

DO CICADAS RADIATE SOUND THROUGH THEIR EAR-DRUMS?

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Summary

1. Sound output was investigated in males of two cicada species, *Cyclochila australasiae* Donovan and *Macrotristria angularis* Ståhl. These are large insects, about 4.5 cm in length, with a typical arrangement of sound-producing organs.

2. Songs produced by both species consist of continuous trains of sound pulses, with a fundamental frequency close to 4 kHz. Higher harmonics fall below the 4 kHz peak by 20–30 dB. These songs are the loudest yet recorded among insects: 110 dB SPL at 20 cm for the protest songs of both species, and values as high as 115 dB for the vigorous calling songs of *C. australasiae* (mean 113 dB).

3. The male tympanum (ear-drum) is between 3.3 (*M. angularis*) and 5.5 (*C. australasiae*) times greater in area than that of the female, which does not sing. The tympana and folded membranes, as well as the sound-generating tymbals, vibrate vigorously during singing; other parts of the insect do not vibrate.

4. Sound output is greatest at the gap between the tympana and their protective coverings, the opercula. High values are also found close to the tymbals but not over the rest of the body. When the gap between tympana and opercula is held closed, rather than open, sound output falls by 11 dB. In the field, calling males adopt a characteristic posture, which keeps this opercular gap wide open.

5. Ablating the tympana makes no difference to the sound output. But ablating the posterior half of the abdominal air sac produces a mean fall of 8.6 dB, together with a great broadening of the song's frequency content.

6. The above results support the conclusion that the majority of sound is radiated through the tympanal opening in typical cicadas, with the tympana being driven passively by the resonant vibrations of air in the air sac. This system can be modelled as a Helmholtz resonator, with the tympanal opening representing the neck of the resonator.

Introduction

Any animal that is capable of producing a loud sound must possess a highly specialised mechanism in order to do so. Such a mechanism may be resolved into

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four functional elements: a generator that produces audio frequencies, a power source to drive the generator, a resonator that amplifies selected frequencies from the generator, and a radiator, which is a surface that transmits the resonant vibration to the surrounding air. In a calling frog, for example, the vocal folds are the generator, air expelled from the lungs by muscular action is the power source, the vocal tract is the resonator and the vocal sac provides the surface that radiates the sound into the environment.

Many species of insect communicate by means of airborne sound, and male cicadas (Homoptera: Cicadidae) are among the noisiest exponents of this means of intraspecific signalling. The first three functional elements mentioned above have been clearly identified in the sound-producing mechanism of cicadas. Sound frequencies are generated by a bilateral pair of stiff membranes or tymbals on the abdomen, and the power to drive each tymbal is provided by a single large muscle, the tymbal muscle. Evidence for this was provided by early workers who scrutinised the various membranes and muscles and, in some cases, conducted ablation experiments to assess their importance in sound production (e.g. Carlet, 1877; Lucas, 1887). With the advent of electronic equipment for recording and analysing both sounds and muscular activity, the role of the tymbals and tymbal muscles was demonstrated clearly (Pringle, 1954; Hagiwara, 1955). Later the same basic mechanism was shown to apply to a variety of cicadas around the world (Moore and Sawyer, 1966; Aidley, 1969; Reid, 1971).

There is a large air sac associated with the tymbals and tymbal muscles within the abdomen of male cicadas. The view that this air chamber acts as a resonator was advocated by Carlet (1877) and others, but it was Pringle (1954) who provided experimental evidence that this is the case. The most striking example of the air sac's role as a resonator is that of the bladder cicada, *Cystosoma saundersii*, in which the air-filled abdomen is much enlarged (Fletcher and Hill, 1978; Simmons and Young, 1978).

However, the question of the fourth functional element, of how sound is radiated by a cicada, has not been so clearly settled. Although Pringle (1954) demonstrated the importance of the air sac as a resonator, he did not specifically address the question of sound radiation. Michelsen and Nocke (1974) state that sound is radiated by the tymbals but they did not consider the role of the air sac. In the bladder cicada, the whole surface of the abdomen appears to act as a radiating surface (Fletcher and Hill, 1978; Simmons and Young, 1978), but this is less likely to be the case in typical cicadas, where most of the abdominal wall is relatively thick and inflexible. In cicadas of more typical appearance, the ear-drums or tympana provide a large membranous opening to the air sac, in addition to that provided by the tymbals (see Results, Fig. 1). It is entirely possible, therefore, that sound might be radiated from the air sac *via* the tympana. Weber *et al.* (1987) have pointed out that the way abdominal movements alter the song in certain species implies that this is the case.

The present report directly examines the question of whether sound is radiated through the tympana in a singing cicada, using two large species of Australian

cicadas, *Cyclochila australasiae* and *Macrotristria angularis*. These two species are of typical appearance and are very similar to one another.

Materials and methods

Specimens of *Cyclochila australasiae* were collected by hand during the day from parks and gardens around Melbourne, Victoria, in November and December. Specimens of *Macrotristria angularis* were obtained from areas of relatively undisturbed bush around Brisbane, Queensland, in January. They were collected using an ultraviolet light soon after it became dark, at the conclusion of the dusk chorus. The insects were either kept in soft mesh cages and supplied with fresh twigs or they were sleeved onto living shrubs. Since cicadas do not keep well in captivity, all experiments on sound production were conducted within 24 h of capture.

