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THE MECHANISM AND EFFICIENCY OF SOUND PRODUCTION IN MOLE CRICKETS

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INTRODUCTION

The song of the mole cricket has been described as 'a low dull jarring note, continued for a long time without interruption' by Gilbert White (1789), writing about '*gryllus gryllotalpa*'. Chopard (1951) describes the song as 'assez doux, comparable à une sorte de roulement'. By contrast, the song of a French species termed *Gryllotalpa vulgaris* is 'assez fort et perçant' according to Latreille (1804).

The song of a French mole cricket, termed *Gryllotalpa gryllotalpa*, has been examined by M.-C. Busnel (1953). She found that the song has a frequency of 3·2 kHz at 24° C. and is an almost pure note with very little harmonic content. She did not examine the animals in detail as her apparatus was very heavy and the animals are sensitive to ground-borne vibrations. The song is described as being so loud that the ground vibrates over a radius of 20 cm. around the hole.

These insects are large, by some accounts noisy, and sing from a fixed point, the mouth of the burrow. For these reasons they are ideal material for a study of the energetics of sound production.

MATERIAL

Two species of mole cricket were examined. They are *Gryllotalpa gryllotalpa* L. and *Gryllotalpa vineae*, Bennet-Clark (1970). Both species were found near Meyrals, Dordogne, France, and were abundant in their respective habitats; *G. gryllotalpa* lives in water-meadows, gardens and potato fields and *G. vineae* lives in hill-pastures, cornfields and vineyards.

Males of both species sang after sunset most evenings from the middle of April until mid-May, when I left the area. *G. gryllotalpa* produces the sound described by White (1789) and Chopard (1951), and *G. vineae* the sound described by Latreille (1804) and Busnel (1953). Fuller descriptions of the songs appear in §§ 3 and 6 of the results.

For comparison with that of *Gryllotalpa*, the song of the field cricket, *Gryllus campestris* L., was examined. This species was also common in the area.

METHODS

1. *Measurement of sound-pressure*

Observations of sound-pressure must be made with various precautions. Measurements with continuous pure tones are the easiest and, so long as care is taken to avoid

* The field work of this project was performed at Le Station Biologique, Les Eyzies, 24 Dordogne, France.

reflexion and diffraction artifacts, a measure of the sound output of a source can be made by plotting the sound-pressure levels in the whole of its field (Olson, 1957). Here the terminology follows that proposed by Beranek (1949).

Sound-pressure level is the root-mean-square (r.m.s.) sound-pressure and may be measured by a combination of microphone and a.c. voltmeter with an overall flat frequency response. A meter was built for this project.

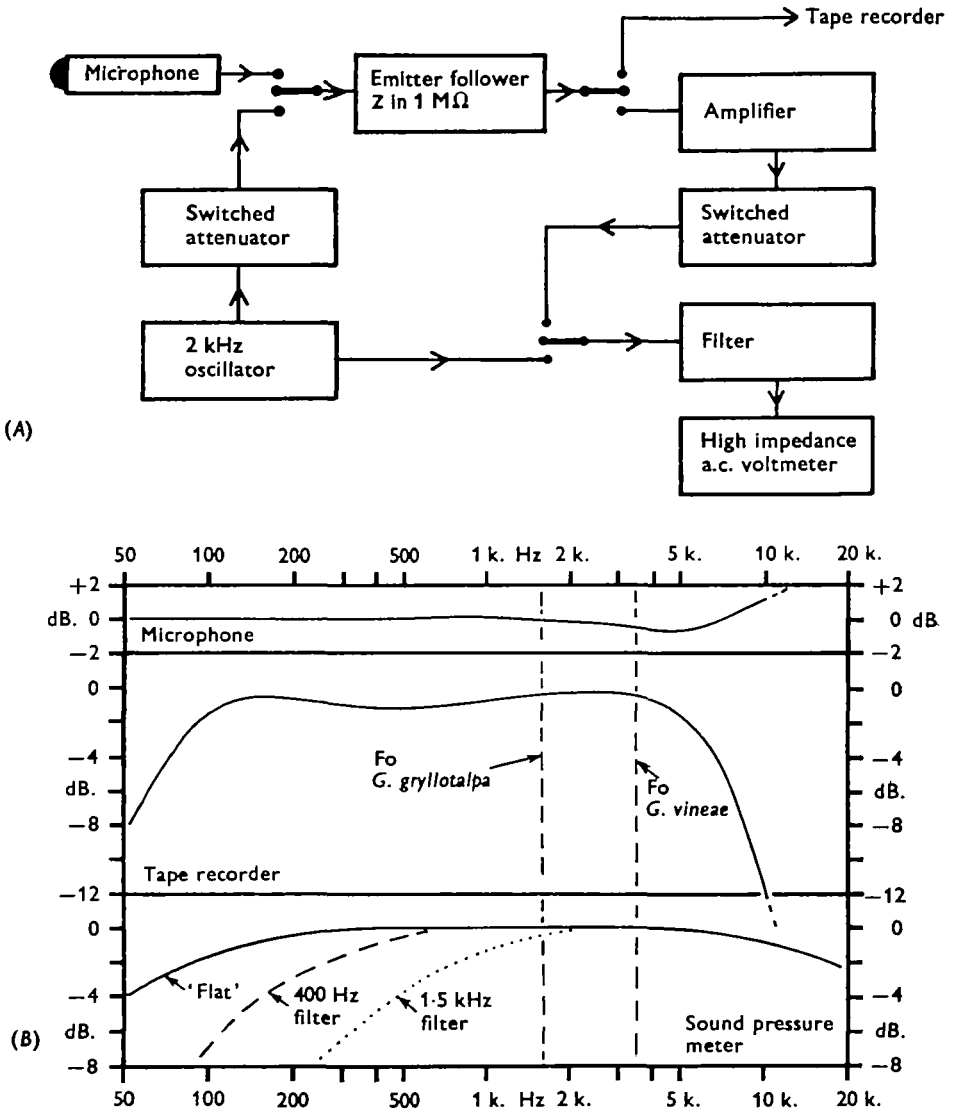

Fig. 1 (*A*). Block schematic diagram of the sound-pressure meter and reference oscillator. The oscillator is used either to provide a reference signal on the recorder or to test the functioning of the sound-pressure meter. 1 (*B*) Graphs of the frequency response of the components of the system illustrated in Fig. 1 *A*. Top. Frequency response of the microphone, Bruel and Kjaer, type 4117. Middle. Frequency response of the Philips recorder type EL 3302 A measured about 10 dB. below peak recording level. Bottom. Frequency response of the sound-pressure meter of Fig. 1 *A*.

A Bruel and Kjaer type-4117 microphone was used. This is a piezo-electric microphone and the frequency response of the example used is flat in free-field conditions within $\frac{1}{4}$ dB. from 20 Hz to 2 kHz, with a slight trough of $-0{\cdot}75$ dB. at 5 kHz and a peak of $+1$ dB. at 10 kHz (Fig. 1*B*). Above 2 kHz the response off-axis is not linear. The recommended load impedance is 1 MΩ.

A block diagram of the sound-pressure meter is shown in Fig. 1*A*. The lead connecting it to the microphone is 2 m. long and of low capacitance. Silicon transistors are used throughout and the different active circuits have individually stabilized 6 V. supplies from the common 9 V. battery. D.c. current drain is 9 mA and the meter weights 1·9 kg.

The output from the microphone feeds a 'bootstrapped' emitter-follower with a Z_{in} of 1 MΩ and Z_{out} of 100 Ω over the bandwidth 10 Hz to 20 kHz. This output can either feed a tape recorder or an internal amplifier. The internal amplifier has high gain and provides an output of 0·4 V. r.m.s. when driven by voltages equivalent to 70 dB. sounds. A switched attenuator alters the effective gain of the amplifier to give the same output for 80, 90, 100 or 110 dB. sounds. The residual noise level is equivalent to a 50 dB. sound.

The electronic voltmeter has a high Z_{in} and drives a 50 μA meter calibrated in decibels. The reading is the r.m.s. value of the voltage. The voltmeter is driven via a single-section filter giving 6 dB. per octave cut-off below 100 Hz, 400 Hz or 1·5 kHz (Fig. 1*B*).

The reference oscillator provides a 2 kHz signal of 0·2 V. r.m.s. which can either be fed to the voltmeter direct or through a switched attenuator giving outputs equivalent to 70, 80, 90 or 100 dB. sounds at the input of the emitter follower. In this way the oscillator can be used to check the performance of the sound-pressure meter in the field, and this was done every time before use.

The meter was tested carefully before the visit to France and after returning. The response of the electronic circuits was flat $\pm\frac{1}{4}$ dB. from 200 Hz to 7 kHz and -1 dB. at 10 kHz (Fig. 1*B*). The very small positive effect of temperature change between 5 and 35° C. is compensated by a similar negative coefficient in the microphone. The calibration accuracy within and between ranges is $\pm\frac{1}{2}$ dB.

2. *Measurements in the field*

As the animals sang from their burrows, it was possible to set the microphone at a known distance from the source.

The microphone was mounted on a lightweight photographic tripod with telescopic legs 1·2 m. long and 11 mm. in diameter. By arranging the legs of the tripod it was possible to direct the microphone at the mouth of the burrow from any point on a hemisphere of 1 m. radius; one leg was used to measure the radius and the other two to measure chords of this hemisphere. After positioning the microphone, care was taken to move the radial leg so that its tip was at least 300 mm. from the mouth of the burrow.

As a check that vibrations and reflexions arising from the legs of the tripod were not important the microphone was suspended by its cord during the course of one series of measurements.

In a typical measurement the sound-pressure level was noted at 30° intervals all round the burrow at angles of 30°, 45°, 60° and 75° from the vertical and at 1 m. vertically above the burrow. Care was always taken to point the microphone directly at the burrow and to avoid spurious effects caused by reflexion from the observer's body. As checks on the constancy of the insect's performance, the original measurement and the vertical reading were checked after each cycle of measurements at a given azimuth.

3. *Tape recordings*

For reasons of economy, lightness and convenience when working in darkness in muddy fields, a Philips cassette recorder model 3302 A weighing 1·9 kg., with batteries, was used. The response of the recorder was carefully checked at various input levels and at 10 dB. below peak level the response was flat ± 1 dB. between 100 Hz and 5 kHz (Fig. 1*B*). With respect to the 2 kHz reference frequency the response at 1·5 kHz was level and at 3·5 kHz was −0·4 dB. Harmonic distortion was under 1 % at the recording level used in the field.

All records were made at about 10 dB. below peak level; this procedure minimizes distortion, gives the greatest bandwidth and reduces the risk of tape print-through. New Hitachi C 60 cassettes were used throughout and a tape, made with pulsed sine waves to test for print-through (a spurious signal arising from excitation and magnetization of hyper-sensitive domains in adjacent layers of the roll of tape), showed that the print-through level was less than the residual noise level. The actual noise level was about 40 dB. below the signal frequency at the recording level used.

No attempt has been made to correct the frequency response of the recorder by electrical means since such procedures tend to introduce distortion and phase shift.

Recordings made in the field used the Bruel and Kjaer microphone, via the tape-recorder outlet of the sound-pressure meter. The records were voice-cued with information about the weather, air temperature, time of day and vertical sound-pressure level. A 2 kHz calibration signal of appropriate level was added. In this way the recorder was used to check the validity of measurements made with the sound-pressure meter.

The use of a recorder with such a limited bandwidth is only justifiable when pure tones are being examined. From the work of Busnel (1953) and the present work this appears to be the case.

4. *Analysis of records*

The tape records have been played back and examined visually on a Telequipment D 53 oscilloscope, photographed using a 35 mm. camera focussed on the oscilloscope screen or a Cossor moving-paper camera. Time markers have been added afterwards, but as the long-term and short-term speed stability of the tape recorder is better than 0·5 %, this is acceptable. Some of the moving-paper records were made by re-recording the tape on an Ampex SP 300 Instrumentation Recorder running at 15 in. sec^{-1} and replaying this at $1\frac{7}{8}$ in. sec^{-1}. This technique improves resolution of photographic records but increases the noise level appreciably.

Sound frequencies were measured by using a Radiometer FRA 2B wavemeter, a Kay Sonagraph type 7029A and by measurement from oscillograms. The first method was used to measure the harmonic content of the records.

5. *Measurements of burrows*

Plaster casts were made of burrows when detailed readings of sound-pressure levels had been completed. The casts were made by pouring a liquid mixture of plaster of Paris and water into one opening of the burrow and then over the surrounding surface and leaving this to harden until the following morning. After it was dug up the cast was washed of adherent soil. This procedure meant that it was not possible to capture the animal but as burrows were chosen by the flatness of the terrain, and as other animals producing similar sound levels at 1 m. above the burrow were dug up, this is not a serious disadvantage.

Further procedures and methods are dealt with as they arise.

6. *Units*

The following conventions are followed: the unit of sound-pressure, the Newton.metre^{-2} is regarded as equivalent to 2·5 mW.m.$^{-2}$ of acoustic power. This is general practice in acoustic measurements. Acoustic power may also be expressed in decibels (dB.), and for this purpose 0 dB. is taken as 10^{-12} W.m.$^{-2}$. Thus a sound power of 90 dB. is $10^{9} \times 10^{-12}$ W.m.$^{-2}$ or 1 mW.m.$^{-2}$. For a fuller discussion of the derivation of these units see Olson (1957).

For the purposes of this paper it is assumed that the units of pressure are freely interchangeable with those of power and that the effect of temperature on this interchangeability is negligible and also that the attenuation of sounds in air at the frequencies encountered here is negligible.

RESULTS

1. *The stridulating mechanism of* Gryllotalpa

This has not been described in detail before. In the present description, the terminology is that used by Ragge (1955). Fig. 2 shows the underside of the right forewing of *Gryllotalpa vineae*.

