ACOUSTICS OF A SMALL AUSTRALIAN BURROWING CRICKET: THE CONTROL OF LOW-FREQUENCY PURE-TONE SONGS

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Summary

For most insects, size determines the call frequency. This paper describes the acoustics of a small brachypterous cricket (*Rufocephalus* sp.; body length 9.6 mm) producing a call with a carrier frequency of approximately 3.2 kHz from a subterranean burrow. Crickets such as *Gryllus campestris* are approximately twice this length and produce a call frequency close to 5 kHz. The burrow of *Rufocephalus* opens *via* a small hole with a diameter of 3.2 mm. The neck of the hole at approximately 1.4 mm depth opens to a vertical two-part burrow with an upper vase-shaped chamber 16.1 mm in height with a diameter of 9.4 mm. This top chamber connects *via* a 6.4 mm high (diameter 5.2 mm) neck to a more irregular chamber approximately 18 mm high with a width of approximately 11 mm. The walls of the top chamber neck and of the upper part of the lower chamber are smooth and appear to be sealed with saliva.

The song has a mean centre frequency of 3.2 kHz and is made up of variable-length trills of pulses of mean duration 15.8 ms. Many song pulses had smooth envelopes and their frequency did not vary by more than ±40 Hz from the centre frequency, with a relative bandwidth Q_{-3dB} of over 50. Other pulses showed considerable amplitude and frequency modulation within the pulse.

When driven by external sound, burrows resonated at a mean frequency of 3.5 kHz with a mean quality factor Q of 7.4. Natural-size model burrows resonated at similar frequencies with similar Q values. One cricket, which had previously called from its own burrow at 2.95 kHz, sang at 3.27 kHz from a burrow that resonated at the same frequency.

Life-size model burrows driven by external sound resonated at similar frequencies to the actual burrows; models three times life size resonated at one-third of this frequency. In all models, the sound pressure was more-or-less constant throughout the top chamber but fell rapidly in the neck of the burrow; the phase of the sound was effectively constant in the top chamber and neck and fell through approximately 180° in passing from the neck into the lower chamber. A numerical model of the sound flow from region to region gave essentially similar results.

A resonant electrical model fed from a high-impedance source with discrete tone bursts at different frequencies showed similar amplitude and frequency modulation to the various types of song pulses that were observed. It is suggested that the high purity of the songs results from close entrainment of the sound-producing mechanism of the insect's wings to the sharply resonant burrow.

Introduction

Sound communication among animals is constrained by their size and, because insects tend to be small, there are physical limits to both the power and frequency of the signal they can produce (Bailey, 1991; Bennet-Clark, 1998). As a consequence, there is a close correlation between the size of the sound-producing structure and the song frequency (Bennet-Clark, 1998). Because high frequencies are attenuated by the environment at a greater rate than low frequencies and because, for the most part, insects gain by transmitting the signal over the furthest distance, there is a constant trade-off between the

production of signals at high frequencies, which can be produced more efficiently, *versus* at low frequencies, which can travel further (Römer, 1993).

Insects have exploited three strategies to achieve effective sound transmission. First, concentrating the sound power within a narrow frequency band improves the effective signal-to-noise ratio and is achieved by the use of resonant sound-producing structures. The second requirement is for efficient coupling or impedance matching between the sound-producing structures and the surrounding air. Finally, related to both

sound power and increasing the insect's effective size, insects have exploited external structures that are larger than themselves (Forrest, 1982; Bennet-Clark, 1998).

The forewings of male crickets are specialised for sound production: a plectrum on the posterior edge of one wing engages with the teeth of a file on the underside of the opposite wing. Crickets sing by closing the forewings and thereby creating a series of catch-and-release actions between the plectrum and file, which in turn distorts specialised veins of the wings (the harp), exciting their resonant vibration (Nocke, 1971; for reviews, see Bennet-Clark, 1989; Bennet-Clark, 1999b). Each wing-closure causes a series of excitations of the harp resonators, which merge into a sustained coherent vibration that is radiated as a sound pulse.

Because the resonant frequencies of the harp regions of the two wings are similar and sharply tuned, cricket songs are musical and most songs are confined to a narrow frequency band corresponding closely to the resonant frequency of the harps (Nocke, 1971). However, this rather simplistically suggests that crickets produce pure-tone calls, although this is seldom observed: in many crickets, the frequency of the signal decreases within each pulse (Leroy, 1966; Simmons and Ritchie, 1996); the effective resonant frequency appears to decrease throughout the closing stroke (Bennet-Clark, 1999b). In this paper, we examine the extent to which a pure-tone carrier frequency can be maintained by a calling insect.

Efficient impedance matching between a vibrating structure and the surrounding fluid medium depends on the effective size of the sound-producing structure. For example, the radius of a monopole source that radiates sound from only one side should exceed one-sixth of the carrier frequency wavelength; if the source is a doublet, radiating sound from both sides, the effective radius should exceed one-quarter wavelength (Olson, 1957; Fletcher, 1992). Not surprisingly, where there has been strong selection on low-frequency pure-tone signals, insects have evolved second-stage transduction devices that effectively increase the size of the sound source.

Many insects that produce pure-tone sounds increase the power of the signal by coupling the sound-producing organ to a resonator (Forrest, 1982). These resonators can form part of the sound-producing structures themselves, but the insect may also use external structures to enhance the signal further. Such devices may include leaves as baffles (Forrest, 1982) or the specially shaped burrows of mole crickets that are tuned to the resonant frequency of the sound-producing wings (Bennet-Clark, 1970; Bennet-Clark, 1987; Daws et al., 1996). In cicadas, the primary resonators are small paired tymbals on the side of the abdomen which, in many cicadas, drive a Helmholtz resonator consisting of the abdominal air sac and ear drums (Young, 1990; Bennet-Clark and Young, 1992). A feature of both the mole cricket and the cicada systems is that the second stage of impedance matching increases the effective size of the sound source to close to the optimum and, since it is tuned to the carrier frequency of the song, tonal purity is maintained.

This paper describes a grylline system analogous to that of the mole cricket (Gryllotalpidae). The remarkably low frequency of the song, with its almost pure tone, is produced by a very small cricket, thus challenging the notion that small insects can produce only high-frequency calls. This example of an insect that uses external means to enhance its calling performance represents, to the best of our knowledge, the first description of a member of the Gryllidae using a complex tuned burrow for this purpose. We test the acoustics of such a system by natural experiment and also by developing both model burrows and model crickets. Finally, we draw comparisons between the subject of this paper, an undescribed species of *Rufocephalus*, and the acoustics of mole crickets.

Materials and methods

Insects

The cricket described in this paper is tentatively assigned to the genus *Rufocephalus* Otte and Alexander, 1983. The four *Rufocephalus* species described by Otte and Alexander (Otte and Alexander, 1983) occur several hundred kilometres north of our study site, extending from the Pilbara Ranges to the Kimberley Plateau in Western Australia. The song types of these four species are different from those described here, as are their carrier frequencies. It is almost certainly a new species within the genus and, throughout this paper, we therefore refer to it as *Rufocephalus*. Voucher specimens are lodged with the Australian National Insect Collection, Canberra.

Male insects were collected from the Coalseam Nature Reserve on the Irwin River north of Mingenew in Western Australia on three occasions in October and November 1999. Insects were located by their song during the night and dug up immediately after song recordings had been made. The insects made their burrows in red alluvial sandstone clays where the top 20–30 mm hardens to a crust-like cap. Some burrows were photographed while the insect was calling, enabling a measurement of the exposed length of their antennae. Insects were brought back live to Perth in separate specimen jars and were subsequently preserved in 70 % ethanol. Body dimensions of preserved insects were measured to the nearest 0.1 mm using a graticule eyepiece in an Olympus binocular microscope.

Measurements of song parameters

After the burrow opening had been located, recordings were made from a distance of approximately 150 mm. The microphone was a Tandy tie-clip microphone (catalogue no. 33-1052) fastened to the end of a 400 mm long 7 mm diameter plastic pipe; this was calibrated against a Bruel and Kjaer microphone (type 4165) and Bruel and Kjaer sound level meter (type 2209); its response was flat ±2 dB between 1 and 20 kHz. Recordings were made at 12 dB below peak level into one channel of a Sony TCD-D8 digital audio tape recorder, with a specified and measured frequency response that was flat ±1 dB from 20 Hz to 22 kHz. Recordings were voice-cued with the date and serial number of the insect. Between 30 and 60 s of recording were made for each insect.

Sound level measurements were made in the field using a

Bruel and Kjaer (type 2231) sound level meter with integrating module (type BZ7100) and microphone (type 4155). Both mean sound pressure and peak sound pressure levels were measured with a distance of 200 mm between the mouth of the burrow and the face of the microphone.

Tape recordings were analysed either using Signal (Engineering Design, Belmont, MA, USA) data-acquisition and analysis software or using the sound-acquisition input of an Apple Macintosh Powerbook 3400C and Canary 1.2.1 sound-analysis software sampling at 44.1 kilosamples s^{-1}. Pulse duration was measured directly from oscillograms; the dominant frequency was measured by Fast Fourier Transform (FFT), and cycle-by-cycle frequency was measured by zero-crossing analysis.

Most FFT analyses using the Canary software were made using a Hamming window and a 2048-point analysis window giving a filter bandwidth of 87 Hz. Most recordings were analysed without filtering, but in some cases where there was intrusive wind noise, frequencies below 500 Hz and above 12 kHz were removed before signal analysis with the 'filter out' tool in the Canary software; this filters by 30 dB in 50 Hz, regardless of the frequency. The harmonic content of different parts of song pulses was observed by similar filtering-out of the frequency band from 1 to 4.5 kHz and comparing the filtered pulse with the unfiltered one. The frequency spectra of short sections of sound pulses were analysed by copying part of the pulse and pasting it into the middle of a 0.5 s duration blank recording. To improve the resolution of the FFT analysis, single song pulses were analysed by copying them into a 0.5 s duration blank recording and making a 16 384-point analysis, giving a filter bandwidth of 10.9 Hz.

