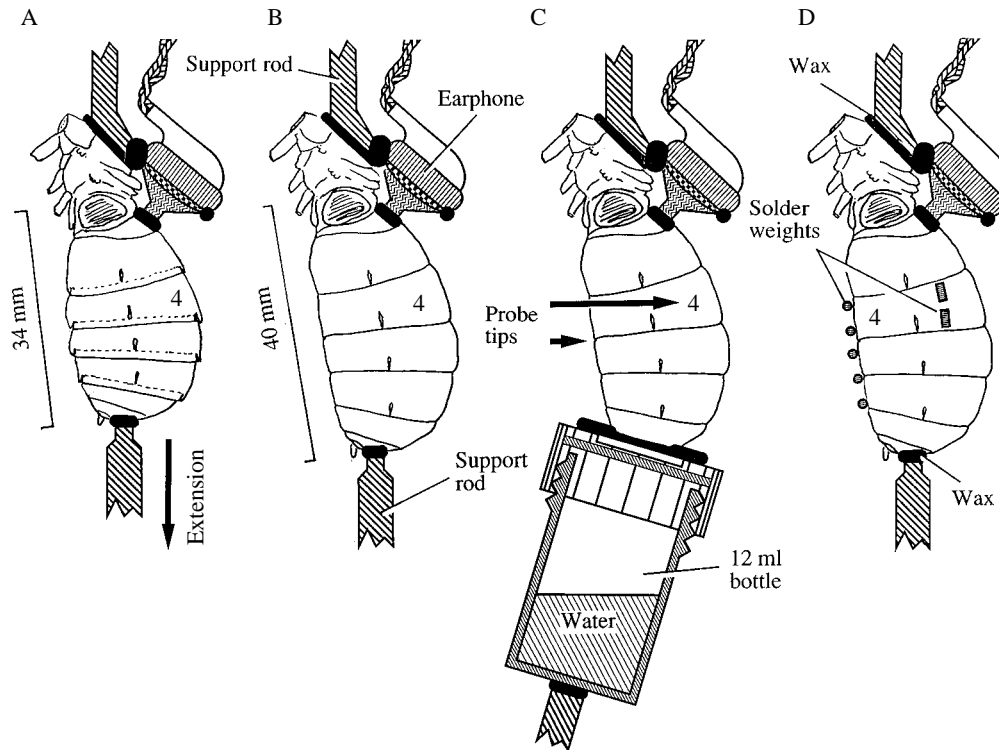


Fig. 1. Diagrams of the experimental arrangements used to examine the acoustics of the abdomen of *C. saundersii* when driven by an internal sound source. (A,B) Arrangement used to test for the effect of changes in abdomen length. (A) The shortened resting length, where the intersegmental membranes are folded. (B) The length when the insect is singing, where the intersegmental membranes are fully extended. (C) Arrangement used to test for the effect of increasing the effective volume of the abdomen. A plastic bottle was waxed onto the end of the abdomen, and the tip of the abdomen was then cut away so that the interior of the bottle was connected to the large abdominal air sac. The volume of air was adjusted by filling the bottle with known volumes of water. By placing a washer across the mouth of the bottle, a system volume similar to that of the intact insect was achieved. The arrows show the standard positions at which the tips of the probe microphones were placed. (D) Arrangement used to test for the effect of increasing the effective mass of the vibrating regions of the abdominal cuticle. Equal weights were put at the anterior and posterior ends of the dimple on both sides of tergite 4 (see Fig. 2) and a total mass equal to 1.5 times that on either dimple was placed on the mid-line of the surfaces of sternites 4–6. Tergite 4 is labelled in A–D.

that lasted for up to 2 h: at the end of this period, repeat measurements of resonant frequency were within $\pm 5\%$ and of Q were within 10% of those made at the start of the series and, in all cases, the heart could be seen beating along the length of the abdomen.

After removal of the abdomen posterior to segment 2, tymbal clicks were produced by pulling on the tymbal apodeme with flat-nosed forceps, thereby simulating the action of the tymbal muscle.

Portions of the abdominal wall were cut out and fixed in glutaraldehyde, dehydrated through an alcohol series and embedded in Araldite. Sections were cut with a glass knife and stained with Toluidine Blue for observation under the light microscope.

Internal sound source

Internal sound pulses were delivered *via* a 3 mm diameter hole cut in the anterior left side of abdominal tergite 2. A Sony miniature earphone was waxed to the conical end of a 10 ml polycarbonate syringe. To damp internal resonances, the cavity in the end of the syringe was packed with fine wire wool. The

needle adaptor tube at the end of the syringe was cut to a length of 4 mm. This tube was waxed to the previously cut hole in abdominal tergite 2, and the weight of the earphone was supported by waxing it to the brass rod that supported the insect (see Fig. 1).

The earphone was driven with tone bursts or continuous sine waves produced by a Tektronix function generator (FG 501) controlled by another Tektronix function generator (FG 505) feeding a Toshiba SB-M30 power amplifier. The carrier frequency of the tone bursts was set to the nearest 1 Hz using a Testlab TL 3400 multimeter. Tests of the validity of this method are described in Results.

Acoustic measurements

Two specially constructed probe microphones with a tip diameter of 1.25 mm were used. The design and specification of these microphones have already been described in detail (Young and Bennet-Clark, 1995; Bennet-Clark, 1997a). In summary, between 100 Hz and 2 kHz, their response was flat to less than ± 1 dB and they were matched to better than ± 0.5 dB and $\pm 2 \mu$ s difference in response time. The polarity

of the microphones meant that compression produced a negative voltage; however, for clarity, all oscillograms shown here have been inverted so that compression is shown as positive.

The probe microphones were mounted on 6 mm diameter rods held in micromanipulators fastened to the steel baseplate to which the insect was attached. The tips of the probe tubes of the microphones were normally placed 2 mm away from the surfaces being measured. Altering this distance from 1 to 3 mm caused a decrease of only 1 dB in the readings.

Comparative measurements of sound levels were made from the output of the microphone preamplifier using the Testlab TL 3400 multimeter. The response of this multimeter was found to be flat to within ± 0.1 dB from 50 Hz to 2 kHz.

Other measurements, including the relative sound pressure, frequency and rate of decay of sound pulses, were made *via* an Analog Digital Instruments MacLab 4 data acquisition system using MacScope 3.2 signal acquisition and data analysis software. Two-channel measurements were normally made at 20 kilosamples per second or with 50 μ s resolution of the 850 Hz (1.18 ms period) dominant frequency of the insect's song. Because the tips of the probe microphones were placed 2 mm from the sound-radiating surfaces, signal-to-echo and signal-to-noise ratios both exceeded 50 dB.

The instantaneous frequency within song pulses (see Fig. 4B) was obtained by measuring the period of single cycles of oscillograms of the waveform, starting at the zero-crossing of either the positive-going or negative-going half-cycle of the waveform: the frequency resolution by this method is better than 40 Hz at 850 Hz. Resonant frequencies were obtained either by using the Fast Fourier Transform (FFT) software of MacScope or by direct measurement from oscillograms of the period of the decaying part of waveforms. A few measurements were made by observing the frequency at which the amplitude of the sound output of the abdomen was maximal. All these methods gave closely similar values.

The quality factor (Q) is standard measure of sharpness of tuning or of resistive damping of a resonance or vibration (see, for example, Morse, 1948, chapter 2; Fletcher, 1992, section 2.5). Throughout the present study, Q was calculated from

measurements of the rate of decay d of vibrations from oscillograms of the waveforms and is given by:

$$Q = \pi / \log_e d. \quad (1)$$

The significance of the quality factor in the context of cicada song is discussed elsewhere (Bennet-Clark and Young, 1992; Young and Bennet-Clark, 1995). The repeatability of successive measurements or comparisons of Q was better than $\pm 10\%$.

When a simple system is driven at its resonant frequency, the phase of the response lags that of the drive by 90° (Morse, 1948; Fletcher, 1992). Thus, measurements of relative phase can be used to confirm whether a driving waveform has excited a resonance. This property of a driven resonance can be seen in Fig. 12.

Terminology of the sound-producing movements and sounds

The inward tymbal buckling movement brought about by the contraction of the ipsilateral tymbal muscle is termed inwards, and the pulse of sound that this buckling produces is termed the IN pulse. The return movement of the tymbal that follows relaxation of the tymbal muscle is termed outwards, and the pulse of sound that this movement produces is termed the OUT pulse (Pringle, 1954; Young, 1972).

