Calling songs of some South African cicadas (Homoptera: Cicadidae)

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The spectral and temporal characters of the calls of 12 species of cicada are illustrated and described. Variation within populations of conspecifics appears to be greater in temporal than in spectral properties. Conspecific calls recorded at widely separated localities have essentially the same characteristics. Details of behaviour during singing are also noted. Cicada calling songs are very useful in the identification of species in the field.

Die strukturele karakters van die roepstemme van 12 sonbesiespesies word uitgebeeld en beskryf. Variasie binne bevolkings van die selfde spesie blyk groter in temporale as in spektrale eienskappe te wees. Details van gedrag gedurende geroep is ook aangeteken. Sonbesieroepstemme is baie nuttig by die identifikasie van spesies in die natuur.

The usefulness of animal signals in identifying the animal is well known (Maclean 1985; Otte & Cade 1984; Passmore & Carruthers 1979). Because of their species-specificity and their similarity between localities, calling songs are ideal identification characters for the identification of cicadas. Calling songs can also be used as taxonomic characters if they are preserved as tape-recordings or sonagrams along with the specimens. It was the distinctiveness of their calls that led to the recognition of the cicadas *Magicicada septendecula* (Alexander & Moore 1958), *Platypleura maytenophila* (Villet 1987), *Terpnosia ridens* (Pringle 1954a) and several *Maoricicada* species (Dugdale & Fleming 1978) as distinct species. There is, therefore, considerable scope for the use of cicada calling songs in taxonomic and ecological studies of these insects.

The calling songs of male cicadas have drawn attention since at least the time of the ancient Greeks, who wrote odes to these insects. Cicada songs have been described phonetically or even in musical notation (Myers 1929; Pringle 1954b), but these methods seldom convey accurate information concerning their structure. More precise (though less poetic) quantitative descriptions can be made from spectrographic analyses of tape-recorded songs. The songs of about 60 species of cicada have been analysed in this way (Aidley 1969; Claridge, Wilson & Singhrao 1979; Dugdale & Fleming 1969, 1978; Fleming 1971, 1973, 1975; Hagiwara & Ogura 1960; Huber, Wholers & Moore 1980; Josephson & Young 1985; Moore 1962; Moulds 1975; Popov 1981; Pringle 1954b; Young 1972, 1980; Young & Josephson 1983a, 1983b), including one African species (Boulard 1977). This work has revealed a rich variety of sounds, both in terms of frequency composition (spectral structure) and amplitude modulation patterns (temporal structure).

In this paper the calls of several South African species are described for the first time, as an aid to their identification. Variability in calling songs is examined within populations from Natal, South Africa. Some conspecific calls from widely separated localities are also compared.

Methods

Tape recordings of calling males were made at various times of day, between October, 1984 and February, 1985 at Mtunzini (28°59′S / 31°46′E), on the north coast of Natal, South Africa. Recordings were also made incidentally at several other localities which are marked on Figure 1. The identity of the species singing each song

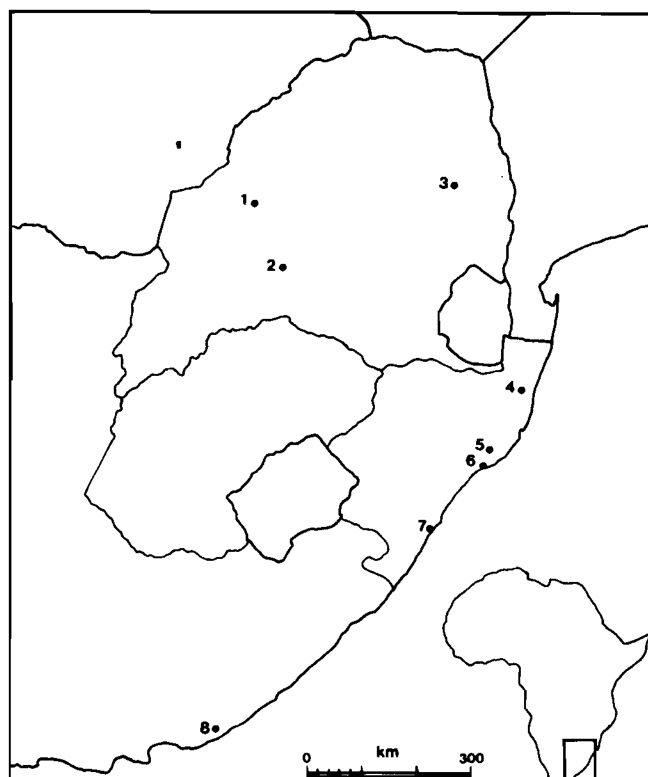

Figure 1 Localities at which calling songs were recorded. 1. Northam (24°48′S / 27°16′E) 2. Broederstroom (25°51′S / 27°53′E) 3. Dunstable Farm (24°27′S / 30°44′E) 4. Mkuzi (26°39′S / 32°10′E) 5. Nyala Park (28°43′S / 31°49′E) 6. Mtunzini (28°59′S / 31°46′E) 7. Illfracombe (30°11′S / 30°48′E) 8. Grahamstown (33°17′S / 26°32′E).

was established by collecting several specimens in each case.