Resolution of the cycle-by-cycle or instantaneous frequency within the pulses was performed using ZeroCrossing ZC version 3 software written by K. N. Prestwich, which measures the time of zero crossing of the wave form to a precision of approximately 0.5 μs by exploiting the interpolation between sample points provided by the Canary software. Tests with 3 kHz sine-wave signals showed that the frequency of individual cycles was measured to less than ±5 Hz. Further tests showed that the method can give anomalous results with signals with any direct current component or where the signal-to-noise ratio is poor: the analyses reported here were made after using the software to filter out all signal components below 500 Hz and normally only with signals for which the signal-to-noise ratio exceeded 40 dB.

Burrows

Casts of burrows were made in the field by pouring dental plaster made up to a fluid consistency through the surface hole of the burrow. A 15 mm high ring of plastic water pipe was used to confine the plaster to the region of the mouth of the burrow. The casts were dug up the next day, and adherent soil was washed away.

Most dimensions of the washed plaster casts were measured to the nearest 0.1 mm using Mitutoyo digital callipers. Actual burrows in the soil were fragile, so the dimensions of the surface holes and other regions were measured optically in the laboratory or from photographs taken in the field with a reference scale. Further measurements were made directly from casts of burrows, which were dug up and then sectioned in the laboratory.

The porosity of different regions of the burrows was assessed by painting the inside of the burrow with cellulose paint and subsequent washing to remove soil particles. Surface roughness was measured from sections of the burrow cut after embedding the parts of the burrow in epoxy resin.

For acoustic tests, blocks of approximately the top 50–100 mm of soil, each containing a burrow, were dug up and transported to the laboratory. Acoustic testing was carried out after placing the block of soil containing the burrow on a 10 mm thick layer of cotton wool on top of a 100 mm thick layer of acoustic foam.

Tests with model burrows

Natural-size models of the burrow cavity were carved from paraffin wax to dimensions taken from representative plaster casts of the insects' burrows; any rough carved marks were smoothed with a warm soldering iron. The models were carved so that the dimensions of the surface hole, upper and lower chambers and neck (see Fig. 1) were within ±0.2 mm of the dimensions of the plaster casts of burrows, but the models were made with a longer neck at the surface hole and a long exit tunnel, giving a total length of 150 mm and without the natural and occasional deformations that occurred in the casts of the burrows. The wax models were cast in the centre of a 30 mm square block of plaster, so the wall thickness of the cast exceeded 10 mm. After the cast had set, it was dried and heated to melt out the wax. Holes 1.3 mm in diameter were drilled through the walls of the cast into the model cavity to allow the insertion of probe microphones; when not in use, these holes were plugged with wooden pegs. The sharp lip of the surface hole of the real burrow was simulated by grinding away any excess plaster left after the casting process.

The natural-size models were driven by an external sound source placed 40 mm from the top surface of the model, and measurements were made at 5 mm intervals along the length of the cavity as well as across the outside of the models at the plane of the surface hole (see Fig. 1). The strong resonances due to the 100–120 mm length of the cavity were damped by filling the lower half of the models with cotton wool; tests with a probe microphone inserted into the cotton wool showed (i) that the resonance seen in the upper part of the model did not appear at the bottom end of the model and (ii) that the sound was attenuated by over 40 dB relative to the peak pressures in the upper part of the models. Further, measurements in the upper parts of the model with the bottom end of the model sealed with modelling clay were the same as those with the end open.

A model cricket body was made from a cylinder (10 mm long and 3 mm in diameter) of modelling clay mounted on a straight length of 0.2 mm wire, which was inserted through the

bottom end of the plaster model. Using a scale attached to the wire, this was moved to measured positions along the length of the burrow.

A series of model burrows approximately three times natural size was made from 30 mm internal diameter by 45 mm internal length polyethylene film canisters, joined by lengths of 14.5 mm internal diameter polystyrene tubing. A variety of surface holes was provided by washers in which the hole had been chamfered to give a sharp edge. Holes 1.5 mm in diameter were drilled along the length of the model for the insertion of probe microphones. A 3 mm wide slot cut along the length of the top chamber of the model allowed the sound source to be moved along the chamber, where it was sealed in place with modelling clay. The modular construction allowed the dimensions of the models to be altered. Termination in the models was provided by a 300 mm length of 14 mm internal diameter plastic tubing filled with cotton wool. Variable porosity was provided by rows of 1.5 mm diameter holes in the walls of the model which could be sealed with modelling clay.

The relative amplitudes and phases of the inputs and responses of the models were measured directly from an oscilloscope. Phase was measured in degrees, and phase lead relative to that at the datum was, for convenience, given a positive value.

An electrical model of the burrow was made from a parallel LCR (inductor, capacitor and resistor: Fig. 12C, inset) resonant circuit in which a 20 mH inductor was tuned by a 0.15 μF capacitor to 2.9 kHz and adjusted with a 20 kΩ shunt resistor to a quality factor Q of 10. This was driven *via* a 22 kΩ resistor, which provided a source of similar impedance to that of the resonant circuit at its resonant frequency, from a Tektronix FG 501A function generator gated to produce tone bursts by pulses from a Digitimer DS9A stimulator, and measurements were made of the response across the inductor. The frequency within the tone bursts was set to the nearest 10 Hz using a Testlab M2365 multimeter.

Sound sources

The wings of crickets are held above the body, so there is sound leakage from the two sides around the edges of the wings. An appropriate model is a doublet source consisting of a moving diaphragm open on both sides so that the anti-phase sound radiated from one side interacts with that from the other side. A high-quality Sony 15 mm diameter earphone was removed from its housing and glued to a 2 mm square support rod parallel to the plane of its diaphragm. The back of the diaphragm radiates sound through small ports in the earphone surround anti-phase with that radiated from the front of the diaphragm. To balance the output from the two sides of the diaphragm, a 12 mm diameter disc of adhesive tape was attached to occlude the central part of the front face of the earphone. The following tests confirmed that the source acted as a suitable dipole or doublet source: first, the phase of the sound output at the front of the source differed by 180 ° from that at the back; second, measurements made by moving a probe microphone in a straight line normal to the plane of the diaphragm, 1 mm away from the edge of the earphone, showed a nearly symmetrical V-shaped distribution of sound pressure on either side of the diaphragm with a null at the plane of the diaphragm and a 180 ° phase shift either side of the null.

Burrows and models were also driven externally by an unmodified Sony earphone mounted on a 2 mm square support rod at a range of 50 mm from the surface hole with the centre of the diaphragm on the axis of the burrow.

Both sound sources were driven directly by a Hewlett Packard 8111A pulse and function generator gated to produce discrete tone bursts of complete sinusoidal cycles by pulses generated by a Neurolog pulse and delay-width generator. Both sources were effectively aperiodic when driven by tone bursts between 0.8 and 5 kHz; in other words, there were no significant resonances in the frequency band studied here and, when the source was driven by a tone burst of 10 cycles, it produced 10 cycles of sound.

Probe microphones

Measurements of the acoustics of burrows, casts and models were made using a pair of probe microphones similar to those described by Young and Bennet-Clark (Young and Bennet-Clark, 1995) made from Realistic Electret tie-pin microphones (Tandy catalogue 33-1052) but with 18 mm long probe tubes of 1.25 mm external diameter and 0.8 mm internal diameter. The microphones were used in conjunction with a specially constructed two-channel preamplifier and, overall, the responses were amplitude-matched to less than ±0.5 dB from 200 Hz to 6 kHz with a time difference of less than ±5 μs equivalent to ±5 ° at 3 kHz.

Terminology

The sharpness of tuning of resonances is quoted as the quality factor (or Q), given by $\pi/\log_e$(decrement) of the free decay of an oscillation. The Q value is also the ratio of the resonance frequency of a system to the width of the response curve at 50 % amplitude or at 3 dB below the peak response (Morse, 1948).

The relative bandwidth of frequency spectra is quoted as Q_{-3dB}, given by the frequency at which amplitude is maximal divided by the bandwidth at 3 dB below the maximum.

Two separate terms are used here because they concern different aspects of the sound signals we describe. The contexts in which the use of different measurements of Q are appropriate are discussed in Bennet-Clark (Bennet-Clark, 1999a).

The frequency at which the acoustic response to a sinusoidal drive is maximal is termed the resonant frequency, F_o. The frequency of maximum power in a frequency *versus* relative power spectrum is termed the best or centre frequency, F_c.

In power spectra, the relative power is given in decibels (dB) relative to the peak power: 10 dB is a 10-fold change in power; 20 dB is a 10-fold change in amplitude.

Table 1. *Body dimensions of male* Rufocephalus

Head width (mm)	3.02±0.23 (19)
Antenna length (mm)	18.9±0.63 (4)
Body length (mm)	9.60±0.89 (16)
Forewing width (mm)	3.22±0.22 (19)
Forewing length (mm)	4.56±0.31 (19)
Pronotum length (mm)	1.55±0.11 (19)
Pronotum width (mm)	2.75±0.27 (19)
Pronotum height (mm)	1.73±0.22 (19)
Calculated body volume (mm^3)	39.93±8.77 (19)
Calculated height to tips of raised wings (mm)	7.15±0.50 (19)

Values are means ± S.D. (*N*).

The body volume was calculated as the product of body length × pronotum width × pronotum height.

The height to the tips of the raised wings was calculated as the sum of 1.5 × pronotum height plus forewing length.

Table 2. *Dimensions of casts of the burrows of male* Rufocephalus

	Dimensions	Coefficient of variation
Mean diameter of surface hole (mm)	3.19±0.20 (19)	0.063
Area of surface hole (mm^2)	9.92±0.63 (19)	0.070
Length of surface hole (mm)	1.4±0.55 (4)	0.39
Height of top chamber (mm)	16.1±3.30 (17)	0.205
Mean diameter of top chamber (mm)	9.37±0.89 (17)	0.095
Volume of top chamber (mm^3)	697±192 (15)	0.275
Length of neck (mm)	6.43±2.13 (13)	0.33
Diameter of neck (mm)	5.15±0.49 (12)	0.095
Height of lower chamber (mm)	17.70±4.35 (11)	0.25
Mean width of lower chamber (mm)	10.67±2.11 (11)	0.20
Volume of lower chamber (mm^3)	1164±798 (11)	0.69
Mean width of exit tunnel (mm)	6.8±1.70 (10)	0.25

Values are means ± S.D. (*N*).