Results

The anatomy of male Cystosoma saundersii

At rest, the overall length of the body of male *C. saundersii* is approximately 47 mm (47.2 ± 1.7 mm, mean \pm S.D., $N=5$). The head and thorax of *C. saundersii* males resemble those of other cicadas but the abdomen is a thin-walled bladder (Fig. 2; see also Simmons and Young, 1978). The testes are confined to the convex posterior end, in segments 8 and 9, and other internal organs such as the heart, gut, intersegmental muscles, etc., are thin and greatly reduced in size.

When the insect is at rest and silent, the abdomen is shortened by the folding the intersegmental membranes at the anterior borders of segments 4, 5, 6 and 7 (Fig. 2). Each intersegmental membrane allows a telescopic movement of

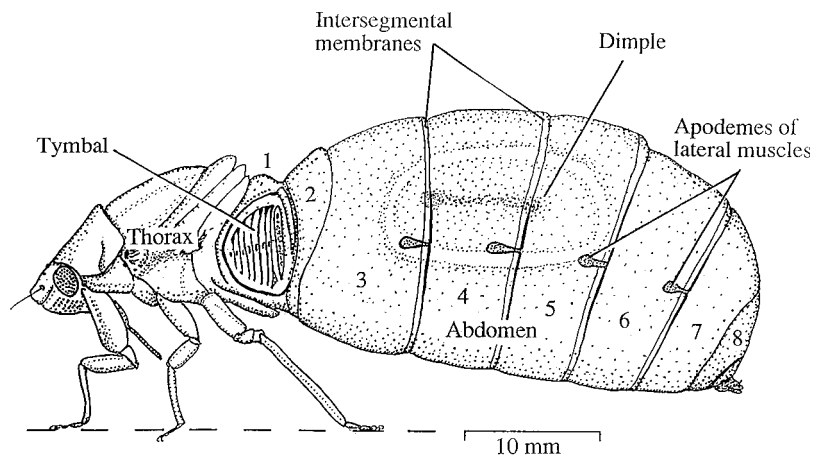


Fig. 2. Drawing of a male *C. saundersii* in the singing position, in which the abdomen is fully extended, stretching the intersegmental membranes. The wings are omitted for clarity. The spatulate apodemes situated at the anterior edges of segments 4, 5, 6 and 7 can be seen through the thin cuticle of the abdomen. A cross section of the abdomen at segment 4 is shown in Fig. 6B.

2–2.5 mm. In four different insects at rest, the abdomen length ranged from 32 to 34 mm, measured from the anterior end of the tymbals to the tip of the pygophore. When extended during production of the calling song, the abdomen of these insects ranged from 39 to 42 mm in length. At segment 4, the abdominal circumference of these same insects ranged from 58 to 62 mm. The volume of the abdominal air sac when fully extended varied in different insects between 5.6 and 9.6 ml (the mean value for nine insects was 7.6 ml; s.d.=1.4 ml, $N=9$).

Extension of the abdomen is brought about by the action of lateral muscles attached to paired spatulate apodemes at the anterior borders of tergites 4–7 (Fig. 2). Similar apodemes and muscles have been described in *Platypleura capitata* by Pringle (1954) and in *Tibicen chloromera* by Vasvary (1966). These apodemes, which are clearly visible through the sides of the abdomen, extend forwards from the anterior edge of one segment across the intersegmental membrane (Figs 2, 3). Each apodeme consists of a spoon-shaped extension of an internal cuticular ridge at the anterior end of the segment. This ridge runs dorsally and ventrally as a hoop around each segment, and appears to transmit the force of the apodeme muscles from the spatulate apodeme to the apodeme-bearing segment of the abdomen (Fig. 3).

There are separate dorsal and ventral muscles of the apodeme (Vasvary, 1966). The muscle fibres are attached to the outer (lateral) surface of the broad, flat region of the apodeme and pass diagonally backwards to the inner surface of the abdominal cuticle of the preceding segment (Fig. 3). Contraction of these muscles has the effect of moving the spatulate apodeme posteriorly and hence extending the intersegmental membrane. When the abdomen is fully extended, the intersegmental membranes are unfolded and

appear shiny. Shortening of the abdomen is brought about by other muscles located laterally, ventrally and dorsally; at the latitude of the spatulate apodemes, these muscles run internally (medially) to the muscles of the apodemes (Fig. 3). They are referred to here as abdomen shortener muscles.

When the abdomen is extended, its cross section at the level of segments 3–6 is approximately pear-shaped, with nearly flat regions in the middle of the tergites on either side and on the sternites along the mid-ventral line (see Fig. 6B). On the tergites, each of these flat regions constitutes a shallow dimple, which is roughly oval in shape and extends forwards into segment 3 and backwards almost to the posterior edge of segment 5. This oval area is indicated in Fig. 2 by a clear ring bordered by stipple (see also the colour photograph on the cover of *J. exp. Biol.* **144**, 1989, where the lower edge of the dimple catches the light). In the centre of this oval area, a slight further concavity usually appears on tergite 4, as indicated by the central area of dense stipple in Fig. 2.

The thickness of the abdominal cuticle, measured in segment 4, varies between 20 and 30 μm over most of the circumference of the segment, except for the ridges on the anterior and posterior borders of the segment. The cuticle is not noticeably thicker or thinner in the region of the lateral dimples. The thickness of the tissue of the body wall in segment 4 generally varied between 50 and 150 μm but was up to 300 μm locally, especially in dorsal and ventral areas in the presence of fat body, muscle, tracheae, Malpighian tubules, etc.

The wet mass of a recently fixed patch of cuticle plus epidermis of area 130 mm² cut from the dimple region of tergite 4 (Fig. 2) was 36 mg. This gives a specific mass of 0.28 mg mm⁻². This specific mass, equivalent to a mean tissue thickness of approximately 270 μm , is compatible with the range of cuticle and tissue thicknesses reported above.

The tymbals of *C. saundersii* are unusually large and almost hemispherical. The sclerotised posterior tymbal plate, to which the tymbal muscle attaches, is set at an angle of approximately 75° to the sagittal axis of the body. Anterior to the tymbal plate, a series of seven sclerotised ribs runs dorso-ventrally over the convex surface of the tymbal (see Fig. 4 in Simmons and Young, 1978). These long ribs are separated by a series of short ribs (see Fig. 5 in Simmons and Young, 1978), and all the sclerotised parts are supported by sheets of resilin-containing cuticle, as occurs in *Cyclochila australasiae* (Young and Bennet-Clark, 1995).

Calling song and protest song

The bimodal pulses of calling song (Fig. 4A) are produced by the sequential action of the two tymbals, one of which starts to buckle inwards between 5 and 7 ms before the other (Simmons and Young, 1978), which represents a delay at the motor neurone level of one-quarter of the cycle period (Simmons, 1977). Each part of the pulse is normally produced by the buckling of three ribs of one tymbal, which buckle in a posterior-to-anterior sequence, starting at the tymbal plate. Either the left or the right tymbal can lead, and the buckling of

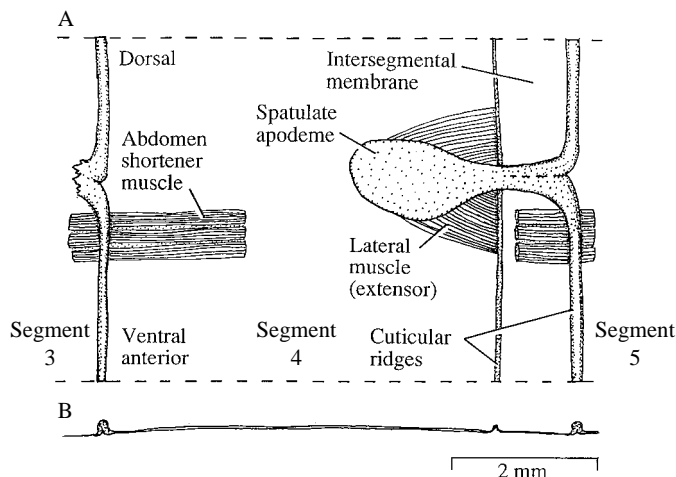
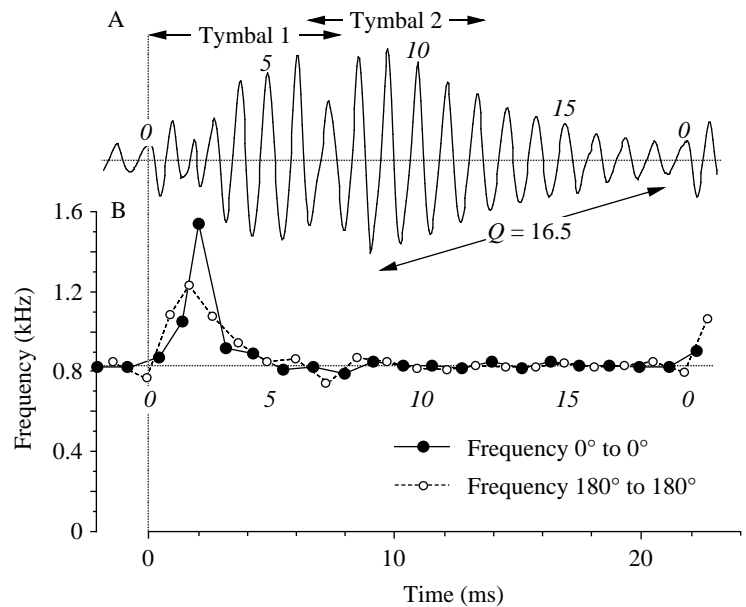


