

## THE TUNED SINGING BURROW OF MOLE CRICKETS

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### SUMMARY

During burrow digging by the mole cricket *Scapteriscus acletus* Rehn and Hubbard, the burrow is enlarged and shaped in a series of digging cycles, each lasting 1–2 min, and song chirps are produced after every cycle. The song becomes up to 18 dB louder and acoustically purer during burrow building. The shape of the song pulse envelope changes so that its average power density becomes greater and its build-up and decay become more gradual.

The forewings show a single resonance of the harp (Cu 1 cell) regions at 2.5–3.0 kHz: the normal song carrier frequency is 2.5–2.7 kHz. Removal of the outer parts of the forewings does not affect the radiated sound power.

The singing burrow has an exponential horn opening at the soil surface and an internal bulb. The calculated cut-off frequency of the horn is 1.34 kHz and that of the first resonance is 2.5–2.7 kHz. The volume of the bulb is close to that required to tune the throat: obliteration of the burrow bulb causes a substantial decrease in the radiated sound pressure levels before singing ceases.

The horn mouth acts as a finite sound source, with large acoustic reactance. The acoustics of the burrow were measured with a small doublet source inserted at the position at which the cricket sings. At this position, the burrow resonates at 2.75–3 kHz, with a quality factor (Q), measured both by the –3 dB bandwidth and by the build-up and decay of tone bursts, of 2.5–2.7. The sound pressure produced by the doublet source is up to 24 dB louder when it is in the burrow than when it is in free air. Further in or out from the insect's singing position, the effective gain of the burrow is reduced and other resonances and anti-resonances are observed. Obliteration of the burrow bulb reduces the effective gain of the burrow by 6–10 dB and the burrow ceases to resonate at 2.75 kHz.

It is proposed that the tuned burrow acts as a resistive load on the vibrating harps, so allowing good coupling between the small wings and the surrounding medium while allowing a pure carrier frequency to be radiated.

### INTRODUCTION

Mole crickets are large burrowing orthopterans. The songs of various species have been described (e.g. Bennet-Clark, 1970; Ulagaraj, 1976). As is typical in the Orthoptera–Ensifera, the song of the male insect is produced by the closure of the

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forewings, causing the plectrum on one wing periodically to catch and trip across the teeth of the file on the other wing, exciting a resonant vibration of the 'harp' (Cu 1) cell of the wings adjacent to the file (see e.g. Bennet-Clark, 1970; Nocke, 1971).

The song of mole crickets is remarkably pure. The carrier frequency does not change much and the level of the higher harmonics is low. This implies that the resonant vibration of the harp is either lightly damped or is sustained by an appropriate driving force. The song is also, in the case of one species, remarkably loud, which implies good coupling to the medium or good acoustic damping. This paradox has been discussed elsewhere (Bennet-Clark, 1970, 1971, 1975). As the effective diameter of the wings of mole crickets is only a small fraction of the sound wavelength, their acoustic radiation resistance can be expected to be less than that of air in the free field (Olson, 1957; Bennet-Clark, 1971), so the acoustic impedance matching should be poor and the song should be neither loud nor produced at as high efficiency as has been suggested (Bennet-Clark, 1970). However, mole crickets sing from specially constructed horn-shaped burrows which open to the surface (Bennet-Clark, 1970; Nickerson, Snyder & Oliver, 1979). These are in the form of a single or divided exponential horn which suggests that the burrow may act as an acoustic transformer that matches the acoustic impedance of the small wings to that of the air in the free field.

This paper addresses three aspects of the acoustics of the song of mole crickets: how the singing burrow is constructed by the insect; whether the burrow acts as an acoustic transformer that maximizes the insect's sound power output; how, if the insect's wings are acoustically well-damped, the carrier frequency is kept so constant.

#### MATERIALS AND METHODS

Singing male *Scapteriscus acletus* (the southern mole cricket) were collected after sunset from fields near the University of Florida, Gainesville. These insects were used for the majority of experiments. Further insects were caught in sound traps (Walker, 1982). Insects were subsequently kept singly in 6-litre buckets of soil (this laboratory procedure was devised by T. J. Walker). This sandy local soil was kept nearly saturated with water (see Results for the reason) throughout the period of observation and experimentation.

Insects in their numbered buckets were placed in a sound-proofed room kept at 27°–28°C. The lighting in the room was arranged to go off at 09.00 h and to come on at 19.00 h. Insects were thus induced to sing for up to 1 h daily after 09.00 h.

The normal calling song of this species has a carrier frequency of 2.5–2.7 kHz and a pulse repetition rate of 55 s<sup>-1</sup> (Ulgaraj & Walker, 1973; Ulgaraj, 1976).

Periodically, insects were fed with powdered dog biscuit and with fresh vegetables. No insect died during the 4-week period of observation and experimentation.

#### *Observations and measurements with singing insects*

All visual observations were made using a battery-powered lamp on a head band. The lamp had a red filter and its light did not appear to disturb the insects.

Tape recordings were made on a Nagra IV full-track recorder at  $19\text{ cm s}^{-1}$ . The microphone was either a Bruel & Kjaer type 4117 or an Electro-Voice Model 655C, both of which have an essentially flat frequency response to above 10 kHz, though, since all measurements and analyses are comparative, the overall response of the chain is comparatively unimportant. During a recording, the microphone was placed at a standard distance of either 100 or 150 mm vertically above the mouth of the singing burrow and the gain control of the recorder was set to a standard level so allowing direct comparison between sections of that particular recording.

Tape recordings were analysed using a Unigon Real-Time Spectrum Analyser type 4512 and Scan Converter model SC 1, either using the 10 kHz range, with a resolution of 80 Hz and averaging over eight sweeps of total duration 200 ms, or using the 5 kHz range, with a resolution of 40 Hz, averaging over 16 sweeps of total duration 800 ms. The measurements so obtained give the average relative power, directly in dB, within the sampling period.

Oscillograms were made *via* a Tektronix type 502A oscilloscope and Nihon Kohden moving paper camera type PC2A. Other electrical measurements of microphone outputs were made directly from the screen of a Tektronix type 5030 oscilloscope. Both these methods give the instantaneous amplitude of sound pressure which is proportional to (instantaneous sound power)<sup>0.5</sup>, for which correction has been made in the relevant graphs (e.g. Figs 6, 10, 11).

Sound levels are expressed either as absolute sound pressure levels (absolute SPL), referred to a threshold of  $20\text{ }\mu\text{Pa}$ , measured with a Bruel & Kjaer Sound Level Meter type 2213 on the slow setting, or as relative sound pressure levels (relative SPL) between a series of similar measurements all made with either a Bruel & Kjaer type 4117 or a Tandy stock no. 270-090.

#### *Measurements of the acoustic properties of the burrow*

Simultaneous measurements of the particle velocity and sound pressure in the song were made using a purpose-built two-headed microphone. One head was a Tandy Electret Pressure Microphone stock no. 270-090 and the other, as a particle velocity microphone, was built using the electret transducer from another Tandy 270-090 (Bennet-Clark, 1984a). The two transducers were mounted with the electret membranes co-planar in the face of a head  $21\text{ mm} \times 12\text{ mm}$  with maximum sensitivity to sound sources normal to the plane of the membranes and face of the head. The output of the pressure head was fed to a linear amplifier and that of the particle velocity head to an integrating amplifier (Bennet-Clark, 1984a). The frequency and phase response of the two outputs were within 1 dB and  $10^\circ$  of each other, as measured in anechoic plane wave conditions, from 100 Hz to 4 kHz.

Particle velocity levels are expressed as relative values compared to those expected in plane waves of the same absolute SPL (for the absolute relationship, see Bennet-Clark, 1971, 1984b:  $0\text{ dB} = 48 \times 10^{-9}\text{ m s}^{-1}$ ).

A small electret doublet sound (EDS) source was made using the electret membrane and fixed electrode from a Tandy Electret Microphone (270-090) which were mounted in a 10 mm diameter brass housing brazed to a 200 mm brass strip on

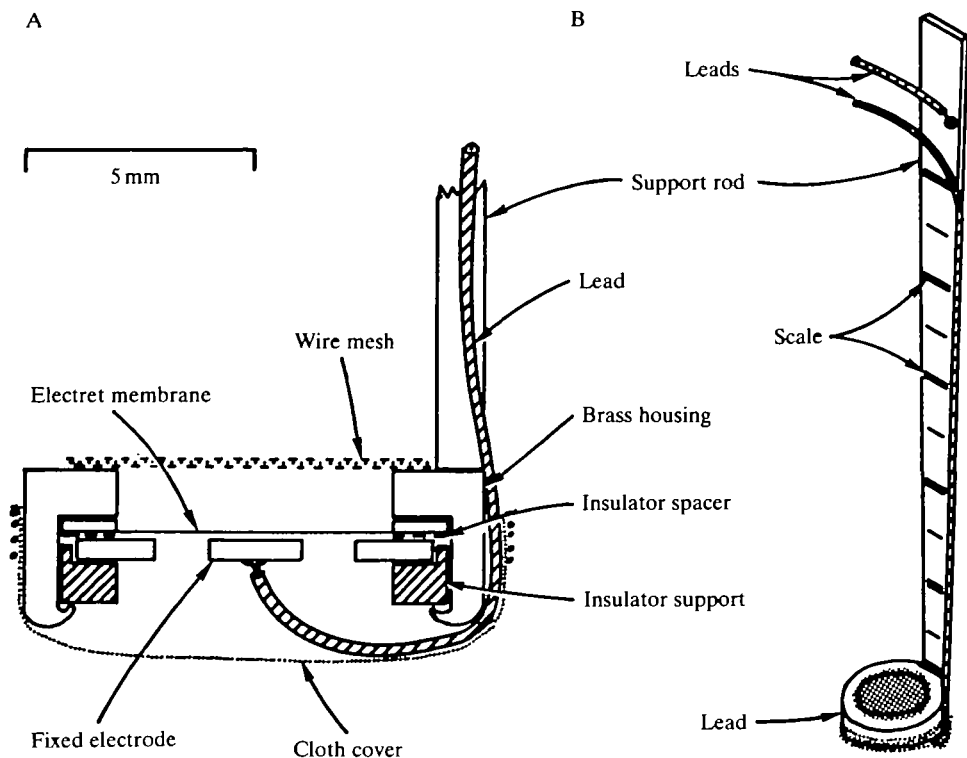


Fig. 1. Diagram of the electret doublet source used to examine the acoustics of the singing burrow. (A) A section of the head to show the electret membrane in its brass housing. (B) An isometric view of the head on its graduated support rod.

which was glued a scale measuring from the plane of the electret membrane (Fig. 1). The size of the source compared with that of the insect's wings is shown in Fig. 7B. This source was driven from a Hewlett Packard oscillator type 200 CD *via* a General Radio Toneburst Generator type 1398A, a high quality audio amplifier and a Tandy 120 V to 6.3 V transformer stock no. 273-050. The amplifier was connected to the 6.3 V winding and the electret source to the 120 V winding. The electrical response of this chain was flat within 1 dB from 200 Hz to over 10 kHz.