Calling songs were recorded on high quality magnetic tape (Scotch, standard play) at a speed of 38 cm/sec with a Nagra III tape recorder and a Beyer M69N dynamic microphone. The microphone was held about 0,5 m from the insect, as close to the midline as conditions would allow, to avoid asymmetrical recording from the paired tymbals (Aidley 1969). Reference numbers were spoken onto the tape before each recording.

Sonagrams of the recordings were prepared on a Kay 7029A sound spectrum analyser using a wide band (300 Hz) filter, which allows fine temporal resolution of the call. A narrow band (45 Hz) filter was used to generate power spectra (amplitude/frequency displays) with fine spectral resolution on the same analyser. The time axis was calibrated with a Kay 6077A time marker. The frequency band width and emphasized frequency of the call were measured from the power spectra. Pulse rates were measured from wide band (300 Hz filter) sonagrams made from recordings replayed at 9,5 cm/sec.

Results

Descriptions of calling songs

Severiana lindiana. Distant (Figures 2a, b)

Frequency range: 6,5–11,5 kHz; emphasized frequency: 7,7 kHz; pulse rate: 440–490 pulses/s.

The call is a continuous train of groups of six pulses, which give it a rattling quality. The groups are 15 ms long and 6 ms apart.

Brevisana brevis. Walker (Figures 2c, d; Table 1)

Frequency range: 7,0–11,0 kHz; emphasized frequency: 8,7 kHz; pulse rate: 380–510 pulses/s.

A sustained noise composed of evenly spaced double pulses. Narrow band sonagrams show a slight frequency modulation at a rate of 115 modulations/s, corresponding to groups of four double pulses in wide band sonagrams.

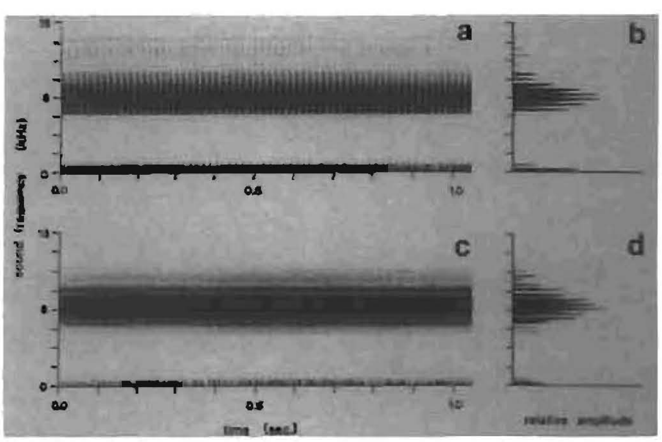

Figure 2 (a–b) Calling song of *Severiana lindiana*. (a) Sonagram, (b) power spectrum. (c–d) Calling song of *Brevisana brevis*. (c) Sonagram, (d) power spectrum.

Table 1 Descriptive statistics for the call parameters of eight species of African cicada. *S.D.* = standard deviation; *C.V.* = coefficient of variation