Fig. 3. (A) Drawing of an internal view of part of the right third, fourth and fifth tergites of *C. saundersii*, fixed with the abdomen fully extended, to show the spatulate apodeme of the fifth segment and various intersegmental muscles. The lateral longitudinal abdomen shortener muscle is drawn cut away where it passes over the apodeme and the dorsal and ventral lateral muscles of the apodeme. (B) A section of the ventral cuticle of the same region as A to show the ridges onto which the intersegmental muscles attach.

Fig. 4. The calling song of *Cystosoma saundersii*. (A) Oscillogram of a single song pulse, recorded 2 mm from the outer surface of tergite 4. The bimodal pulse envelope results from drive produced by the buckling of one tymbal then the other (Simmons and Young, 1978), as shown by the two arrows. The quality factor Q was measured from the reciprocal of the natural logarithm of the decrement of the pulse amplitude during the last 10 cycles of the pulse. The dotted line shows the zero crossing of the waveform. (B) Plots of the instantaneous frequency of the calling song waveform against time, on the same scale as A, measured as the reciprocal of the period of one cycle from the zero crossing to zero crossing of the next waveform. The period was measured either from 0° of one cycle to 0° of the next cycle or from the 180° crossing to the next 180° crossing. The dotted line is drawn at 830 Hz. In A and B, the cycles in the song pulse are numbered in italics.



rib 3 of the leading tymbal overlaps the buckling of rib 1 of the following tymbal.

The waveform is nearly coherent (Fig. 4A), and the instantaneous frequency of its dominant component, measured as the reciprocal of the period of each cycle, does not vary much from the value of 800–850 Hz of the insect's song (Fig. 4B). However, there is an irregular low-amplitude component at the start of the pulse (between 0 and 2.5 ms on Fig. 4) when the dominant frequency varies rapidly.

The song pulses analysed here are representative of the normal calling song of this species. The Q of 16.5 measured from the decay of the pulse shown in Fig. 4A is similar to values found using the same method for song pulses of *Cyclochila australasiae* (see Fig. 6 in Bennet-Clark and Young, 1992) but higher than the Q values of up to 9.4 reported by Young (1980). The discrepancy between our present measurements and those reported previously by Young (1980) is probably due to uncertainties arising from the short sampling window used for Young's measurements.

When the singing insect is held, vibration of the abdomen can be felt. Vibration of the tergal cuticle in the dimple area can be seen clearly through a dissecting microscope.

Tests of the internal sound delivery system

In order to test the validity of the results obtained using the earphone internal sound source, three series of measurements were carried out.

In the first, tone bursts of one, two, three or four sinusoidal cycles at the previously measured resonant frequency of the abdomen were delivered to the interior of a *C. saundersii* abdomen that had been extended to a length of 40 mm. The sounds that resulted from these tone bursts were recorded 2 mm outside the dimple region on tergite 4 (Fig. 1C). Fig. 5A shows a set of four oscillograms superimposed so that the build-up of the sound pulses can be compared. All pulses, whether one or

four cycles long, show the same exponential build-up but, of course, the four-cycle pulse builds up to the largest final amplitude. All pulses also show a similar exponential decay.

The decay of such pulses was tested more directly in the second experiment in which the drives were four-cycle tone bursts at 500 or 740 Hz (Fig. 5B). In this case, the oscillograms have been aligned so that the decay of the waveforms can be compared. The driven part of the response to the 500 Hz drive has a somewhat irregular envelope, but decays exponentially at a higher frequency (720 Hz). The driven part of the response to the 740 Hz builds up smoothly, showing that the abdomen is being driven at close to its resonant frequency, and the decay of the waveform is closely similar to that seen with the 500 Hz drive.

In the third test, the earphone was used to provide a drive into a 7.5 ml polycarbonate syringe, into which a probe microphone was sealed. Using frequencies at 500 Hz and 1 kHz, tone bursts were reproduced with the correct number of cycles as well as similar phase between drive and response and without sharp resonances (Fig. 5C).

We conclude that the earphone driver provides a valid model of the sort of drive that is provided by the tymbal. This justifies the use of the earphone for comparative measurements of the acoustic properties of the abdomen.

Mapping the sound radiation of the abdomen

Because of their sensitivity to disturbance, it was difficult to obtain a complete series of measurements along the full length of the abdomen and around its circumference with insects producing the calling song naturally. However, one nearly complete map and another confirmatory map were obtained from naturally singing insects. Thereafter, detailed measurements were made using the internal sound source (set up as in Fig. 1B with the abdomen fully extended), driven by equal mark-to-space eight-cycle tone bursts at the previously

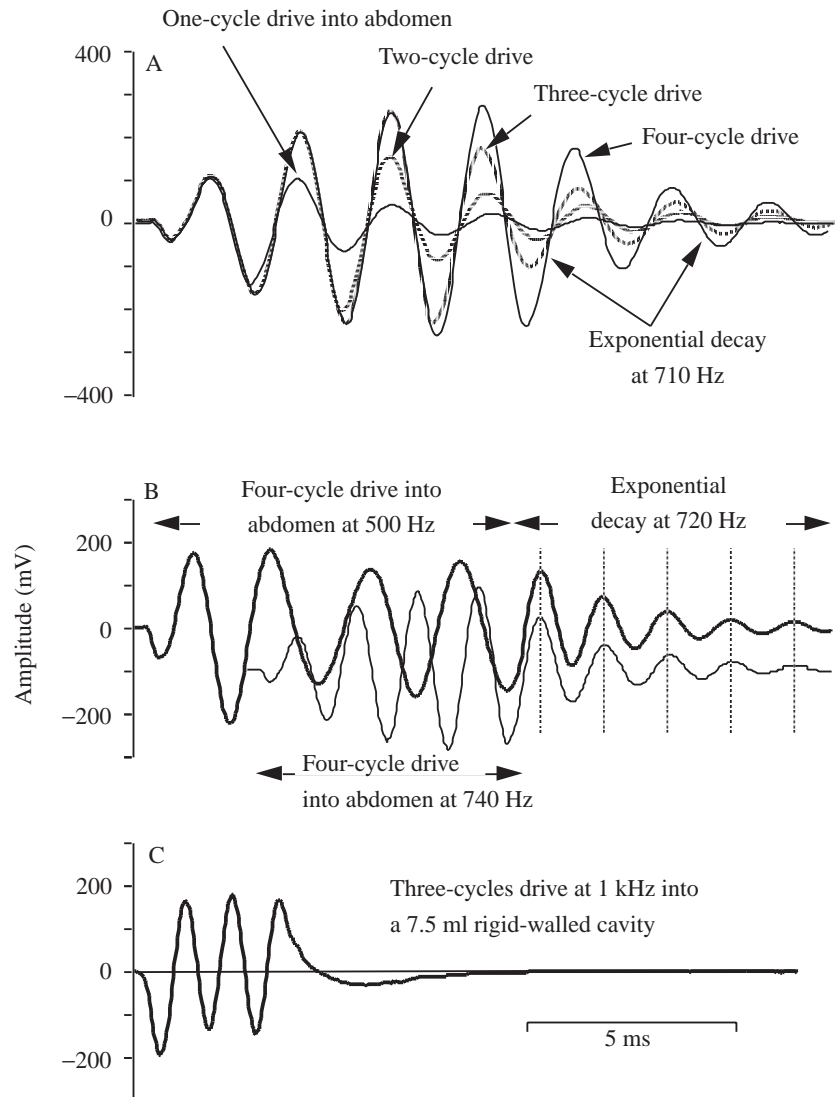


Fig. 5. Results from tests of the validity of the internal sound source (see Fig. 1). (A) A set of four superimposed oscillograms of the sound recorded outside tergite 4 produced by tone bursts of one, two, three or four cycles delivered inside the abdomen of *C. saundersii*. The build-ups at the start of the pulses are very similar. (B) Oscillograms of the response to four-cycle tone bursts delivered inside the abdomen of *C. saundersii*, the upper (thick line) at 500 Hz and the lower (thin line) at 740 Hz, recorded outside tergite 4. The responses to these different signals decay at the same frequency and the same rate. The oscillograms have been aligned for easy comparison. (C) Oscillogram of the sound pressure recorded inside a 7.5 ml rigid-walled cavity when driven with a three-cycle 1 kHz tone burst delivered inside the cavity.

measured resonant frequency of the abdomen. Complete sound pressure maps were obtained from three such preparations, with the abdomen fully extended. The two incomplete maps from the freely singing insects and the three maps obtained using the internal sound source showed essentially the same pattern of sound distribution.