Sound recordings were made with a Sennheiser MKH 816 directional microphone and a Nagra IV S tape recorder at a tape speed of 19 cm s^{-1} . The recorded songs were analysed using a Kay Elemetrics model 5500 signal analysis workstation. Measurements of sound pressure were made with a Bruel & Kjaer type 4155 microphone connected by a 3 m long cable to a Bruel & Kjaer type 2230 sound level meter, displaying peak sound pressure in dB re $20 \mu\text{Pa}$. The sound level meter and microphone were calibrated with a noise source, Bruel & Kjaer type 4230.

Sound pressure measurements were made with the microphone at a distance of 20 cm from the singing insect to avoid any near-field effects that might bias readings made close to a sound source (Michelsen and Nocke, 1974). Since both species have peak frequencies close to 4 kHz, the sound level meter was used with the 4 kHz octave filter in place, to reduce the influence of extraneous noises. The sounds produced by undisturbed insects were recorded and measured in the field. The sounds produced under various experimental conditions were recorded and measured in the centre of a room, approximately $4 \text{ m} \times 4 \text{ m}$, in a quiet suburban home without audible distractions. Ambient temperatures were between 25 and 33°C.

During experiments involving the sounds made by captive insects (see Results), the microphones of the tape recorder and sound level meter were placed beside one another in a secure position. Then the captive insect was held by the thorax at a distance of 20 cm from the microphones and prodded or squeezed to elicit sound production. In one test, the opercular gap was held open or closed with a mounted needle. Superglue was used to keep the opercular gap closed in another trial; this gave similar results but was less convenient.

In another experiment, measurements were made of sound pressure around an insect using a probe microphone with a diameter of 2.5 mm from the Bruel & Kjaer probe microphone kit, in conjunction with the sound level meter. Here also, the microphone was secured and the insect was then held with its body surface about 2 mm away from the orifice of the probe microphone. The insect was

manipulated to bring different parts of its body close to the probe microphone while sound production was elicited from the insect.

The dimensions of the tympana (see Table 2) were measured from drawings prepared using a dissecting microscope with a squared graticule in the eyepiece and drawing paper with corresponding squares on it. The area of each tympanum was calculated from these drawings using a Zeiss MOP. Anatomical drawings (Figs 1, 3) were prepared from colour transparencies of the dissected insect, supplemented with details drawn under a dissecting microscope.

Results

Structural features

Both the species studied here, *Cyclochila australasiae* and *Macrotristria angularis*, are large, robust insects between 4 and 5 cm in length (Table 1). Males and females are similar in size, though the males are generally a little shorter and wider than the females.

The organs of sound production are very similar in the two species, and they conform to the typical pattern for cicadas, described by Myers (1928, 1929) and Pringle (1954). Fig. 1 shows the principal sound-producing structures, which are found only in the males. The tymbal is a ribbed cuticular membrane located dorsolaterally on the first abdominal segment. Further details of the tymbal are given for *C. australasiae* in Josephson and Young (1981) and Young (1975, Fig. 1); the tymbal of *M. angularis* is very similar. In both *C. australasiae* and *M. angularis*, the tymbal is largely hidden externally by a skeletal fold, the tymbal cover, which projects forward from the second abdominal segment (Fig. 1B). The large tymbal muscle inserts near the dorsal corner of the tymbal, on a cuticular plate, and has its origin on a strong ventral infolding of the exoskeleton (Fig. 1A).

There are two regions of thin, unsclerotised cuticle on the ventral surface, close to the origin of the tymbal muscle. Anteriorly, there is the folded membrane, which is opaque and thrown into irregular folds (Fig. 1A, C). The flexibility of this membrane allows the abdomen to be raised and lowered with respect to the thorax; the folded membrane is stretched as the abdomen is raised. Posteriorly, there is the tympanum, which is a relatively taut membrane, approximately circular in shape (Fig. 1C; cover photograph, this volume). Over most of its area,

Table 1. *Body size in male and female cicadas*

	Length (cm)	Width (cm)
<i>Cyclochila australasiae</i> male	4.53±0.21	1.76±0.06
<i>C. australasiae</i> female	4.6±0.25	1.71±0.05
<i>Macrotristria angularis</i> male	4.45±0.15	1.68±0.04
<i>M. angularis</i> female	4.64±0.27	1.66±0.07

Values of each characteristic are means and standard deviations from 10 individuals.