Parameter	Mean	*S.D.*	Range	*C.V.*
Platypleura argentata (n = 17)				
emphasized frequency (kHz)	14,5	1,2	13,0 – 16,7	8,1
midpoint frequency (kHz)	15,1	0,5	14,3 – 15,8	3,1
band width (kHz)	6,6	1,1	4,5 – 9,0	16,4
phrase duration (s)	13,8	3,1	10,0 – 21,0	22,1
part A duration (s)	4,8	0,9	3,2 – 6,5	22,2
part B duration (s)	9,4	2,9	6,5 – 16,9	31,2
intensity peaks/part A	4,6	1,1	3 – 7	23,9
intensity peaks/part B	7,5	3,7	2,5 – 16,5	49,2
Platypleura divisa (n = 10)				
emphasized frequency (kHz)	11,3	0,5	10,5 – 12,0	4,2
midpoint frequency (kHz)	11,4	0,4	11,0 – 12,0	3,3
band width (kHz)	4,7	1,0	2,5 – 6,0	22,1
phrase duration (s)	25,3	7,3	14,0 – 35,0	28,7
part A duration (s)	12,8	5,0	7,0 – 20,0	38,6
part B duration (s)	12,5	3,6	7,0 – 17,0	28,5
intensity peaks/part A	9,5	2,0	7,0 – 12,0	21,8
Platypleura maytenophila (n = 33)				
emphasized frequency (kHz)	8,7	0,5	7,7 – 10,0	6,3
midpoint frequency (kHz)	9,3	0,4	8,5 – 10,2	4,7
band width (kHz)	4,4	0,7	3,5 – 6,0	15,7
phrase duration (s)	5,1	1,0	3,0 – 8,0	20,2
part A duration (s)	3,7	0,8	2,0 – 5,5	20,4
part B duration (s)	1,3	0,6	0,5 – 3,0	48,9
Platypleura haglundi (n = 10)				
emphasized frequency (kHz)	13,4	0,7	12,5 – 14,7	5,5
midpoint frequency (kHz)	13,5	0,5	12,7 – 14,0	3,7
band width (kHz)	4,7	0,9	3,5 – 6,0	19,9
Platypleura zuluensis (n = 34)				
emphasized frequency (kHz)	11,6	0,8	10,0 – 13,0	7,1
midpoint frequency (kHz)	11,6	0,4	10,5 – 12,8	3,8
band width (kHz)	4,5	0,7	3,5 – 6,5	16,0
phrase duration (s)	13,6	3,1	10,0 – 24,0	22,7
part A duration (s)	6,6	2,0	3,0 – 11,0	29,6
part B duration (s)	6,9	3,5	3,0 – 19,0	50,4
Oxypleura lenihani (n = 20)				
emphasized frequency (kHz)	6,9	0,4	6,0 – 7,5	6,5
midpoint frequency (kHz)	7,5	0,3	6,7 – 8,0	4,6
band width (kHz)	5,1	0,8	3,5 – 7,0	16,0
phrase duration (s)	33,7	5,5	24,0 – 39,0	16,4
part A duration (s)	18,3	4,9	11,0 – 25,0	26,7
part B duration (s)	15,9	6,9	9,0 – 27,0	43,7
Brevisana brevis (n = 40)				
emphasized frequency (kHz)	8,8	0,3	8,0 – 9,5	3,8
midpoint frequency (kHz)	8,9	0,3	8,5 – 9,5	3,4
band width (kHz)	3,2	0,4	2,5 – 4,0	12,1
Pycna semiclara				
Full Call (n = 57)				
emphasized frequency (kHz)	4,8	0,2	4,4 – 5,3	3,8
Encounter Call (n = 12)				
emphasized frequency (kHz)	4,7	0,1	4,5 – 4,9	3,1

Platypleura haglundi. Stal (Figures 3a, b; Table 1)

Frequency range: 10,5–17,0 kHz; emphasized frequency: 13,4 kHz; pulse rate: 330–350 pulses/s.

The call of this small cicadine is a high-pitched, continuous train of double pulses, with a broad peak of emphasized frequencies. These frequencies are very slightly modulated about 50 times per second.

Platypleura hirta. Karsch (Figures 3c, d)

Frequency range: 8,0–13,0 kHz; emphasized frequency: 9,5 kHz; pulse rate: 350–410 pulses/s.

Another song composed of a sustained train of paired pulses. There is a slight, cyclical frequency modulation at a rate of about 38 modulations/s.

Platypleura argentata. Villet (Figures 4, 5a, b; Table 1)

Frequency range: 11,0–20,0 kHz; emphasized frequency: 14,5 kHz; pulse rate: 280–480 pulses/s.

The gross structure of this call features a series of three to seven crescendos lasting 3–6 s (part A, Figure 4), followed by a 6–17 s train of sound which has 2–16 amplitude peaks (part B, Figure 4). When a male encounters another cicada, it shortens its call by omitting several intensity peaks in part A of its call. Figure 5a illustrates a segment of part B.

Platypleura divisa. Germar (Figures 4, 5c, d; Table 1)

Frequency range: 8,5–15,0 kHz; emphasized frequency: 11,3 kHz; pulse rate: 360–440 pulses/s.

A phrase of this song begins with a 7–20 s series of prolonged notes (part A, Figure 4) leading into a louder, 7–17 s continuous sound (part B, Figure 4). Part of two prolonged notes and the intervening pause are shown in Figure 5c.

Platypleura maytenophila. Villet (Figures 4, 6a, b; Table 1)

Frequency range: 6,5–13,0 kHz; emphasized frequency: 8,8 kHz; pulse rate: 310–510 pulses/s.

The complex gross temporal pattern of this call makes it quite distinctive. The first section (part A, Figure 4) lasts about 4 s. It is a series of pulse groups 25–40 ms long and approximately 5 ms apart which fuse into a continuous sound (part B, Figure 4) for 1–3 s before becoming distinct again. The entire phrase rises in a crescendo. Each pulse group contains a small frequency modulation, and each pulse has two subpulses. The transition from part A to part B is show in Figure 6a.