Results

Insects and burrows

Male *Rufocephalus* are small and lack hindwings, but the forewings are well developed and oblong in shape. Dimensions measured from 19 individuals are given in Table 1. The antennae are approximately twice as long as the body but, because the antennae were very fragile, we have only been able to present data from four insects. If disturbed, the male either withdrew into its burrow or occluded the surface hole with its broad frons. Males could be induced to emerge from their burrows by tickling their antennae with a fine grass stem: presumably, they were expecting to meet searching females. At the end of a bout of singing, the insect sealed the surface hole from within using what appeared to be a cement made from fine soil particles.

Insects sang from within their burrows, which were often situated on flat regions of bare or sparsely covered hardened red clay. The burrow is complex and has an extremely consistent structure (Fig. 1). The surface hole opens into an ovoid flask-like top chamber connected *via* a narrower neck to a roughly ovoid lower chamber. An exit tunnel extends downwards from the lower chamber often to 200–300 mm below the soil surface. The sharp-edged surface hole expands into the top chamber at a depth of between 1 and 2 mm; the diameter of the surface hole is only slightly larger than the width of the insect's head (Table 1, Table 2). The dimensions of the top chamber and neck of the burrow were less variable than those of the lower chamber (Table 2). The interior of the top chamber, neck and top half of the lower chamber were smoothed or plastered to a surface roughness of less than 0.2 mm, compared with a roughness of more than 0.5 mm in the lower regions of the burrow. The smooth regions appeared to have been coated with some secretion, such as saliva, which consolidated and sealed the surface (Fig. 1); cellulose paint applied to these regions did not penetrate deeper than 0.2 mm but penetrated to over 0.5 mm in the rougher unsmoothed lower regions of the burrow. In some burrows, the lower parts of the
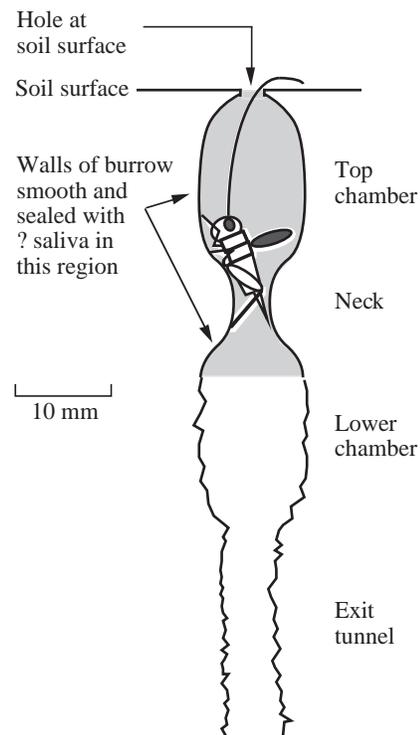

Fig. 1. Diagram of the singing burrow of *Rufocephalus* to show the dimensions and terminology used to describe the burrow. The position of the insect in the burrow was estimated from the length of antennae that were seen projecting through the surface hole and the measured dimensions of the insect (see Table 1, Table 2).

lower chamber appeared to link up with larger cavities or chambers made by termites.

It was not possible to see where the insects were situated while singing, but we are able to estimate the singing position indirectly: while singing, the tips of the insect's antennae were visible extending from the surface hole. The length extending outside the burrow, measured from photographs, was
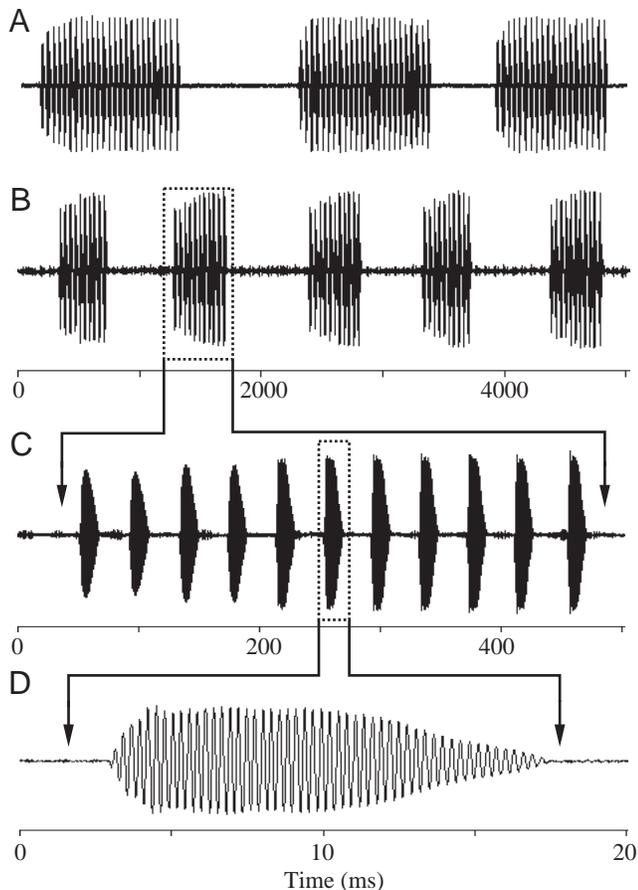
Fig. 2. Song structure of *Rufocephalus*. (A,B) Oscillograms of 5 s sections of the song of two different insects with different trill lengths to show the basic song structure. (C) Detail (500 ms duration) of the second trill of the section of song shown in B. (D) Detail (20 ms duration) of the sixth pulse of the trill shown in C.

4.1±1.3 mm (mean ± S.D., *N*=5). The mean length of the antennae is 18.9 mm (Table 1) so, using the dimensions of the surface hole and top chamber, we estimate that the anterior of the insect's head was probably between 13 and 14 mm below the soil surface and between 4 and 5 mm above the burrow neck, with the posterior half of the body extending into the neck and the wings extended across the lower end of the top chamber (Fig. 1).

Songs

Insects sang in three periods, first for approximately 1 h starting approximately 30 min after sunset, second for approximately 2 h starting just before midnight and third for approximately 1 h starting 1 h before dawn.

The songs of more than 40 insects were recorded. Overall, the songs had a remarkable bell-like purity. The song is made up of a long-duration series of trills with a variable number of pulses and variable intervals between the trills, ranging from trills made up of from two to over 50 pulses, with intervals lasting from 0.4 s to over 1 s (Fig. 2). Within each trill, the first two or three pulses were approximately 2 dB quieter than the

Table 3. *Principal parameters of the song pulses of male Rufocephalus*

		Range
Centre frequency, F_c (kHz)	3.18±0.24 (17)	2.85–3.64
Pulse period (ms)	47.4±7.5 (18)	35.5–64.9
Pulse duration (ms)	15.8±2.21 (18)	10.28–18.55
Peak sound pressure at 200 mm (dB)	84.4±2.3 (6)	79–88

Values are means ± S.D. (*N*).

Pulse period is defined as the time between the start of one pulse and the start of the next.

Pulse duration is defined as the time between the start of the first cycle of the pulse and the end of the cycle at the end of the pulse in which the amplitude had decayed to 0.1 of the peak amplitude or 20 dB below peak level.
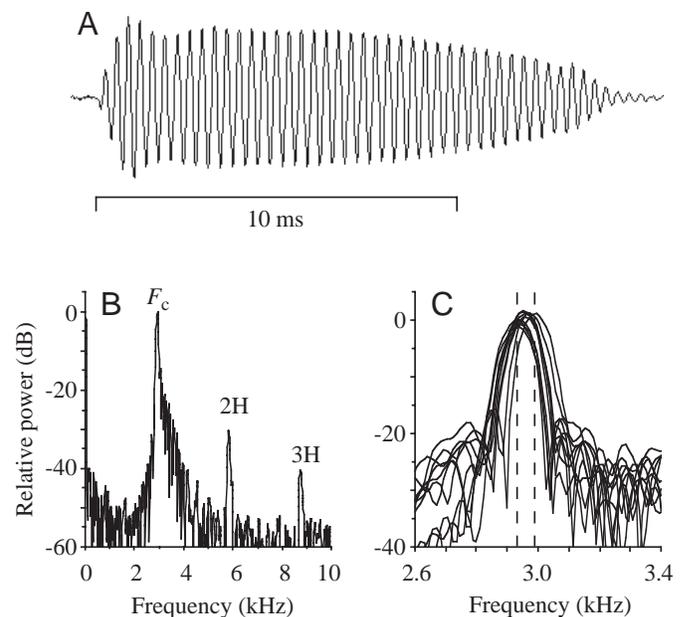

Fig. 3. Consistent song pulses from a single individual *Rufocephalus*. (A) Oscillogram of a single song pulse; the next nine pulses in the trill had closely similar envelopes and duration (cf. the pulses shown in Fig. 5A) (B) Frequency *versus* relative power spectrum of the pulse shown in A, showing the best frequency (F_c) and second (2H) and third (3H) harmonics. (C) Detail of the superimposed frequency *versus* relative power spectra of 10 consecutive pulses from the same insect to show the small range in F_c and peak amplitude that was observed; the broken lines show the frequencies of the highest and lowest F_c.

later pulses (Fig. 2), which usually did not vary in amplitude by more than 1–2 dB. Different insects produced songs with different pulse duration and pulse period, but each individual tended to produce trills of similar pulses. Mean values of certain song parameters are shown in Table 3.