The sound-producing mechanism is similar to that of all grylloids: a plectrum on the posterior margin of the left forewing strikes the toothed under-surface of the contralateral vein Cu 2. The under-surface of this vein in both forewings of male mole crickets bears teeth and these teeth are asymmetric, with the sharper edge facing the posterior wing margin (Fig. 3). The plectrum, on the upper side of the posterior wing margin, also has its sharper edge facing backwards; if the toothed vein, or pars stridens, is rubbed against the contralateral plectrum, it will move quite easily and quietly outwards, but on the inward stroke each tooth gathers on the plectrum and drops only after the applied force has increased considerably.

The manner in which the wing produces a sound is not immediately obvious. The harp area, area Cu 1, is roughly triangular and is slightly convex. The proximal ends of veins Cu 1 and Cu 2 are not fused but are joined by a very flexible region (Fig. 4 *A*). Pressure along the length of the pars stridens (Cu 2) tends to force the proximal end of that vein towards the wing tip, causing a change in the geometry of the harp area triangle. This causes the already convex vein, the distal oblique, to become more convex (Fig. 4 *B*).

The actual cycle is probably that the plectrum gathers a tooth of the pars stridens, pushes this inwards, causing the middle of the harp to buckle upwards, then drops the tooth which allows the harp to return to its original position. The plectrum-bearing left wing behaves in a similar manner since the wing-closing force is also transmitted from the plectrum across the anal veins to the pars stridens (Fig. 4 *A*). As the plectrum

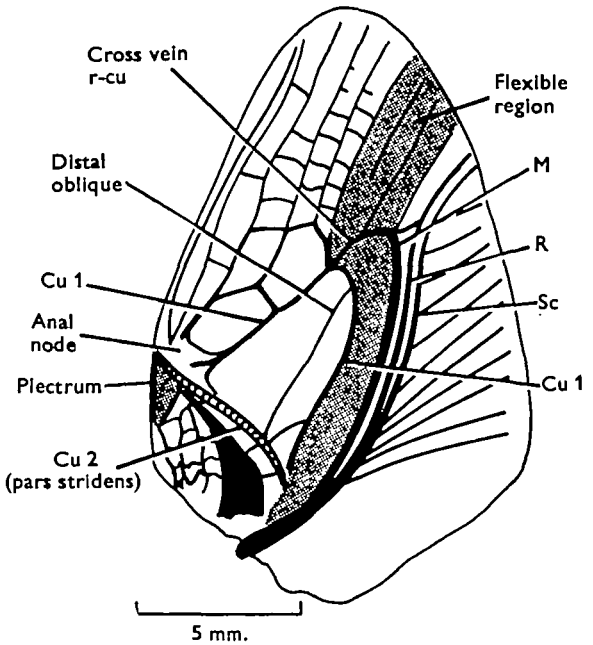

Fig. 2. Underside of the right forewing of male *Gryllotalpa vineae*. The stippled regions are very flexible; the mechanical connexion between veins Sc, R and M of the lateral field and vein Cu 1 of the dorsal field is the cross-vein r-cu and the plectrum is supported only at its ends.

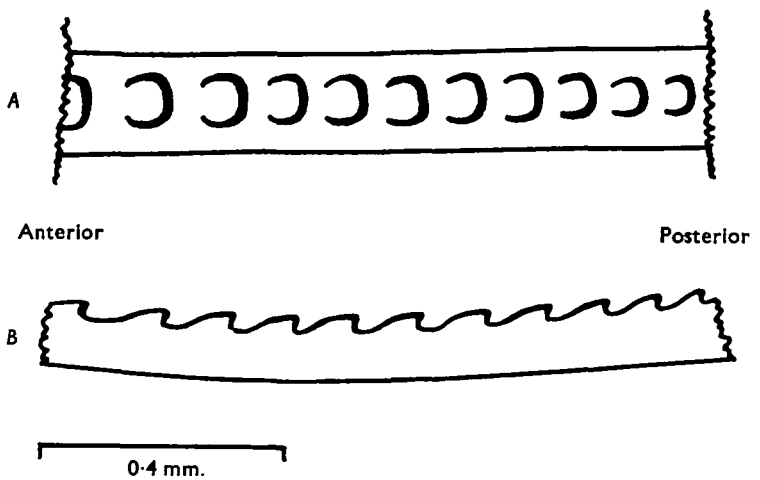

Fig. 3. Diagram of the teeth of the pars stridens (vein Cu 2) of *G. vineae*. (*A*) Seen from the underside of the wing; the anal edge is to the right and the diagram shows that the teeth increase in size towards the middle of the pars stridens. (*B*) shows the teeth from the side.

is not a rigid continuation of the surface of the wing but is only connected at each end, it can rotate along its length to drop the teeth of the pars stridens. As the mass of the plectrum is very small, its torsional resonant frequency is likely to be above the frequency of the song and the force required to cause rotation and drop of a tooth will be determined solely by the stiffness of the plectrum.

A more direct examination of the mode of operation of the two wings was obtained by rubbing a pair of wings together using Bailey's actuator technique (1970). This

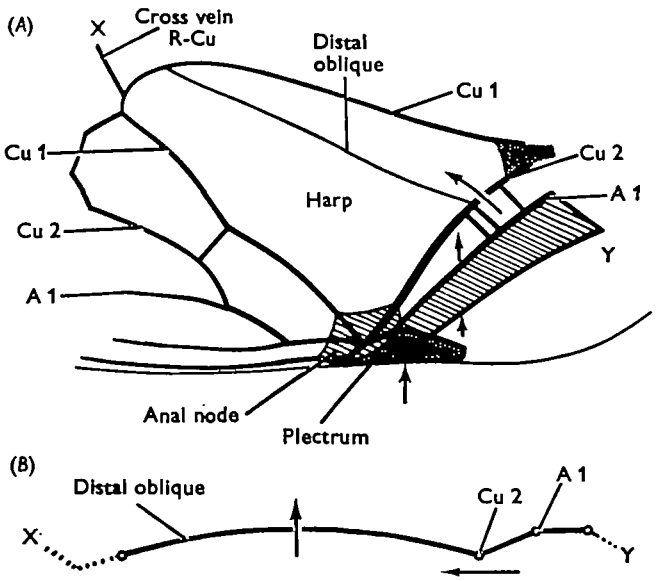

Fig. 4. Diagram of the manner in which the harp area of the wing is deformed by the action of the plectrum on the pars stridens. (*A*) The force on the plectrum or pars stridens is transmitted along the pars stridens and causes the proximal end to rotate. These forces are shown by arrows. The stippled region between the proximal ends of Cu 1 and Cu 2 is flexible. The plectrum is separated from the rest of the wing by a flexible region. (*B*) This shows a vertical section of the line X–Y of Fig. 4*A*. The distal oblique vein is somewhat convex; a force applied to the right hand end will cause it to become more convex. For both these figures it is assumed that point is × fixed.

technique strikes the two wings together in a manner similar to that occurring in the animal. In the experiment the sound produced decreased considerably when the harp area of the plectrum-bearing wing was covered with Evo-stik. A very much more marked decrease attended the subsequent covering of the harp area of the opposite wing with Evo-stik. This confirms that both wings radiate sound. Bailey (1970) has found that in *Homorocoryphus* the vertical movement of the mirror frame and the plecrum are opposite in phase; the two wings are different and the wing that bears the pars stridens is mute.

In a mechanism of this type the vibration that will cause a sound is that normal to the surface. Owing to the complex geometry of the harp area and as it has been demonstrated to me by Bailey that the harp frame is a resonant system in *Gryllotalpa*, it is not easy to estimate from the size of the teeth on the pars stridens what the amplitude

of vibration or the area of the vibrating surfaces will be. It is shown later that there is a close relationship between tooth size and song amplitude (§ 3, Fig. 10).

The stridulation causes an up-and-down vibration of part of the dorsal fields of both wings. The dorsal field is but loosely connected to the thorax and is connected to the lateral field by the very flexible medial area (Fig. 2). Across this flexible region a single rigid cross-vein connects the distal corner of the harp to the fused veins Sc, R and M of the lateral field. The whole driving force of the thorax is transmitted along these rigid lateral-field veins, through this cross-vein, and down the veins surrounding the harp to the pars stridens and the plectrum. The harp region is relatively undamped by the lateral field and so is able to resonate freely. This arrangement appears to be typical of the grylloids and doubtless accounts for the tonal purity of their songs.

Table 1. *Dimensions of mole crickets*

Dimension	*G. vineae*	*G. gryllotalpa*
Forewing length	19·57 ± 0·57 mm., n = 24	15·87 ± 0·93 mm., n = 28
Forewing width	12·43 ± 0·56 mm., n = 24	9·64 ± 0·53 mm., n = 28
Area of harp	13·6 ± 1·25 mm.^{2}, n = 8	8·1 ± 0·66 mm.^{2}, n = 12
Length of pars stridens	3·98 ± 0·25 mm., n = 24	3·22 ± 0·23 mm., n = 28
No. of teeth on pars stridens	46·0 ± 3·8, n = 24	81·4 ± 5·5, n = 28
Length of body, newly killed	54·2 ± 3·6 mm., n = 12	44·1 ± 3·7 mm., n = 10
Weight, newly killed	3·3 ± 0·45 g., n = 13	3·0 ± 0·52 g., n = 9

The wings of the males of the two species differ. In *G. vineae* the median vein is fused to the cross-vein r-cu but is free in *G. gryllotalpa*. The dorsal field is far larger and the wing appears more rigid in *G. vineae*. Table 1 compares wing size and body weight for males of the two species; measurements and counts are for both wings, where these were intact.

Probably the most important specific differences are in the size of the harp and in the number of teeth on the pars stridens; the latter is of use as a taxonomic character (Bennet-Clark, 1970).

2. *The thoracic musculature and available power*

The mesothoracic muscles of *Gryllus* have recently been thoroughly re-described (Bentley & Kutsch, 1966) and their study has been used as a guide for the present work. Dissection of newly killed mole crickets showed that the anatomy was very similar to that of *Gryllus*, the principle difference being the loss, in mole crickets, of the dorsal longitudinal indirect wing levator (81 in Bentley and Kutsch's terminology). Wing depression is performed largely by the contraction of the second basalar muscle, 98.

The sound-producing stroke is a wing levation or closing stroke. This is produced by contraction of the large muscles inserted on the tergum. These are the tergal promotor (89a), the tergal remotor (90) of the coxa, and the depressor of the trochanter (103a). There are no indirect dorso-ventral muscles and the other mesothoracic muscles are relatively small and so, in a study of the energetics, can probably be ignored.

Muscles were dissected from newly killed animals and weighed. In making the weighings extreme speed was needed to avoid drying of the excised muscle and a check was made by comparing the weights from one side with those from the other.

The weight of muscle for the various species is shown in Table 2. For *G. gryllotalpa* and for *Gryllus campestris* this is the total mesothoracic muscle weight as it was not easy, with their smaller muscles, to weigh them with the same confidence as with the large muscles of *G. vineae*.

Table 2. *Mesothoracic muscle weights of male crickets and mole crickets*

Gryllus campestris	Total, both sides	19·8 ± 3·7 mg.	$n = 5$
Gryllotalpa gryllotalpa	Total, both sides	16·4 ± 2·6 mg.	$n = 5$
Gryllotalpa vineae	Levators, both sides	50·3 ± 7·7 mg.	$n = 6$
	Depressors, both sides	8·3 ± 1·6 mg.	$n = 6$

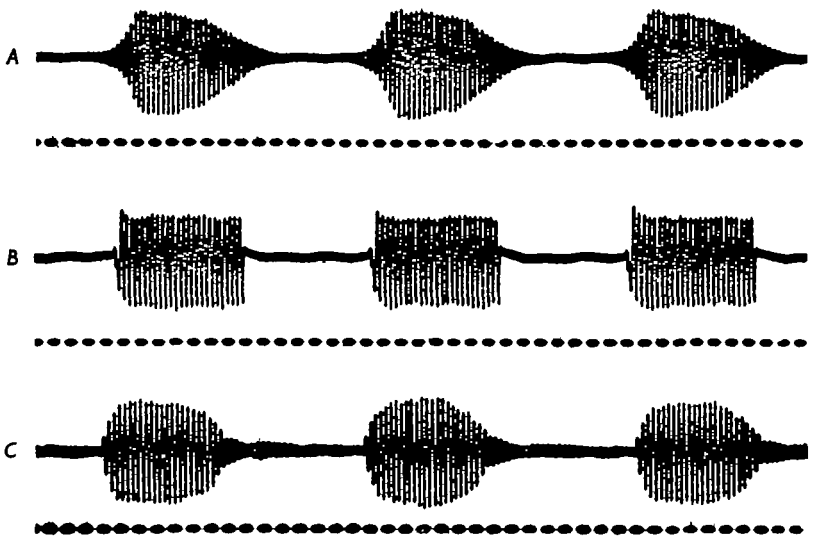

Fig. 5. Oscillograms of tape recordings of the song of *G. vineae* and of simulations of the song. (*A*) Simulation made by modulating a 3·5 kHz oscillator with a 66 Hz sine wave. (*B*) Simulation made by modulating a 3·5 kHz oscillator with a 66 Hz square wave. (*C*) Song of the insect recorded at 12° C. In all these records the time markers are at intervals of 1 msec.

The power output of insect muscle depends on the operating conditions and on the temperature. The maximum that has been observed is from double-excited isolated locust muscle at 36° C. Under these rather extreme conditions Neville (1965) calculates a power output of 130–160 W. kg.$^{-1}$. This is for a 50 msec. load cycle, where a second activation follows 4–8 msec. after the first and increases the twitch force. In *Gryllotalpa vineae*, the load cycle is only 14 msec. (§ 3), which is near the uppermost limit for synchronous-firing muscle, and so it is probable that the muscle is not developing so much power and that it is not double-excited. Instead, it seems that the power will not exceed 70 W.kg.$^{-1}$, a figure found for various insect muscles at around 30° C. (quoted by Neville).