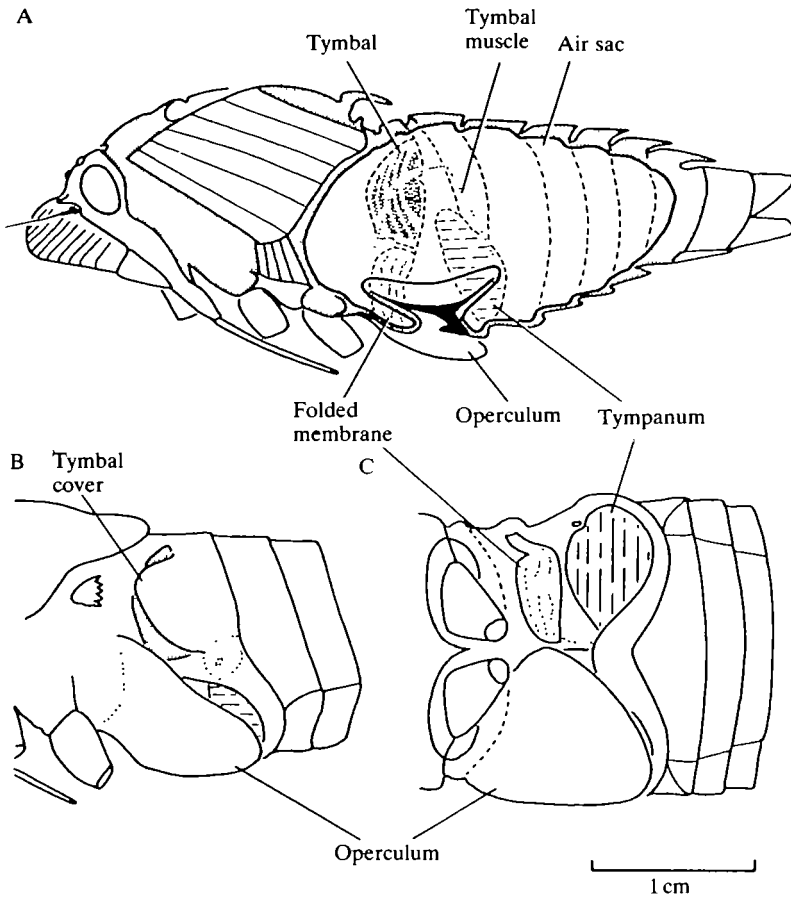


Fig. 1. Sound-producing structures in males of the cicada *Cyclochila australasiae*. (A) The insect cut open along the mid-line to give a medial view of the right side of the body, showing the large air sac and its relationship to other elements of the sound-producing mechanism. (B) Lateral view of the insect's left side (anterior to the left), to show the exoskeletal folds which cover the tymbal (tymbal cover) and tympanum (operculum) on each side. (C) Ventral view of the same region as in B (anterior to the left) to show the arrangement of the folded membrane and the tympanum, which are rendered visible on the insect's left side by removing the operculum. The scale at bottom right applies to all three drawings.

the tympanum is uniformly thin and transparent. In *C. australasiae*, it was found to be between 1 and 2 μm thick, measured in the light microscope from methacrylate sections. Near its lateral edge, a special thickening, the tympanal ridge, connects the tympanum with the auditory sensillae (Vogel, 1923; Michel, 1975; Young and Hill, 1977). The tympanum is covered externally by the operculum, which is an exoskeletal fold that extends backwards from the metathorax (Fig. 1B,C). The opercula are rigidly fixed to the metathorax and cannot be moved by muscles; the gap between the opercula and the tympana is increased by raising the abdomen.

Table 2. *Dimensions of the tympanum in male and female cicadas*

	Width (mm)	Area (mm ²)
<i>Cyclochila australasiae</i> male (N=5)	8.37±0.53	42.9±5.5
<i>C. australasiae</i> female (N=3)	4.46±0.057	7.7±0.36
<i>Macrotristria angularis</i> male (N=5)	7.0±0.32	28.2±1.94
<i>M. angularis</i> female (N=3)	4.33±0.15	8.57±0.4
<i>Cystosoma saundersii</i> male		4.1
<i>C. saundersii</i> female		3.9

Values are means and standard deviations.

Data for *Cystosoma saundersii* are taken from Young and Hill (1977).

At rest, the opercula usually touch the outer rim of cuticle around the tympana but there is always a space of a few millimetres between the opercula and the surface of the tympana.

Internally, much of the abdomen is occupied by a large air sac, which displaces the viscera dorsally (Fig. 1A). The tracheal lining of this air sac is closely adpressed to the inner surface of the tymbals, the folded membranes and the tympana. It also enfolds the tymbal muscle. The tracheal lining is so tightly pressed against the inner surface of the tympanum that coloured interference rings are often apparent (Vogel, 1923; cover photograph, this volume). Thus the tympana, the folded membranes and the tymbals are all coupled into a single large air chamber.

Although most of the above structures are absent in female cicadas, the females do possess a pair of tympana and an associated small air sac as part of their auditory system (Vogel, 1923; Myers, 1928; Young and Hill, 1977). In *C. australasiae* and *M. angularis*, the female tympanum is approximately oval in shape and is much smaller than that of the male. The area of the male tympanum is between 3.3 (*M. angularis*) and 5.5 (*C. australasiae*) times as great as that of the female (Table 2). The greater area of the male tympanum does not reflect a difference in size between males and females, which are very similar in size (Table 1).