The songs of many insects showed smooth pulse envelopes (Fig. 3A) and more-or-less constant pulse durations. In such songs, the level of the second and third
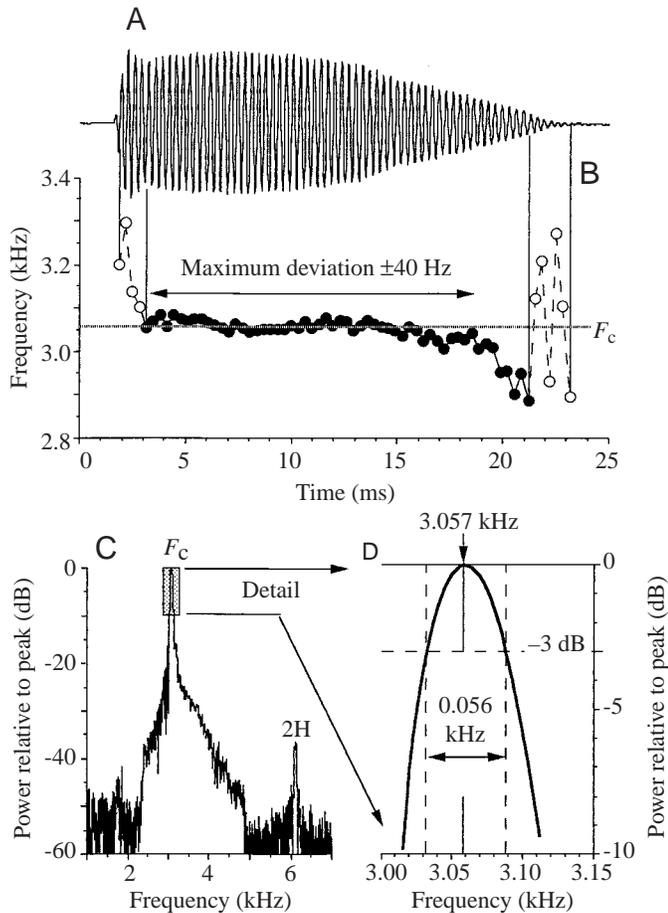
Fig. 4. (A) Oscillogram of a single song pulse of *Rufocephalus*. (B) Cycle-by-cycle frequency within the pulse shown in A to show the deviation from the best frequency, F_c, plotted using zero-crossing analysis; the varying frequency at the start of the pulse (shown between the vertical lines) can also be seen in Fig. 5, Fig. 6 and Fig. 12. The varying frequency seen after 21 ms is partly due to noise in the recording. The horizontal dotted line shows F_c within the pulse. (C) Broad-band frequency *versus* relative power spectrum of the pulse shown in A. 2H, second harmonic. (D) Detail of the frequency *versus* relative power spectrum shown in B. The FFT bandwidth was set to 10.9 Hz. The solid lines show the peak power and F_c, and the dashed lines show the −3 dB level and −3 dB bandwidth, which give a relative bandwidth Q_{-3dB} of 55.
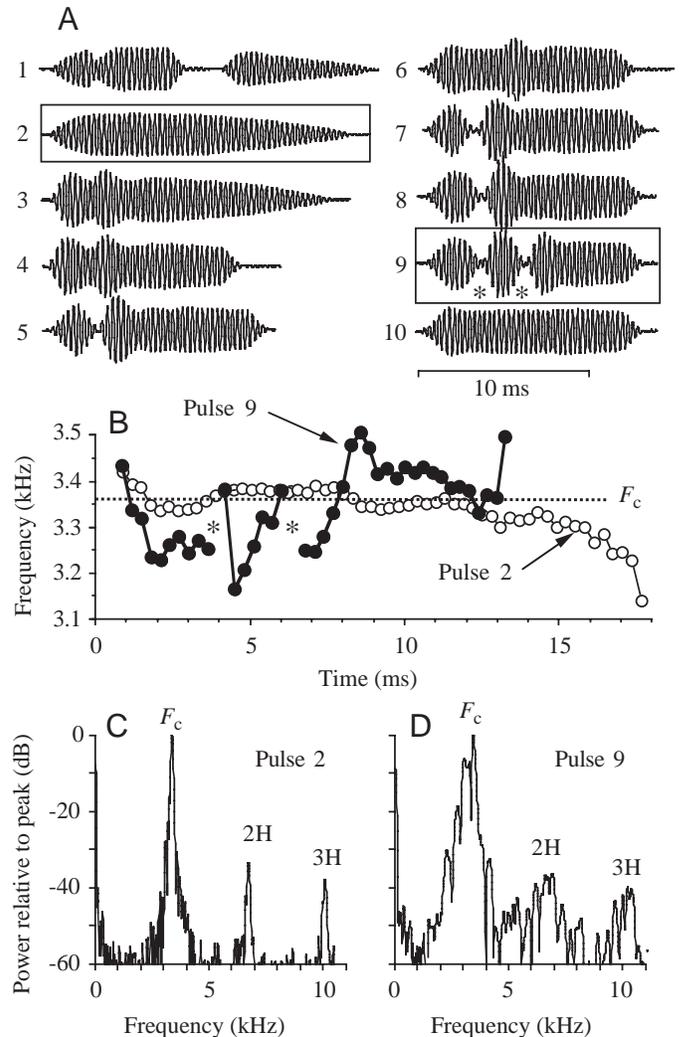
Fig. 5. (A) Oscillograms of 10 consecutive song pulses of a single individual of *Rufocephalus* to show the variation. Analyses of the pulses enclosed in boxes are shown in B–D. (B) Instantaneous frequency within the unimodal pulse 2 and the trimodal pulse 9 shown in A to compare the variation in frequency. The smooth envelope of pulse 2 is accompanied by slow changes in the cycle-by-cycle frequency, whereas the rapid changes in amplitude of pulse 9 are accompanied by rapid changes in cycle-by-cycle frequency. For pulse 9, parts of the analysis of the waveforms between the first and second and the second and third sub-pulses, where there are very large deviations in frequency (shown by an asterisk), have been deleted. (C) Frequency *versus* relative power spectrum of pulse 2 in A. Note the narrow bandwidth of the best frequency F_c and of the second and third harmonics, 2H and 3H. (D) Frequency *versus* relative power spectrum of pulse 9 in A. Note the multiple peaks around F_c and around harmonics 2H and 3H due, in part, to the rapid irregular modulation in the trimodal pulse.

harmonics was typically at least 30 dB below that of the best frequency, F_c (Fig. 3B, Fig. 4C). F_c showed some inter-individual variation (Table 3), but tended to be constant to less than ±40 Hz in successive pulses of the song of an individual (Fig. 3C). The song pulses of most crickets show considerable frequency modulation (Leroy, 1966; Simmons and Ritchie, 1996; Bennet-Clark, 1999b) but, in many of the songs analysed here, particularly where the pulse envelope was smooth (e.g. Fig. 4A), the frequency varied by as little as ±40 Hz for the major part of the pulse (Fig. 4B). Frequency spectra of this type of song showed that the song power was confined to a narrow frequency band: the example shown in Fig. 4C,D has a Q_{-3dB} of 55. Q_{-3dB} values of over

30 were measured from the song pulses of 10 other insects. In many pulses, the cycle-by-cycle frequency varied rapidly at the start and at the end of the pulse. Similar phenomena are described below for the results of tests using an electrical model.

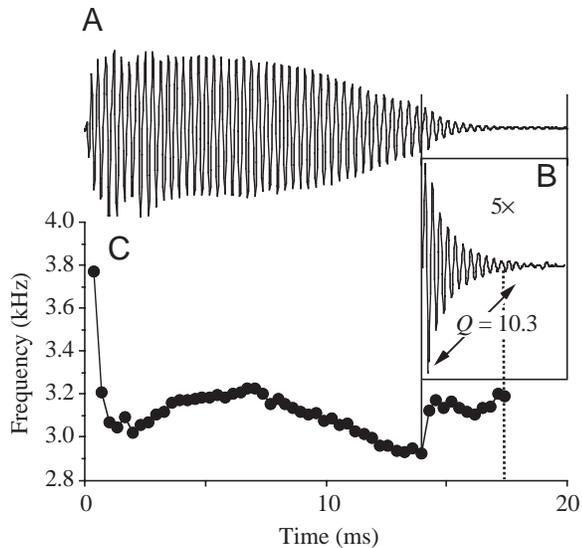Songs of other individuals were highly variable: some of the

Fig. 6. (A) Oscillogram of a single song pulse of *Rufocephalus*. (B) Detail of the decay at the end of the pulse shown in A, with the *y*-axis magnified five times, to show the exponential decay that is seen in some song pulses and the quality factor Q, which was calculated from the rate of decay. (C) Cycle-by-cycle frequency within the pulse shown in A, plotted by zero-crossing analysis. Note the rapid change in frequency at the start of the pulse (cf. Fig. 4 and Fig. 12), that changes in frequency between 1 and 10 ms are associated with rapid changes in the pulse amplitude and the abrupt increase in frequency during the exponential decay at the end of the pulse. The erratic cycle-by-cycle frequency that occurs during the noisy final decay of the pulse (after the dotted line) has been deleted.

pulses from within the same trill had smooth unimodal envelopes (e.g. pulses 2 and 10 in Fig. 5A), while others were bimodal or even trimodal (Fig. 5A pulse 9). These variable pulses showed contrasting distributions of the cycle-by-cycle frequency: when the envelope was smooth, the frequency tended to show a similar constancy to that in Fig. 4B or to vary slowly with time, but the pulses with ragged envelopes showed rapid changes of frequency associated with the modulation of the envelope (Fig. 5B). There was similar contrast in the frequency *versus* power spectra: those of the smooth pulses showed a single sharply tuned peak (Fig. 5C), whereas the pulses with irregular envelopes showed both broader spectra and a series of side-bands due to the rapid and irregular amplitude modulation of the signal (Fig. 5D).