Measurements of the sound pressure were made at 5 mm intervals, first along the length of one side of the abdomen in a series of horizontal lines 5 mm apart between the widest part of the abdomen, where it curves in towards the ventral surface and the mid-dorsal line, then as a series of sagittal lines along the flat ventral surface of the abdomen, outwards from the mid-ventral line (Fig. 6B). The map of the sound field shown in Fig. 6A treats the abdomen as if it were a flat sheet and plots the distribution of the sound pressure expressed as dB relative to the maximum measured value. These values were initially plotted onto a 5 mm square grid drawn on the same projection as Fig. 6A, and equal sound pressure isobars at 2 dB intervals were then interpolated.

Maximum sound pressure was recorded from close to the

lateral dimple on tergites 3–5. The 0 dB sound isobar corresponds to the centre of the dimple. The -4 dB isobar corresponds closely to the extent of the dimple (compare Fig. 6A with Fig. 2). The approximate dimensions of various isobars are shown in Table 1, together with the calculated mass of these regions

A subsidiary area of sound radiation was centred on sternite 5 of the flat ventral surface of the abdomen (Fig. 6; Table 1). Although the peak sound pressure in this region is 10 dB below that produced at the tergites (or one-tenth of the power per unit area), the area is nearly three times greater, so its overall contribution to sound radiation by the abdomen is likely to be approximately one-third of that radiated each tergite.

The phases of the sounds radiated from the two sides of the abdomen and from the ventral surface were identical. This suggests that all three sound-radiating regions of the abdomen act as parts of a single vibrating system.

These three sound-radiating regions are nearly flat oval regions in the fully extended abdomen. There was very little sound radiation either in the naturally singing insects or from

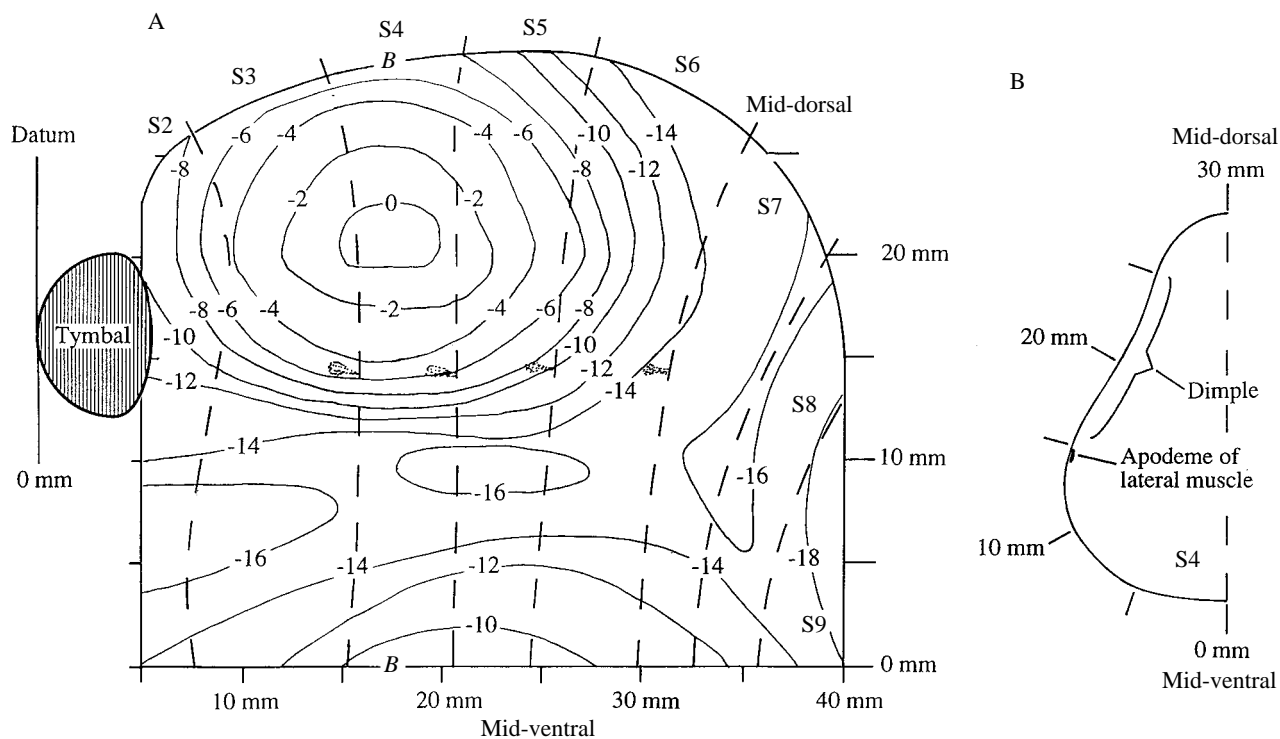


Fig. 6. (A) Map of the distribution of sound pressure at 2 mm distance from the surface of the fully extended abdomen of a *C. saundersii* driven by the internal sound source (see Fig. 1B). Values are in dB relative to the maximum value measured. The initial data were collected along a 5 mm×5 mm grid over the surface of the abdomen, as indicated at the bottom and right-hand side of the map. Contour lines of equal sound pressure were then drawn by interpolation. The segmental boundaries are shown by dashes, and the spatulate apodemes (see Fig. 2) of the lateral muscles are shown as dotted outlines. B–B shows the plane of the section drawn in B. (B) Drawing of the cross section of the left side of the abdomen through the middle of segment 4, drawn to the same scale as A. The shape of the cross section and the positions of the lines of latitude used in Fig. 6A are shown. S2–S9, segments 2–9.

the abdomens driven by the internal sound source from the curved ventro-lateral edge of the abdomen or in the domed anterior segment 2 and domed posterior segments 7–9. This suggests that sound is radiated by the vibration of these flat compliant discs of cuticle set in the less compliant curved surrounds.

The effects of changing the length of the abdomen

The length of the abdomen was changed while it was driven by the internal sound source using a five-cycle tone burst at the resonant frequency. Measurements of the sound pressure were made at the centre of the dimple on tergite 4 and at the junction

between sternites 4 and 5 at the mid-line. Both the amplitude and the *Q* of the sound waveform rose dramatically as the abdomen lengthened (Fig. 7B). When fully stretched, it produced a long sound pulse (Fig. 7A). The maximum amplitude and *Q* of the decay of the waveforms with 2 mm stepwise changes of abdomen length in one experiment are shown in Fig. 7B. Similar values have been measured from three other insects, ranging in fully stretched abdomen length from 39 to 42 mm. These observations show that the abdomen behaves as a resonator and that full extension is necessary if it is to resonate sharply and radiate the maximum amplitude of sound.

Table 1. *Dimensions of the isobars of sound radiation from the abdomen of Cystosoma saundersii*

| Sound-radiating region | Sound pressure relative to peak (dB) | Length of isobar (mm) | Height or width of isobar (mm) | Area of isobar, as an ellipse (mm ²) | Approximate mass of region (mg) |
|------------------------|--------------------------------------|-----------------------|--------------------------------|--------------------------------------------------|---------------------------------|
| Tergite 4 | 0 | 5 | 4 | 16 | 4.5 |
| Tergites 3–5 | –2 | 10 | 8 | 64 | 18 |
| Tergites 3–5 | –4 | 15 | 12 | 140 | 39 |
| Sternites 4–6 | –10 | 12.5 | 5 | 50 | 14 |
| Sternites 3–7 | –12 | 22 | 10 | 170 | 48 |

The dimensions are taken from the map of sound radiation (Fig. 6A), and the mass is calculated using a specific mass of 0.28 mg mm^{–2}.