The EDS was calibrated in the free field using a Tandy 270-090 pressure microphone (the frequency response is effectively flat from 100 Hz to over 10 kHz and the sensitivity is far higher than that of the other microphones that were available) placed 50 mm from the EDS and normal to the plane of its membrane. The source output was measured thus between 2 and 6 kHz, with the EDS driven by 150 V peak to peak.

The EDS was then placed inside the singing burrow and the sound output was again measured with the same Tandy 270-090 microphone but placed at the ground plane in the mouth of the burrow. Two types of measurement were made: (i) using continuous tones at different frequencies and with the source at different distances from the mouth of the burrow; this allowed the sound output of the source to be compared with that when it was operating outside the burrow; (ii) using tone burst

of 2 or 4 cycles of different carrier frequencies, which allowed the build-up and decay time of the sound radiated from the burrow to be measured. Both the EDS source with its associated electronics and the Tandy 270-090 are essentially aperiodic over the frequency range 2–6 kHz.

### *Burrows and casts*

Burrows for experiments were obtained by chasing the singing insects from fully formed burrows. Burrows were made in compacted moist soil, so they were mechanically stable enough for the bucket to be moved about and they did not collapse when the EDS, which was smaller in diameter than the narrowest part of the burrow, was inserted.

Permanent casts of burrows were made by pouring in about 250 ml of a plaster of Paris/water mixture made fluid enough to pour easily. The casts were dug out the same evening and measured with Vernier callipers.

### *Resonances of the wing*

These were observed by holding the newly detached wing at the mouth of a Tandy 40-1381 piezoelectric horn-loaded loudspeaker driven to produce a sound pressure level at the position of the wing of 120–125 dB over the range from 2 to 10 kHz. The position of vibration antinodes was observed by sprinkling cork powder onto the wing: such light powders tend to aggregate as vibrating heaps at areas of maximum air movement (Savart, 1827; Faraday, 1831; Nocke, 1971). As there was no readily available way of measuring the amplitude of vibration, these measurements were subjective and qualitative.

### *Wing operations and measurements*

Insects were dug out of their buckets and anaesthetized lightly with ether. Parts of one or both wings were removed by cutting with scissors (see Fig. 7C for an example). The vibration of regions of the wings was modified by painting with a layer of cellulose nail varnish. The insect was allowed to recover and then replaced in the bucket. In practice, recovery was so quick that the song of the operated insect could be recorded the next day, allowing direct comparison with the song that was produced immediately before the operation.

The height and distance separating teeth on the file were measured by examining the file in profile using a Malies Curtain Measuring Eyepiece and a Leitz L 20/0.32 objective. The repeatability of measurements was within  $\pm 1$  eyepiece division or  $\pm 0.5 \mu\text{m}$  and the accuracy of readings, measured with a graticule slide, was also within  $\pm 1$  eyepiece division or  $\pm 0.5 \mu\text{m}$ .

## RESULTS

### *The normal pattern of burrow building*

In *Scapteriscus acletus* the singing burrow is opened to the surface as a 15 mm diameter hole a few minutes after lights-out (equivalent to sunset). Thereafter, the

insect goes through a stereotyped burrow-building behaviour which shows the following stages: (i) the insect faces the outside and shapes the mouth of the burrow by pushing soil away with a spreading movement of the forelegs (this stage lasts about 0.5 min); (ii) the insect retreats backwards into its burrow, turns so that its posterior end is outwards, walks backwards so that its posterior end is about 30 mm from the mouth of the burrow and then makes a short chirp of song lasting upwards of 0.5 s; (iii) the insect moves deeper into the burrow and makes a series of scooping and pushing movements to the soil, again with the forelegs. The insect may dig downwards or turn onto its back or one side so as to manipulate the top or sides of the burrow, in this stage adjusting the shape and volume of the bulb (see Fig. 8; this stage lasts about 0.5 min); (iv) the insect repeats stage i, gradually increasing the diameter of the mouth of the burrow and making it flare by making wider spreading movements of the forelegs as it nears the soil surface. At this stage, the insect turns so that the whole of the circumference of the horn (Fig. 8), is shaped. If, at this stage, any soil falls into the burrow, it is either compacted into the walls or lifted to the outside and pushed away. This stage also lasts about 0.5 min. Stages ii, iii and iv then continue in sequence for several cycles, totalling 20–50 min, with the song chirps becoming longer and louder and sometimes being repeated several times during stage iii with the insect moving inwards or outwards along the throat of the horn (see below) between or during the chirps.

Finally, the insect starts to sing steadily and may then sing the calling song continuously (see Materials and Methods) with changes in absolute SPL of not more than 1 dB over a 30- to 60-min period. After abruptly stopping singing, the insect once more turns to face outwards and seals the burrow opening by pushing up soil from the inside. Burrows on later days are made close to the site of earlier burrows.

#### *Sound production during burrow building*

The chirps produced during burrow building change considerably during the succession of building cycles that precede continuous singing. This is shown particularly clearly in analyses of sound production during a burrow-building sequence recorded over a 50-min period. At the start, a single chirp which lasted about 0.5 s was produced in each cycle of burrow building but, after 10–20 min, more than one chirp was often produced, at 1- to 4-s intervals, and each lengthened to about 1.5 s. Later, singing extended to several 2-s or longer chirps as burrow building was completed. The relative SPL produced during the chirps increased over the 50 min by 18 dB (a 60-fold power increase) (Fig. 2). At the same time the relative intensity of the second harmonic (at about 5.6 kHz) to that of the carrier became less, changing from –18 dB at the start of burrow building to –23 dB after the song became continuous (Fig. 2). The third harmonic, at about 8 kHz, shows a different pattern. Initially, the level was some 28 dB below that of the carrier and decreased slightly during burrow building but it then increased suddenly to –25 dB after the song became continuous (Fig. 2). Other recordings of burrow building

showed a similar trend of e.g. a 12-dB increase in relative SPL during an 18-min period of burrow building, and a 6-dB decrease in the level of the second harmonic.

The frequency at which peak intensity of the carrier occurred was also examined. Though this remained fairly constant at 2.64–2.72 kHz in most of the chirps, the second (6 min) and fifth (12 min) chirps, which were 4 and 6 dB, respectively, below the adjacent chirps, also had different peak frequencies of 2.80 and 2.84 kHz, respectively (Fig. 3). The sharpness of the frequency: intensity curves also changed

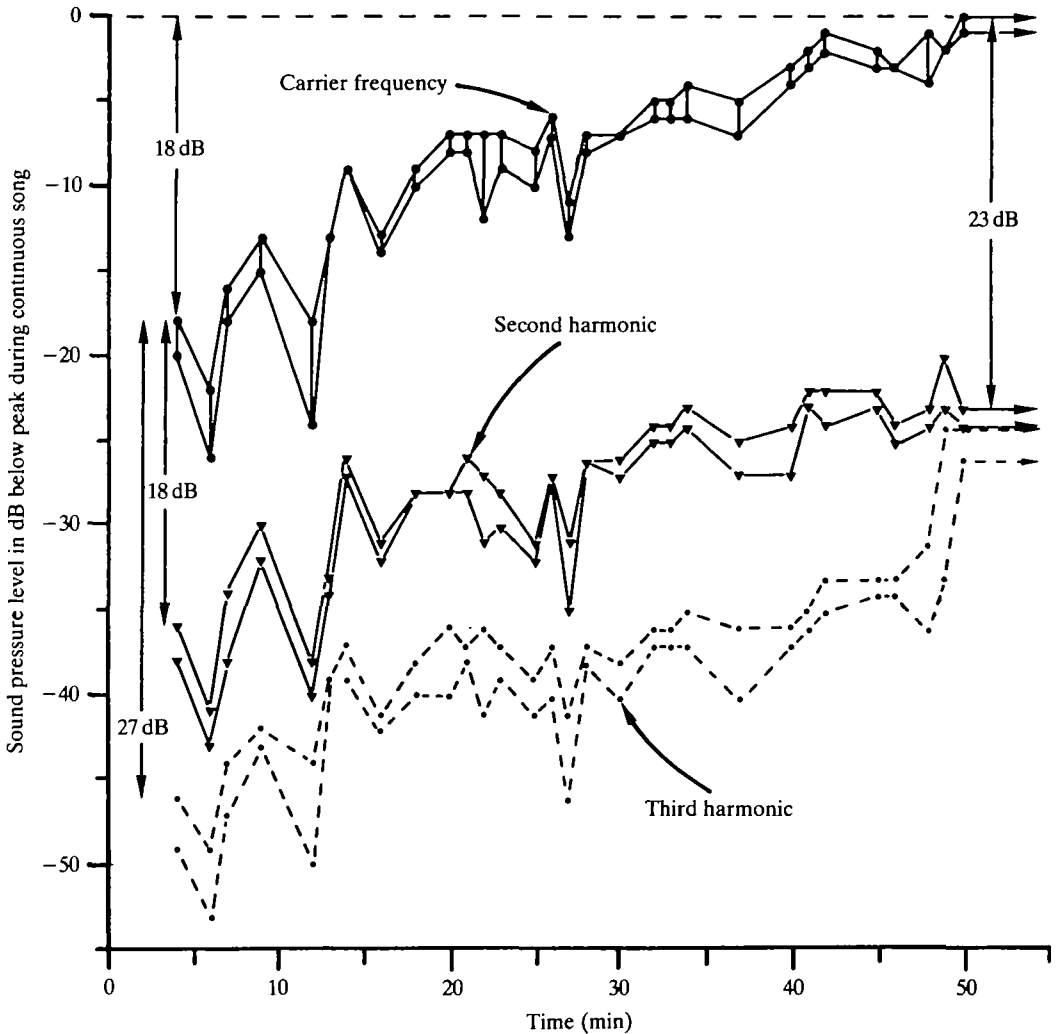


Fig. 2. Relative sound pressure in the successive chirps produced by a *Scapteriscus acletus* male during building of the singing burrow. The sound pressures are expressed in decibels (dB) relative to the peak level produced during continuous singing (which started after 50 min). The three plots show the average sound pressure levels (SPL) of the carrier frequency (2.64–2.84 kHz) and its second and third harmonics, with the range shown by three separate samples during each chirp. The average relative SPL of the carrier increases by 18 dB during burrow building.