The decay of amplitude at the end of the pulse in many cases appeared to be nearly linear (Fig. 2D, Fig. 5A pulses 1, 2 and 3), but in others the decay appeared to be exponential (e.g. Fig. 3A, Fig. 6B). In certain cases, the frequency during this exponential decay differed markedly from the frequency in the adjacent parts of the pulse (Fig. 6C). The mean Q for the decay of the pulses from 10 insects was 6.91±2.33 (mean ± S.D.; maximum 11.0, minimum 4.1), which is similar to the measured Q for the burrows (see below and Fig. 8) and suggests that these exponential decay components are due to the resonance of the burrow. During the exponential decay of
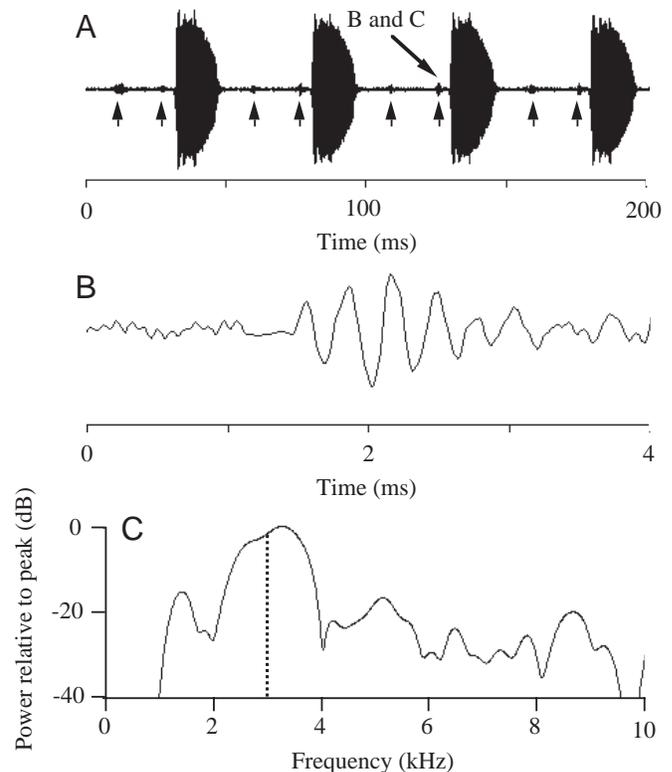

Fig. 7. Oscillogram of a 200 ms region of a song of *Rufocephalus*. The short arrows below the trace show the quiet pulses that occur between the loud song pulses of many recordings. The long arrow above the trace indicates the pulse that is shown in detail in B and C. (B) Oscillogram on expanded amplitude and time scales to show the pulse indicated by the arrow in A in greater detail. (C) Frequency *versus* relative power spectrum of the pulse shown by the arrow in A. The best frequency F_c of this pulse is similar to that of the loud song pulses (shown by the vertical dotted line) but, because the pulse is brief, the width of the spectral peak is broader.

the pulse, the amplitude of the second and third harmonics in the sound fell by 10–15 dB; this is consistent with the behaviour of a freely decaying resonant system.

In many recordings, one or two brief quiet sound pulses occurred during the interval between the normal song pulses (Fig. 7A,B). The interval between these pulses was similar to the duration of the normal song pulses. The F_c of these pulses was similar to that of the normal pulses but, because the pulses were brief (Fig. 7B), the bandwidth of the frequency *versus* power spectra was far broader that those of the normal pulses (cf. Fig. 4C and Fig. 7C). These quiet pulses are probably caused during the wing opening movement; typically one or two are seen before the first pulse in a trill and another after the last pulse.

Acoustics of burrows and the effect of the burrow on the insect's song

Five burrows were used: of these, three included the whole of the lower chamber and part of the exit tunnel and the other two were broken off approximately halfway down the lower
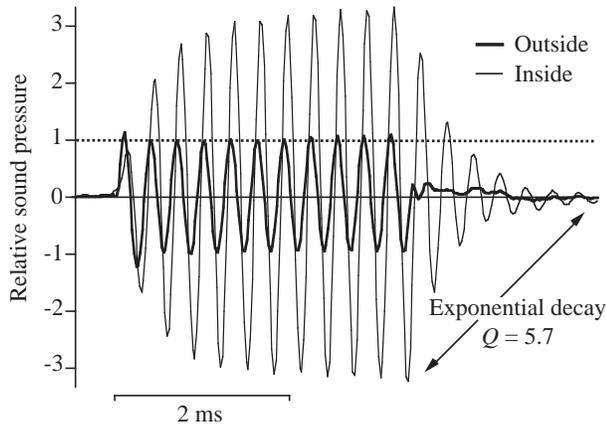
Fig. 8. Acoustics of a burrow of *Rufocephalus*. Oscillograms of an 11-cycle tone burst at 3.27 kHz used to drive the burrow (thick line) and the resonant response measured 5 mm inside the burrow (thin line). The amplitude of the internal sound pressure is shown relative to that of the external driving sound (horizontal dotted line). The quality factor Q of the resonance of the burrow, measured from the $\log_e$(decrement) of the decay of the response, was 5.7.

chamber. The pressure and phase of the sound were measured 5 mm inside the top chamber (see Fig. 1). All burrows showed resonant properties: the mean F_o was 3.48±0.18 kHz (mean ± S.D., $N=5$; range 3.22–3.67 kHz) and the mean Q was 7.44±2.56 (mean ± S.D., $N=5$; range 4.0–9.7). The resonant response of one complete burrow (8/23Nov99) to a discrete 11-cycle tone burst at 3.27 kHz is shown in Fig. 8. The sound pressure within the burrow builds up and decays exponentially; the Q of the decay of the response was 5.7. After the initial build-up of the response, the phase of the internal sound lags by approximately 90° that of the driving sound measured outside the burrow. Because the burrows were fragile, more elaborate tests were not carried out.

Two insects for which both song recordings and complete burrows were obtained showed a close correspondence between the song F_c and burrow F_o: for the first, the song F_c was 3.43 kHz and the burrow F_o was 3.47 kHz; for the second, the song F_c was 3.15 kHz and the burrow F_o was 3.22 kHz.

Another cricket which had previously been recorded in its own burrow was dug up (destroying its burrow) and transferred to burrow 8/23Nov99, which was placed in a large bucket of earth. This insect subsequently sang on three successive evenings following its re-location. In both burrows, the insect was able to produce song pulses with smooth envelopes (Fig. 9A). In its own burrow, the F_c of the song was 2.95 kHz, but in burrow 8/23Nov99 the F_c of its song was close to the measured F_o of the burrow, 3.27 kHz (Fig. 9B,C), and the lack of overlap in the cycle-by-cycle frequency of the song pulses in the two burrows suggests that the burrow is a major determinant of the song frequency. Unfortunately, because of the lateness of the season and the extreme fragility of the dry soil surrounding the burrows, we were unable to extend these important experiments.
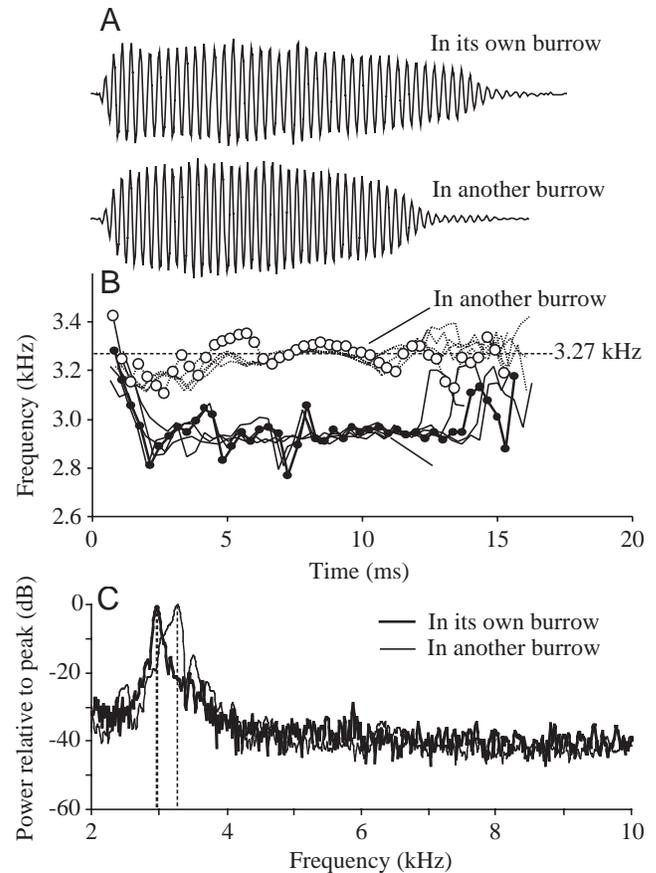

Fig. 9. Songs of the same cricket singing in its own burrow and after transfer to another burrow. (A) Oscillograms of single song pulses. Upper: singing in its own burrow. Lower: singing from the burrow used for the tests shown in Fig. 8. (B) Cycle-by-cycle frequency within song pulses produced either from the insect's own burrow (continuous line traces and filled circles) or from the burrow shown in Fig. 8 (dotted line traces and open circles). The analyses of the pulses shown in A are shown by circles and lines, and those of four other pulses are shown by lines. The horizontal broken line shows the measured resonant frequency of the burrow into which the cricket was transferred. (C) Frequency *versus* relative power spectra for the two song pulses shown in A. The vertical broken lines mark the best frequencies F_c of the two spectra: in the insect's own burrow (thick line) and after transfer to the burrow tested in Fig. 8 (thin line).