Taking this figure, 70 W.kg.$^{-1}$, 50 mg. of wing levator muscle gives a total available mechanical power output of 3·5 mW. for *G. vineae*. There will be about 1 mW. in *G. gryllotalpa* and about 1·2 mW. in *Gryllus campestris*.

3. *Description of the calling song of* Gryllotalpa vineae

The average value for the fundamental frequency of the calling song is 3512 Hz, s.d. 105 Hz, recorded from 33 individuals in the field at air temperatures above 10° C. A particularly long record was made (Fig. 5*C*) and this has been examined with a wave analyser. The analysis shows a bandwidth at −20 dB. points of about 600 Hz, the presence of a second harmonic at 6·8 kHz, 26 dB. below the fundamental and a third harmonic of −35 dB. at 10·2 kHz (Fig. 6*C*).

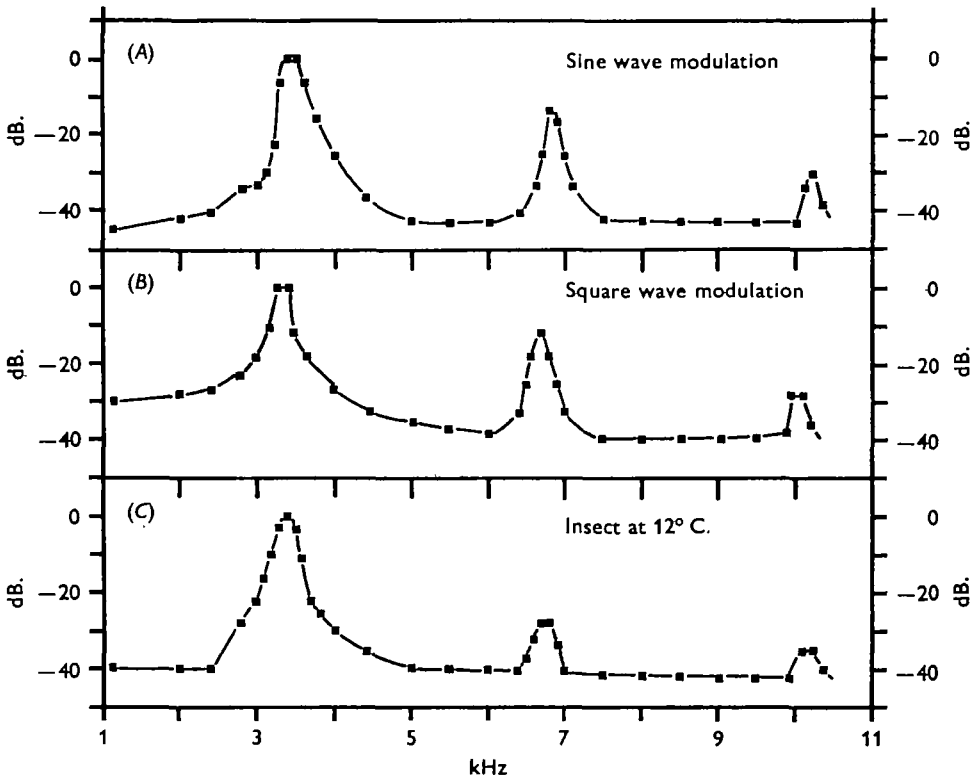

Fig. 6. Frequency analyses of tape records of the signals shown in Fig. 5. The analyses were made with a wave analyser and are plots of power against frequency; the peak intensity of the fundamental is taken as 0 dB. The noise level is about 40 dB. below the peak signal level and the measurements are corrected for the recording characteristic of the tape recorder. (*A*) 3·5 kHz modulated by 66 Hz sine wave. (*B*) 3·5 kHz modulated by 66 Hz square wave. (*C*) Song of *G. vineae* at 12° C.

Simulations of this song were made by modulating a simple 3·5 kHz oscillator with a 66 Hz modulation. Two types of modulation were used; Fig. 5*A* shows the oscillator output modulated by a 66 Hz sine wave to a depth of about 180% and Fig. 5*B* shows the same fundamental but with 100% modulation by a 66 Hz square wave. Of these, the first sounded extremely like the song of the insect. The modulated 3·5 kHz signals were examined with the wave analyser and were also recorded on the tape recorder and re-analysed on playback. Since the harmonic content of the oscillator output and

tape-recorder output were (after allowing for the overall record-replay characteristic of the recorder) within 1 dB. of each other it appears that the recordings can be used for assessing the harmonic content of mole cricket's song.

The bandwidth of the recorded simulations at −20 dB. points is also about 600 Hz (Fig. 6*A*, *B*) and this can be used to suggest that the song of the insect approximates to a pure tone deeply modulated by another pure tone; when the modulation depth exceeds about 30% the side bands of the fundamental frequency tend to be a series consisting of the fundamental plus and minus the modulating frequency and its harmonics. With extreme modulation the rise and fall time of the modulation may be different and so produce two series of side bands.

From the preceding argument it appears that the calling song of *Gryllotalpa vineae* may be regarded as a modulated pure tone. The implications of this are considered further in §§ 4 and 5.

It should be noted that this type of analysis is only possible where a long homogeneous recording is available. In the general description of the song that now follows the records were far briefer, and so the Kay Sonagraph was used to provide a less detailed qualitative analysis. In addition, oscillograms of the songs have been made.

It should be noted here that considerable difficulties can result from the indiscriminate use of the Kay Sonagraph. Fig. 7*A* shows an analysis of the sine-wave modulated simulation, 7*B* the square-wave modulated simulation and 7*C* the insect song record analysed with the narrow-band filter and after speed reduction to improve the temporal resolution. Fig. 7*D* shows the same record as 7*B* but here the effective tape speed was increased to improve frequency resolution at the expense of temporal resolution. In this case the individual pulses are not resolved, but a long series of side bands due to the harmonics of the modulating waveform are shown.

Where the original recording has considerable speed irregularity (wow and flutter) the side bands can be completely obscured, and the effect that is seen for a sharply modulated pure waveform is similar to that obtained from a narrow-band noise spectrum.

Careful analysis of insect song records photographed on a much expanded time scale (as in Fig. 11) show that there is some change in the fundamental frequency during the pulse. In the first quarter of the pulse the frequency is about 3·6 kHz, in the middle about 3·45 kHz and in the last quarter about 3·3 kHz. The frequency change seems to be continuous and is probably due to an increase in the effective mass of the resonant system resulting from an increase in the mechanical coupling between the wings with increasing overlap during the sound-producing stroke.

Since the frequency change is so slight, and since it is continuous through the pulse, the song may still be regarded as a modulated pure note for the purposes of sound-pressure measurements. As the total harmonic content is only about 5%, the effect of the harmonics upon the total power will be negligible. Further implications of this finding are considered in § 4.

In singing insects the pulse length was somewhat variable, between 5 and 9 msec., consisting of 17–31 cycles of the tone. In general, pulse length was greater at higher temperatures where the pulse repetition rate was greatest; at the highest rate observed the pulse length was 8 msec. and the interval between the start of one pulse and the

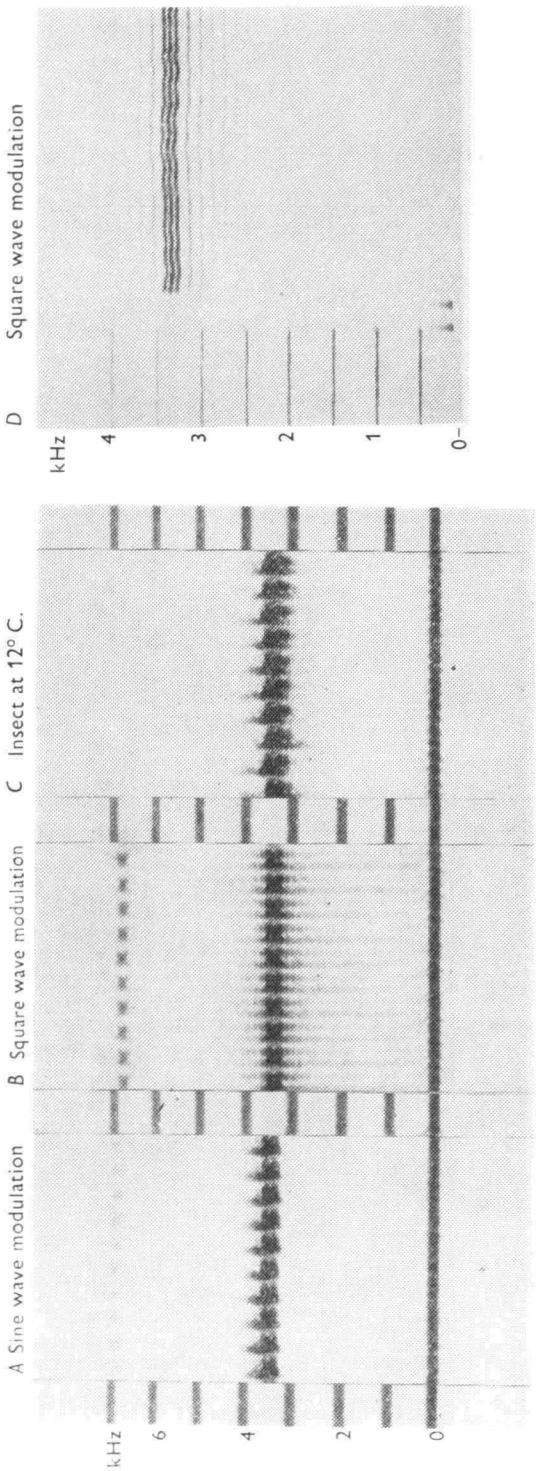

Fig. 7. Sound spectrographs of the signals shown in Fig. 5 made with the Kay Sonagraph. These were made after re-recording the signals at 7·5 in. sec^{-1} and re-playing at 3·75 in. sec^{-1}. (*A*) 3·5 kHz modulated by 66 Hz sine wave. (*B*) 3·5 kHz modulated by 66 Hz square wave. (*C*) Song of *G. vineae* at 12° C. (*D*) Sound spectrograph of the signal shown in Figs. 5*B* and 7*B* but analysed after re-recording at 3·75 in. sec^{-1} and playing back at 7·5 in. sec^{-1}. The side bands have become sharper but the individual pulses are not resolved.

start of the next (the pulse interval) was 14 msec. (Fig. 8*D*) at an air temperature of 16° C.

The longer pulse intervals were found during 'warm up' at the start of an evening's singing. The first sound was a few irregular ticks or chirps, typically followed by a slow, erratic trill (Fig. 8*A*). As singing proceeds, the trilling becomes more regular, the note becomes purer (Fig. 8*B*) and the pulse envelope becomes cleaner, the pulse interval falling and the pulse length increasing. While this has not been studied systematically, the initial pulses seem to show erratic excitation of a resonant system. This could happen in the present system if the teeth of the pars stridens were caught and released irregularly at first and more regularly later. During warm up the sound consists of a far broader band of frequencies (Fig. 9*A*) than when singing has settled at the final rate (Fig. 9*B*, *C*, *D*).

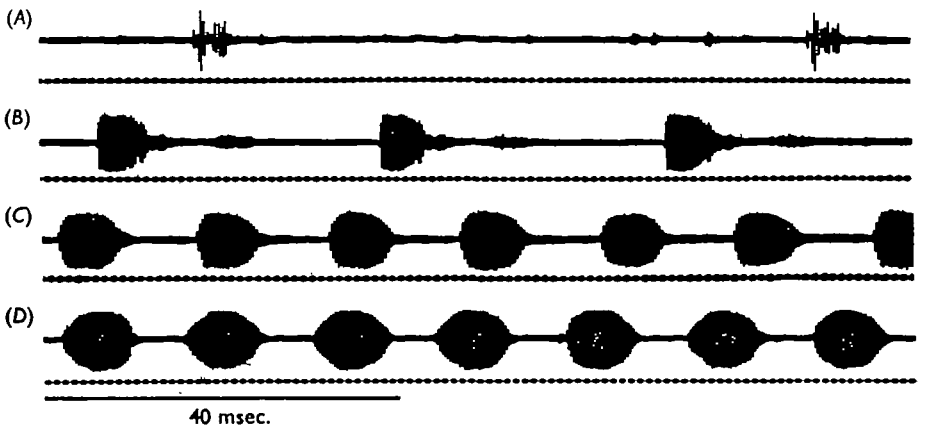

Fig. 8. Recordings of the songs of *Gryllotalpa vineae* made in the field. *A* at 8° C.; *B* at 9° C.; *C* at 12° C.; *D* at 16° C., air temperature. Time markers at 1 msec. intervals in all records.

No attempt has been made to measure temperatures within the animal or within the burrows. Singing may start at an air temperature as low as 8° C. but does not become established below about 9° C. and reaches maximum power and rate at rather higher temperatures; since this aspect has not been studied systematically, no further comment can be made.

The normal pulse of the established song consists of a coherent waveform. The interpulse period is not quiet but includes one or more trains or waves of similar frequency but lower amplitude. This is seen most clearly at low temperatures (Fig. 8*B*) but is always present. It appears that the rubbing together of the wings during the opening stroke excites the same resonant system as in the closing stroke.

For any individual the modulation envelope of the pulse is of constant shape. While this has not been examined in detail it is likely that this is related to the teeth on the pars stridens which vary in depth and in pitch along the length. Fig. 10 compares tooth pitch and depth with the amplitude of sound-pressure for the one individual where adequate song records exist and the insect's right wing was available for measurement. It will be seen that there is a fairly close relationship between the song amplitude and the tooth pitch and this conforms with the mechanism proposed in § 1.