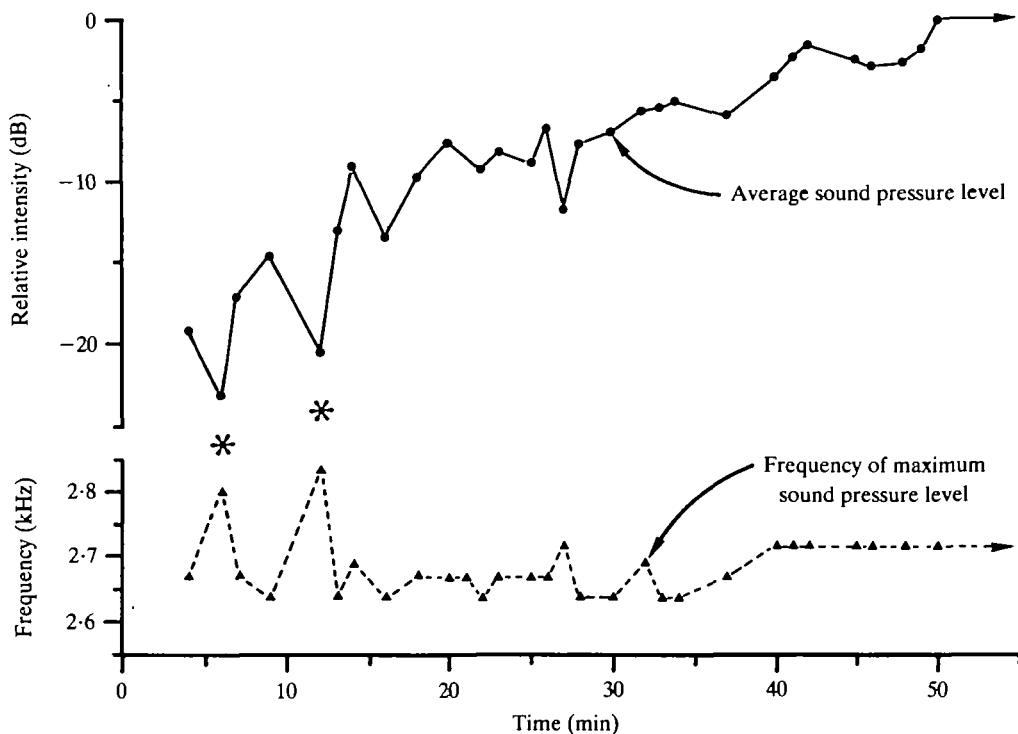


Fig. 3. Average sound pressure level (SPL) at the carrier frequency (●—●) and the frequency for maximum SPL (the carrier frequency) (▲—▲) for successive chirps made during burrow building. Note particularly that the second and fifth chirps (\*) are quieter and have higher carrier frequencies.

somewhat from chirp to chirp during burrow building (Fig. 4). This can be expressed in terms of the  $Q$ , or quality factor, of the curve given by:

$$Q = \frac{\text{carrier or peak-intensity frequency}}{\text{bandwidth at } -3 \text{ dB}} \quad (1)$$

Fig. 4 shows that the  $Q$  of the song increases slightly from  $Q = 21$  in the first chirp (4 min) to  $Q = 25$  during continuous song (50 min) at the end of burrow building. The second (6 min) and fifth (12 min) chirps, in which the sound level decreased, also show far lower  $Q$  values, 16 and 14, respectively.

The form of the song pulses in the chirps changes during burrow building. The amplitude of successive cycles in each pulse has been compared with the dimensions of the file teeth. In the insect that produced the burrow-building chirps described above and which sang with the left file over the right plectrum, the left file bore 58 teeth. The height of the teeth is more constant than the horizontal distance between teeth: these parameters are plotted in Fig. 5A against the amplitude of successive cycles of a typical pulse of the first (4 min) and second (6 min) chirps and of the continuous (50 min) song. Oscillograms of pulses are shown in Fig. 5B and other oscillograms are analysed in Fig. 6, where the natural logarithm of the amplitude is



plotted for every cycle of a series of song pulses produced throughout the burrow-building process. The  $Q$  value for a vibration that shows an exponential build-up or decay can be calculated from:

$$Q = \frac{\pi}{\ln \text{ decrement}} = \frac{\pi}{\ln \text{ increment}}, \quad (2)$$

where  $\ln$  decrement (or increment) is the natural logarithm of the amplitude ratio of successive cycles in the decay or build-up of the response.

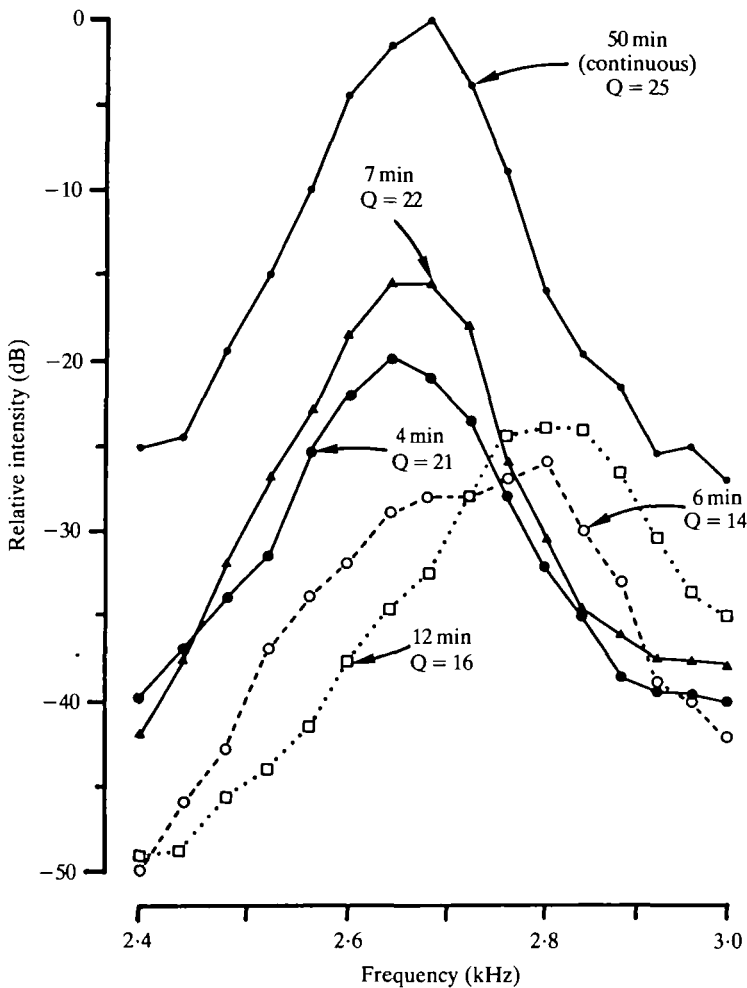


Fig. 4. Frequency *vs* intensity spectra for successive chirps from the burrow-building recording used for Figs 2 and 3. The sound pressure is referred to the average relative sound pressure level (SPL) in the continuously produced song at the end of burrow building. The relative SPL increases from the first to third and from the third chirp to continuous singing (solid lines and solid symbols) but decreases from that in the preceding chirp in the second and fifth chirps (broken lines and open symbols). See also Fig. 3.

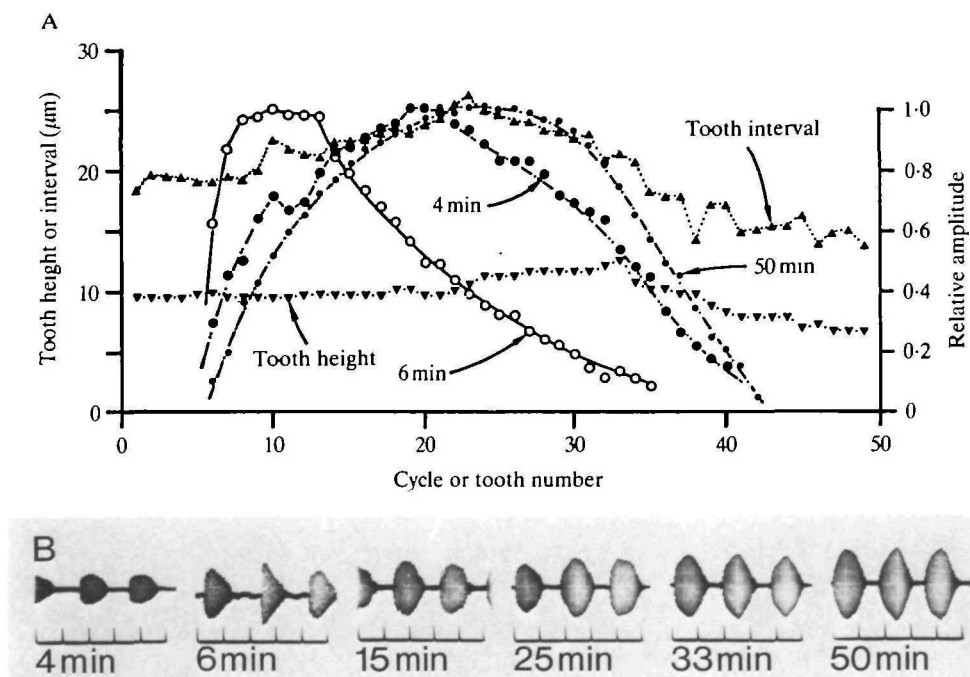


Fig. 5. (A) Plots of the tooth interval (▲···▲) and tooth height (▼··▼) along the length of the file *vs* tooth number, counting in the direction in which the file is struck during singing, and of the relative amplitude of successive cycles of representative pulses produced in chirps during burrow building and in continuous song *vs* the cycle number in the pulse. The data were all obtained from the same insect. The first three and last five small irregular teeth of the file have been ignored. The song pulses are drawn as if they started at the fifth measured tooth of the file and amplitude is referred to the peak amplitude (=1.0) measured in each pulse. The symbols used for the pulses are the same as those used in Fig. 6. (B) Oscillograms of 50 ms sections of the chirps produced during burrow building. The oscilloscope gain control was adjusted so that the peak amplitude for all pulses was similar. Time marker: vertical bars every 10 ms.