Tests with model burrows

In total, five natural-size plaster model burrows were tested. All showed resonant properties with F_o between 3.35 and 3.8 kHz and Q values between 5.8 and 9.5, which are similar to the values measured for the natural burrows. The sound pressure and sound phase for one model, relative to that of the external sound drive, are shown in Fig. 10A. The sound pressure rose approximately threefold and remained approximately constant within the top chamber, then fell within the length of the neck to a value similar to that outside the model in the lower chamber. The phase fell outside the surface hole as the hole was approached then fell to −90° within the top chamber; there was a further rapid phase lag of
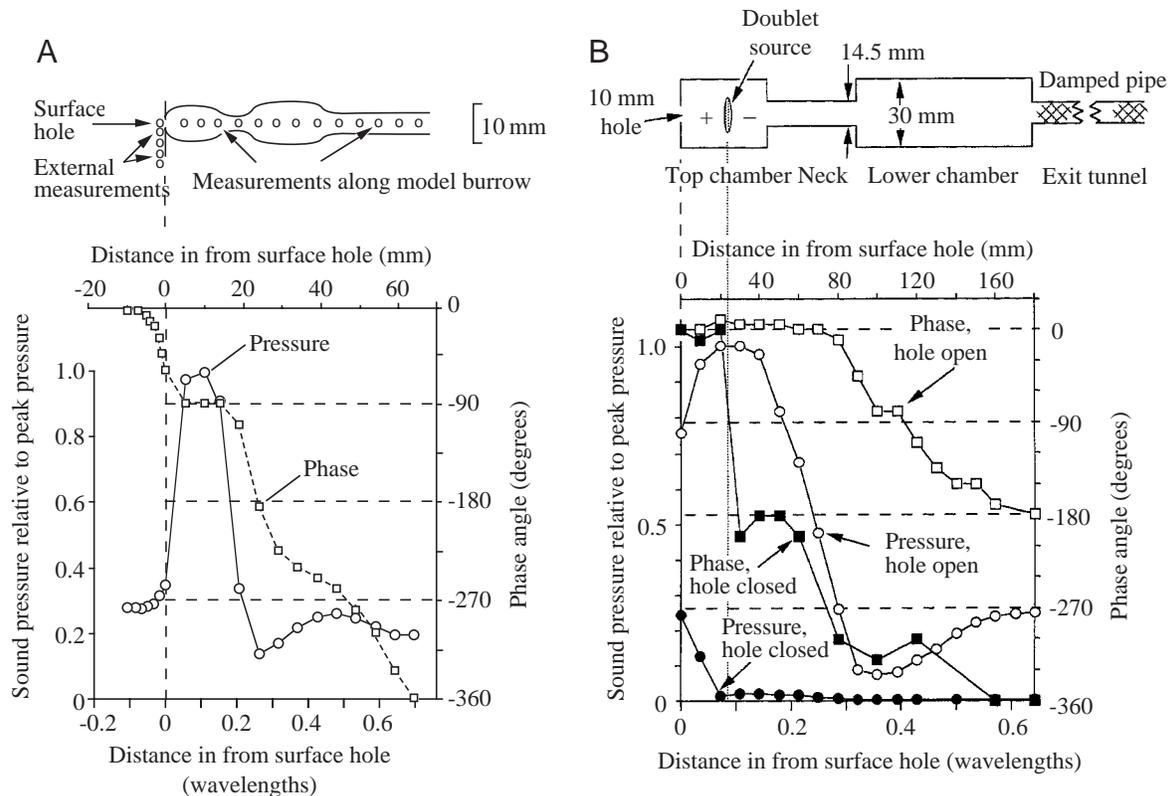
Fig. 10. Graphs of sound pressure and phase in two different models of the burrow of *Rufocephalus*. (A) Response of a natural-size plaster cast to an external sound source at its resonant frequency F_o, 3.72 kHz. Upper: diagram of the model scaled to the distance axis of the graphs below, showing the points at which measurements were made. Lower: the bottom horizontal scale shows distance in terms of the wavelength of the driving sound. Phase is referred to the sound outside the model: there is a 90° phase lag between the sound outside the model and that in the top chamber (cf. Fig. 8). (B) Response of a model approximately three times natural size driven by an internal doublet sound source at its F_o, 1.06 kHz. Upper: diagram of the model scaled to the distance axis of the graphs and showing the position of the doublet source; the terminology for the regions of the burrow follows that used in Fig. 1. Lower: sound pressure and phase data obtained either with the surface hole open (open symbols) or with the hole closed (filled symbols). The bottom horizontal scale shows distance in terms of the wavelength of the driving sound. Phase is referred to that at the surface hole of the model.

approximately 135° in the length of the neck followed by a further slower phase lag in the lower chamber and exit tunnel. From these measurements, it appears that the top chamber acts as a unit and that rapid phase and amplitude changes occur at both ends. The sound pressure and phase changes that occurred outside the model close to the surface hole are probably due to near-field effects that are likely to occur in the vicinity of a cavity of this type.

The effect of moving a model cricket along the length of the model burrow is shown in Fig. 11. When the model was moved from the top chamber into the neck, the resonant frequency fell and then rose again as the model was moved into the lower chamber. The insect appears to sing with the tip of its abdomen within the neck of the burrow (see above). This experiment shows that the resonant frequency of the model burrow is sensitive to the effective diameter of the neck and that the insect may be able to tune the burrow by ±0.1 kHz by moving 2.5 mm up or down the burrow.

Further tests used models approximately three times natural size made from film canisters, which were driven internally by

a doublet source. The model shown in Fig. 10B had an F_o of 1.06 kHz and a Q of 9.9. The sound pressure and phase of the sound are shown in Fig. 10B, with the 'surface hole' both open and closed. With the hole open, the sound pressure and phase are approximately constant throughout the major part of the 'top chamber', but the sound pressure drops in the length of the neck. Within the 'lower chamber', the sound pressure rises but the phase falls through approximately 180°. When plotted against the sound wavelength, the behaviour within this model closely parallels that within the natural-size plaster model shown in Fig. 10A; with the plaster model, driven externally, there is a 90° phase lag between the outside and immediate inside of the model. With the 'surface hole' closed, the sound pressure within all regions of the film canister model when driven at 1.06 kHz was greatly reduced; the phase, in this configuration, changed through 180° either side of the plane of the doublet source, but there was a similar phase lag of approximately 180° between the neck and the end of the 'lower chamber'. With the surface hole open or closed, the phase of the sound was inverted if the polarity of the doublet
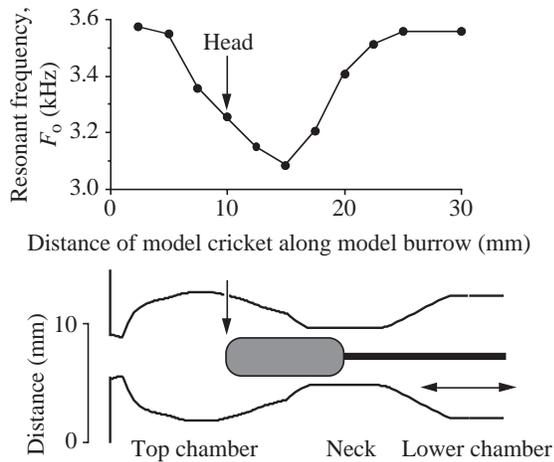
Fig. 11. The effect on the resonant frequency, F_o, of a plaster model burrow of moving a model cricket along the length of the model burrow. The graph shows resonant frequency *versus* distance of the 'head' (left) end of the model cricket from the surface hole. The vertical arrows show the approximate position of the head of a singing cricket in a natural burrow (cf. Fig. 1), and the diagram shows the model cricket approximately in the position adopted by a singing cricket. The model cricket was moved along the length of the model burrow using a piece of wire, as shown in the diagram.

source was reversed by rotating it through 180° in the plane of the diaphragm.

The F_o and Q of the film canister model were affected by the diameter of the surface hole, varying from an F_o of 1.35 kHz and Q of 7.2 with an 18 mm diameter surface hole through an F_o of 1.06 kHz and maximum Q of 9.9 with a 10 mm diameter hole to an F_o of 1.01 kHz and Q of 6 with a 6 mm diameter hole. With a hole 4 mm in diameter or smaller, the resonance weakened and became hard to measure. When the porosity of the top chamber was increased by progressively unsealing 1.5 mm diameter holes previously drilled along its length, F_o increased and Q decreased; this effect was reversed by re-sealing the holes. Increasing the porosity of the lower chamber had only a small effect on the acoustics of the top chamber.

These models show similar resonant properties to those of the burrow and also show that F_o scales inversely with burrow size. The models also show that F_o and the sharpness of tuning depend of the dimensions of the surface hole as well as on the porosity of the walls of the top chamber.

Tests with an electrical model

The electrical model, which was tuned to 2.9 kHz with a Q of 10 (Fig. 12C inset), was driven with tone bursts at either 2.9 and 3.2 kHz (Fig. 12A). With 2.9 kHz tone bursts of 40 cycles, the pulse envelope of the output built up exponentially to a sustained maximum and then decayed exponentially (Fig. 12A): the envelope was similar to those shown in Fig. 3 or Fig. 5 pulse 2, and the frequency measured within the pulse and during the decay remained at that of the input ±5 Hz (Fig. 12C). When the model was driven by two tone bursts at

2.9 kHz, separated by a gap of half a cycle duration (Fig. 12D), the pulse envelope of the output showed an interruption and there was a decrease in the cycle-by-cycle frequency for several cycles after the time of interruption but otherwise, throughout both tone bursts and the decay, the output frequency was close to that of the input (Fig. 12F). However, following the interruption, the amplitude of the output fell more rapidly than at the end of the second tone burst; the second exponential build-up, following the interruption, was similar to the build-up at the start of the first tone burst; the final decay was slower and exponential (Fig. 12D). The effects on the amplitude of the output depended on whether the interruption to the input caused the second tone burst to start in-phase or anti-phase with the existing response of the model: gaps of 0.5, 1.5, etc. cycles had the largest effects.

When the electrical model was driven with 3.2 kHz tone bursts of 40 cycles, the amplitude of the response initially rose rapidly, then decreased (Fig. 12B), then rose slightly after 5 ms to a steady value until 12 ms, after which the amplitude decayed exponentially. The cycle-by-cycle frequency rose over the first 3 ms from approximately 3.05 kHz to over 3.2 kHz before decreasing to a steady 3.2 kHz for the remainder of the driven part of the pulse (Fig. 12C). Throughout the exponential decay at the end of the pulse, the frequency was approximately the 2.9 kHz to which the model was tuned (Fig. 12C). When driven at 2.6 kHz, the envelope showed a similar bulge at the beginning of the pulse, but the cycle-by-cycle frequency showed a mirror image of that when the frequency of the input was higher than the F_o of the model. These wave forms resemble the irregular unimodal envelopes seen in, for example, Fig. 3A, Fig. 5 pulse 10 or Fig. 6A.