Song features

In the field, undisturbed males of both species produce a loud piercing song, the calling song, from elevated positions in trees and tall shrubs. The calling songs of both *C. australasiae* and *M. angularis* consist of continuous trains of sound pulses (Fig. 2; Josephson and Young, 1981). The individual sound pulses consist of sinusoidal oscillations, forming the fundamental frequency that dominates the song. This fundamental or carrier frequency is close to 4 kHz in both species (Fig. 2; Table 3). There is a prominent secondary peak around 6 kHz in *M. angularis* but this is less conspicuous in *C. australasiae*. Higher harmonics of the fundamental frequency are evident in the power spectra but even the most

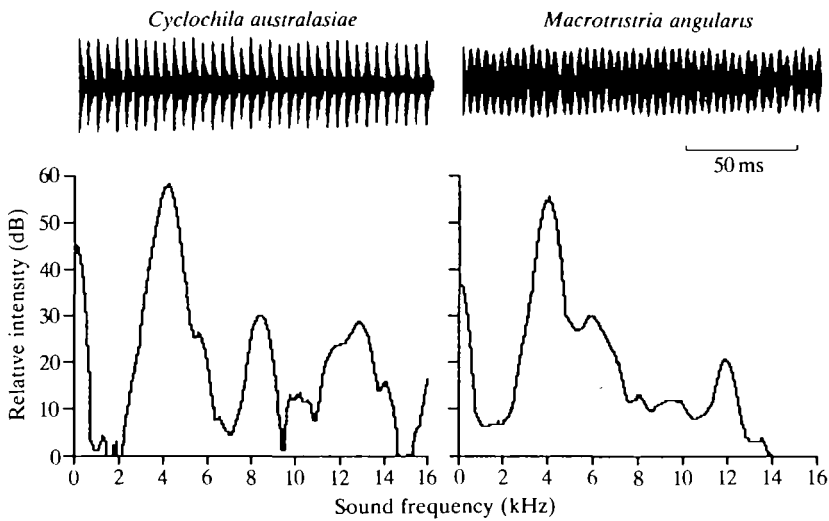


Fig. 2. Calling songs of the cicadas *Cyclochila australasiae* (left) and *Macrotristria angularis* (right). The upper part of the figure shows a small portion of the calling song of each species displayed on an oscilloscope (the time scale applies to both species). The lower part of the figure shows a log power spectrum of the calling song for each species.

Table 3. Measured parameters of cicada song

	Sound pressure level at 20 cm (dB)	Sound frequency (kHz)	Pulse rate (Hz)
<i>Cyclochila australasiae</i> calling song	112.9+2.9 -4.38 (N=8)	4.3±0.2 (N=10)	230.5±15.9 (N=10)
<i>C. australasiae</i> protest song	109.9+1.8 -2.3 (N=5)	—	—
<i>Macrotristria angularis</i> calling song	—	4.0 (N=2)	285 (N=2)
<i>M. angularis</i> protest song	110.3+0.9 -1.0 (N=8)	3.9±0.1 (N=10)	209±23 (N=10)

Values are means and standard deviations; for sound pressure level, the latter are asymmetrical about the means because they were calculated after conversion to absolute units of sound pressure and then converted back to dB.

prominent of these fall below the main peak by 20–30 dB (Fig. 2). The repetition rate of the pulses is consistently higher in *M. angularis* than in *C. australasiae* (Table 3). The very low frequency peak evident in the power spectra probably represents this repetition rate, i.e. the modulation envelope of the sound.

Prodding captive animals elicits protest songs, which resemble the calling songs

but are marked by a lower pulse repetition rate (Table 3; Josephson and Young, 1981). Both *C. australasiae* and *M. angularis* produce prolonged and vigorous protest song, and this facilitates experimental study. In *M. angularis*, which was used in the majority of experiments reported below, the protest song closely resembles the calling song in having the 4 kHz fundamental frequency, a secondary peak around 6 kHz and a 20–30 dB drop from the fundamental to its harmonics (compare Fig. 2 with Fig. 5A).

The most noticeable feature of these songs is that they are extraordinarily loud. A group of males calling in a nearby tree can render conversation impossible, and it is actually painful to hold a protesting insect close to one's ear. Measurements of the sound pressure level at 20 cm from the singing insect were obtained for the different song types (Table 3), except for the calling song of *M. angularis* (males of this species sang too high in the trees to be reached). In both species, the protest song consistently registers about 110 dB SPL, which is indeed a very loud sound for an insect to produce.

In *C. australasiae*, the calling song is sometimes louder than the protest song. The range of values registered for the calling song of *C. australasiae* is fairly wide (Table 3), and this is partly because a singing male can vary the intensity of the song by varying the size and posture of its abdomen (see below). Also, the force exerted by the tymbal muscle varies with ambient temperature (Josephson and Young, 1981). There is therefore quite a wide range of individual variation, from subdued to vigorous calling, judged subjectively. A subdued calling song may be quieter than the protest song, registering about 108 dB SPL, but a vigorously calling male may register 115 dB SPL or more. These values do not represent momentary peaks of sound intensity: males of *C. australasiae* are capable of maintaining their loud song for many minutes on end.