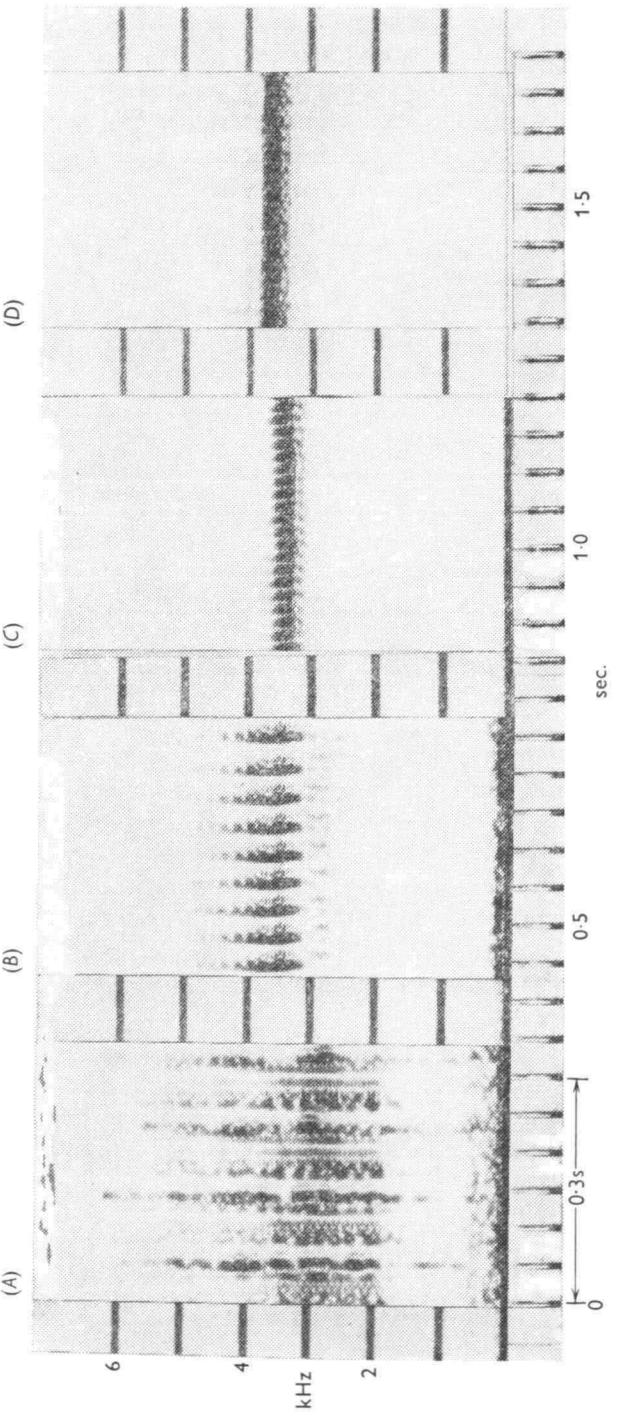

Fig. 9. Sound spectrographs of the songs shown in Fig. 8; frequency is plotted linearly on the horizontal axis. Time markers are at 50 msec. intervals. *A* from record made at 8° C.; *B* at 9° C.; *C* at 12° C.; *D* at 16° C.

4. *The power output of the song of* Gryllotalpa vineae

The song of this insect is the loudest that I have heard. A single individual can be heard in still weather conditions at a distance of 600 m. Singing starts about 30 min. after sunset and may continue for over an hour. By about 10 min. after the start the song has become established and continues with little or no interruption and with not more than 1 dB. change in level.

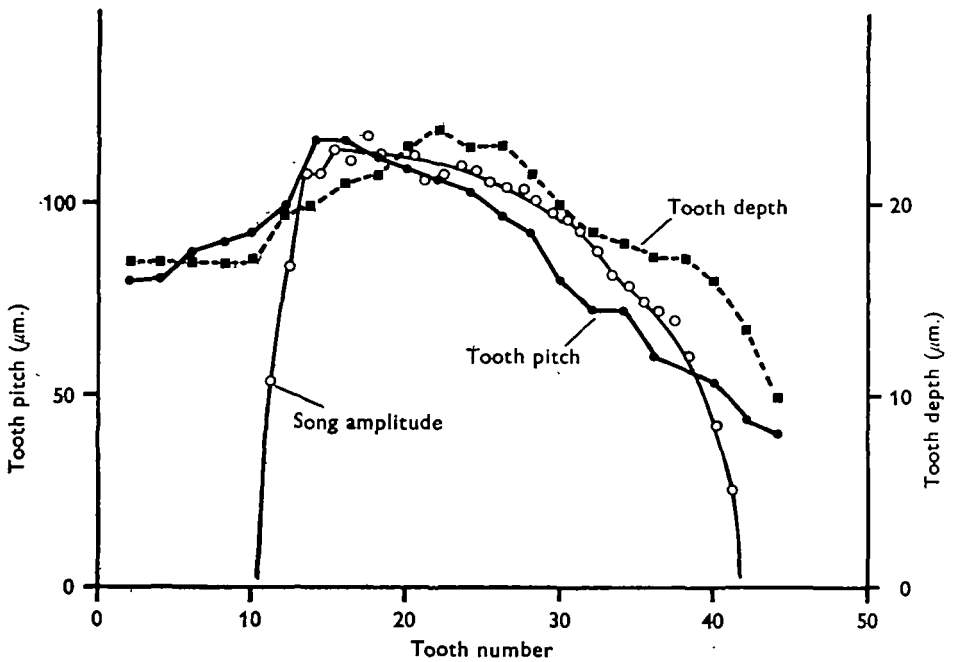

Fig. 10. Graph of various parameters of the song and sound-producing mechanism of a single individual of *G. vineae*. ■--■--, Tooth depth against tooth number; ●–●–●, tooth pitch against tooth number for the right pars stridens, counting from the anal edge of the wing; O–O–O, song amplitude against cycle number, the peak amplitude being arbitrarily chosen and the horizontal position adjusted to give the best fit with the other curves.

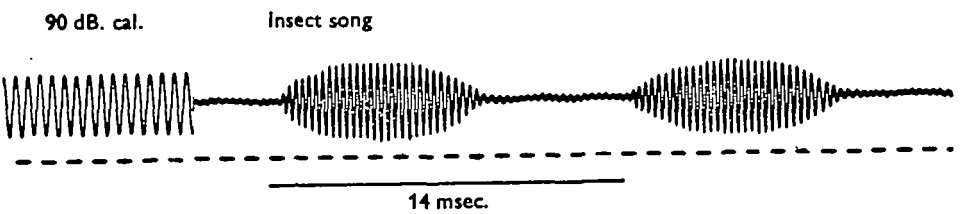

Fig. 11. Oscillogram of the song of a loud individual of *G. vineae* with the 90 dB., 2·1 kHz signal that was recorded as calibration.

The maximum sound-pressure level observed at 1 m. vertically above the singing insect was 90 dB. (1 mW. m.$^{-2}$) as indicated on the meter. The wave form of this song, with the 90 dB. 2·1 kHz calibration signal, is shown in Fig. 11.

Replay of this recording at a suitable level into the sound-level meter showed that the meter underestimated the peak level of these modulated signals by about 2 dB.

The mean acoustic pressure level of the song is found by integrating the instantaneous power over a complete pulse cycle. The instantaneous power is approximately the square of the instantaneous peak to peak amplitude; this may be compared with the square of the amplitude of a waveform of known power. Fig. 12 shows the power throughout the pulse for the waveform shown in Fig. 11 compared with the power of the 90 dB. calibration signal. The peak power is about 92 dB. and the mean power over a complete cycle of wing opening and closing is 88 dB. Analyses of the songs of

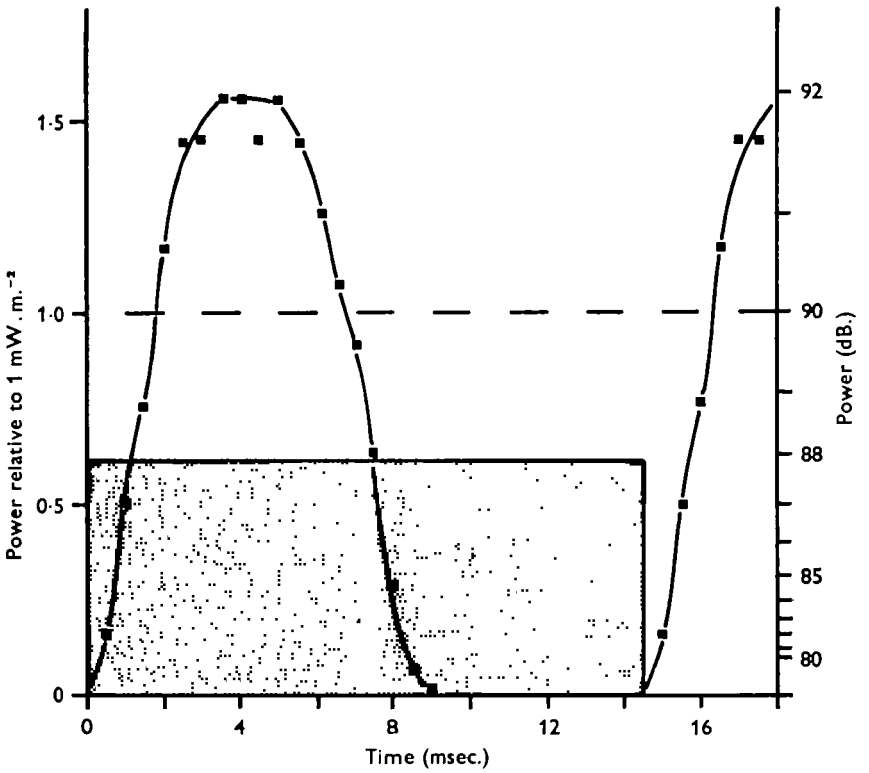

Fig. 12. Plot of the power of the signal shown in Fig. 11, which is the square of the instantaneous amplitude of the song against time. The horizontal dashes indicate the square of the amplitude of the 90 dB. calibration signal and the stippled area shows the mean power through the complete trill.

other individuals have shown that these estimates are realistic; and while this very high mean sound-pressure level was only recorded twice, a mean sound-pressure level of 87 dB. was recorded on five occasions and 86 dB. on eight occasions.

In this context it is useful to note that the peak sound-pressure was greater on damp evenings and with newly made singing burrows. At higher temperatures, and so with shorter pulse intervals, the mean power was greater. The acoustics of the singing burrow are considered in § 5.

Measurements of the sound-pressure level were made over the surface of a hemisphere of radius 1 m. (Methods, § 2) for 12 individuals. The results for one typical individual are displayed in Figs. 13 and 14. The mean sound-pressure level for this animal was 87 dB. at 1 m. vertically above the singing burrow. The results are con-

verted to show radial distance along various latitudes at which the mean sound pressure level is 0·1 mW.m.$^{-2}$ or 80 dB. Thus for a point source, by the inverse square law, 87 dB. at 1 m. is 80 dB. at 2·24 m., and 76 dB. at 1 m. is equivalent to 80 dB. at 0·63 m. Fig. 13 shows these radial distances at angles below the vertical of 30, 45, 60 and 75°.

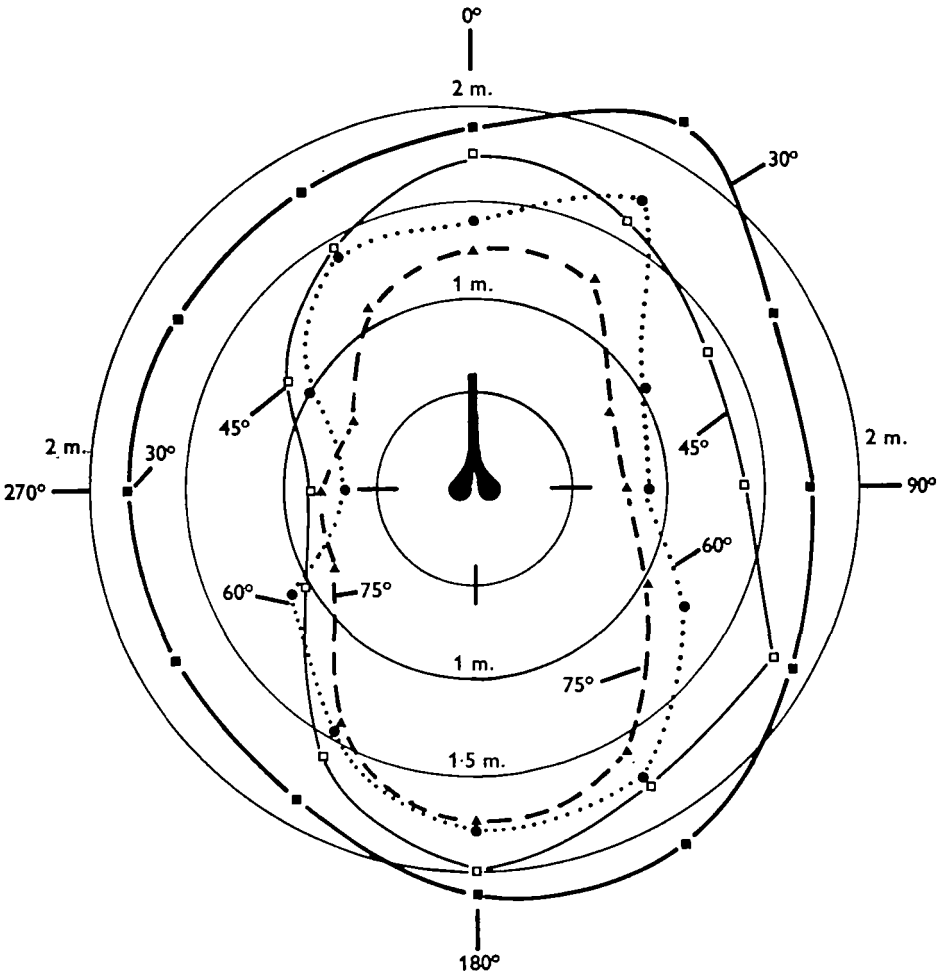

Fig. 13. Plot of the 80 dB. isobar of the song of *G. vineae* for various latitudes. The polar diagram shows radial distance to the isobar. The vertical distance to the isobar is 2·24 m. The vertical is regarded as 0° and ground level as 90° and isobars are plotted –■–■– at 30°, –□–□– at 45°, ··●··● at 60° and –▲– –▲– at 75° from the vertical. The head of the animal is given the longitude 0° and its tail 180°.