The electrical model was also driven by 3.2 kHz 20-cycle tone bursts separated by brief intervals. Fig. 12E shows the input and output of the model to a pair of tone bursts separated by half a cycle of the driving frequency. The output at the start of the first tone burst resembles that to the 40-cycle tone burst (Fig. 12A) but, after the gap between the first and second tone burst, there is an abrupt decrease in amplitude and in frequency, followed by a build-up in amplitude and change in frequency similar to those at the start of the first tone burst. The decay of the output at the end of the second tone burst resembles that of the 40-cycle tone burst. The wave forms and changes in frequency seen when this resonant system is driven by a series of short, interrupted tone bursts at different frequencies resemble those of some of the song pulses shown in Fig. 5.

With lower source impedances with a 3.2 kHz input, the amplitude changes at the start and end of the output occurred more rapidly and were smaller than those shown in Fig. 12, and the cycle-by-cycle frequency reached that of the input more rapidly; in contrast, with higher source impedances, the amplitude changes occurred more slowly, were larger in amplitude and the cycle-by-cycle frequency reached that of the input less rapidly.

Fig. 12. Response of a parallel resonant circuit tuned to 2.9 kHz with a quality factor Q of 10 (the circuit is shown in the inset to C) when driven by tone bursts. In A, B, D and E, the measured amplitude of the input varies by less than ±5 % and the cycle-by-cycle frequency of the input varies by less than ±10 Hz during the tone bursts. For the symbols used in C and F, see F. (A) Oscillograms of the waveforms of the drive (Input) and response (Output) to a 40-cycle tone burst at 2.9 kHz. (B) Oscillograms of the waveforms of the drive (Input) and response (Output) to a 40-cycle tone burst at 3.2 kHz. (C) Graphs of the cycle-by-cycle frequency of the inputs to (open symbols) and the outputs from (filled symbols) the resonant circuit shown in the inset at the two input frequencies, 2.9 and 3.2 kHz. For the 3.2 kHz drive, note that the amplitude and frequency of the response vary during the initial 4 ms of the drive and that during the exponential undriven decay at the end of the response the frequency falls to 2.9 kHz. (D) Oscillograms of the waveforms of the drive (Input) and response (Output) to a sequence of two 20-cycle tone bursts at 2.9 kHz.
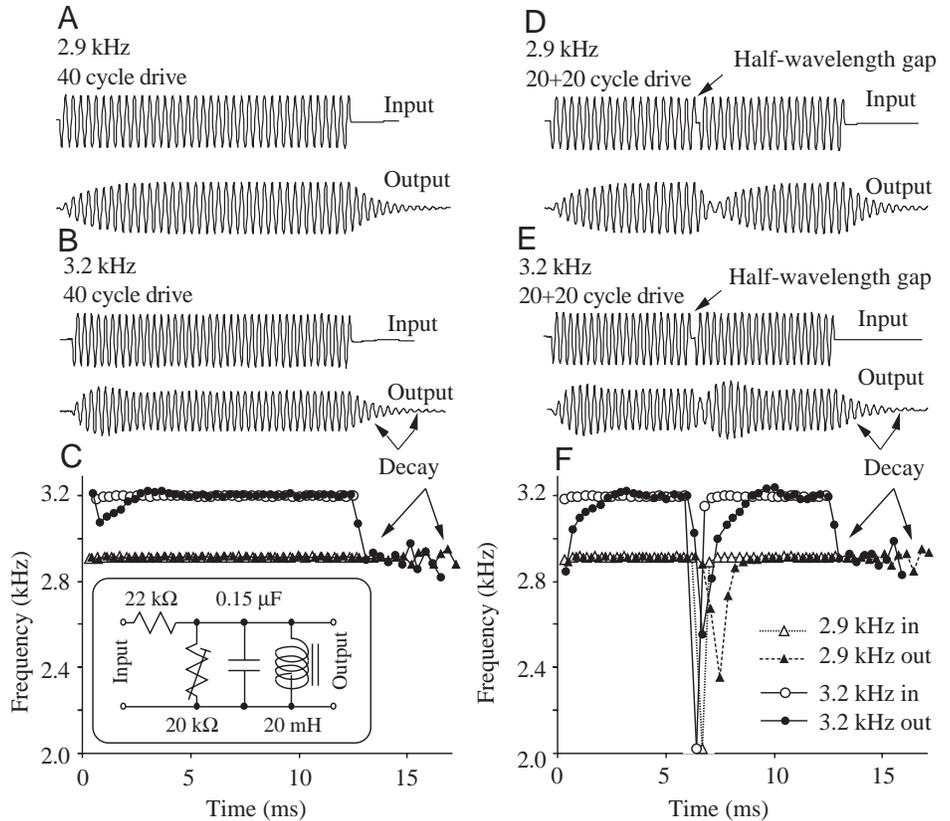
(E) Oscillograms of the waveforms of the drive (Input) and response (Output) to a sequence of two 20-cycle tone bursts at 3.2 kHz. In D and E, the gap between the two tone bursts was half a wavelength, λ. (F) Graphs of the cycle-by-cycle frequency of the inputs to (open symbols) and the outputs from (filled symbols) the resonant circuit shown in the inset to C at the two input frequencies. For the 2.9 kHz drive, note the rapid fall in amplitude of the response after the gap between the two tone bursts; for most of the response, the frequency is closely similar to that of the drive. For the 3.2 kHz drive, note that the amplitude and frequency of the response vary during the initial 4 ms of the drive and again after the gap between the two tone bursts; during the exponential undriven decay at the end of the response, the frequency falls to the 2.9 kHz, to which the resonant circuit is tuned.

Discussion

Impedance matching to the surrounding air

Male *Rufocephalus* are approximately half the total body length of crickets such as *Gryllus campestris* and *Teleogryllus oceanicus* and their sound-producing forewings are approximately one-third the length and half the width of those of males of these species. Despite the relatively small body and wing size, the song has a dominant frequency of approximately 3.2 kHz compared with those of the larger *G. campestris* and *T. oceanicus*, both of which are close to 5 kHz. *Rufocephalus* produces a lower frequency song from substantially smaller structures than the larger species.

Crickets calling from the ground or from exposed foliage typically have calls with their F_c between 4 and 8 kHz (Dumortier, 1963; Leroy, 1966), while the F_c of mole crickets is between 1.6 and 3.5 kHz (Bennet-Clark, 1970). So a general feature of burrow-calling insects is that physical factors that normally constrain song frequency to vary with body size are relaxed. The reason for this is that the acoustic transformation that occurs in the burrow allows small sound-producing structures to be coupled *via* the burrow to the far larger area of the mouth of the burrow from which the sound is radiated (Bennet-Clark, 1995; Bennet-Clark, 1998). The present study describes for the first time a comparable situation in burrow-calling crickets (Gryllidae, Gryllinae).

Consideration of the impedance matching between sound sources and the surrounding air (see, for example, Olson, 1957; Fletcher, 1992) shows that the 3.2 mm diameter hole from which the song of *Rufocephalus* is radiated is a far smaller source than that which would provide optimal impedance matching of the 3.2 kHz song to the air. For optimum impedance matching, the source diameter should exceed one-third of the sound wavelength. For the approximately 3 kHz song of *Rufocephalus*, the wavelength, λ, is close to 100 mm, which requires a burrow with a mouth diameter of approximately 35 mm. However, if the insect were to sing in the open air, the wings would act as a dipole or doublet source with a diameter of approximately 5 mm, or 0.05λ, with a specific acoustic resistance approximately 2×10^{-4} times that of air. By singing from within the burrow and radiating sound from the surface hole, the source becomes a monopole with a specific acoustic resistance 2×10^{-2} times that of air. The
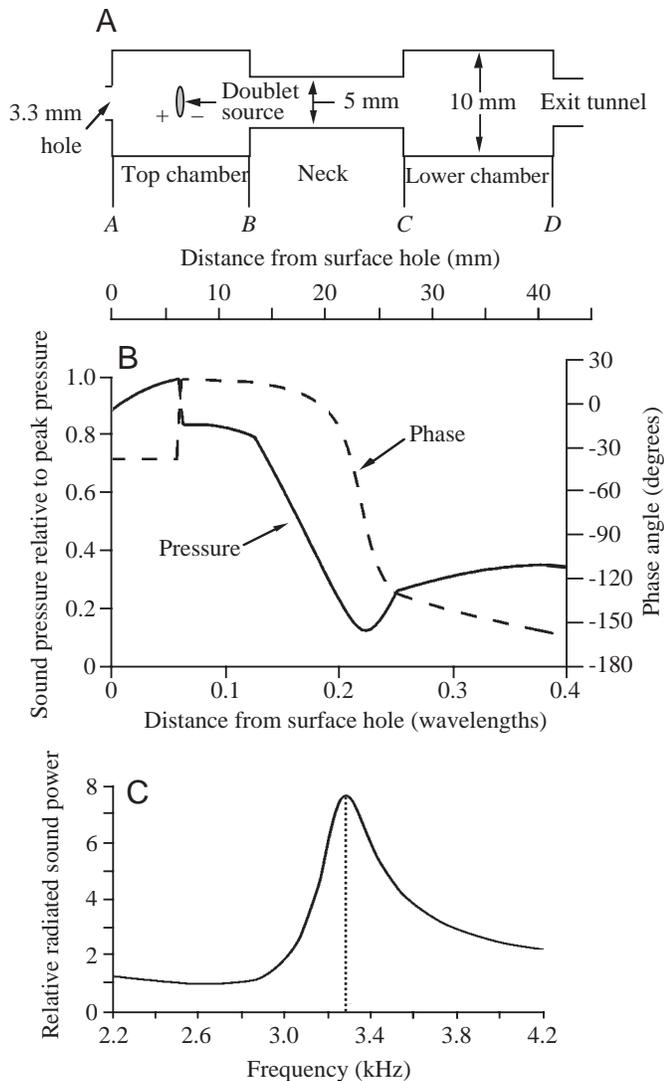
Fig. 13. Dimensions and performance of a numerical model of the burrow. (A) Scale diagram of the model to show the position of the small doublet source in the top chamber and the planes of discontinuity (*A*, *B*, *C*, *D*) used to calculate the acoustics of the model. The dimensions of the model are based on those of actual burrows (see Table 2). (B) Graphs of sound pressure (solid line) and phase (broken line) against distance from the surface hole for the model shown in A at a resonant frequency F_o of 3.25 kHz. Distance along the burrow is expressed in millimetres (upper scale) or in terms of the sound wavelength (lower scale). Phase is given relative to that at the plane of the dipole source. These data can be compared with those obtained with the physical models shown in Fig. 10. (C) Graph of the relative radiated sound pressure from the surface hole against frequency for the model shown in A. F_o is 3.25 kHz with a quality factor Q of 7, which are closely similar to values measured for actual burrows, physical models and of the best frequency F_c of the song (Table 3).

burrow thus provides a 100-fold improvement in the coupling between the insect and the air, permitting far louder and more efficient sound production; similar advantages have been proposed for the singing burrows of mole crickets (Bennet-

Clark, 1987) or the abdominal resonator of cicadas (Bennet-Clark and Young, 1992).