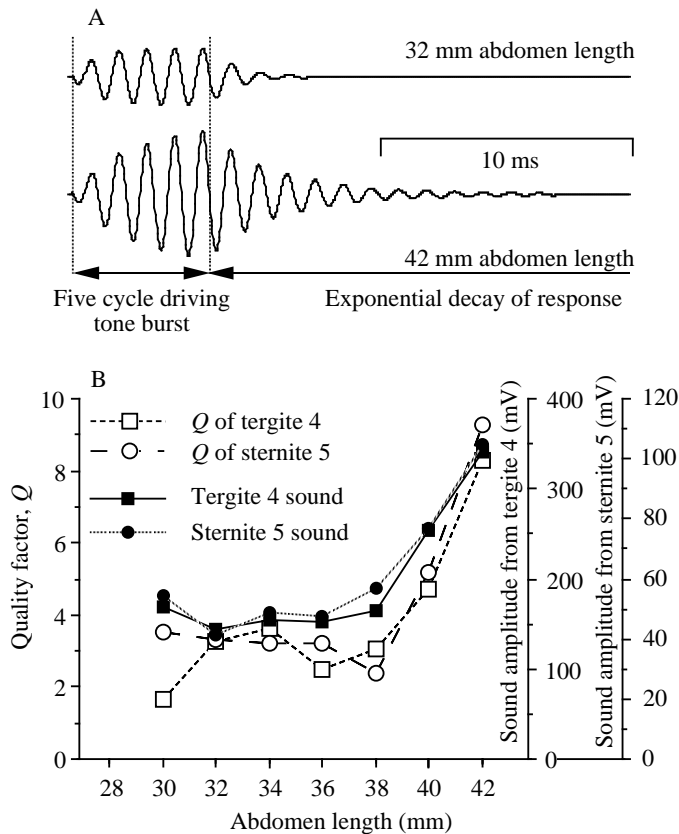


Fig. 7. (A) Oscillograms of the response recorded at tergite 4 of the abdomen of a *C. saundersii* to a five-cycle tone burst delivered by the internal sound source. The upper trace was recorded with an abdomen length of 32 mm, approximately equal to the resting length; the lower trace was recorded with an abdomen length of 42 mm, with the intersegmental membranes fully extended. The dotted lines mark the duration of the driving tone burst. (B) Graphs showing the effect of altering the length of the abdomen of the same *C. saundersii* on the quality factor Q (left-hand scale) and the amplitude (right-hand scales) of the response to an internal sound drive. The sound pressure radiated from tergite 4 was always approximately 10 dB greater than that radiated from sternite 5, but the Q values were very similar.

In another experiment, the resonant frequency was measured at different lengths of abdomen. The resonant frequency fell from 900 Hz at 41 mm abdomen length to 815 Hz at 34 mm length. Possible reasons for this change are discussed below.

Compliant and inertial elements of the abdominal resonator

For a simple resonant system, the resonant frequency is proportional to the reciprocal of the square root of the compliance. In an air chamber of this type, the effective compliance is proportional to the volume (Fletcher and Hill, 1978). The resonant frequency of the abdomen recorded at tergite 4 was measured after various changes to the total volume of the abdominal air sac (see Materials and methods and Fig. 1C), with the intersegmental membranes of the abdomen fully extended. The results are shown in Fig. 8, which plots resonant frequency against $1/\sqrt{(\text{total volume})}$ for

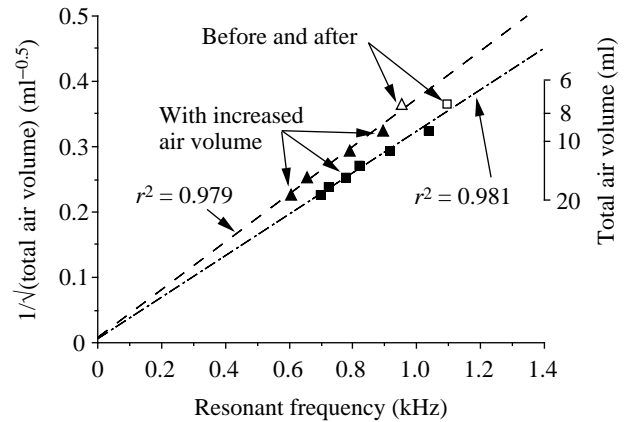


Fig. 8. The effect on the resonant frequency of the abdomen of *C. saundersii* of increasing its effective volume by the method shown in Fig. 1C. The data from two insects are plotted as resonant frequency against $1/\sqrt{(\text{volume})}$ (left-hand scale, with the actual volume shown on the right-hand scale). The experiments were performed with the abdomen at its fully extended length. The open symbols shown the values measured with the mouth of the bottle sealed with a washer at the start and end of the experiment (Fig. 1C). The figure shows the correlation coefficients of linear regressions for the two sets of data with the regression lines plotted to intercept the y axis. The regression equations for the two lines are: for ▲, $y = 7.23 \times 10^{-3} + 0.37 \times 10^{-3}x$ ($P < 0.001$, d.f. = 8) and for ■, $y = 6.67 \times 10^{-3} + 0.32 \times 10^{-3}x$ ($P < 0.001$, d.f. = 12).

two preparations. The regression lines drawn through both sets of values pass very close to the origin, providing strong evidence that air sac volume is the major compliant element in the resonator and confirming Fletcher and Hill's (1978) suggestion.

In calculating the resonant frequency of the abdomen (see below), we have taken 7.5 ml as the effective volume of the abdominal resonator.

An open *C. saundersii* abdomen with the end removed posterior to segment 7 resonated at 3 kHz, even though the air sac volume was similar to that of the intact insect. This appeared to be a Helmholtz-type resonance of the open cavity, and this experiment provides further evidence that the normal 850 Hz resonance depends on the enclosed air volume in the abdomen.

The resonant frequency of a simple resonant system is also proportional to the reciprocal of the square root of mass. A pilot series of experiments was performed in which 15 mg solder weights were glued at 5 mm intervals all over the surface of the abdomen. This brought about a considerable decrease in the resonant frequency, but also greatly lowered the Q of the resonance. In other experiments, it proved possible to excite resonant responses at one frequency from the dimple on tergites 3–5 and at another frequency from sternite 5. Clean lowering of the resonant frequency of the whole abdomen could only be obtained if both sides of the tergites were loaded symmetrically and if the load on the sternites was larger than that on the tergites: if the side of one tergite was loaded, the resonance of the unloaded side tended to persist and dominate.

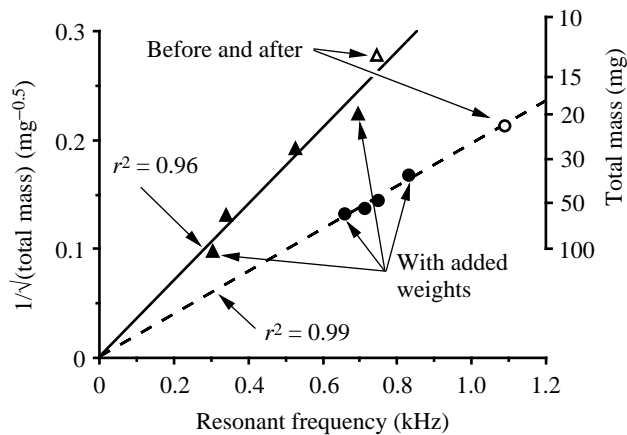


Fig. 9. The effects on the resonant frequency of the abdomen of *C. saundersii* of increasing the effective mass of tergite 4 and the sternites by the method shown in Fig. 1D. The data from two insects are plotted as resonant frequency against $1/\sqrt{\text{total mass}}$ (left-hand scale, with the actual mass shown on the right-hand scale). Both experiments were performed with the abdomen at its fully extended length. The open symbols show the calculated values for the mass for the abdomen, at the measured resonant frequencies before loading and after removal of all the weights, using a regression line calculated to run through the origin. The regression equations for the two lines are: for ▲, $y = 11.59 \times 10^{-3} + 31.6 \times 10^{-3}x$ ($P < 0.001$, d.f. = 8) and for ●, $y = 13.92 \times 10^{-3} + 19.5 \times 10^{-3}x$ ($P < 0.001$, d.f. = 8).