The diagram is made looking downwards and the front of the insect is indicated as longitude 0°. The sound distribution is directional; the sound-pressure level near the ground is about 10 dB. higher along the animal's axis than at right angles to it. This is also seen in Fig. 14, which shows plots of sections of the 80 dB. isobar cut along and across the animal's length. Plotted in this way the irregularities that appear in Fig. 13 are shown to be less significant; they probably arise from small irregularities in the terrain but do not substantially alter the distribution.

The total sound power is given by the surface area of the 80 dB. isobar. The surface of the 80 dB. isobar is too irregular to be regarded as an oblate hemispheroid. A closer measure of its surface area can be obtained by use of Pappus' theorem. By this theorem the surface area of a solid formed by sweeping a plane curve around a point is the product of the perimeter swept by the plane curve and the centroid of the curve.

The transverse vertical section of the isobar (Fig. 14) is concave but may be converted to a convex curve of the same length. The distance around this curve was measured with a map-measurer and its centroid was found by cutting out and finding the centre of gravity.

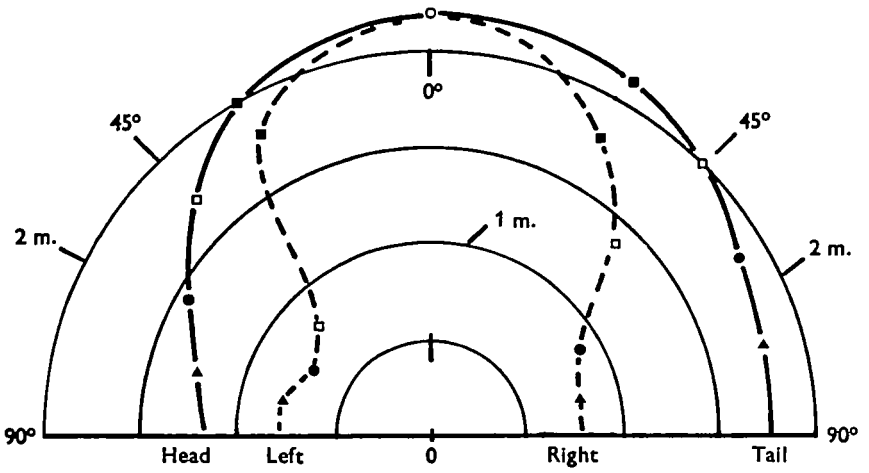

Fig. 14. Vertical plots of the 80 dB. isobar derived from Fig. 13. The complete line shows the radial distance to the isobar measured above the animal's long axis and the dashes show the isobar across the long axis. This is indicated on the diagram by head, tail, left and right where the isobars intersect the horizontal. As in Fig. 13, vertical is termed 0° and this allows comparison with Fig. 17.

Similar curves were drawn for angles of 60° from the vertical above the head and above the tail, and were similarly measured. The surface area was calculated for 60° arcs of rotation of each of these three surfaces, the total surface area being the sum of these areas representing a total of 180° of rotation.

The surface area, A, of a surface of rotation of arc $\theta°$ is given by

$$A = 2\pi\, l\bar{x}\theta/360 \qquad (1)$$

where l is the length of the half-arc of the plane curve and $\bar{x}$ is the distance from the centre of rotation to the centroid of the rotating-plane curve.

Table 3 shows the values that have been measured and calculated for the surface illustrated in Figs. 13 and 14.

The total surface area of the 0·1 m. W.m.$^{-2}$ isobar is 12·2 m.^{2}, giving a total mean power output of 1·2. mW. As this is produced by an estimated total muscular power of 3·5 mW., the efficiency of conversion of muscular to acoustic power is about 35%.

The measurement given here is probably typical of the upper limit of performance of this species. Outputs 1 dB. lower were observed more frequently; for the same muscular power the efficiency then is 28%.

The peak power in any one pulse is 4 dB. above the mean power (Fig. 14). For a mean power output of 1·2 mW., the peak power is 3 mW. This aspect is considered further in § 5.

Table 3. *Calculation of the total area of the* 80 *dB. isobar of the sound produced by* G. vineae, *based on data in Fig.* 16, *and using formula* (1)

Arc of Rotation	i	$\bar{x}$	θ	Area
Ground level to 30° below vertical above head of insect	4·0 m.	0·7 m.	60°	3·0 m.^{2}
30° either side of vertical	5·6 m.	0·9 m.	60°	5·4 m.^{2}
30° from vertical to ground level at tail of insect	4·6 m.	0·8 m.	60°	3·8 m.^{2}
	Total arc and area		180°	12·2 m.^{2}

5. *The singing burrow of* Gryllotalpa vineae

In wet weather and at night the male insect digs openings from the main burrow system to the surface. The mouths of this burrow are of very constant shape and are typical of this species.

The singing burrow is in the form of a paired horn (Fig. 15). The oval mouths are about 30 mm. long and 25 mm. wide and are separated, centre to centre, by about 40 mm. From these mouths two channels lead down and merge about 30 mm. below ground level, and the common channel then turns horizontally, decreasing in width along its length until at a total distance of 70 to 90 mm. from the surface it expands to a spherical bulb of 25 to 35 mm. diameter. From this a horizontal channel 15 mm. diameter leads away to the rest of the burrow. The exit burrow usually bifurcates within 60 mm. of the bulb (Fig. 15 *B*).

The shape of the burrow is remarkably constant and the walls are extremely smooth, with surface irregularities of less than 1 mm. It is not, at present, clear how the animal shapes the burrow but, from the occasional claw marks on the walls, it is probably dug with the forelimbs and then in some way smoothed. Nor is it clear how the animal recognizes the surface of the ground; burrows dug in an irregular terrain are asymmetric and may even have three or more mouths.

These burrows are used for upward of a week. When newly made they are very regular, but with the passage of time they become enlarged, lose the division between the two mouths and may collapse. However, in dry weather following their construction they become remarkably strong structures and can be dug up intact—it is probable that the animal uses some secretion to reinforce the walls.

When singing the animal lies with the posterior end of the abdomen at the confluence of the two upward-turned channels. By comparing the length of the animal with a plaster cast of its burrow, it is established that the head and pronotum lie just inside the bulb, and the forewings (when raised into the singing position) fill the upper part of the burrow just outside the bulb (Fig. 15 *A*). It is difficult to examine the insects while they are singing, but it appears that the forewings are raised to about 40° above the rest position during singing; this is consistent with the description given here.

If disturbed the animal runs away down the exit burrow. It can be dug up by

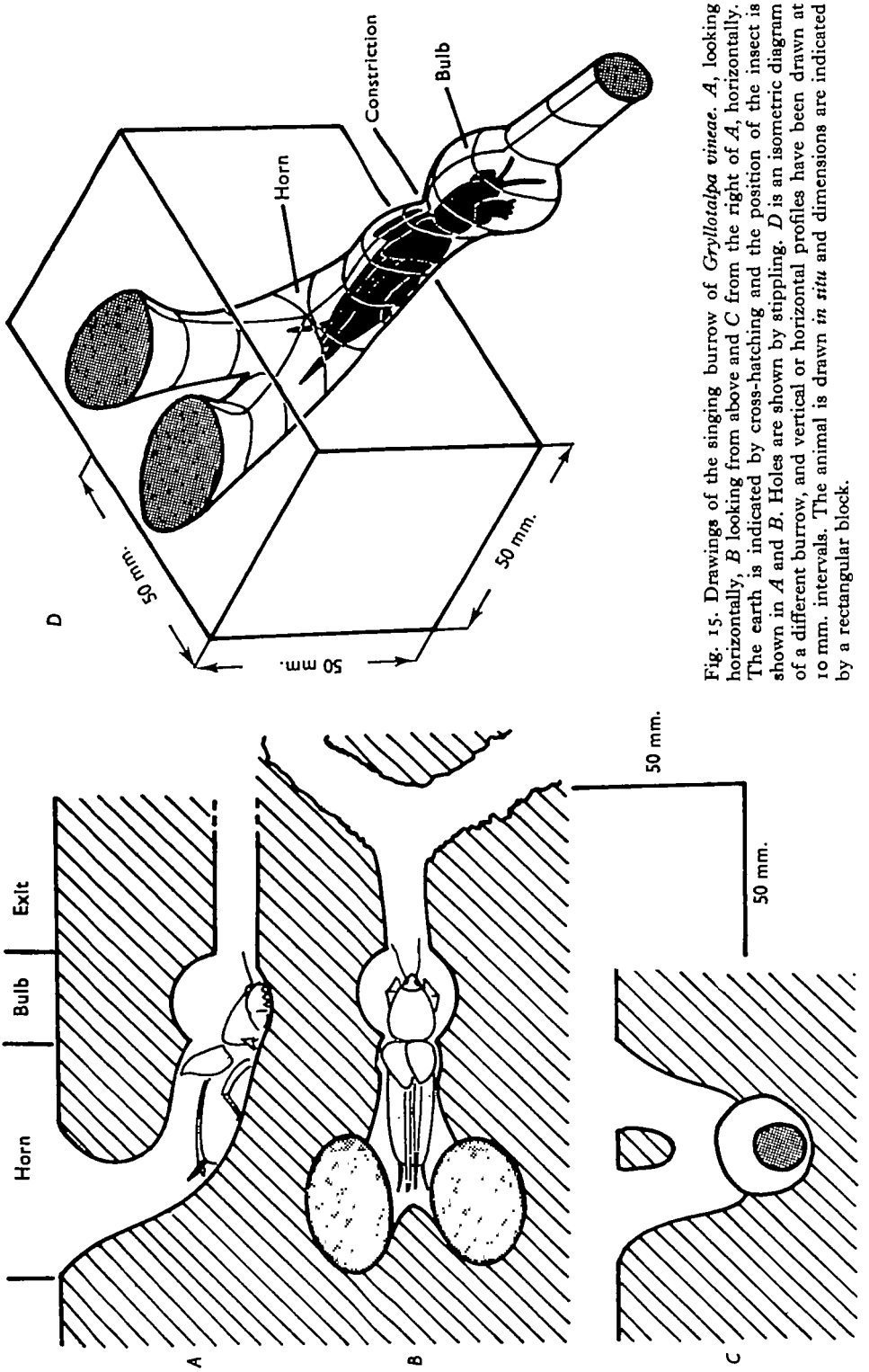

Fig. 15. Drawings of the singing burrow of *Gryllotalpa vineae*. *A*, looking horizontally, *B* looking from above and *C* from the right of *A*, horizontally. The earth is indicated by cross-hatching and the position of the insect is shown in *A* and *B*. Holes are shown by stippling. *D* is an isometric diagram of a different burrow, and vertical or horizontal profiles have been drawn at 10 mm. intervals. The animal is drawn *in situ* and dimensions are indicated by a rectangular block.

placing a trowel (or even a finger) through the inner part of the burrow. While singing it is not greatly affected by ground vibrations; this is hardly surprising as the sound level at the mouths of the burrow is about 115 dB. and this presumably saturates all the insect's mechano-receptors.

The insect does not move appreciably while it is singing; and as the burrow is in the form of a double horn set in a flat infinite baffle, the ground surface, it is reasonable to regard the system as a fixed source operating at a single frequency. This assumption has been made in § 4.

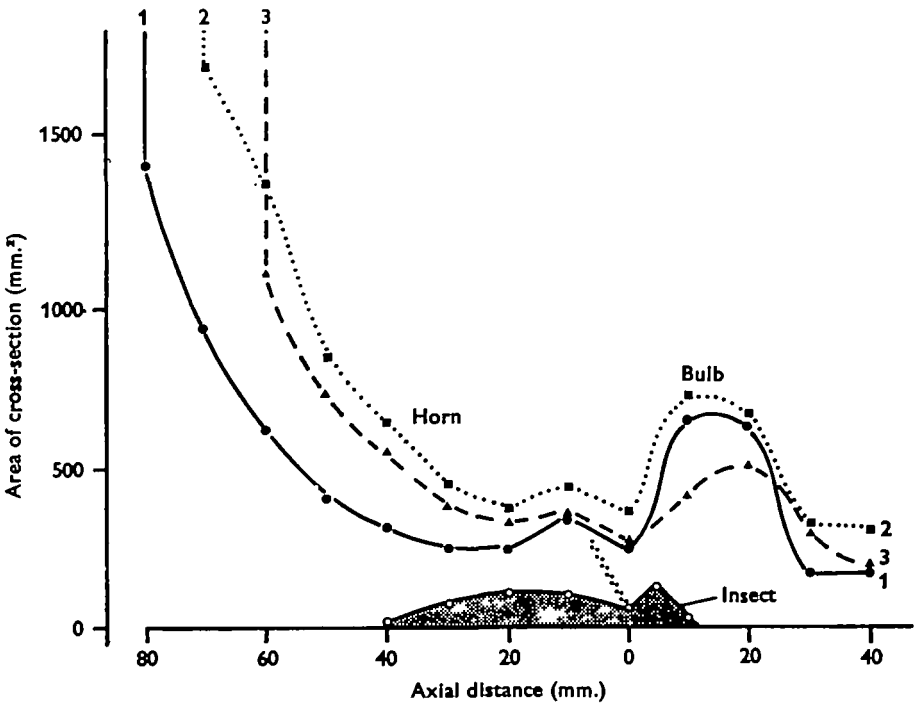

Fig. 16. Plots of the cross-sectional area of three singing burrows of *G. vineae* against the distance along the axis, measuring from the constriction at the outer side of the bulb. The stippled area indicates the position occupied by the animal and its area of cross-section.