In contrast to the tuned low-*Q* singing burrow of mole crickets (Bennet-Clark, 1987; Daws et al., 1996), that of *Rufocephalus* is far more sharply tuned, typically with a *Q* of over 7. This is achieved by radiating a relatively small proportion of the sound energy in the burrow *via* the small surface hole, in contrast to the far larger burrows (and hence far larger resonant mass) of mole crickets, which radiate sound from surface holes that approach the optimal size for impedance matching with the surrounding air (Bennet-Clark, 1995). Mole crickets are large robust insects that weigh between 10 and 50 times as much as *Rufocephalus* and are, hence, capable of transducing a commensurately greater mechanical power into sound. Also, by virtue of their far greater size, mole crickets are able to build large burrows with surface hole dimensions approaching that of the sound wavelength, which would be extremely energy-demanding for an insect as small as *Rufocephalus*.

A numerical model of the burrow

A theoretical model is helpful in understanding the observed tonal purity of the insects' songs and the resonant properties of the burrow. For this purpose, we adopt the simplest model possible and require that it have no adjustable parameters.

The geometry of the real cricket burrow is complex, so the theoretical model is constructed using the dimensions of the real burrows but with simplified geometry, as shown in Fig. 13A (and resembling that in Fig. 10B). The form of the theory provides simple scaling. Its results are unchanged if all dimensions are altered by a factor *K* and the frequency is changed by a factor 1/*K*; this accords with the measurements for two different sizes of physical model, as reported above.

The theory to be formulated is essentially one-dimensional, by which it is implied that all parameters are averaged over the cross section of the appropriate part of the burrow, so that they depend only upon a single parameter, the distance from the burrow mouth. Given these constraints, the major difficulty is then the modelling of the cricket sound source. In reality, there will be a complex flow of air around the vibrating wings, and a detailed solution of this aerodynamic problem is far beyond the demands of the present study. Instead, it is assumed that the cricket behaves as a simple dipole source, generating an oscillating pressure step, and hence an acoustic volume flow *U* along the axis of the burrow, and presenting no obstacle to other flow. The limitations of this model will be discussed below.

The acoustic pressure waves generated by the wings of the cricket are partially reflected at each discontinuity in the burrow, so that, in addition to the initial flow *U*, allowance must be made for two counter-propagating acoustic flows in each burrow chamber. If the amplitude and phase of each of these flows are initially taken as independent variables, then the model contains 12 such variables, four for each chamber of the burrow. On each of the four planes *A*, *B*, *C* and *D* of Fig. 13A, however, there are equations relating these variables.

At *A* the connection is through the impedance of the surface hole, at *D* through the impedance of the exit tunnel, assumed to be infinitely long, while at *B* and *C* there are continuity conditions on both acoustic pressure and acoustic flow. This makes 12 equations in all, when both amplitude and phase are taken into account, which is a sufficient number to determine all the variables. The loss of energy as sound passes through the surface hole is actually very small, and most acoustic energy is dissipated as losses to the rough walls and as propagation into the non-reflecting lower large exit tunnel.

The results of the calculations show good agreement with experiment in most respects. Fig. 13B shows the calculated variation of acoustic pressure along the burrow and the calculated variation of acoustic phase for a cricket-source position in the middle of the top chamber; these results can be compared with those shown in Fig. 10. Of more interest is the calculated acoustic output from the mouth of the burrow as a function of frequency, as shown in Fig. 13C. There is a sharp resonance at 3.25 kHz, which is near the measured song frequencies, suggesting that the cricket must adapt its song frequency to the burrow in which it is singing (or, of course, the other way round). Changing the diameter and wall thickness of the surface hole can vary the frequency of the resonance. The *Q* of the resonance depends upon the value assumed for the wall absorption. However, even with the rather large wall damping coefficient of 10, which has been assumed in these calculations, the resonance is still quite sharp, with a *Q* of approximately 7, which again agrees with the measured *Q* values for real burrows. A further calculation shows that the acoustic output from the burrow is not greatly affected by the length of the lower chamber *CD*. The calculation further shows a minimum in the output power for a lower chamber length of approximately 7 mm, but only a small increase in output for both longer and shorter chambers. This insensitivity accords with the observed variability in the length of the lower chamber (Table 2). If acoustics were the only function of the burrow, one might have expected the insect to opt for a very short lower chamber in the interests of economy, but the extended burrow may provide the insect with access to water in a very dry environment or may be used as an oviposition site for mated females.

Calculations suggest that the optimal singing position of the cricket would be close to one end or the other of the top chamber, which agrees well with our observations on where the insect sings (see Fig. 1); the variation in output is quite large. However, the model source adopted here was that of a very small dipole oscillating with a rather large amplitude, whereas the source provided by the cricket's wings may be better approximated by a much larger source oscillating with small amplitude. It is not simple to introduce this refinement into the numerical model, but an argument on general physical grounds suggests that an increase in source size will move the optimum singing position progressively towards the middle of the chamber, where the acoustic flow is smallest.

Song frequency and song purity

As has been indicated, the songs of *Rufocephalus* are, for their size, unusually low in frequency, while the loudness (Table 3) compares, size-for-size, favourably with that of the far larger *G. campestris*, which is approximately 95 dB at the same distance (from data in Bennet-Clark, 1970). In many examples, the songs were also unusually constant in frequency, both within and between pulses, with Q_{-3dB} of greater than 30 and with harmonics at levels of less than 3 % of the amplitude at F_o. In *Rufocephalus*, the *Q* of the burrow is greater than that reported for mole crickets (Bennet-Clark, 1987). Because of this high *Q*, the burrow will be most easily driven at its resonant frequency. And, as a consequence, the high *Q* and the close coupling between the insect and the burrow will tend to entrain the frequency of catch-and-release of the plectrum-and-file mechanism to that of the burrow; the system acts as a resonator with its frequency set by the burrow. Such a system appears to maintain the song frequency and coherence, as can be seen in Fig. 3 and Fig. 4. Indeed, if the coupling between the insect and the burrow is tight and the difference between the natural frequency of the insect's wings and the F_o of its burrow is small, there may be no alternative. This appears to have been the case with the burrow exchange experiment shown in Fig. 9.

However, several of the songs we measured contained pulses with gaps, and showed both frequency and amplitude modulation. From the measurements made with the electrical model shown in Fig. 12, pulses of this type may result from a frequency mismatch between the insect and its burrow that causes an erratic cycle of catch-and-release of the plectrum against the file. The results with the electrical model (Fig. 12) suggest that the file-and-plectrum mechanism may act in two different ways during the production of the pulse.

First, the cycle of catch-and-release of the file teeth may become entrained to the F_o of the burrow. In this case, the pulse envelope will be comparatively smooth and the cycle-by-cycle frequency will be fairly constant. The sound pulses shown in Fig. 4A,B are examples of this phenomenon and are associated with the very high Q_{-3dB} for this type of song pulse. However, the initial process of entrainment at the start of the pulse may be accompanied by rapid amplitude modulation of the waveform of the pulse. This amplitude modulation may rise rapidly and then fall (see Fig. 3, Fig. 4A, Fig. 12A) and be accompanied by frequency modulation. This is shown in the first 2 ms of the pulse in Fig. 4 or the first 4 ms of that in Fig. 12A. What is not clear is whether the insect's wings are being entrained to the F_o of the burrow or the burrow is being driven by the cycle-by-cycle frequency determined by the file-and-plectrum mechanism of the wings. The latter would explain the sudden jump in frequency that occurs at the end of pulses of the type shown in Fig. 6, where the amplitude decays exponentially at a nearly constant but different frequency from that in the preceding part of the pulse and with a lower harmonic content.

The second alternative is that the file-and-plectrum mechanism does not become entrained or does not remain entrained to the F_o of the burrow. This was modelled in

Fig. 12B, which shows that even a brief irregularity in the cycle-by-cycle input to a resonant load can result in rapid amplitude and frequency modulation of the output, particularly when the frequency of the input differs from the F_o of the load. An initial lack of entrainment would explain the brevity of the first sub-pulse of pulse 9 in Fig. 5, which occurs at a different cycle-by-cycle frequency from that of pulse 2 from the same insect, with a slow amplitude modulation and comparative constancy of frequency. Subsequent loss or failure of entrainment may then result in an interruption to the input from the insect's wings to the burrow. In this case, if entrainment fails, causing irregular movement of the insect's wings, the frequency generated by the catch-and-release of the file-and-plectrum mechanism of the wings may show considerable variation during the wing-closing movement. Our preliminary studies here, and those with the songs of other species of cricket, show a clear relationship between rapid changes in amplitude or frequency and the relative amplitude of harmonics of the F_c of the sound (H. C. Bennet-Clark and W. J. Bailey, in preparation).

The comparatively sharply tuned burrow appears to be an important determinant of the song frequency (Fig. 9) and it appears that even very brief sounds, such as the 'ticks' produced during the wing-opening movements, are capable of exciting the resonance (Fig. 7). Transduction from the small wings of the insect to the surrounding air *via* two resonant stages offers advantages in impedance matching and maintenance of song purity that have been considered elsewhere (e.g. Bennet-Clark, 1995). The resonant singing burrow of mole crickets (Bennet-Clark, 1987; Daws et al., 1996) offers similar advantages but, as described above, its acoustics differs.

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