By selective removal and addition of weights, the critical areas at which loading caused a general reduction of the frequency of a single abdomen resonant frequency were found. A pattern of loading that met this criterion was to place equal weights as two lengths of solder along both dimples on tergite 4 and a further row of weights, totalling 1.5 times that on either dimple, close to the intersegmental membranes of sternites 3 and 4, 4 and 5, and 5 and 6 (Fig. 1D).

The data obtained for the reduction in the resonant frequency by loading tergite 4 allowed us to calculate, for each side of tergite 4, the effective unloaded mass of the tergite. The results for two insects are plotted on Fig. 9, giving unloaded masses of 13 and 22 mg. Two other preparations gave estimates of mass of 17 and 30 mg. The measured resonant frequencies of the unloaded abdomens differed somewhat from the frequency of the natural song. These discrepancies probably result from differences between the artificial extension of the experimental abdomens and the natural extension that occurs in the singing insect.

In calculating the resonant frequency of the abdomen (see below), we have taken 20 mg as the effective mass of the resonant region.

These experiments suggest that the mass elements of the abdominal resonator are the areas of cuticle making up the dimples on tergites 3–5 and a ventral patch centred on sternite 5. From the interdependence of their resonances, these areas appear to be loosely coupled; although these masses are separated by regions that do not vibrate appreciably, they share the air sac as a common compliant element.

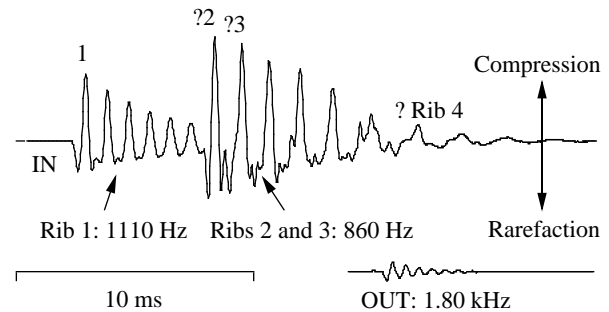


Fig. 10. Oscillograms of the sounds produced by tymbal buckling driven by muscle contraction, recorded from a *C. saundersii* from which the abdomen had been removed posterior to segment 2. The upper trace shows a sequence of IN pulses indicating the ribs that produced the various pulses in the sequence and the frequency that was measured for the various parts of the waveform. The lower trace shows the OUT pulse that was produced by the outward buckling of the tymbal after relaxation of the tymbal muscle.

The drive provided by the tymbal

After removal of the abdomen posterior to segment 2, the tymbal muscle was stimulated. Stimulation was provided by single pulses 2 V in amplitude and 5 ms in duration from the MacLab stimulator facility applied by a pair of stainless-steel pins directly to the lateral ventral end of the tymbal muscle. The muscle contractions caused the inward buckling of one or more tymbal ribs. Our results confirmed the report by Simmons and Young (1978) that the initial buckling of rib 1 is followed after 4–6 ms by the buckling of rib 2, followed rapidly by that of rib 3. In some preparations, there was also a weak pulse produced by the buckling of rib 4 (Fig. 10).

The frequency of the IN pulse produced by the buckling of rib 1 in four different insects varied between 1030 and 1110 Hz. That from ribs 2 and 3 varied between 830 and 870 Hz, and that from rib 4 between 630 and 750 Hz. The peak amplitude of the IN pulses produced by the buckling of ribs 2 and 3 was always 4–6 dB louder than that produced by rib 1. That from rib 4 was variable but quieter than that from the other ribs.

As the tymbal muscle relaxed, the tymbal buckled outwards approximately 20–30 ms after the start of the inward movement, producing an OUT pulse (Fig. 10). The frequency of the OUT pulses from the same four insects varied between 1.6 and 1.9 kHz.

The inward buckling of the separate tymbal ribs occurred so rapidly, when produced by the tymbal muscle, that their effects could not be separated clearly for analysis. Hence, other experiments were performed in which the tymbal was buckled by pulling on the apodeme of the tymbal muscle by hand (Fig. 11) (see Fig. 8c in Simmons and Young, 1978). The normal pattern of IN pulses, which was easy to produce, was similar to that produced by muscle contraction, but occurred over a longer period (compare Figs 10 and 11A). However, by altering the rate at which the tymbal muscle was pulled, it was possible to obtain trains of well-separated pulses

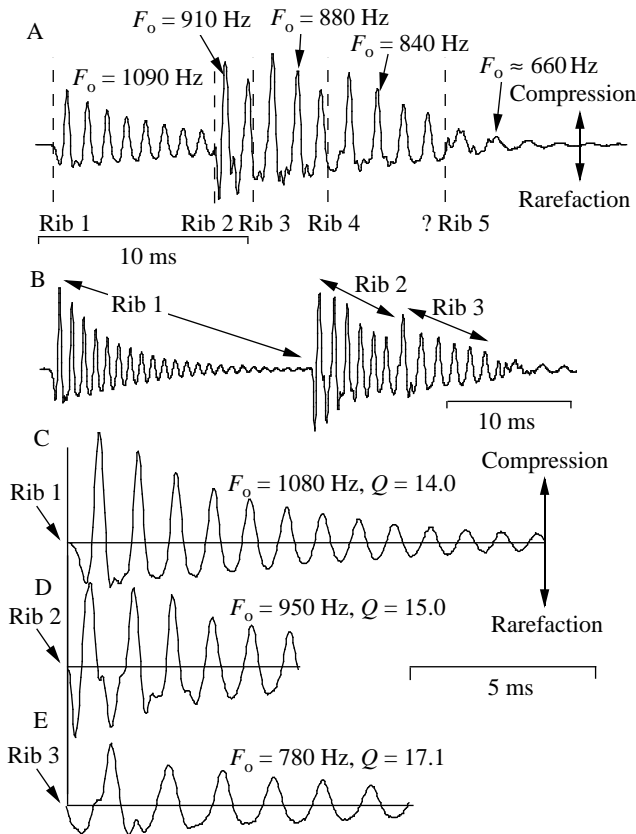


Fig. 11. Oscillograms of the sound pulses produced by tymbal buckling when the apodeme is pulled with forceps, recorded from a *C. saundersii* from which the abdomen had been removed posterior to segment 2. The resonant frequency (F_o) and quality factor Q for different parts of the waveforms are shown. The time markers for A and B differ, but C–E share a common time marker. (A) Typical train of IN pulses from a rapid pull, showing the IN pulses produced by the buckling of five of the seven tymbal ribs. (B) Train of IN pulses produced by a slower pull, showing a similar sequence to that in A. In this example, the second and third IN pulses are more widely separated than in A. (C–E) Details of the separate IN pulses produced by the buckling of ribs 1–3 to show the resonant frequency and Q calculated from the rate of decay of the waveform. The vertical lines indicate the start of the inward buckling of each pulse. All pulses are plotted at the same gain, so the traces show the relative amplitude of the different pulses.

(Fig. 11B). It was very difficult to obtain sequences with identical frequencies from successive pulls from the same preparation: the frequency and amplitude of the sound produced depended critically on the direction of the pull (compare Fig. 11A and 11B). However, the typical pattern was that the first IN pulse was at over 1.05 kHz, the second plus third at 850–950 Hz, the fourth at 750–850 Hz and the fifth at 650–750 Hz (Fig. 11).

Fig. 11A,B shows oscillograms of two complete sequences of pulses each produced by a single pull, and Fig. 11C–E shows details of the sequence in Fig. 11B. Note that the terms ‘compression’ and ‘rarefaction’ used in Figs 10 and 11 follow standard acoustic terminology in referring to sound pressure

recorded at the microphone on the outer surface of the tymbal, rather than referring to sound pressures inside the cicada’s abdominal air chamber. In all cases, the waveforms produced were highly asymmetrical, with the rarefactions produced by the initial inward movements of the tymbal being far smaller in amplitude than the compressions produced by the subsequent outward rebound. The amplitude of the pulses produced by the inward buckling of each rib is greatest during the first cycle and thereafter decays more or less exponentially (Fig. 11). The frequency during the decay of the vibration decreases from IN pulse 1 to IN pulse 4, and the Q of the resonance increases in this sequence.