The burrow expands in cross-sectional area from the bulb outwards. By measuring a number of burrows at intervals along their length, the rate of expansion of the horn-like mouths has been calculated. The burrow is treated here as if it were a single horn; after it has divided, near the surface, the cross-sectional area is taken as the sum of the areas of the two channels. Fig. 16 is a plot of the cross-sectional area along the length of three typical burrows. The datum that is adopted for the long axis is the constriction at the outer end of the bulb; this is where the forewings (or diaphragm of the transducer) are placed during singing (Fig. 15*A*, *D*). The stippled area in Fig. 16 represents the insect. The area of the cross-section of the insect has been calculated from measurements of dead insects and makes a considerable difference to the effective size of the burrow.

The burrows expand at a nearly exponential rate. They can thus be considered as exponential horns.

The acoustic performance of exponential horns has been treated in detail by Olson (1957). An exponential horn is an acoustic transformer which presents a high resistive air load to a small diaphragm and thus increases the efficiency with which energy is radiated since a larger proportion of the mechanical work performed by the driving system is converted to sound.

Thus the acoustical resistance presented to the diaphragm by the throat of the horn is important in determining the efficiency of the system. The resistance of the horn throat can be calculated when its rate of expansion or flare is known.

The flaring constant, m, measured in inverse millimetres, is given by

$$S = S_0 e^{mx}, \tag{2}$$

where S is the cross-sectional area in mm.^{2} at an axial distance of x mm. from a point where the cross-sectional area is S_0 mm^2. The flaring constant can be used to determine the frequency at which the throat resistance of the horn falls to zero, or the lowest frequency that can be radiated. This frequency, f, is given by

$$f = mc/4\pi, \tag{3}$$

where m is the flaring constant and c is the velocity of sound in air.

The flaring constant and the cut-off frequency have been calculated for the three horns illustrated graphically in Fig. 16. These parameters are shown in Table 4.

Table 4. *Various measurements of the singing burrows of* G. vineae *shown in Fig.* 16

Burrow number	1	2	3
Distance in which area of cross-section doubles, near mouth	19 mm.	20 mm.	20 mm.
Area of throat, corrected for presence of the insect	240 mm.^{2}	340 mm.^{2}	220 mm.^{2}
Measured volume of bulb	11,700 mm.^{3}	15,500 mm.^{3}	10,250 mm.^{3}
Calculated volume of bulb from formula (4)	13,200 mm.^{3}	19,700 mm.^{3}	12,700 mm.^{3}
Flaring constant of horn, in inverse mm., from formula (2)	0·0365	0·0345	0·0345
Cut-off frequency from formula (3)	980 Hz	930 Hz	930 Hz

It will be seen that the cut-off frequency for all the horns is about one-third of the frequency produced by the animal. The situation described above only applies strictly to infinite horns and is more complex for horns of finite length. Here the throat resistance does not fall sharply to zero near the cut-off frequency but falls more gradually and may fluctuate in value at higher frequencies. In addition, the horn throat shows considerable inertance, or inductance, at low frequencies. While a detailed treatment of the properties of horns is not necessary for an understanding of the acoustics of the mole cricket's horn, two factors are important.

Since at frequencies above but close to the cut-off frequency the throat resistance is low, the efficiency of the horn as a transformer is reduced. More important, since

the throat has substantial inductance at these frequencies, the particle velocity in the throat will not be in the same phase as diaphragm velocity in a simple horn.

This property of horns has been considered by Klipsch (1941), who suggests that the throat inductance can be offset or tuned by a suitable acoustic capacitance or air chamber placed behind the diaphragm. When this is done the acoustic load of the diaphragm becomes resistive since the horn acts as a series resonant circuit.

Klipsch simplifies the calculations and shows that the volume of the air chamber can be calculated from the area of the throat of the horn and length in which the horn cross-sectional area doubles; the volume, V, in cubic millimetres, is given by

$$V = 2{\cdot}9\,AR, \tag{4}$$

where A is the throat area in mm.^{2} and R is the axial distance in which the cross-sectional area doubles in mm.

He points out that the theoretical calculation does not apply precisely to practical horns as the inductance is less for a finite horn than for an infinite one and that, in practice, the optimum volume of the air chamber should be less than the formula provides.

Klipsch's formula tunes the horn inductance at or close to its flare cut-off frequency. If the bulb in the mole cricket's horn is regarded in the same way, various factors must be considered. The insect is producing a sound at a frequency rather above the horn cut-off frequency and so the horn must be tuned to this frequency. Unlike the Klipsch horn, the insect's air chamber has two outlets, the horn throat and the exit hole to the rest of the burrow; these must be regarded as inductances in parallel. The true inductance of the system is lower than a study of the horn alone would indicate, and so the horn will be tuned at any given frequency by a larger air chamber than simple theory predicts.

In Table 4 the terms in Klipsch's formula (4) are given for the three horns of Fig. 16. From these the volume of the air chamber is calculated, and this may be compared with the measured value for the volume. It will be seen that the agreement is quite close and that, within the conditions given in the previous paragraph, it may be assumed that the insect modifies its burrow so that it presents a resistive load at its throat to the diaphragm formed by its wings. The reason for this is quite clear. The wings do not hug the walls of the burrow very closely nor can they be made to do so by the nature of the wing movement that produces the sound. If the horn throat presents considerable inductive reactance, the particle movement will not be in phase with the wing vibration and so a component of the sound will escape around the edges of the wings to the inner side of the burrow. If the horn throat is tuned, however, energy will not be lost in this manner but will be transformed in the horn and radiated. A component of the energy will still be lost in the inner part of the burrow, but this will be lost anyway so the overall efficiency of the system is greatly improved.

It is a striking support of the present hypothesis that the song is louder on wet evenings when, presumably, the walls of the horn do not absorb sound to the same extent as dry porous soil.

Unfortunately, there are too many unknown factors in the acoustics of the complete system to make a rigorous treatment of the horn at all easy. I feel that the explanation given here is sufficient to justify the argument.

The horn is, in fact, double. There are two mouths which are separated by a distance of about $\frac{1}{2}$ the sound wavelength and which are about $\frac{1}{3}$ the wavelength in diameter.

Double sources have directional properties but it is probably more realistic to treat the mole cricket's horn as a line source because the directional properties of horns that have lost the plug that divides the mouth are very similar to those of the usual double horn. With a line source the directional response can be calculated using a formula quoted by Olson (1957). The response at an angle $\alpha°$, $R\alpha$, relative to the response normal to the source is given by

$$R\alpha = \frac{\sin\left[(\pi l/\lambda)\sin\alpha\right]}{(\pi l/\lambda)\sin\alpha}, \tag{5}$$

where l is the total length of the source and λ is the wavelength of the sound. The mole cricket's horn, consisting as it does of two finite sources, cannot justly be considered as a pair of point sources though this treatment gives similar results. Fig. 17 plots the isobars along the long axis and along the short axis for a source 50 mm. long and 25 mm. across, radiating a sound of wavelength 95 mm. The sound level normal to this source is taken as unity and the isobar has been plotted using the inverse square law. The three-dimensional isobar is a surface of rotation of one curve upon the other. It will be seen that the shape of this curve is closely similar to the radiation pattern produced by the animal (Fig. 14). The directional properties of model burrows of the same size are closely similar to those of the insect's horn.

The insect builds quite a complex burrow to provide a suitable acoustic load to its wings for the efficient production of the calling song. The advantage of producing a beam of sound is discussed in greater detail later.

The present assertion is that the horn loads the insect's wings in a resistive manner. If this is the case it should be possible to calculate the amplitude through which the wings must vibrate to produce the power output that has been observed.

The power output P, in watts, may be calculated from a formula quoted by Olson (1957)

$$P = \frac{\rho c\,(2\pi f)^2\, d^2 A_d^2\, 10^3}{2A_h}\ \text{watts}, \tag{6}$$

where ρ is the density of air, c is the velocity of sound, f is the frequency, d is the amplitude of the vibration, A_d is the diaphragm area and A_h is the area of the horn throat, all in S.I. units.

The throat area of the horn is about 200 mm.^{2}. The amplitude of vibration of a diaphragm in this horn is plotted against the area of the diaphragm for powers of 1·5, 3 and 6 mW. in Fig. 18. The area of both harps is about 26 mm.^{2}, the area of the proximal rather rigid part of the two dorsal fields is about 80 mm.^{2} and the area of the two wings is about 280 mm.^{2}. The depth of the teeth on the pars stridens is about 25 μm. and the tooth pitch is about 115 μm. It will be seen that the requisite power is either produced by both harps vibrating with the amplitude of the tooth pitch or by both dorsal fields vibrating through slightly more than the tooth depth. While this finding is a gross simplification, it suggests that the mechanism proposed here is feasible. A more rigorous treatment is not possible without more detailed knowledge of the mode of vibration of the dorsal field of the wing.

6. *The calling song of* Gryllotalpa gryllotalpa

This insect is very much quieter than *G. vineae*. The fundamental frequency of the song is 1·6 kHz and the pulse consists of about 20 cycles of the tone (Fig. 19). The teeth of the pars stridens are far smaller and more numerous than those of *G. vineae*, with a maximum pitch of 35 μm. and depth of 10 μm. The total area of the two harps is about 16 mm.^{2}. The singing insect is far more sensitive to ground vibrations than *G. vineae*, and so it is very difficult to measure the sound-pressure level of the song in sufficient detail to estimate the total power output. A typical value of peak sound-

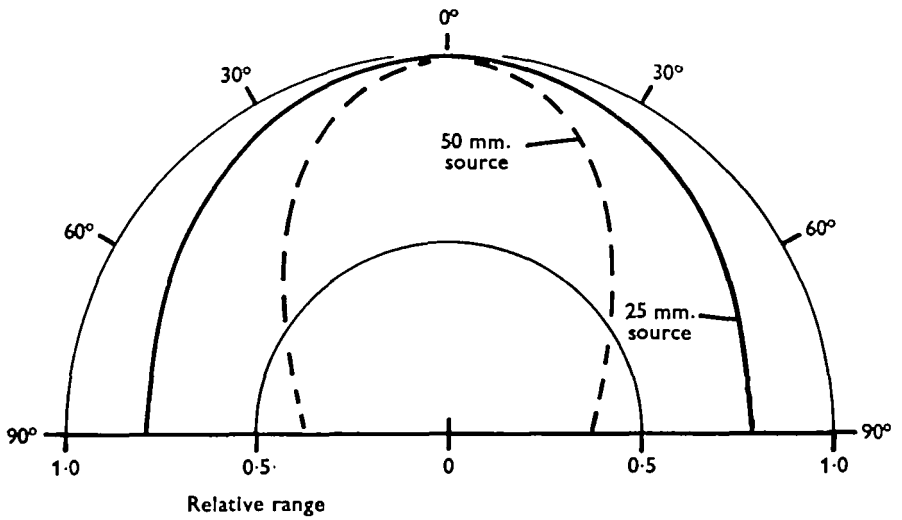

Fig. 17. Directional properties of a line source 50 mm. long and 25 mm. wide radiating a sound wavelength of 95 mm. Formula 5 is used to calculate the response relative to the axial response and this data is re-treated to give the radial distance to the isobar. The properties in three dimensions are given by a surface of rotation of one line on the other. - - - - -, The isobar for a 50 mm. long source; ——, the isobar for a 25 mm. long source.

pressure level at 1 m. vertically above the burrow is 72 dB. or $1{\cdot}25 \times 10^{-5}$ W.m.^{2} and the mean sound-pressure level is about 66 dB. The sound distribution is probably similar to that of *G. vineae*. Assuming a hemispherical distribution over a total area of about 6 m.^{2}, the mean power output of this species is about $2{\cdot}5 \times 10^{-5}$ W. and the peak power is $7{\cdot}5 \times 10^{-5}$ W. However, these estimates are probably too high.

The wings of this species are far smaller than those of *G. vineae*, and as the teeth of the pars stridens are smaller and the song frequency lower it is not surprising that the song is quieter.

The singing burrow is far larger than that of *G. vineae*. It is very irregular, but a typical structure seems to be that there is a double horn with mouths spanning an area about 100 mm. wide and 30 mm. long. This chamber is constricted in its middle and it is thought that the insect places its wings at the outer side of this constriction (Fig. 20). The burrow may have up to six holes at the surface, and these are approximately in line. As the sound wavelength is 210 mm., the source is a line about $\frac{1}{2}$ wavelength long and will have similar directional properties to the horn of *G. vineae*. This

has not been established with confidence owing to the rather low sound level and to the extreme care that is required to avoid disturbing the animal.