The normal pattern, during continuous song, is that the amplitude of the pulse builds up relatively rapidly, with a  $Q$  of 10 or less (Fig. 6). In the middle third of the pulse, the amplitude changes more slowly over a broad peak, in which the power is close to maximum (Fig. 6) and the amplitude of successive cycles in the pulse follows the spacing of the file teeth (curve for 50-min pulse in Fig. 5A) then the amplitude decays. The final decay, over the last few cycles, is rapid, again with a low value of  $Q$ . The pulse in the earlier chirps tends to build up to peak amplitude more abruptly than those produced during continuous song (Figs 5A,B, 6): this is seen clearly in pulses of the chirp produced at 4 min and, more clearly, in that produced at 6 min (Fig. 5) in which the relative SPL was about 4 dB less than with the preceding and succeeding chirps (Figs 2, 3). The form of the pulse envelope also tends to change more from pulse to pulse during these earlier chirps than when the insect is singing continuously (Fig. 5B).

When the insect is singing continuously, the pulse duration tends to be about 3 cycles longer than during the earlier chirps, but the pulse period is reduced from between 19 and 20 ms ( $50\text{--}53\text{ pulses s}^{-1}$ ) in the first chirps to between 16 and 18 ms ( $56\text{--}62\text{ pulses s}^{-1}$ ) in continuous song (Fig. 5B), so the effective sound:silence ratio of the song increases during burrow building. There appear to be additional gains: that a larger proportion, over half the duration, of the pulse has an instantaneous sound power that is within 3 dB of the peak power, or above half the peak

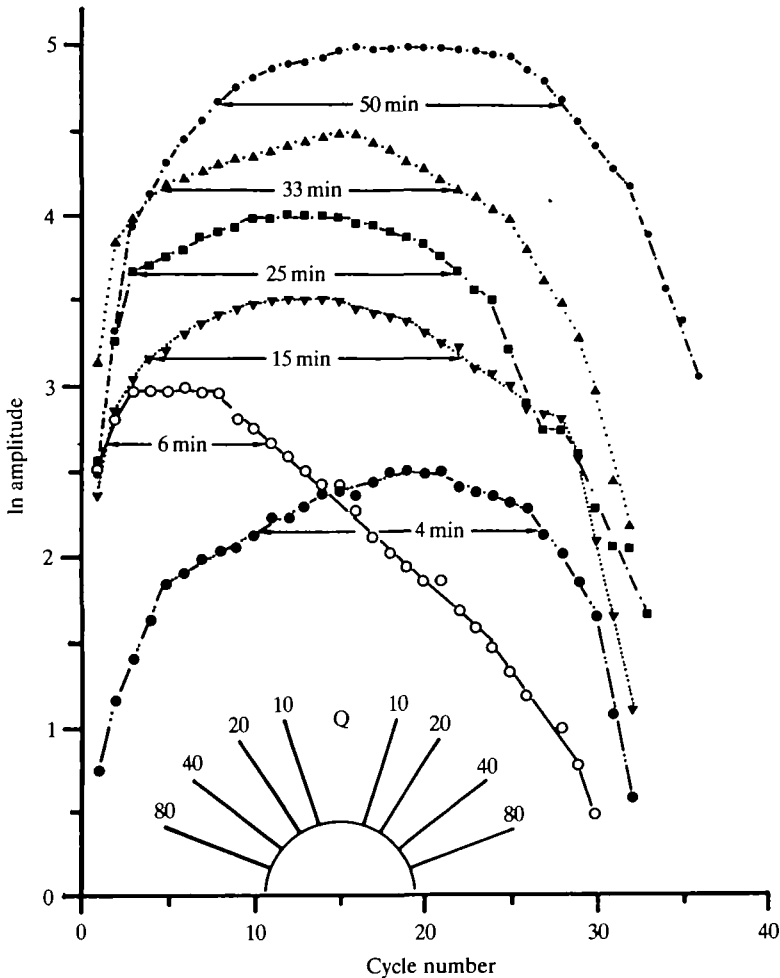


Fig. 6. The natural logarithm of the amplitude *vs* cycle number within pulses for representative pulses produced as burrow building progresses. For clarity, successive plots are referred to peak levels that differ by 0.5 ln units from those of their neighbours. For each plot, horizontal arrows ( $\leftarrow \rightarrow$ ) are drawn 0.35 ln units below the peak level, or 3 dB below the peak instantaneous power. The radiating plot centred on cycle 15 of the x-axis shows the slope of the ln decrement (left side) and ln increment (right side) associated with the Q values indicated (equation 2). The relative SPL increases between the 4-min chirp and continuous singing (solid symbols) but decreases between the 4-min and 6-min chirps (symbol  $\text{---}\bigcirc\text{---}$ ). See also Figs 3 and 4.

instantaneous power; and that the central part of the pulse has a plateau over which the instantaneous power is close to the peak power (Fig. 6). By contrast, during the chirp produced at 6 min, only about one-quarter of the pulse duration is within 3 dB of the peak instantaneous power. During continuous song, the insect appears to be able to produce a higher power density through the pulse and, from the reasonably close correspondence between the shape of the pulse envelope and that of the file teeth (Fig. 5A), appears to be able to drive the wing more effectively than during the earlier chirps, when this correspondence is less good and where the natural logarithm of the rate of change of amplitude tends to be greater and so the  $Q$  of any excited resonance will be lower.

Because the rate of change of amplitude with time is low during most of the duration of the 4-min, 15-min to 33-min and continuous song pulses, these songs have a higher effective  $Q$  than that produced in the 6-min chirp: this is also seen, using a different method of analysis, in Fig. 4.

These observations on the chirps produced during burrow building suggest that they have an important biological function: that the insect uses them in some way to test the progress of burrow building. It should be noted that, between the start and continuous singing, not only does the sound become far louder, as the acoustic loading increases, but it also becomes rather more pure, suggesting that the acoustic transformer produced during burrow building does not merely provide a simple damping load to the wings: this idea is examined below.

#### *Resonances of the wing*

Vibration of the harp region of the wing was observed with five pairs of wings driven with high-intensity sound. With freshly removed wings, maximal amplitude of vibration occurred in the centre of the harp, either side of the distal oblique cross-vein (Fig. 7A), at from 2.5 to 3 kHz with different wings. Only the harp region vibrated significantly in the range 2–10 kHz. With a typical wing, vibrating maximally at 2.7 kHz, the vibration could not be seen below 2.4 or above 3.1 kHz. With wings that had been allowed to dry overnight, the maximal vibration occurred between 4 and 5 kHz.

Vibration of the harp membrane was abolished either by cutting a hole in, or by painting varnish over, the harp area, but the vibration was unchanged when the lateral field or the distal part of the wing was either removed or painted with varnish. When held by the wing base, by the large subcostal, median and radial veins (Fig. 7A), by the plectrum or by the anal node, harp vibration was unaffected but it was much reduced when the wing was held by the Cu 1 (cubital) vein or by the file (Cu 2) vein. It thus appears that the harp is the resonant structure of the wing, as with *Gryllotalpa* (Bennet-Clark, 1970) or *Gryllus* (Nocke, 1971), and that its resonant frequency is consonant with the typical 2.5–2.75 kHz carrier frequency of the insect's song. Both the aggressive and courtship songs in this species have the same carrier frequency (Ulagaraj, 1976) which is to be expected if the harp is the only resonant structure on the wing.

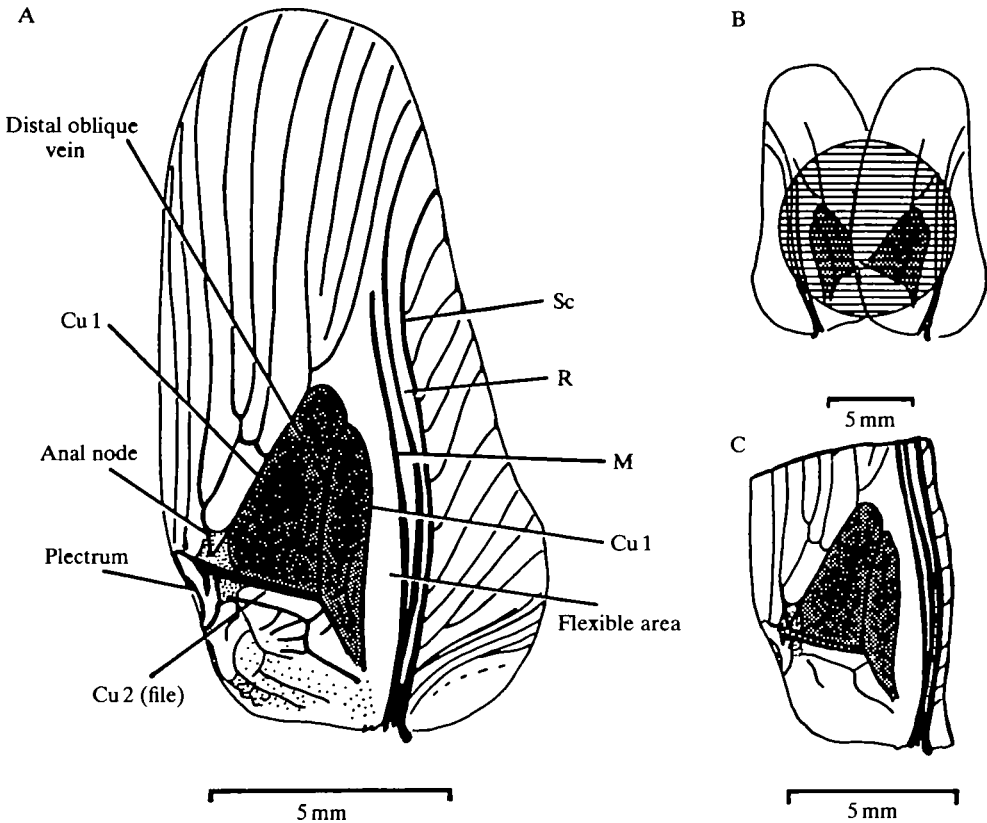


Fig. 7. The forewing of male *Scapteriscus acletus*. (A) View of the underside of the right wing. The harp is shown stippled. The region of maximum amplitude of vibration runs along the distal oblique vein. The harp is separated from the thick subcostal, radial and median veins by a flexible area. (B) The size of both wings when held in the singing position. In practice, the wings are held at  $30^{\circ}$ – $40^{\circ}$  above the abdomen (see Fig. 8) so their aspect area, viewed along the singing burrow, is smaller than the diagram indicates. The harps are shown stippled and the cross-hatched circle shows the relative size of the electret doublet source. (C) The size of one wing of an insect that continued to sing normally after operations to remove most of the anterior and distal parts of both wings. Cu 1, 2, cubital veins.