When one rib buckles shortly after another, the IN pulses merge into one another coherently (Figs 10, 11A). A similar observation has been made with the IN pulses produced by the tymbal of *Cyclochila australasiae* (Bennet-Clark, 1997). The IN pulses produced by buckling of the tymbal ribs of *C. australasiae* are also distorted, but to a far smaller extent (Bennet-Clark, 1997). The decline in frequency with successive pulses is also seen in *C. australasiae*, but the relative decrease in resonant frequency between the pulses produced as successive ribs buckle is far greater in *Cystosoma saundersii*.

In summary, the results described in this section show that, as rib 1 buckles, the tymbal produces a low-amplitude IN pulse at a higher frequency than that of the song; this is followed by a larger-amplitude sustained IN pulse at a similar frequency to that of the song, produced by the buckling of ribs 2 and 3. From this, it appears that the pulses produced by the buckling of ribs 2 and 3 are likely to dominate the excitation of the abdominal resonance during singing and, because a long coherent sound pulse is produced by ribs 2 and 3, this will excite, then augment and sustain, a sympathetic resonance of the abdomen.

Protest song at varying abdomen lengths

Protest song is both quieter and more erratic than calling song (Simmons and Young, 1978). However, it is easily elicited and allows the relationship between the tymbal drive and sound radiation from the abdomen to be examined.

Insects with their legs and wings removed were prepared as shown in Fig. 1A,B to test the effects of changing the length of the abdomen. Measurements with short and long abdomens showed that, although the amplitude of the sound recorded at the tymbal was closely similar with both short and long abdomens, the amplitude of the sound recorded at tergite 4 with the abdomen fully stretched was approximately 6 dB louder than with the abdomen at the resting (short) length. In all cases, the phase of the response from tergite 4 lagged behind the sound produced by the tymbal by approximately 90° (as was found with natural calling song; see Fig. 12) suggesting that a sympathetic resonance was excited in the abdomen.

Although the sound that was produced in this condition did not show the high Q of the calling song, the tymbal drive did appear to excite a sympathetic resonance in the abdomen.

Discussion

The elements of the resonant system

The present study provides experimental support for the general mechanism of sound radiation from the abdomen of *C. saundersii* that was proposed by Fletcher and Hill (1978). In their model, the abdomen acts as a resonator in which the reactive elements are the compliance of the air sac and the mass of the abdominal cuticle.

We can now attempt to fit our data to a new model of how the abdominal resonance is determined.

The resonant frequency, F_o , of a simple resonant system of this type is given by:

$$F_o = \frac{1}{2\pi} \sqrt{\left(\frac{1}{A \times m} \right)}, \quad (2)$$

where A is compliance and m is mass. The treatment given by Fletcher and Hill (1978) expresses this in terms of the electrical analogues of compliance and mass, capacitance (C) and inductance (L), respectively. Equation 2 then becomes equivalent to:

$$F_o = \frac{1}{2\pi} \sqrt{\left(\frac{1}{C \times L} \right)}. \quad (3)$$

Following Fletcher and Hill, the capacitance of the air sac volume, $C_{\text{air sac}}$, is:

$$C_{\text{air sac}} = \frac{V_{\text{air sac}}}{\rho_{\text{air}} \times c_{\text{air}}^2}, \quad (4)$$

where $V_{\text{air sac}}$ is the volume of the air sac, ρ_{air} is the air density and c_{air} is the velocity of sound in air.

The effective inductance (L) of the vibrating area, following Fletcher and Hill (1978), is:

$$L = \frac{\rho_{\text{cuticle}} \times T_{\text{cuticle}}}{S_{\text{cuticle}}}, \quad (5)$$

where T_{cuticle} is the thickness of the cuticle, S_{cuticle} is the area of vibrating cuticle and ρ_{cuticle} is the cuticle density. This can be expressed in terms of mass and area as:

$$L = \frac{m_{\text{cuticle}}}{A_{\text{cuticle}}^2}, \quad (6)$$

where m_{cuticle} is the mass of the cuticle. After rearrangement, the resonant frequency is now given by:

$$F_o = \frac{1}{2\pi} \sqrt{\left(\frac{S_{\text{cuticle}}^2 \times \rho_{\text{air}} \times c_{\text{air}}^2}{m_{\text{cuticle}} \times V_{\text{air sac}}} \right)}. \quad (7)$$

Using equation 6, we can calculate the effective vibrating area from the following values: $F_o=850$ Hz; $\rho_{\text{air}}=1.2$ kg.m⁻³; $c_{\text{air}}=340$ m.s⁻¹; $m_{\text{cuticle}}=20 \times 10^{-6}$ kg; $V_{\text{air sac}}=7.5 \times 10^{-6}$ m³. This gives an area of 35×10^{-6} m² or 35 mm². This is broadly compatible with the area of one of the paired -2 dB isobars of sound radiation that were mapped on the outside surfaces of abdominal tergites 3–5 (see Results and Table 1).

In making this calculation, we have ignored reactive components due to the acoustic loading of the abdomen. The justification for this simplification is that the radiating regions of the abdomen are only approximately 10 mm long but are radiating sound at 850 Hz with a wavelength, λ , of 425 mm. The sources thus have a maximum dimension of less than $\lambda/40$, which have small specific acoustic resistances and reactances (Olson, 1957). Also, the Q values greater than 7 that have been obtained suggest that the damping on the abdomen, whether from the acoustic load or from viscosity within the cuticle, is a minor element of the resonant system.

This model is an over-simplification and ignores the reduction in compliance of the cuticle that may occur when it is stretched tightly (N. Fletcher, personal communication). This effect may explain two of our findings: first, that the Q of the resonance rises rapidly as the abdomen becomes fully stretched (Fig. 7); second, that the resonant frequency of the abdomen rises as it is stretched whereas, from equation 7, the frequency should fall as the air sac volume increases. These two findings suggest that both the compliance and the mass in the system can be altered by the extent to which the abdomen is extended; this may also explain why, in some of our experimental preparations, the resonant frequency of the abdomen differed from the typical 850 Hz of the insect's song (see, for example, Fig. 9).

An earlier model of sound radiation from the abdomen of *Cystosoma saundersii* (Fletcher and Hill, 1978) suggested that lengthwise telescoping of a series of stiff segmental rings of abdominal cuticle, driven by the internal sound pressure produced by tymbal buckling, caused the body to resonate at the song frequency. The dimensions of the body were broadly compatible with the model they proposed.

Our findings confirm Fletcher and Hill's (1978) suggestion that the major compliant element of the abdominal resonator is the air sac volume. However, our results suggest that the mass elements are the two dimples on tergites 3–5 and the flat ventral region of the abdominal sternites. These masses appear to be loosely coupled, presumably by the coupling action of the shared air sac.

Driving the abdominal resonator

The two tymbals buckle asynchronously, the first between 5 and 7 ms before the second. This produces a bimodal song pulse envelope (Fig. 4A) which has been analysed previously by Young (1980). Our present measurements confirm Young's earlier findings and also allow us to consider the role of the two tymbals as complementary drives that first build up and then sustain the abdominal resonance.

A possible model of what is happening is given in Fig. 12A,B, which shows a complete cycle of buckling of both tymbals. In Fig. 12A, the sound pulse starts with the buckling of the contralateral tymbal, which leads to an initial build-up of the abdominal resonance (Fig. 12B). This is followed after approximately 5 ms by the buckling of ipsilateral rib 1 (Fig. 12A), which produces a sound pulse at approximately 1100 Hz which does not have much effect on the sound being