Measurements made on three of the more regularly shaped burrows have been treated in the same way as those for *G. vineae* and the results are displayed in Table 5. It is surprising that the burrow appears to have a cut-off frequency that is higher than

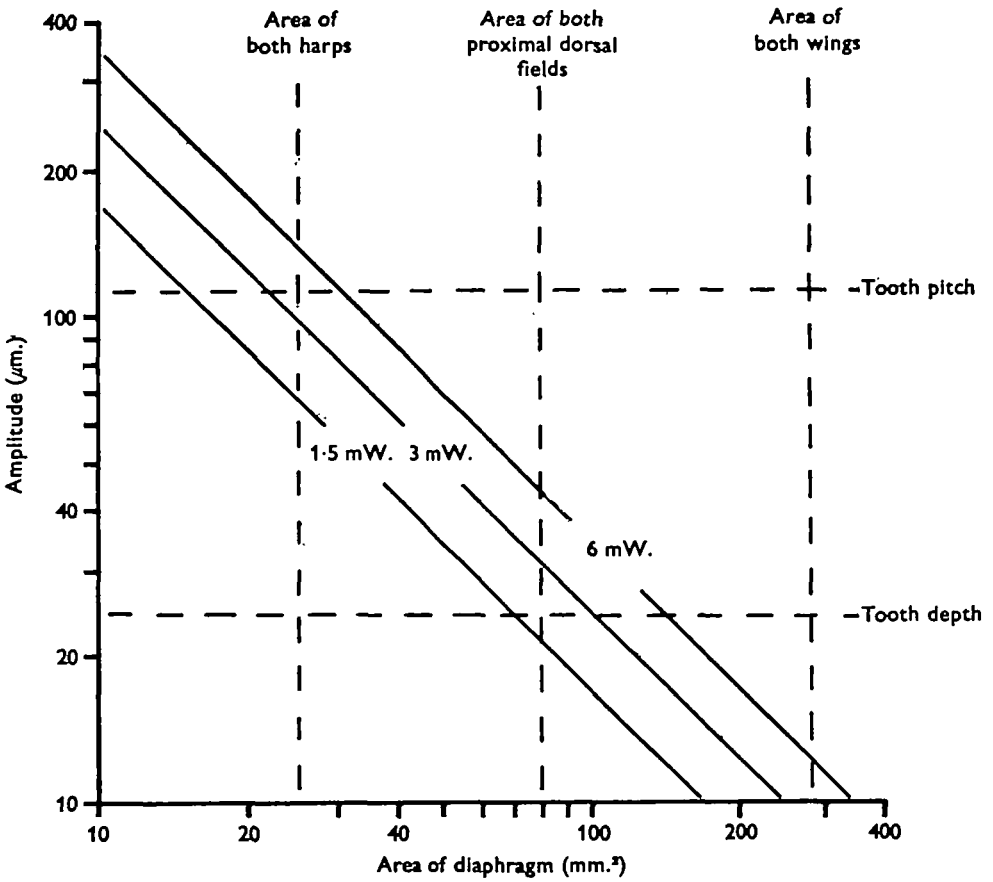

Fig. 18. Graphs of amplitude of vibration of a diaphragm against the area of the diaphragm for a horn-throat area of 200 mm.² and a frequency of 3·5 kHz. The graphs are calculated from formula (6).

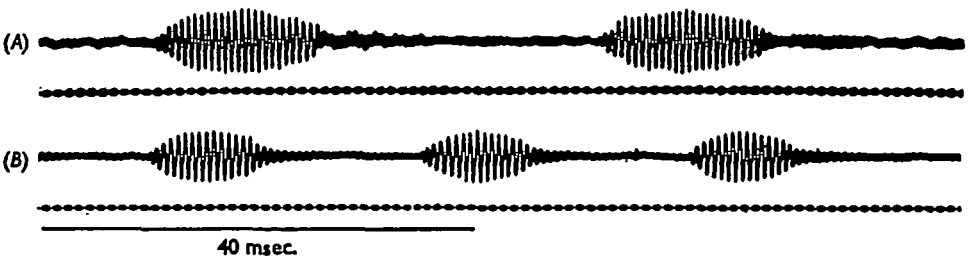

Fig. 19. Oscillograms of the song of *Gryllotalpa gryllotalpa* recorded in the field. *A*, at 12° C., has a longer pulse than *B*, at 16° C. The former signal shows some evidence of double firing of the muscles. Time markers at 1 msec. intervals.

that of *G. vineae*. The volume of the inner bulb is larger but is also close to the value predicted by formula (4). It seems quite likely that the mechanism is very similar to that of *G. vineae*.

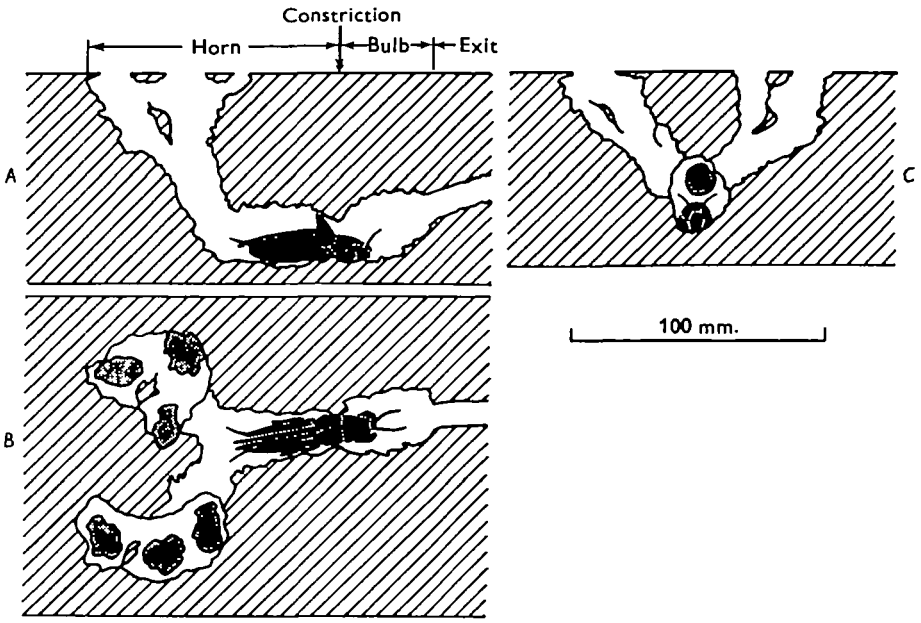

Fig. 20. Diagrams of the singing burrow of *Gryllotalpa gryllotalpa*. (*A*) Side view; (*B*) from above, with the holes at the surface stippled; (*C*) looking from the right of (*A*). In all, the position of the insect is shown. This diagram is made from a plaster cast; the burrows of this species are far less regular than those of *G. vineae*.

Table 5. *Various measurements of the singing burrows of* G. gryllotalpa

Burrow number	1	2	3
Distance in which area of cross-section doubles	*c.* 18 mm.	*c.* 18 mm.	*c.* 16 mm.
Area of throat, corrected for the presence of the insect	*c.* 300 mm.^{2}	*c.* 400 mm.^{2}	*c.* 330 mm.^{2}
Measured volume of bulb	*c.* 12,500 mm.^{3}	*c.* 16,000 mm.^{3}	*c.* 13,000 mm.^{3}
Calculated volume of bulb from formula (4)	15,600 mm.^{3}	21,000 mm.^{3}	16,000 mm.^{3}
Flaring constant of horn in inverse mm.	0·038	0·038	0·043
Cut-off frequency	1030 Hz	1030 Hz	1150 Hz

Owing to the difficulty of measuring the burrows of this species, these values are only approximate.

A calculation, using formula (6), of the diaphragm amplitude required to produce the estimated $7{\cdot}5 \times 10^{-5}$ W. at 1600 Hz from a diaphragm of area 16 mm.^{2} with a horn throat of 250 mm.^{2} is 59 μm. As the tooth pitch on the pars stridens is 35 μm., the mechanism suggested here is plausible.

Gryllotalpa vineae appears to produce its song from single-excited muscle twitches, but there is some evidence, from the two pulse lengths found with *G. gryllotalpa*

(Fig. 19), that the song pulse is sometimes produced from double-excited twitches; in *G. gryllotalpa*, the normal pulse lasts about 15 msec. and the abbreviated pulse lasts about 9 msec. The wing mechanism, the diaphragm, of *G. gryllotalpa* appears to be loaded by an acoustic resistance. Even so, the acoustic output is very much less than in *G. vineae*. It is likely that in *G. gryllotalpa* a far smaller proportion of the mesothoracic musculature is involved in sound production; the available power is about 1 mW. but the mean sound power output is $\frac{1}{40}$ of this—$2{\cdot}5 \times 10^{-2}$ mW.

7. *The song of* Gryllus campestris

This insect was observed on several afternoons, when the air temperature was rather high, from 26° to 35° C. The insects sing regularly but the song consists of trills of three or four long syllables, each containing about 60 cycles of fundamental frequency 4·3–4·5 kHz. Since the insect sits above the ground, with the wings at about $\frac{1}{5}$ wavelength above the surface, reflexion cannot be ignored, though an estimate of the sound output of the insect can be made. The mean sound-pressure level at 1 m. vertically above the insect does not exceed 70 dB. and is similar over the surface of a hemisphere of this radius. As all the major dorso-ventral muscles are activated during the sound-producing stroke (Bentley & Kutsch, 1966), the muscular power input to the system probably approaches the value of 1·2 mW. estimated in § 2.

Fig. 21. Oscillograms of the sound produced by aggressive stridulation of *G. vineae*. Though the fundamental frequency is about 3 kHz, the sound lacks the purity of the calling song. Time markers are at 1 msec. intervals.

There is a fundamental difference in the configuration of the wing in this insect. In *Gryllotalpa* radiation is from one side of the wing and the acoustic load is mainly resistive and a high conversion efficiency is achieved. In *Gryllus* the source may be regarded as a small diaphragm, the harp, set in the surface of the wing which acts as a baffle. As the sound wavelength is about 75 mm., and as the path from front to back of the harp is 20 to 25 mm., about $\frac{1}{3}$ wavelength, considerable destructive interference of radiation from the back and front of the wing is to be expected. Simple and approximate calculations based on data in Olson's chapter 5 suggests that if the system is treated as a disk of radius 10 mm., the radiation resistance will be about 0·02 that of the same disk set in a suitable horn. In practice, since the system is resonant, this is a gross simplification as it takes no account of the losses that must occur in the wing membrane or of the possibility of slight horn loading of the lower side of the wing by the ground and abdomen. The point is that for such a vibrating system the resistance of the air load is far smaller than for the horn-loaded wing and so the efficiency that

will be realized in a practical system is far less. The mean sound power of *Gryllus* is about 6×10^{-5} W. and the efficiency is about 5%. The mechanical input is $1{\cdot}2 \times 10^{-3}$ W. This is to be compared with a similar efficiency, at a far lower frequency, and from far smaller wings for *Gryllotalpa gryllotalpa* and an efficiency of about 30% at a similar frequency and with similar-sized wings for *Gryllotalpa vineae*.

8. *Aggressive stridulation of* Gryllotalpa vineae

On various occasions *Gryllotalpa vineae* was induced to chirp outside its burrow. The mole cricket reacted to mechanical stimuli with a very brisk aggressive stridulation in which the wings were raised about 40° above the rest position and were closed through about 20°. The sound was somewhat impure (Fig. 21) and, at a distance of 1 m. and at 25° C., had an intensity of 74 dB.; although little reliance can be placed on measurements made on these impure waveforms the apparent power is $\frac{1}{25}$ of that produced by the insect in its burrow.

DISCUSSION

The calling song of *Gryllotalpa* is far purer and shows far less change of frequency in the pulse than does that of other gryllids. Analysis of the song of *Gryllus* by Leroy (1962) has shown second harmonics at about −15 dB. and a frequency shift in the pulse of 10%. In tree crickets Walker (1962) has shown that both the pulse rate and the pulse fundamental frequency are lower at lower temperatures, and this all suggests that the resonance of the frame of the harp found by Bailey (1970) may have a different function in crickets from that in bush crickets.

The wings of singing crickets are held about 40° above the body to form a sector of a sphere. In stridulation, the diameter of this spherical surface collapses, and from the action of the plectrum and pars stridens this collapse will contain a harmonic component whose frequency is more or less determined by the resonance of the harp frame. Thus it may be more realistic to regard the radiating system as a pulsating sphere whose frequency is determined by the harp resonance. The pars stridens can then be regarded as an escapement which determines the amplitude of pulsation of the sphere and this would appear to fit the evidence on singing better than the alternative, an analogy of Bailey's work on *Homorocoryphus* (1970), that regards the veins of the frame of the harp as the radiating surface. This is not to reject Bailey's findings but to ascribe to them a different function in the lower-frequency song of crickets.

The actual frequency of the vibration is determined by many factors, one of which, the effective mass of the two wings, has been considered in § 1. The frequency will also depend on the driving force and the mass of the air load. In *Gryllotalpa* the air load is large and the body temperature is probably high and constant so the effect of the change of effective wing mass during the pulse is far smaller than in *Gryllus*. The substantially resistive acoustic load will greatly increase the coupling between the two harps in *Gryllotalpa* and hence tend to sharpen the resonance; this coupling is less in *Gryllus* and still less in those gryllids that hold their wings more or less vertical (*Oecanthus*, *Orocharis*, *Anaxipha* and *Cyrtoxipha*; Alexander, 1962) and have rather low-frequency songs (*Oecanthus*), or have very small wings (*Nemobius*). In these, the song frequency can be driven over a wide range of up to half an octave (Walker, 1962),

butt he song of *Gryllus*, produced from the pulsating sphere type of source considered earlier, where the coupling between the wings will be greater, is very much less variable. It is not surprising that the song made by *Gryllotalpa* outside the burrow lacks the purity of the song from the burrow (Fig. 21).

An efficiency of 30% for an acoustical transducer is fairly high; a typical domestic loudspeaker, covering a band of frequencies, has an efficiency of less than 2%. However, an efficiency of less than 100% implies that other resistance or damping exists in the system. Some of the more obvious losses will occur by the absorption of energy dy the membrane of the wing and by the substrate.