#### *Effect on sound production of removal of parts of the wing*

The experiments reported in this section were performed with a small number of animals and so are preliminary.

With two animals, the major part of the lateral and distal parts of the wings was removed, leaving only large Sc, M and R veins, their connection with the harp region, the plectrum and anal field intact: in other words, only those parts of each wing involved in sound production were left, an area about 5 mm wide by 7 mm long, compared with the 8 mm by 16 mm of the intact wing (Fig. 7A,C). The absolute SPL produced on the 2 days after the operation was within 1 dB of that produced by the same insect on the 2 days preceding the operation. The insects produced normal burrows after the operation and a gap of about 4 mm could be seen between the wings and the sides and top of the singing burrow (with normal insects the gaps are only 1

or 2 mm). It appears that normal sound production in the singing burrow does not depend, as with conventional horn-loaded loudspeakers, on a close fit between the vibrating structure and the throat of the horn.

With two further insects, one harp area (Fig. 7) was carefully painted with nail varnish over its dorsal surface (the file is on the ventral side of vein Cu 2 which is the proximal margin of the harp). After the operation, the absolute SPL was 2–4 dB quieter than that produced before painting. In a third insect, when the painted left wing was being moved under the file of the right wing, the sound that was produced was too quiet to measure with confidence. It appears that the sound is radiated from both wings and that, if the normal plectrum–file escapement mechanism operates (Bennet-Clark, 1970; Elliott & Koch, 1985), about half the total sound power is produced by each wing.

### *The singing burrow*

This was described by Nickerson *et al.* (1979) but, since there is an arithmetical error in the y axis of their fig. 2 and a misinterpretation of my description of the burrow of *Gryllotalpa vineae* (Bennet-Clark, 1970), a redescription is appropriate here.

The burrow is shown in Fig. 8. The burrow opens to the outside *via* a single horn. The insect sings facing inwards with the tip of its abdomen visible in the mouth of the burrow, its prothorax in the bulb of the burrow and its wings raised in an ovoid bulge at the throat of the horn. An exit tunnel leads from one or other side of the bulb. The bulb is large enough to allow the insect to turn (it is termed the ‘turn-around’ by Nickerson *et al.* 1979). The position in the burrow of the constriction between the ovoid bulge and the bulb is taken as the datum plane for all measurements that follow: it can readily be equated with the constriction that occurs in the burrow of *Gryllotalpa vineae* (Bennet-Clark, 1970, fig. 15).

The rate of flare of one burrow horn is shown in Fig. 9: another four horns that were measured showed similar rates of flare and horn lengths (see below). As with that of *G. vineae*, the horn expands exponentially, but the rate of flare and the cross-sectional area at the mouth are different. The lowest frequency, or cut-off,  $f_c$ , at which a horn acts as an acoustic transformer, at which the throat impedance is zero, depends on the rate of flare and is given by:

$$f_c = \frac{mc}{4\pi}, \quad (3)$$

where  $c$  is the velocity of sound in air and  $m$  is the flaring constant in  $m^{-1}$ , given by:

$$m = \frac{1}{D_0} \ln \left( \frac{S_1}{S_0} \right), \quad (4)$$

where  $D_0$  is the distance along the horn at which the area of cross-section changes from  $S_0$  to  $S_1$ . For the horn of *S. acletus*,  $m$  is  $49.5 m^{-1}$  and so, from equation 3,  $f_c$  is 1.34 kHz. For practical horns, it is usual to arrange that  $f_c$  is about an octave below the lowest frequency to be radiated.

The measured volume of the bulb, between the datum constriction and the opening of the entrance tunnel, is about  $7 \times 10^{-6} \text{ m}^3$ . This may be related to the volume that was calculated by Klipsch (1941) for the volume of the acoustic capacitance required to tune the inertial reactance of the throat impedance of a finite horn. This volume,  $V$ , is given by:

$$V = 2.9AR, \quad (5)$$

where  $A$  is the throat area of cross-section and  $R$  is the distance along the horn at which that area of cross-section doubles. For five horns of *S. acletus*,  $A$  ranged from  $110$  to  $150 \times 10^{-6} \text{ m}^2$  and  $R$  ranged from  $13$  to  $15 \text{ mm}$ , so  $V$  is, from equation 5, between  $4.1$  and  $6.5 \times 10^{-6} \text{ m}^3$ : this compares adequately with the measured volume

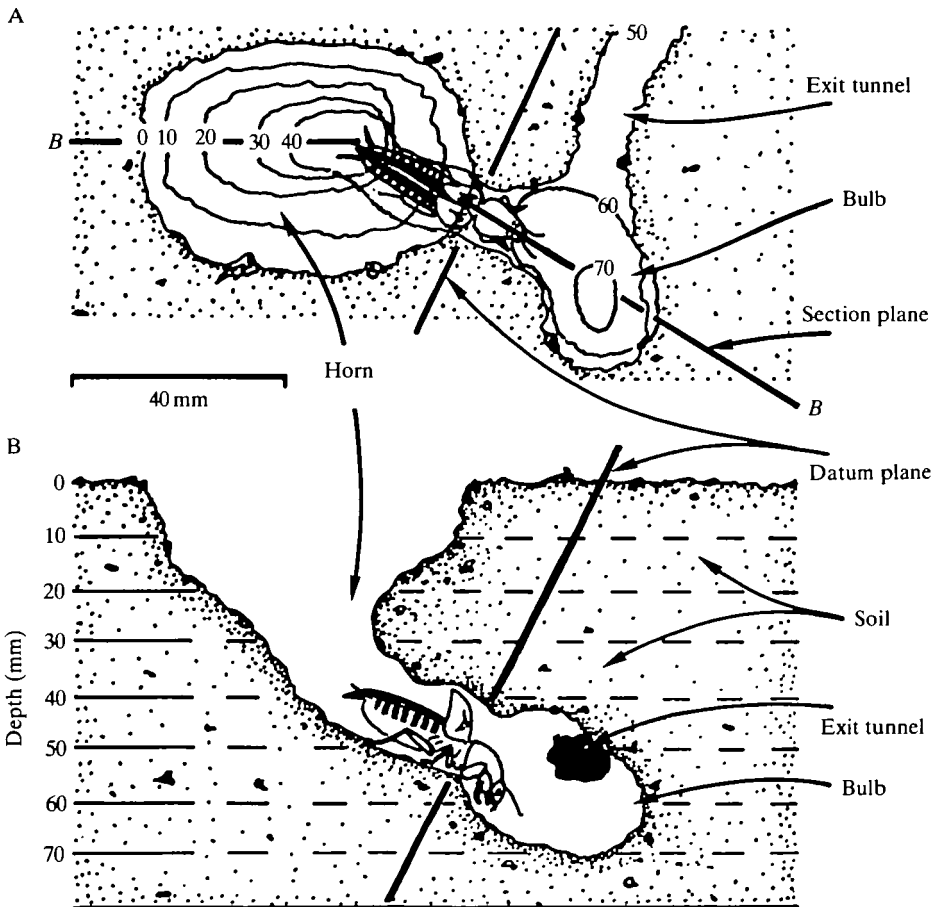


Fig. 8. Diagrams of the singing burrow of *Scapteriscus acletus*. (A) A plan view with contours drawn at 10 mm intervals below the surface plane (labelled 0). (B) A vertical section drawn along the centre line of the burrow (shown by a kinked line B—B in the top diagram). The position of the singing insect in the throat of the horn is shown. The datum line is at the constriction between the horn throat and the bulb. In other burrows, the bulb opened either to the left or to the right of the burrow.