Role of the tympana

The possibility that the tympana might contribute to the radiation of these intense sounds was investigated with a series of experimental tests involving the protest songs. An initial test was to dust parts of the insect's body with lycopodium powder, following the technique of Nocke (1971), and then elicit protest song. When powder was placed on a tympanum, it was seen to be vigorously agitated during bursts of protest song. The vibration of the tympanum was sufficiently vigorous to throw the powder clear during the course of several seconds of song. The folded membranes were also seen to vibrate during protest song when dusted with powder; this was true whether the membranes were relaxed (folded) or stretched. When powder was placed on a tymbal, it was all thrown clear immediately the tymbal was activated in protest song. By contrast, powder placed on other parts of the abdomen remained at rest. Nor were there any signs of vibration on any parts of the head or thorax. The same results were obtained in both species. These results suggest that the three membranous openings to the air sac, the tymbals, folded membranes and tympana, all vibrate during sound production but that other parts of the abdominal wall are unmoved.

Table 4. Relative sound output at different body positions (shown in Fig. 3), measured with a probe microphone in three specimens of *Macrotristria angularis*

Position	Specimen 1	Specimen 2	Specimen 3
A	-15	-18	-17
B	-13	-16	-14
C	-11	-14	-12
D	-13	-17	-16
E	-13	-17	-15
F	-7	-9	-9
G	-11	-12	-13
H	-9	-11	-12
I	-4	-6	-5
J	0	0	0
K	-8	-10	-10
L	-11	-16	-14

Values are dB relative to the loudest position (=0 dB).

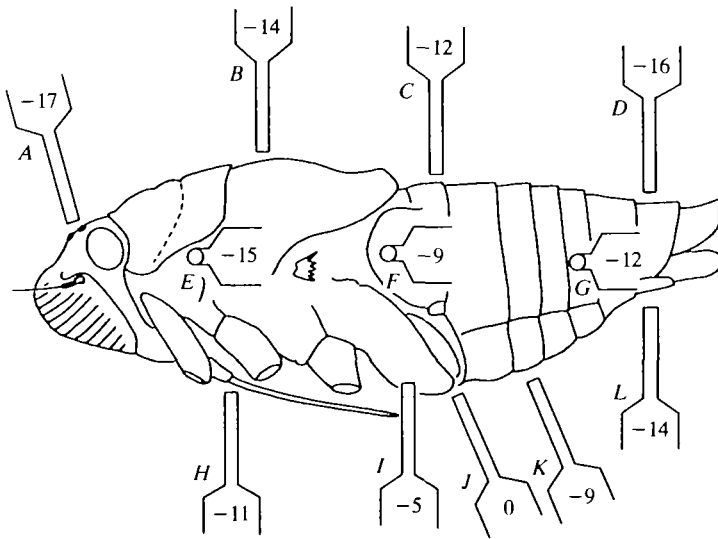


Fig. 3. Sound output from different parts of the body in males of *Macrotristria angularis*, measured with a probe microphone. Mean values for each position are shown within a symbol indicating the placement of the probe microphone. The means are derived from the values given in Table 4 and are expressed in decibels relative to the loudest position. Each position is identified in Table 4 by the letter shown in this figure.

A second test was to measure the sound pressure level at different parts of the body surface with a probe microphone during protest song. The results obtained with three males of *M. angularis* are listed individually in Table 4 and are shown as mean values in Fig. 3. It can be seen that the three specimens gave very consistent

results and that the highest sound output was always found at the gap between an operculum and a tympanum (position *J*). The actual values obtained at this position were over 130 dB SPL, which is consistent with the values obtained at 20 cm. The next highest value was obtained close to the outer surface of an operculum, which is to be expected when the highest value occurs at the opercular gap. The third highest was found close to the outer surface of the tymbal cover (position *F*). The gap between the tymbal and its cover is so small in *M. angularis* that the probe microphone could not be fitted into it. Readings made as close as possible to this gap were 3 or 4 dB greater than on the outer surface of the tymbal cover but never as high as the reading from the opercular gap. The values obtained over the rest of the abdomen were lower and the lowest values of all were obtained from the anterior and posterior extremities of the insect.

It would appear from these readings with the probe microphone that the greater part of the sound output is being radiated from the tympana, and possibly the folded membranes, and is emerging through the gap between the opercula and the tympana. It also seems that a lesser sound output is being radiated from the tymbals, but that the rest of the body surface does not make any significant contribution to radiating the sound.

A third test involved experimentally manipulating the size of the gap between the opercula and the tympana during protest song, while measuring the sound pressure level of the song at 20 cm. If a major part of the insect's sound is emerging through this gap, then there should be a significant difference in the sound pressure level of the song when this gap is held open compared to when it is held closed. Here, a closed gap means that the opercula were touching the cuticular rim of the tympana, and an open gap means that a space of about 5 mm between opercula and tympanal rim was obtained by raising the abdomen. Among five individuals of *M. angularis* tested, the mean value with the opercular gap open was 110.7 dB SPL (+s.d.=1.7; -s.d.=2.2) and with the gap closed it was 99.6 dB SPL (+s.d.=2.1; -s.d.=2.7), giving a mean difference of 11.1 dB. This shows that opening or closing the opercular gap does make a significant difference to the level of sound output.