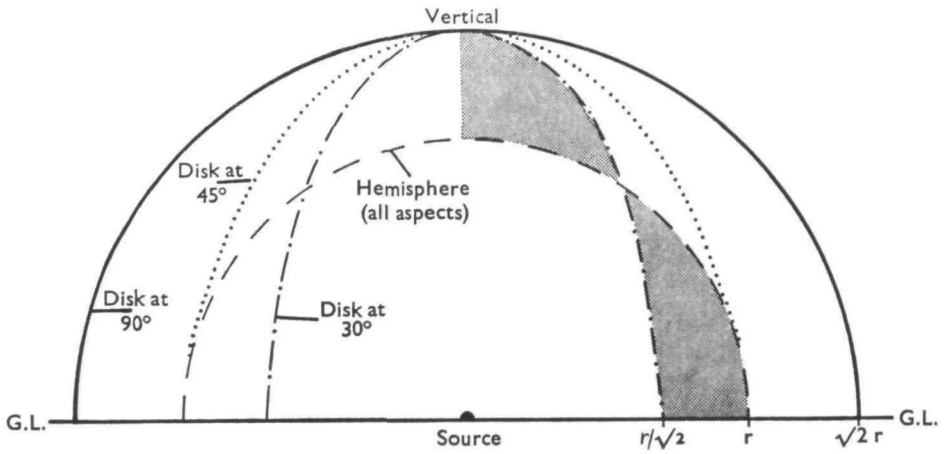

Fig. 22. Diagram comparing the apparent surface areas of a hemisphere and a semicircular disk when viewed from a distance. The radius of the disk is $\sqrt{2}$ times the radius of the hemisphere; their true surface areas are thus identical but the apparent surface area of the disk, viewed normal to its centre, is twice that of the hemisphere. The aspect at an angle of 30° to the plane of the disk is of the same area as the hemisphere at any aspect; the stippled regions are equal in area. For a fuller description, see text.

Even though the harp system is resonant, the surround consisting of the anal node and the distal parts of veins A and Cu 2 are probably not important to the resonant system but all the same are considerable masses of wing that are subjected to oscillation at the song frequency. These masses will cause loss regardless of the air load upon the wing. Unfortunately, I do not have sufficient data to make an accurate calculation of the loss from this cause; an indication of its probable magnitude is given by the following considerations.

In the course of the sound-producing stroke the dorsal fields of the two wings close step-wise and, very approximately, the length of this step is 100 μm. in *G. vineae*. Each step lasts about 0·3 msec., the period of the cycle of the sound. When the dorsal field is brought to rest by the gathering of the next tooth on the pars stridens the kinetic energy is dissipated, some as sound and some as heat. A proportion of the energy may be stored by the elasticity of the wing membrane and cross-vein, r-cu, but at this frequency the stored energy is likely to be a small proportion of the total.

If the assumption is made that the dorsal field is accelerated from rest to move

100 μm. in 0·3 msec., the power to perform this task can be calculated. Power, in watts, is given by

$$P = x^2 m/t^3 \tag{7}$$

where x is the linear displacement in metres, m is the mass of the system in kg. and t is the time in seconds. The whole wing of *Gryllotalpa vineae* weighs some 12 mg. and the dorsal field about 5 mg.; to move 5 mg. from rest through 100 μm. in 0·3 msec. requires a power of 1·85 mW.

For *Gryllus campestris*, where the dorsal field of the wing weighs about 4 mg., the tooth pitch on the pars stridens is about 40 μm. and the song has a period of 0·23 msec., the power involved in a step-wise closing of the wings is 0·53 mW. A simple consideration of the energetics favours the flexible coupling between the dorsal and lateral fields of the wings (§ 1 of the Results and Fig. 2) since it halves the mass of the wing that must vibrate at the fundamental frequency of the song as well as reducing the damping on the harp area.

While this estimate takes no account of the possibility that the wing does not move in a linear manner, it is valuable as an indication of the sort of losses that will occur in a system of this type. The difference between *Gryllotalpa vineae* and *Gryllus campestris* now becomes clearer; in the former, where the wing has a substantial air load, the proportion of the total power input that is radiated as sound energy is far higher than in *Gryllus*, where the air loading is far smaller.

This attempt to draw up a balance sheet for the energetics is unashamedly incomplete. By the very nature of the radiation it is difficult to measure sound powers to an accuracy of better than 1 dB., an accuracy of $\pm 25\%$, and throughout this work I have erred on the side of under-estimation; the efficiency of sound production in *Gryllotalpa vineae* may be nearly 50% and the energy balance offered here may be nearly perfect.

I have assumed that the muscles of *Gryllotalpa* are producing the same power as locust muscle at 30° C. Although the air temperature was far lower, at 12° to 16° C., it is likely that the singing insect is somewhat insulated by its dense thoracic pilosity and by its burrow. There is a warm-up period of about 10 min. and such a period serves in a moth (*Celerio lineata*) to warm the body muscles by 18° C. (Adams & Heath, 1964).

In this context it is interesting to note that in the two species of *Gryllotalpa* the song differences are of fundamental frequency where in gryllids (Walker, 1957, 1962) the interval between pulses may be more important. Where the two sexes of gryllids are likely to be at similar temperatures this is not so for *Gryllotalpa* where the male is insulated in his burrow but the questing female is at the far lower temperature of the surrounding air. In resonant pulse-producing systems of the type found in grylloids, the fundamental frequency within the pulse is not much affected by temperature but the pulse repetition rate is (Fig. 10). The fundamental frequency of the pulse and the continuous nature of the trill should be sufficient to ensure positive identification of appropriate male mole crickets by the females.

I have not seen mole crickets of either species in flight but White (1789) writes 'When mole crickets fly they move "curso undoso", rising and falling in curves'. Those *Gryllotalpa gryllotalpa* of both sexes that I dissected had only very small metathoracic flight muscles, weighing in all some 70 mg., but these were evidently

in an undeveloped state. By contrast, the flight muscles of *G. vineae* were large, weighing some 300 mg. or about $\frac{1}{10}$ of the total weight of the insect. It is likely that the latter species, at any rate, could fly.

The sensitivity to sound of a gryllid, *Gryllus abbreviatus*, is about 60 dB. at 5 kHz (Wever & Vernon, 1959). With the same sensitivity, for *Gryllotalpa vineae* and a sound-pressure level of the calling song of 90 dB. at 1 m., the maximum range of the song is 30 m. By contrast, the range of *Gryllus* is only about 5 m. However, the song of *Gryllotalpa vineae* is beamed and the maximum range is only achieved along the axis of the horn. At ground level, in line with the two mouths of the horn, the range is about $\frac{1}{4}$ of the maximum (Fig. 16). As this is a feature of the sound distribution of both species, and as it is the result of an increase in the complexity of the horn, such a sound distribution must have some selective advantage.

The surface area of the 80 dB. isobar of *G. vineae* is 12 m.^{2}. A hemisphere of similar surface area has a radius of 1·38 m. When the sound distribution is a disk, the maximum range is increased; the maximum range of the 80 dB. sound pattern of *G. vineae* is 2·23 m. (Fig. 16). It is useful to consider what the optimal sound distribution for a calling song may be.

It is assumed that the female insect is flying horizontally, at an unspecified height but fairly near the ground, on a random bearing. Two simple sound distributions will be examined: a hemisphere, as will be produced by a point source in an infinite baffle, and a semicircular disk of the same power, as will be produced by a line source in an infinite baffle. As the sound power is the same, the total surface areas of the two surfaces will be the same. The surface area of a hemisphere is $2\pi r_s^2$, but the area of a circle is πr_c^2.

For $2\pi r_s^2 = \pi r_c^2, r_c = \sqrt{(2r_s)}$. This is shown diagrammatically in Fig. 22. When a hemisphere of radius r is viewed from a distance it appears of the same area as a semicircle of radius r. By contrast, the semicircle of radius $\sqrt{2}r$ has twice the area of the hemisphere when viewed from a position normal to its centre. When viewed from an angle 60° off centre, it appears as an ellipse of major axis $\sqrt{(2r)}$ and minor axis $r/\sqrt{2}$ and thus of the same area as the hemisphere. Since the average angle of intersection of a horizontally flying insect with vertical disk will be 45°, it is clear that the ratio of effectiveness of the disk and the hemisphere in capturing a flying insect will be the ratio of the area of the disk, viewed at 45°, to that of the hemisphere viewed from any angle. Fig. 22 shows that the disk has a larger effective area; in fact, it will be $\sqrt{2}$ or 1·41 times as effective as the hemisphere. Even for very low-flying insects the disk beam is as effective as the hemisphere but its effectiveness increases with height. It is likely that a large insect will not fly very close to the ground at night so an increase in the effective range of the calling song will be of considerable advantage, particularly in an insect that lives, as does *G. vineae*, at a very low density.

Mole crickets appear to be the only animals that modify their surroundings for acoustic purposes; it has been the aim in this paper to show how important such modification could be to the success of the insect.

SUMMARY

1. Sound production in the mole crickets *Gryllotalpa vineae* and *G. gryllotalpa* is compared with that in *Gryllus campestris*.

2. In all species action of the plectrum of the left forewing on the file or pars stridens of the right wing causes the harp areas of both wings to vibrate in phase with each other. As the lateral and dorsal fields of the wing are coupled flexibly, the dorsal field resonates freely.

3. The available muscular power of *G. vineae* is about 3·5 mW., of *G. gryllotalpa* about 1 mW., and of *Gryllus* about 1·2 mW. The mesothoracic musculature of *Gryllotalpa* is fairly similar to that of *Gryllus*.

4. The calling song of *G. vineae* has a fundamental frequency of 3·5 kHz, a pulse length of 8 msec. and a pulse interval of 14 msec. at 16° C. The song is very pure with a second harmonic of −26 dB. Simulations of the song made with modulated oscillators are of similar purity; the song can be regarded as a modulated pure note.

5. The sound distribution has been measured, and from the area of an isobar plot and calculation of the mean power of each pulse, the total mean sound power output is 1·2 mW. and the peak power 3 mW. The efficiency of conversion of muscular to acoustic power is about 35%.

6. *G. vineae* builds a double-mouthed horn-shaped burrow for singing. This contains a bulb which probably tunes the horn to act as a resistive load to the vibrating wings. The double mouths act as a line source with directional properties which concentrate the sound in a disk above the length of the burrow.

7. The probable advantage of a directed sound output in attracting mates is considered; the disk-shaped pattern will be better than a hemispherical pattern of similar power.

8. *G. gryllotalpa* also builds a horn, but this is larger than that of *G. vineae* and the song frequency is far lower, at 1·6 kHz. Although the sound power is far lower, about $2{\cdot}5 \times 10^{-5}$ W., the horn appears to act as a resistive load to the wings.

9. *Gryllus* produces only about 6×10^{-5} W. at 30° C. This is attributed to the small size and hence low radiation resistance of the wings.

10. Estimates are made of inertial losses that occur in sound production and these are shown to account for a substantial part of the mechanical power in the systems of both *G. vineae* and *Gryllus*.

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REFERENCES

ADAMS, P. A. & HEATH, J. E. (1964). Temperature regulation in the Sphinx moth, *Celerio lineata*. *Nature, Lond.* **201**, 20–2.

ALEXANDER, R. D. (1962). Evolutionary change in cricket acoustical communication. *Evolution, Lancaster, Pa.* **16**, 443–67.

BAILEY, W. J. (1970). The stridulatory mechanics of bush crickets: I. The tegmenal generator. (in the Press).

BENNET-CLARK, H. C. (1970). A new French mole cricket, differing in song and morphology from *Gryllotalpa gryllotalpa* L. (Orthoptera: Gryllotalpidae). *Proc. R. ent. Soc. Lond.* (B) **39**, (in the Press).

BENTLEY, D. R. & KUTSCH, W. (1966). The neuromuscular mechanism of stridulation in crickets (Orthoptera: Gryllidae). *J. exp. Biol.* **45**, 151–64.

BERANEK, L. L. (1949). *Acoustic Measurements*. Pp. vii+914. New York: Wiley.

BUSNEL, M-C. (1953). Contributions à l'étude des émissions acoustiques des Orthoptères: 1. Récherches sur les spectres de fréquence et sur les intensités. *Annls Épiphyt.* **4**, 333–421.

CHOPARD, L. (1951). *Faune de France*. Vol. 56, *Orthopteroides*. 359 pp. Paris: Lechevalier.

KLIPSCH, P. W. (1941). A low frequency horn of small dimensions. *J. acoust. Soc. Am.* **13**, 137–44.

LATREILLE, P. A. (1804). *Histoire Naturelle et Particulière des Crustacés et des Insectes*. Vol. 12, 424 pp. Paris: Dufart.

LEROY, Y. (1962). Le signal sonore d'appel sexuel comme caractère specifique chez les Gryllides. *Bull. biol. Fr. Belg.* **96**, 755–74.

NEVILLE, A. C. (1965). Energy and economy in insect flight. *Sci. Progr.* **53**, 203–19.

OLSON, H. F. (1957). *Acoustical Engineering*. Pp. xix+718. Princeton: Van Nostrand.

RAGGE, D. R. (1955). *The Wing Venation of the Orthoptera Saltatoria*. Pp. vi+159. London: British Museum (Nat. Hist.).

WALKER, T. J. (1957). Specificity in the response of female tree-crickets (Orthoptera. Gryllidae Oecanthinae) to calling songs of the males. *Ann. ent. Soc. Am.* **50**, 626–36.

WALKER, T. J. (1962). Factors responsible for intraspecific variation in the calling song of crickets. *Evolution Lancaster, Pa.* **16**, 407–28.

WEVER, E. G. & VERNON, J. A. (1959). The auditory sensitivity of Orthoptera. *Proc. natn. Acad. Sci. U.S.A.* **45**, 413–19.

WHITE, G. (1789). *The Natural History and Antiquities of Selbourne in the County of Southampton*. Pp. v+468+index. London: B. White & Son.