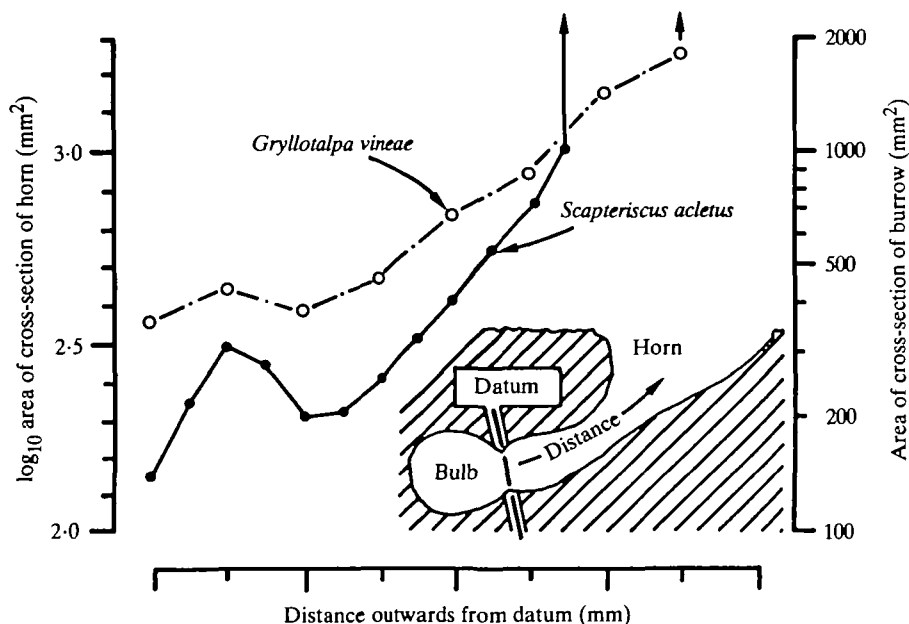


Fig. 9. Plot of the  $\log_{10}$  of the area of cross-section of the horn against distance along the central axis of the horn for the typical burrows of *Scapteriscus acletus* —●— (from present data) and of *Gryllotalpa vineae* -○- (data from Bennet-Clark, 1970). The vertical arrows show the mouth of the horn and ground plane and distance is measured from the constriction between the throat of the horn and the bulb. The inset is a diagrammatic vertical section of a singing burrow to show the position of the datum plane from which measurements were made.

of about  $7 \times 10^{-6} \text{ m}^3$  and may be compared with a similar correspondence described earlier for the horn flare rate and bulb volumes in the singing burrows of two species of *Gryllotalpa* (Bennet-Clark, 1970).

A finite horn will have resonances related to its length. It is difficult to calculate exact values for the frequencies,  $F_n$ , at which resonances will occur but approximate values are given, from Morse (1948), by:

$$F_n \approx \left( \frac{c}{2L} \right) \sqrt{n^2 + \left( \frac{L}{\pi h} \right)^2}, \quad (6)$$

where  $n$  is the order of the resonance, in this case 1 (for the lowest-order resonance),  $c$  is the velocity of sound in air,  $h$  is the distance along the horn over which its diameter increases by  $e$  and  $L$  is the effective length of the horn ( $\approx$  its real length + 0.6 mouth radius). In the present case, values of  $h$  of about 40 mm, burrow lengths of between 65 and 85 mm and mouth radii of 20–25 mm have been measured, so  $F_n$  for the first resonance is 2.6–2.8 kHz.

The calculations based on the dimensions of the horn (equations 3–6) suggest that the design and dimensions of the horn are appropriate for it to act as a tuned acoustic transformer that resonates at the carrier frequency of the insect's song and in which the throat impedance is resistive.



*Effect on sound production of manipulations to the burrow*

When the soil above the bulb is pushed in, the song becomes quieter and broken into an erratic series of trills and, as the bulb is pushed in further, it ceases. In three records of such manipulations, the relative SPL decreased by 6–12 dB before the insects stopped singing but the song carrier frequency and the Q of its intensity–frequency spectra did not change appreciably. After such manipulations, the insect tended to rebuild the burrow, using an abbreviated version of the normal pattern (see above).

Placing one or two 25 mm × 50 mm glass microscope slides to block off the horn mouth at the ground plane caused a dramatic lowering of the relative SPL measured outside the burrow but did not affect singing behaviour. Placing a slide vertically across the burrow about 30 mm inside the mouth, so that the horn was effectively shortened by 30 mm and its opening was shut off, caused the song to become erratic and then cease; but placing a slide vertically along the horn axis so that the effective horn mouth area was halved merely caused about 6 dB decrease in the relative SPL.

The insect is sensitive to certain types of external manipulation of the burrow.

*Acoustics of the singing burrow*

The particle velocity and sound pressure were measured simultaneously in and above the burrow mouths of insects singing normally. From between 50 mm vertically above the burrow and 10 mm below the plane of the mouth, the relative magnitude of the particle velocity to that of the sound pressure changes from +0.5 dB to +2 dB and changes in relative phase from 15° to 50° (Fig. 10). The relative magnitude and phase angle for a source of known effective radius is given by Beranek (1949). Here the effective radius,  $r$ , of the source is about 25 mm (Fig. 8) so that the source size constant,  $k_r$ , can be calculated from:

$$k_r = \frac{2\pi fr}{c} = \frac{2\pi r}{\lambda}, \quad (7)$$

where  $f$  is the frequency (2.75 kHz),  $c$  is the velocity of sound in air (340 m s<sup>-1</sup>) and  $\lambda$  is the sound wavelength. This gives a value of 1.25 for the  $k_r$  of the burrow, for which the calculated relative magnitude of the sound pressure to particle velocity is 0.8 or -1.9 dB and the relative phase angle is 40° (Beranek, 1949), so it appears that radiation at the mouth of the horn is not a simple plane wave but is better modelled as a divergent spherical wave. Similar results were obtained when singing burrows were driven by the EDS.

The effective source position is determined by measuring the rate of attenuation of the sound pressure and the relative phase angle of the particle velocity with distance from the source. Using as a datum the measured value of the sound pressure at a distance of 50 mm above the mouth of the burrow, it can be seen that the inverse square law is followed to about 10 mm above the mouth but that, entering the horn, a different rate of increment occurs. The relative phase angle of the particle velocity is always less than would be expected if the mouth of the burrow acted as a point source (Fig. 10). These two observations are consistent with the view that the mouth of the

horn acts as a radiating surface in the form of a sector of a sphere rather than as a plane or as a point source. This means that the horn, as a source, is finite and its impedance has both resistive and reactive components which, in the present case, are

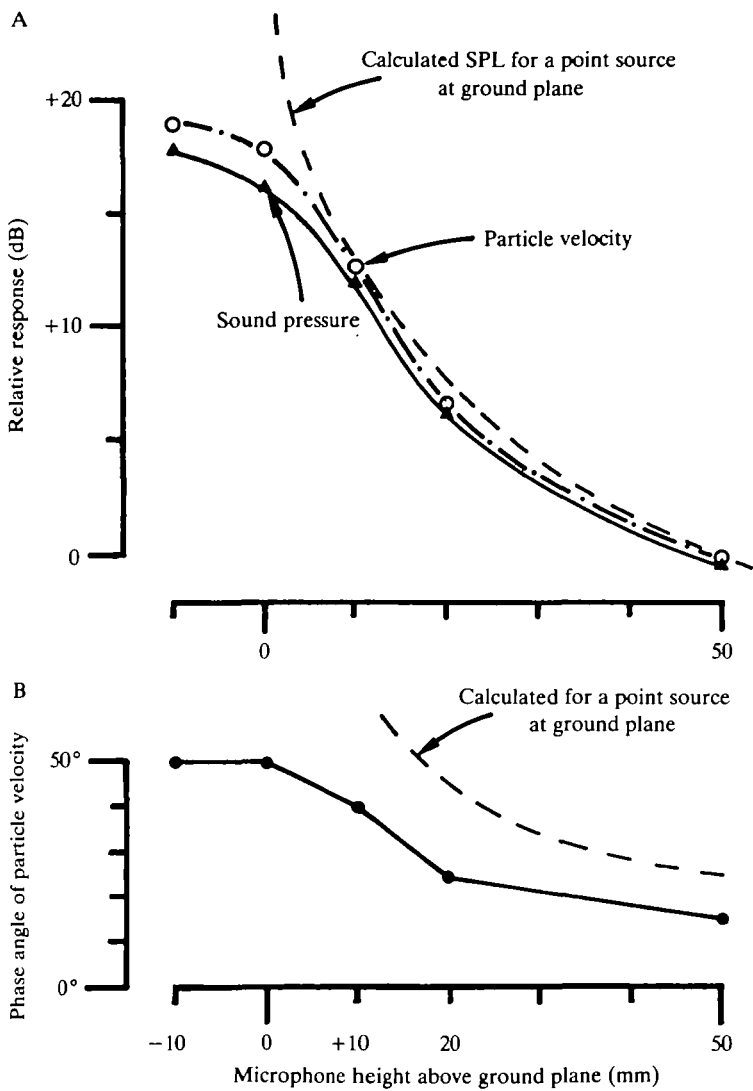


Fig. 10. Plots of the components of the sound produced by a singing *Scapteriscus acletus*. (A) Sound pressure and particle velocity against distance of the microphone above the ground plane vertically above the mouth of the singing burrow. Sound pressure —▲— is plotted relative to that at a height of 50 mm and particle velocity ---○--- is plotted relative to the expected particle velocity (---) in a plane wave. The dashed line shows the expected sound pressure level (SPL) for a point source located at the centre of the burrow mouth. (B) Phase angle of the particle velocity relative to the sound pressure *vs* height of the microphone above the singing burrow. The dashed line shows the calculated phase angle for a point source located at the centre of the mouth of the singing burrow.

approximately equal. If it were a point source, its impedance would be purely reactive and, if it were a large plane source, its impedance would be purely resistive (see e.g. Olson, 1957). The horn described here might be expected to reflect both resistive and reactive components of impedance from its mouth to its throat. A tuning mechanism for the throat of the horn has already been described (see Results and Discussion).

The mouth of the horn measures about  $0.3\lambda$  by  $0.45\lambda$ . Measurements made during singing, at 150 mm from the centre of the mouth over a spherical surface, showed that the absolute SPL decreased by about 2 dB from a maximum of 86 dB vertically above the mouth to 84 dB in a circle  $30^\circ$  above the plane of the soil. This is approximately the response expected for a source of this size (Olson, 1957) but may be contrasted with the disc-shaped radiation pattern produced by the two-mouthed singing burrow of *Gryllotalpa vineae* (Bennet-Clark, 1970).

Using the electret doublet source (EDS) (see Materials and Methods), the acoustic response of the burrow to continuous sine wave input was measured. The results are summarized in Fig. 11, which shows the relative response at the mouth of the burrow compared with that of the source in the free field. Because the source is a small *doublet*, which has a different frequency/sound pressure response to that of a *point* source of the same size (Olson, 1957), the increase in relative SPL that is observed at the mouth of the burrow results partly from the change in configuration of the source when it is placed in the burrow and partly from the gain of the burrow. This is termed the *effective gain* of the burrow.