However, opening or closing the opercular gap does not make a significant difference to the frequency of sound produced. In the above five individuals, the peak frequency of the song fell only a little (100–200 Hz) or not at all when the opercular gap was changed from open to closed (Fig. 4). The large difference in sound level between the main peak and the second harmonic also remained virtually unchanged. Thus, closing the opercular gap makes little difference to the frequency content of the song, even though it significantly reduces its volume.

As a fourth test, the effect of ablating the tympana was examined while measuring the sound pressure level at 20 cm. Removing the tympana necessarily meant removing the air-sac membrane that is so tightly apposed to the back of the tympana. Whether the tympana were merely punctured or were completely cut out, the ablation made no measurable difference to the sound level of the protest song in either *M. angularis* or *C. australasiae*. This indicates that the tympanum

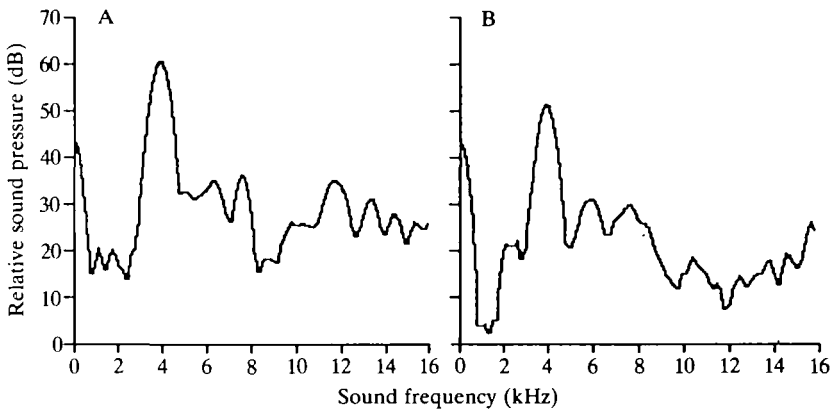


Fig. 4. Log power spectra of the protest song in *Macrotristria angularis*. (A) An individual with the gap between opercula and tympana held open. (B) The same individual with the gap held closed.

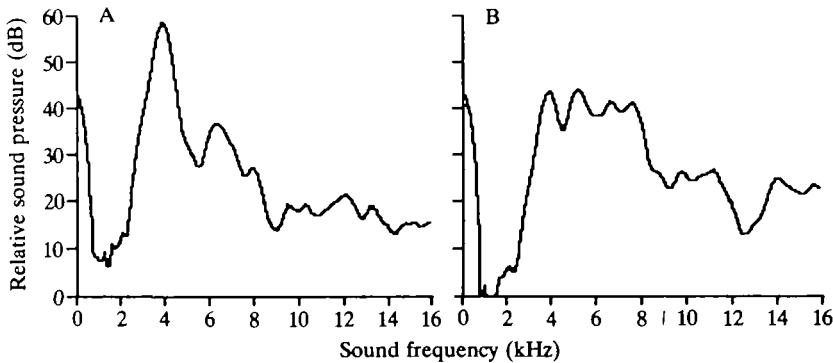


Fig. 5. Log power spectra of the protest song in *Macrotristria angularis*. (A) Protest song of an intact individual. (B) The same individual following ablation of the abdomen posterior to the second abdominal segment.

itself is not acting as a radiating surface, but rather points to the vibrating plug of air in the opening to the air sac as being important.

The role of the air sac was tested by ablating the abdomen, with a cut made as close as possible to the border of the second abdominal segment, in an insect that was otherwise intact. This operation leaves the tymbals, folded membranes and tympana intact but removes the posterior half of the air sac (see Fig. 1). In nine individuals of *M. angularis* tested, the mean level of the protest song at 20 cm was 110.25 dB SPL (+s.d.=2.42; -s.d.=3.36) in the intact insects, and after ablation of the abdomen it was 101.7 dB SPL (+s.d.=2.38; -s.d.=3.27). This is a mean difference of 8.6 dB, which shows that removing much of the air sac produces a significant drop in the level of sound output. In addition, this ablation greatly alters the frequency content of the sound produced (Fig. 5). Although the