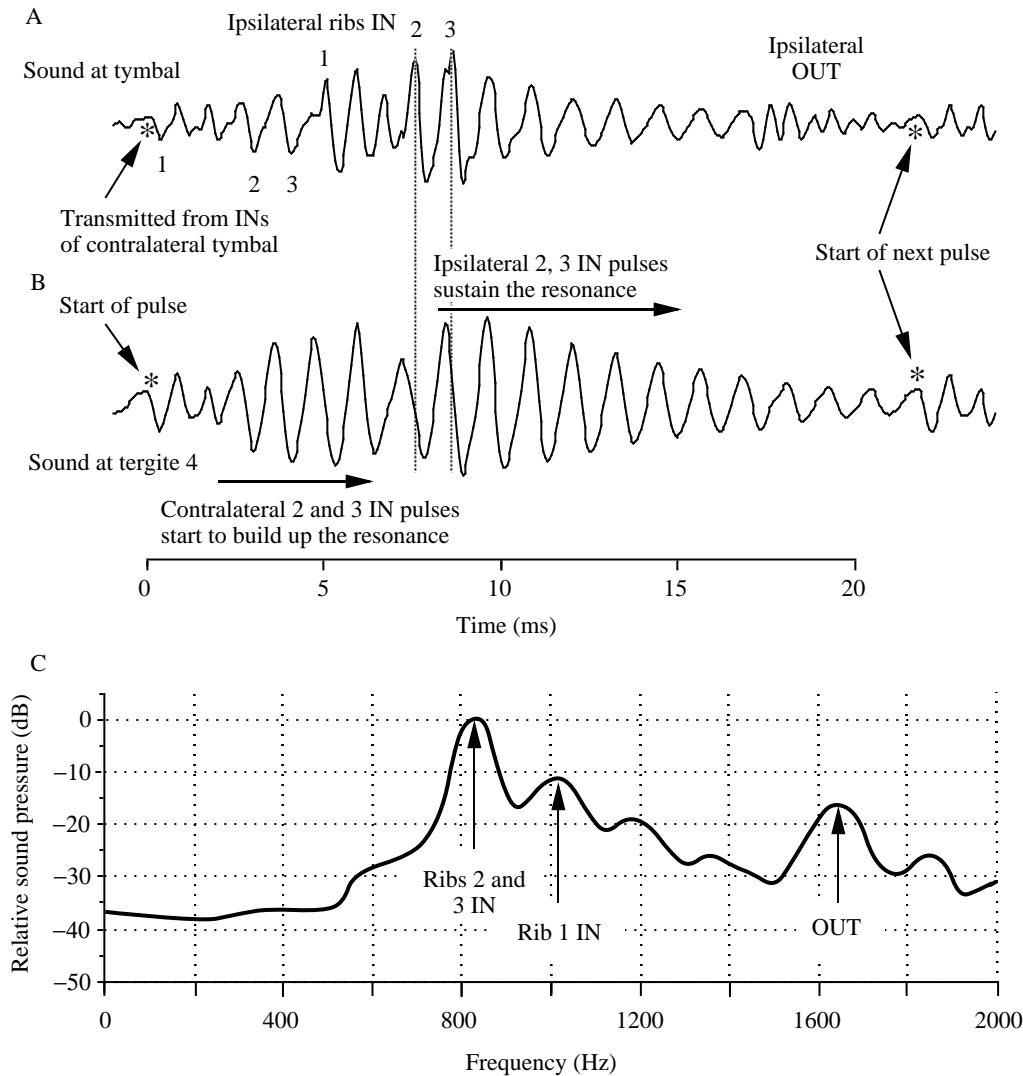


Fig. 12. Oscillograms of a calling song pulse recorded at one tymbal (A) and at tergite 4 (B), with a Fast Fourier Transform of the sound at the tergite (C). The oscillograms include approximately 2 ms of the preceding and succeeding pulses. (A) Sound recorded at the ipsilateral tymbal. Labels above the oscillogram show sound produced by the ipsilateral tymbal and labels below show sounds transmitted from the contralateral tymbal. The pulse starts (at the asterisk) with an IN pulse from contralateral rib 1, followed by two coherent cycles as ribs 2 and 3 buckle in rapid succession. The buckling of ipsilateral ribs 1, then ribs 2 and 3, follows. The ipsilateral OUT pulse, at higher frequency, precedes the start of the next pulse (at the second asterisk). (B) The sound recorded from the tergite shows a ragged waveform at the start of the pulse (asterisk) followed by a build-up of the pulse amplitude as contralateral ribs 2 and 3 buckle and the abdominal resonance increases. This resonance is not consonant with that of ipsilateral rib 1, so the amplitude falls and the waveform becomes ragged, but the pulse is built up again as ipsilateral ribs 2 and 3 buckle. Neither OUT pulse appears as a major component of the sound radiated from the abdomen because their resonant frequencies differ greatly from that of the abdomen. The dotted vertical lines at 8 and 9 ms show that the relative phase between the sound at the tymbal and that at tergite 4 is approximately 90° . (C) Fast Fourier Transform giving a frequency:power spectrum for the song pulse shown in B. The rib bucklings or IN pulses to which three major peaks in the spectrum are attributed are derived from Fig. 11.

radiated by the already-resonating abdomen, first because the internal pressure drive to the resonator from contralateral ribs 2 and 3 is of larger amplitude and, second, because rib 1 produces power at a different frequency.

However, as ipsilateral ribs 2 and 3 buckle, they produce large internal pressure pulses which augment those from contralateral ribs 2 and 3 and further build up the pulse amplitude. The phase of the abdomen response, allowing for

the 180° difference between the sound measured outside the tymbal and the internal drive that the tymbal provides to the abdomen, shows a lag of approximately 90° . Resonant decay of the IN pulse from rib 3 provides a continuing drive which sustains the abdominal resonance until 17 ms from the start of the pulse.

The OUT pulse, at approximately 1.65 kHz, does not appear as a major component of the sound radiated from tergite 4. As

with the pulses produced by rib 1, the frequency of the OUT pulses does not excite a large sympathetic response from the abdomen.

The Q of the decay of the song (16.5; Fig. 4A) is approximately twice that of the decay of the response of the abdomen when driven by internal sound (Fig. 7). We have previously made similar observations with the Q of the song of *Cyclochila australasiae* (see Fig. 6 in Bennet-Clark and Young, 1992) versus the Q of the abdominal resonator (Bennet-Clark and Young, 1992, p. 136), which we ascribed to the presence of two resonant stages in the transduction chain: (1) the Q of the resonant tymbal driving and (2) the Q of the resonant abdomen. A similar mechanism appears to apply in *Cystosoma saundersii*, with the additional complication that the sound pulses are of far longer duration than those of *Cyclochila australasiae* because the frequency of the song is far lower.

These long-duration pulses are produced by the overlapping action of the two tymbals, rather than by the tymbal alternation seen in *Cyclochila*. What is not clear is how the coherence of the song pulses seen in our present records (Fig. 4A) and in earlier records (Fig. 1 in Young, 1980) is produced. A mechanism ensuring coherence of the sound produced by the buckling of successive tymbal ribs in *Cyclochila australasiae* has been proposed (Bennet-Clark, 1997), and we have evidence for a similar mechanism operating in the tymbals of *C. saundersii* (Figs 10, 11A). Presumably the left and right tymbals are coupled through the resonant abdomen, which acts to ensure that the buckling of the second and third ribs of the trailing tymbal occurs in-phase with the resonance already established by the IN pulses of the leading tymbal.

The low-frequency song of Cystosoma saundersii

The song frequency of *Cystosoma*, approximately 850 Hz, is approximately one-quarter that of typical cicadas of the same body length (see Bennet-Clark and Young, 1994). The production of such a low-frequency song requires a relatively large sound source in order to give good impedance matching between the sound source and the surrounding medium (Olson, 1957; for reviews, see Bennet-Clark, 1971, 1995). Thus, the production of an anomalously low sound frequency by *C. saundersii* is accompanied by extreme specialisations of the sound-radiating regions of the abdomen. The abdomen volume is large to provide the large acoustic compliance that reacts with the large, low-mass areas that make up the sound-radiating regions. These areas are considerably greater than the sound-radiating tympana of such conventional cicadas as *Cyclochila australasiae*, which can achieve a similar sharpness of song tuning with smaller structures by singing at a higher frequency. Many of the larger of these conventional cicadas produce piercingly loud songs which are far louder than that of *C. saundersii*.

The advantages of such a low song frequency are a lack of interference from the songs of other insects and good transmission through the acoustically obstructed shrubs from which the insects call (MacNally and Young, 1981; see also

Bennet-Clark, 1998). Male song perches are concentrated between 1 and 1.7 m above ground, which is likely to maximize transmission of the low-frequency sound through the dense shrubbery (Doolan and MacNally, 1981; MacNally and Young, 1981).

The production of low-frequency song is not without problems. Not only is the abdomen of males approximately twice as long as that of female *C. saundersii*, but the volume of the abdominal bladder makes their flight slow, awkward and brief. The large clumsy males are cryptic and tend to remain almost motionless on the host plant for many days (Doolan and MacNally, 1981).

Other cicada species are known to radiate sound through parts of the general abdominal cuticle. *Tympanistalna gastrica* radiates the low-frequency components of its song through the abdominal tergites and sternites and the higher-frequency components through the tympana or directly from the tymbals (Fonseca and Popov, 1994). *C. saundersii* represents an extreme specialisation in which the song is radiated directly from a hypertrophied and highly specialised thin-walled abdomen.

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