Maximum effective gain occurs at a singular point in the range of frequency *vs* distance of the source from the datum that was measured. This value of 24 dB at 2.75 kHz, with the source at datum, represents an effective increase in the radiated sound power of 250 times. It will be seen that the effective gain decreases rapidly as the EDS is pushed further into the burrow. At a distance 20 mm outwards from the datum, the effective gain only varies by a few dB in the frequency range 2–6 kHz but, when moved inwards, becomes more frequency-dependent, becoming most sharply tuned with the EDS at datum. Similar results were obtained with four other burrows, the effective gain of which varied from 20 to 23 dB with the frequency of highest effective gain between 2.5 and 2.8 kHz. The highest effective gain was always found with the EDS between 0 and 5 mm out from the datum plane.

Using the effective gain *vs* frequency data for the EDS at datum, the Q factor of the burrow can be calculated. The –3 dB bandwidth is 1.1 kHz and the frequency for maximal response is between 2.75 kHz and 3 kHz, which, using equation 1 (Results), gives a value for Q of 2.5–2.7 (values of 2.5–3 were obtained with the other burrows).

When the burrow was tested with the EDS driven by 2- or 4-cycle tone bursts, it was found that the response built up and decayed over several cycles. The response of one burrow, driven at 2.75 kHz with the EDS at datum, is shown in Fig. 12. In such a case, Q can be calculated from equation 2 (see Results). The natural logarithm of the amplitude ratio of successive cycles in the decay or build-up of the response is plotted at half-cycle intervals in Fig. 12, from which it can be calculated that Q for

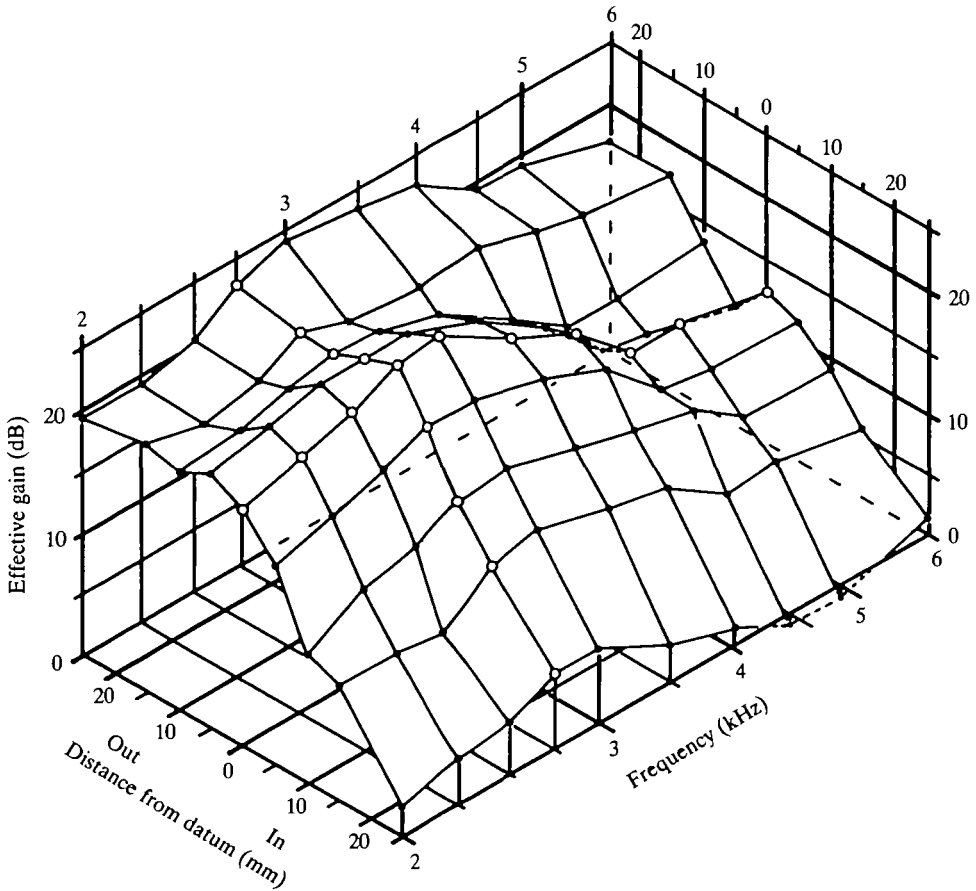


Fig. 11. Three-axis plot of the effective gain (vertical) *vs* frequency and *vs* distance of the electret doublet source (Fig. 1) from the burrow datum (see Fig. 8) for a singing burrow driven with a continuous sine wave. The open circles (—○—) highlight data for the frequency of maximum effective gain, 2.75 kHz, and data with the source at the datum plane.

the burrow is 2.5–2.7. This compares with the same values found by examining the steady-state response of the burrow to different frequencies.

When the EDS is driven with either a square or a saw-tooth wave instead of with a sine wave, the sound emitted when the EDS is in the free field has a ragged waveform. When driven with the same waveform at 2.75 kHz, with the EDS at datum, the burrow response was an almost pure sine wave, so the burrow acts as a frequency-selective filter, presumably because, at this frequency, the effective gain of the horn is maximal. Sometimes, when the EDS is driven by a sine wave at other frequencies and in other positions in the burrow, a ragged waveform is produced. This happens at various frequencies between 2 and 2.75 kHz and at EDS positions between 15 and 25 mm outwards from datum. Thus the burrow shows a strong resonance at 2.75 kHz with the EDS at datum and shows some anti-resonances

elsewhere. There is also a possible weak second resonance at 4 kHz with the EDS at 15 mm out from datum, since the sound produced was a particularly pure sine wave.

Pushing the surface of the soil to collapse the bulb caused the relative SPL, at 2.75 kHz with the EDS at datum, to fall by 6–10 dB; the burrow also ceased to resonate at this frequency but a weaker resonance at about 5 kHz appeared.

It was noticed that if the soil was allowed to dry, the effective gain of the burrows was reduced. Presumably greater losses occurred through the walls of the burrow. It is for this reason that all soil in the experimental buckets was kept almost saturated with water (see Materials and Methods).

## DISCUSSION

### *The advantage of horn loading*

The experiments and observations described above show that the singing burrow greatly increases the effective sound power output of small doublet sources, such as mole cricket wings. The explanation that was offered earlier, that the specific radiation resistance of such sources is far less than that of the free field medium (Bennet-Clark, 1970, 1971), is substantiated. The burrow of *S. acletus* flares to a mouth that is the effective sound source and has  $k_r \approx 1.25$  (see Results, equation 7),

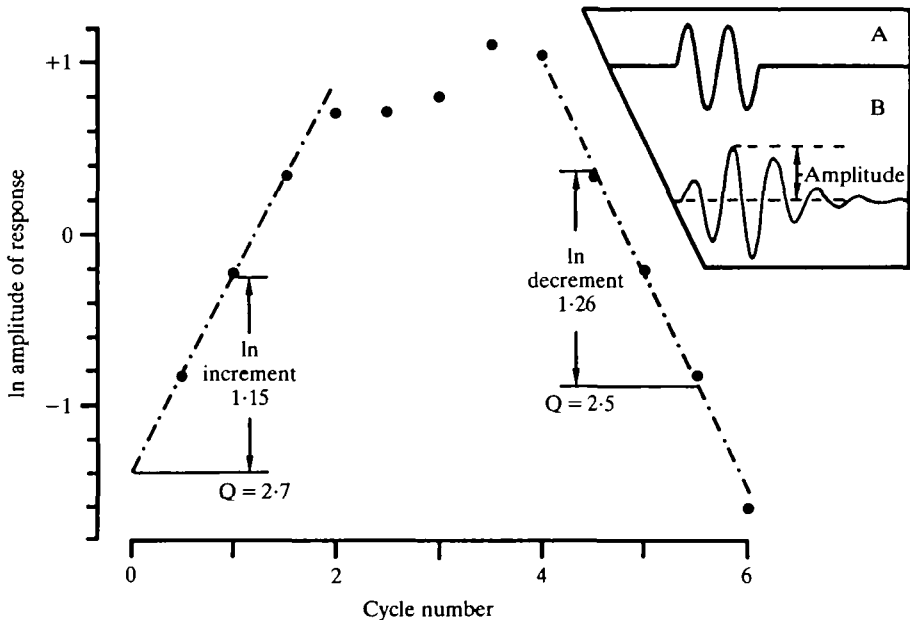


Fig. 12. Graph of the response of a singing burrow to a four-cycle tone burst at 2.75 kHz with the electret doublet source (EDS) at the datum. The natural logarithm of the amplitude of the sound pressure level (SPL) is plotted for every half-cycle of the response and used to obtain the ln increment and ln decrement of the response, from which  $Q$  was calculated using equation 2. The inset shows a representation of (A) a two-cycle tone burst as used to drive the EDS and (B) the response of a damped resonant circuit to this tone burst.

for which the specific radiation resistance, as a vibrating piston or a piston set in an infinite baffle, is about 0.7 times that of air (Olson, 1957). The wings of the insect act as a small doublet source – or, more exactly, a pair of similar small doublets set in small baffles (see Fig. 7C). A doublet source can be regarded as two equal sources, opposite in sense so that their outputs will tend to cancel each other, separated by the plane of the vibrating structure. For the insect wings, the effective source radius is between 5 and 7 mm, for which  $k_r$  is between 0.25 and 0.35 (equation 7). The specific radiation resistance of a doublet source of this effective source radius is between 0.001 and 0.004 that of air, so there is theoretically a 175- to 700-fold increase in the acoustic loading of the wings due to horn loading. The effective gain of the EDS in natural burrows was 24dB or 240-fold. As the burrow is a tuned system, with a gain due to the tuning, the observed effective gains are reasonable fits with the view that the burrow acts as an acoustic transformer or horn.

The sound produced at the mouth of the burrow was radiated as a spherical wave. This has important implications for the acoustics of the throat of the horn because, if the impedance at the mouth is reactive, this will also be seen as a reactive impedance at the throat. If the horn were infinitely long, i.e. if it flared to be continuous with the ground plane, the mouth and throat impedances would be purely resistive and would present only a damping or viscous load to the source at the throat. When, as here, the mouth impedance has similar reactive and resistive components (from the 50° phase angle between the sound pressure and the particle velocity, Fig. 10), the inertance of the horn will be a significant part of the acoustic load at the horn throat.