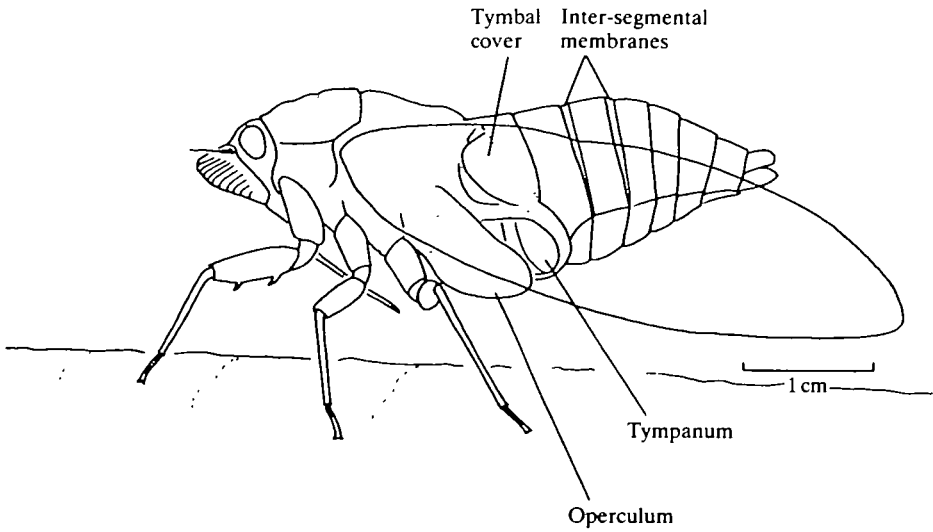


Fig. 6. The singing posture adopted by males of *Cyclochila australasiae* when producing their calling song. This drawing is based on a number of colour transparencies taken in the field. For clarity of illustration, the wings are represented by the outline of the forewing only. The resting position of the abdomen can be seen in Figs 1 and 3.

characteristic peak near 4 kHz is still present, several other frequencies now make an as great or greater contribution to the sound spectrum, including the second harmonic near 8 kHz. Hence the air sac seems to be of critical importance not only in generating the full volume of the song but also in determining its frequency content.

Singing behaviour

It proved possible to examine closely the singing posture adopted by males of *C. australasiae* because they often produce their calling song relatively low down in trees and tall shrubs. As it begins to sing, a calling male adopts a distinctive posture, which becomes more marked as the song becomes more vigorous (Fig. 6). First, the insect stands erect so that no part of the body touches the substratum except for the tarsi of its legs. At the same time, the wings, which meet over the insect's back when at rest, are partly spread laterally, creating a gap between them in the mid-line. Second, the abdomen is raised and protrudes through this gap between the wings. This has the effect of opening up a large gap between the opercula and the tympana. Third, the abdomen is extended longitudinally. In an insect that is singing vigorously, the middle portion of the abdomen is stretched so much that the intersegmental membranes are clearly visible. Whenever calling is interrupted for more than a few seconds, the abdomen is shortened and lowered, the wings close over the back and the insect subsides into a resting position. The same distinctive elements of the singing posture could

be seen in males of *M. angularis*, although it was not possible to observe them as closely.

This distinctive posture is not seen during the protest song. The gap between the opercula and the tympana is opened to a very variable extent by raising of the abdomen, but the abdomen is not usually extended. Apart from this, the movements seen during the protest song are those of a captive insect endeavouring to escape.

Discussion

The combination of evidence presented here consistently supports the conclusion that sound is radiated through the tympana, and possibly the folded membranes, in male cicadas. Indeed, the readings with the probe microphone suggest that the majority of sound is emerging through the gap between the opercula and the tympana. The fact that closing this gap results in a significant drop in sound volume also points in this direction. The dusting with lycopodium powder provides a simple demonstration (Nocke, 1971) that the tympana and the folded membranes do vibrate during sound production, in addition to the tymbals, and that other parts of the abdominal wall do not vibrate. At least three previous reports have noted that the tympana vibrate during sound production (Carlet, 1877; Lucas, 1887; Weber *et al.* 1987) but only the last of these recognises this as evidence for their role in sound radiation.

The much greater size of the tympana in male cicadas is also consistent with this conclusion. From the point of view of sound reception, there is no obvious reason why the male tympana should be larger than those of the female. Certainly, no such difference between the sexes is found in other acoustically active insects. The greater size of the male tympana appears to be usual among cicadas and is not confined to the two species considered here (Vogel, 1923; Myers, 1929; Weber *et al.* 1987). The bladder cicada *Cystosoma saundersii* is an exception since the tympana of the male and female are similar in size in this species (Table 2; Young and Hill, 1977). However, in the bladder cicada, the whole abdominal wall appears to radiate sound (Fletcher and Hill, 1978; Mac Nally and Young, 1981) and there is no reason for the male tympana to play a special role as sound radiators. Hence, this result is consistent with the idea that enlargement of the male tympana is connected with their role in sound radiation.

The singing posture adopted by the males of *C. australasiae* and *M. angularis* also makes sense if the tympana play a major role in radiating sound during the calling song. Raising the abdomen, and hence opening a wide gap between the opercula and the tympana, should contribute significantly to the efficient radiation of sound. The habit of standing erect and spreading the wings may be interpreted as measures that prevent the damping of sound that would occur if the abdomen were in contact with other objects during sound production. The function of extending the abdomen is less clear but it is reasonable to suppose that it contributes to fine tuning of the resonant air sac. Once again, comparison with the

bladder cicada, *Cystosoma saundersii*, is instructive. Males of this species stand erect and spread their wings when calling; they also extend the abdomen noticeably at the onset of singing but they do not raise the abdomen (Simmons and Young, 1978; see also cover photograph, *J. exp. Biol.*, vol. 144). Clearly, raising the abdomen is unnecessary if the tympana play no special role in radiating sound.

Thus, the circumstantial evidence from anatomy and behaviour fits well with the more direct experimental evidence to support the conclusion that the majority of sound is radiated through the tympana in typical cicadas. Given the fact that the tympana open directly into the abdominal air sac, it is hard to see how they could avoid making some contribution to sound radiation. But at first sight, it is surprising to find that ablating the tympana makes no difference to the intensity of sound emitted during protest song. This shows that the tympana do not contribute any gain to the process of sound production but are passively driven by the resonant vibrations of air in the air sac. This result is not really surprising when the extreme thinness of the tympana is taken into account; such delicate membranes must effectively be acoustically transparent in the face of the powerful vibrations within the air sac. Hence, sound radiation is really being effected by the vibrating plug of air in the tympanal opening.

A possible way of modelling this system is in terms of a Helmholtz resonator. Such resonators are influenced by two factors: the volume of the cavity and the volume (area/length) of the neck, whether real or notional, at the opening to the outside. Using these two terms, a first approximation to the resonant frequency (f) is given by the equation:

$$f = \frac{c}{2\pi} \sqrt{\frac{A/l}{V}}$$

where c is the velocity of sound, A is the cross-sectional area of the neck, l is the length of the neck and V is the volume of the cavity (Fender, 1957). In the case of the male cicada, the tympana may be taken to represent the neck and the air sac is obviously the cavity, which is excited by the buckling of the tymbals. Values for the equation may be obtained from Table 1 and Fig. 1 for *C. australasiae*. Treating the air sac as an ellipsoid 2 cm long, 1.2 cm high and 1.5 cm wide gives a cavity volume, V , of $1.88 \times 10^{-6} \text{ m}^3$. The area, A , of both tympana is $85 \times 10^{-6} \text{ m}^2$ and the neck length, l , is about $5 \times 10^{-3} \text{ m}$. The velocity of sound is 340 m s^{-1} . These values give a resonant frequency, f , of 5.1 kHz, which agrees well enough with the observed calling-song frequency of 4.3 kHz in this species. This agreement suggests that the cicada system may be acting as a Helmholtz resonator, with the tympanal opening corresponding to the neck of the resonator.

One obvious question is how damage to the auditory organ is prevented when the tympanum is subjected to such intense sounds from the resonant air sac. This problem was not investigated here, but a possible answer was suggested by Pringle (1954), who described the detensor tympani muscle. He stated that this muscle creases the tympanum before singing commences and so protects the tympanum,

and by inference the auditory organ, from damage. The detensor tympani muscle is certainly present in *C. australasiae* (Young, 1975) and also in *M. angularis*, but it is difficult to see that it has any effect on the strong rim that supports the tympanum. Sometimes the tympanum appears to have a crease running across it during sound production and at other times no such effect is apparent. This problem is clearly one that deserves further investigation, especially since the sound pressures to which the auditory system is exposed are so high.

The exceptionally loud songs produced by these two cicada species appear to be the loudest sounds yet recorded for any insect species. Values around 110 dB SPL at 20 cm for the protest songs and as much as 115 dB for calling songs exceed the values published for other insects known to produce very loud sounds. Counter (1977) gives a figure of 110 dB SPL at 10 cm from a singing tettigoniid, *Neoconocephalus robustus*. There is some uncertainty about this figure (Mac Nally and Young, 1981), but if it is correct it would fall to around 104 dB at 20 cm. Similarly, Bennet-Clark (1970) gives a figure of 92 dB SPL at 1 m for the mole cricket *Gryllotalpa vineae*. This would increase at 20 cm to give a figure comparable to that for *N. robustus*. Both *G. vineae* and *N. robustus* are impressive in their sound output but are not quite as loud as *C. australasiae* or *M. angularis*.

One would expect sound output in cicadas to vary with the power source available, that is with the size and strength of the tymbal muscle, which in turn will vary with the overall size of the insect. Sound output will also vary with the efficiency of the sound radiator, and this is critically dependent on the size of the radiator in relation to the wavelength of the sound (Bennet-Clark, 1971; Michelsen and Nocke, 1974). The high output of *C. australasiae* and *M. angularis* is understandable in these terms since they are very large insects with a large radiating surface in the tympana and tymbal combined and they produce sounds of moderate wavelength (4 kHz). Not all species of cicada are as loud as the two reported here, and their lower output is likely to be accounted for by a combination of body size and frequency of sound produced.

For instance, Mac Nally and Young (1981) give a mean value of 90.6 dB SPL for the bladder cicada *Cystosoma saundersii* and 100 dB SPL for the cicada *Psaltoda argentata*. Although *C. saundersii* is comparable in size to the two species studied here, it produces sound of an exceptionally low frequency (about 850 Hz); hence it is likely to be much less efficient at radiating sound. *P. argentata* is similar in appearance to the two species studied here, but it is somewhat smaller and produces a broader range of sound frequencies. Weber *et al.* (1987) give even lower values for the American periodical cicadas: 80–85 dB SPL for *Magicicada cassini* and 70 dB SPL for *M. septendecim*, measured at 2.5 cm from the singing insect. These values would fall to around 65 dB and just over 50 dB, respectively, at 20 cm. These insects are much smaller than the two studied here and have correspondingly smaller tymbal muscles (Young and Josephson, 1983). Although *M. septendecim* is a little larger than *M. cassini*, it produces sound of a much lower frequency (a little over 1 kHz, Young and Josephson, 1983; Weber *et al.* 1987) and this probably accounts for its particularly poor sound output.

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