It is useful here to consider what determines the resonant frequency of a simple resonant system, such as a mass,  $m$ , suspended on a spring of compliance  $c_m$ . The resonant frequency,  $f_o$ , is given by:

$$f_o = \frac{1}{2\pi} \sqrt{\left(\frac{1}{mc_m}\right)}, \quad (8)$$

and shows that the resonant frequency of a system will be affected by changes in its mass or stiffness: the addition of inertance, which is analogous to mass, as in the acoustic impedance at the throat of a finite horn, will have this effect.

#### *Advantages of a tuned burrow*

It follows from the preceding comments that the acoustic load of the horn, which as will be shown is considerable, could have the effect of changing the  $f_o$  of the harps and so of changing the carrier frequency of the song. This effect was, indeed, seen in Figs 3 and 4, where the insect's modification to the singing burrow caused a change in the carrier frequency it produced. As song carrier frequency tends to be an important species-specific character in Orthoptera–Ensifera (see Leroy, 1966; Ulagaraj & Walker, 1973), such an effect would be biologically undesirable.

The impedance of a resonant system is a reactive mass or inertance far below  $f_o$ , is a reactive spring or stiffness far above  $f_o$ , but is purely resistive at  $f_o$ . A load tuned to the same  $f_o$  as the insect's harps will not change their  $f_o$  but will allow a substantial additional damping load to be added into the system, thus altering the source–load

matching. If, in the process, source and load resistance can be made equal, the power output will be maximized. The biological importance of this is that louder calls attract more flying insects (Ulagaraj & Walker, 1975).

A resonant system tends to have a larger amplitude of vibration than a non-resonant system driven by the same force. This means that the power density in the system is greater than if it were aperiodic; thus, if there is continuous replacement of the power that is dissipated, it is capable of dissipating more power than a simple resistive system. A further biological advantage of the smaller but tuned horn is that the insect is able to dig a far smaller burrow and still obtain a large resistive acoustic load for its wings.

In the present case, formal analysis of the effect of the resonant load on the resonant wings is not easy because the degree of coupling between source and load cannot be ascertained. It should be noted that during burrow building, the insect not only increases its sound power output by up to 18 dB or 64 times (Fig. 2) but also slightly increases the  $Q$  of the sound (Fig. 4). The damping resistance in the system increases by roughly 8 times ( $\sqrt{64}$ ), which should cause the  $Q$  of the song to decrease by the same factor, from about 20 to 2.5. Instead, the  $Q$  rises by more than would be expected from the effect of the extra damping and the  $Q$  factor of the burrow (approx. 2.5), which implies that the system may also be driven more efficiently when it is damped by the extra load of the burrow.

This idea is borne out by the change in shape of the song pulse envelope during burrow building (Fig. 6), which implies that the change in the impedance of the air load is reflected back onto the mechanical vibration of the harp and thence back to the muscular system; this in turn is likely to be designed to be optimally coupled to a heavily loaded harp even though, as an escapement system (Elliott & Koch, 1985), the wing closing movement may be able to trip and excite the resonance of the harp with a wide range of load conditions. In other words, the effect of the burrow building may be to allow the insect to optimize the coupling between the singing muscles and the wings to more than offset any decrease in  $Q$  due to the increased acoustic damping (see Discussion).

#### *The burrow as a tuned system*

Evidence is presented in the Results that the singing burrow is tuned to the carrier frequency of the insect's song. My suggestion (Bennet-Clark, 1970) that this is effected by tuning the throat inductance of the horn by an acoustic capacitance at the other side of the wings is supported by the effect on the song of obliterating the bulb: this causes a decrease in relative SPL of around 10 dB (or 3.2 times) (see Results), which is about the expected decrease if the  $Q$  of 2.5 due to the burrow is removed from the system. Further support is given by the observation that when the insect, during burrow building, makes the burrow 'worse', this affects both the SPL and the carrier frequency of the output.

The contention is that the tuned horn presents resistive conditions at the throat. Since the insect's wings act as a small doublet source (or as two equal adjacent sources, opposite in sense), the outputs from the two sides will tend to cancel each

other and the majority of the output will be a circulation between the two sides of the source. The sound power that can be radiated to a distance by such a small source will be small but will rise, with increasing size of the source, becoming maximal after the source size constant,  $k_r$  (equation 7), exceeds a value of 3, above which its specific acoustic resistance approximately equals that of the free field and its reactance decreases (Olson, 1957).

If a small doublet source is placed in the throat of a simple finite horn, its acoustic load will have a substantial reactive component and there will be considerable circulation from the front to the back of the source. If the throat is tuned, the acoustic load becomes resistive and the effect of the doublet source will be to set the whole air column in the horn throat vibrating along the axis of the horn. In this condition, there will be no leakage around the source as the air in this region will be vibrating in the same phase as the source rather than in antiphase as happens with the same source in free air. There is circumstantial and experimental support for this interpretation: the wings of the singing insect do not fit closely to the walls of the burrow so the potential leakage does not seem to be important; when the size of the wings is reduced dramatically (see Results, Fig. 7C), so that any potential leakage should be much increased, the insect still produces the same sound power.

The acoustic loading due to the horn is difficult to specify because of the uncertainties in the description of the system but a rough estimate of the magnitude can be calculated from the source size constant (equation 7) of the mouth. The mass of the acoustic load on a source  $M_a$  is given by:

$$M_a = \frac{R_a}{2\pi f}, \quad (9)$$

where  $R_a$  is the source acoustic resistance, the product of its specific acoustic resistance and its area. For the mouth of the horn, the specific acoustic resistance is about 0.6 that of air or  $250 \text{ kg m}^{-2} \text{ s}^{-1}$  and the area is about  $2 \times 10^{-3} \text{ m}^2$ , so  $M_a$  is 29 mg. This can be compared with the mass of both wings, 7 mg, and, more importantly, with the very much smaller mass of the two harps. It is clear that the dominant loading in the system is that of the horn.

The system can be regarded as a mechanical chain in which the links are muscle power  $\rightarrow$  stridulation  $\rightarrow$  harp vibration  $\rightarrow$  sound radiation. For the best conversion of muscle power to sound power, the losses in transformation should be kept as low as possible. This can be improved if the masses of the intermediate structures, the wings and the harps, are kept small in relation to the effective masses of the muscles and the air loads, which should be similar. From the foregoing discussion, this seems to be an important consequence of the type of loading given by the tuned singing burrow.

#### *The cues to burrow building and tuning by the insect*

The insect spends a considerable time building its burrow and, between successive cycles of digging and testing, usually succeeds in increasing its sound power output. The clear inference is that the insect is able to monitor its performance and gains



information from the performance, in a test chirp, of the uncompleted burrow and uses it further to modify and improve the burrow. Some possible cues are: the frequency of the radiated song; the sound intensity in the burrow; the power input to the wings from the flight muscles.

A serious impedance mismatch between insect and burrow appears to produce a change in song carrier frequency (Fig. 3): the effect is small and, although the hearing of mole crickets is sharply frequency-dependent (Zhantiev & Korsunovskaya, 1973), the fact that the song carrier frequency changes only slightly over a series of enlargements of the burrow and song chirps argues against this as a major cue.

The sound within the burrow (the insect cannot hear the radiated song!) will have complex phase–amplitude relationships between particle velocity and pressure at the throat of the horn if the horn is tuned to a frequency that differs greatly from that of the harps. The paired tympanal organs of mole crickets, as with most other Ensifera, each have an acoustic input from the prothoracic spiracle and the tibial slit. It is, in principle, possible that the insect can monitor the interaction between these two inputs to assess whether or not the throat of the horn is behaving resistively. This seems unlikely as a cue because it appears that, through most of the later stages of burrow building, the horn is closely tuned to the song carrier frequency, but with an ever-increasing horn mouth area and hence total radiation resistance (see Results, Figs 2, 3).

If, during burrow building, the total radiation resistance increases steadily, the burrow will, in principle, reach a size at which the insect is no longer able to produce sufficient muscle power to sustain the oscillation of its harps. As the harp is driven by an escapement system (Elliott & Koch, 1985), the insect would be unable to make this system trip – and it would only be able to trip at the frequency to which the harps and horn are tuned. This situation was not observed, but before it is reached the burrow will reach a size at which it radiates as much sound power as the insect is capable of producing continuously: support for this mechanism is given by the shape of the pulses in continuous song and their high power density (Figs 5A, 6). The insect's muscle power will be the product of the velocity of wing closure, which is fixed by the escapement mechanism of the file and plectrum, and the muscle force. Cuticular stress receptors might provide appropriate information to indicate that power dissipation is optimal.

### *Resistive acoustic loading*

The present contention is that resistive loading allows direct power transformation in the sound-producing chain (muscle power → wing closure → resonant harp vibration → resonant horn loading → sound radiation) with good source:load impedance matching and a characteristic frequency determined by the common resonant frequency of the harp and horn. Similar advantages would accrue in hearing: there is evidence that the mechanical load due to the receptors on the locust tympanum provides good matching for power transfer of a putative adequate stimulus (Stephen & Bennet-Clark, 1982); there is also evidence, in vertebrate ears,

that the receptors themselves are tuned to their characteristic frequencies (Crawford & Fettiplace, 1981). Similar mechanisms for optimal matching are expected in all biological systems that operate at a single frequency – or that discriminate between frequencies – with high sensitivity or efficiency.

The experimental work for this paper was done while I was a Fulbright Fellow and Visiting Professor at Cornell University and the University of Florida, Gainesville. I thank the Fulbright Foundation for a travel grant and both host universities for their hospitality, for financial assistance and for the loan of facilities. Various people gave invaluable assistance and advice, and lent apparatus: Dr R. R. Hoy, Professor T. J. Walker, Dr J. C. Webb, to all of whom I am grateful for their kindness and patience. In particular, I am deeply indebted to Dr T. G. Forrest for making recordings for me, to replace those that were stolen, and who thereby salvaged that part of the work reported in Results, *Sound production during burrow building*.

#### AUTHOR'S NOTE

Some of the experiments that are reported here are of a preliminary or incomplete nature. On my way back from Florida, all my tape recordings and much of my apparatus were stolen. Fortunately, my notebooks, which contained many analyses done during the course of my experiments, were not lost.

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