Platypleura hirtipennis. Germar (Figures 4, 6c, d)

Frequency range: 6,0–10,0 kHz; emphasized frequency: 7,8 kHz; pulse rate: 360–480 pulses/s.

This call is a series of hissing lisps about 0,55 s long,

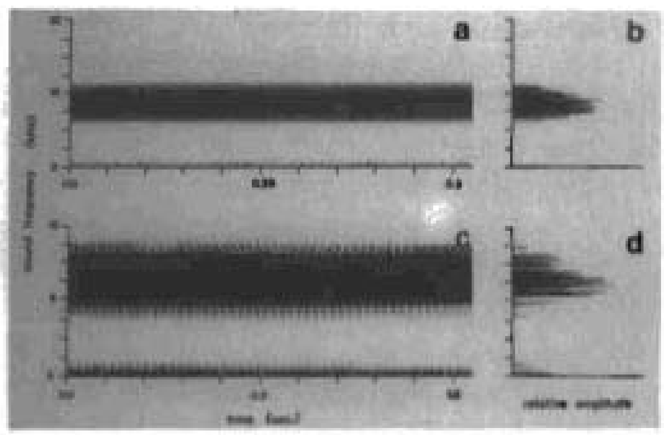

Figure 3 (a–b) Calling song of *Platypleura haglundi.* (a) Sonagram, (b) power spectrum. (c–d) Calling song of *Platypleura hirta.* (c) Sonagram, (d) power spectrum.

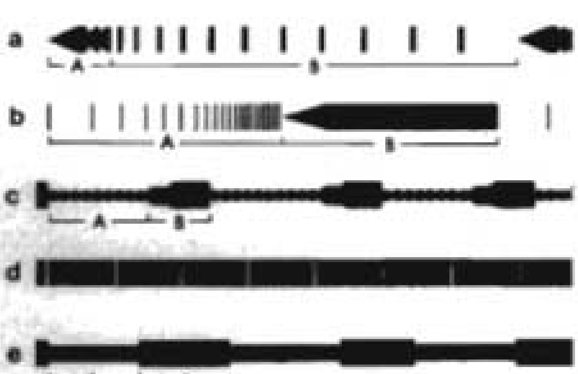

Figure 4 Diagrammatic representations of the gross temporal patterns in amplitude modulation of five species of Platypleurine cicada. The vertical dimension represents amplitude, and the horizontal one time. A and B — parts A and B. Diagrams are not to scale. (a) *Platypleura argentata.* (b) *Platypleura divisa.* (c) *Platypleura maytenophila.* (d) *Platypleura hirtipennis.* (e) *Oxypleura lenihanni.*

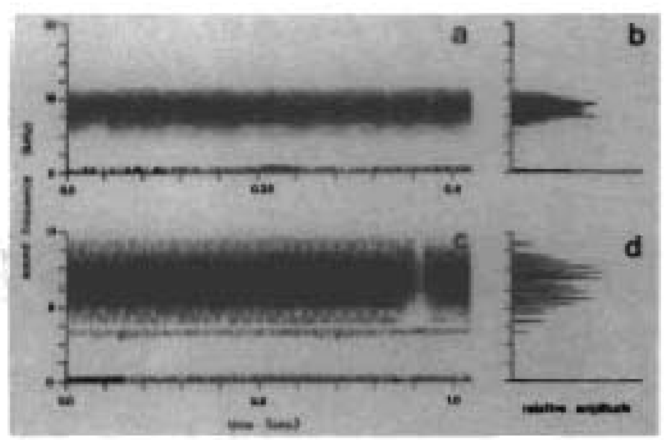

Figure 5 (a–b) Calling song of *Platypleura argentata.* (a) Sonagram of a segment of part B, (b) power spectrum. (c–d) Calling song of *Platypleura divisa.* (c) Sonagram of a segment of part A, (d) power spectrum.

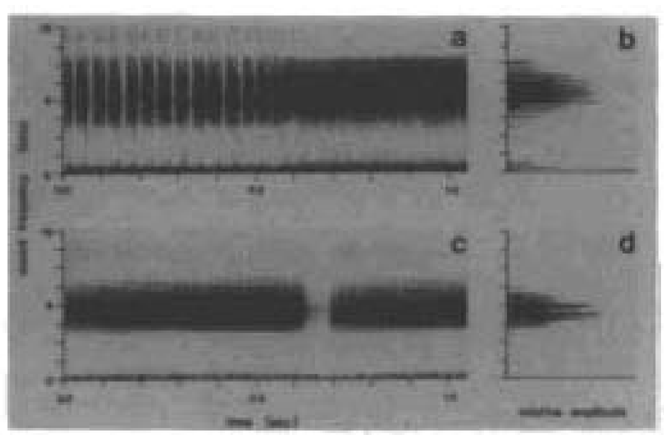

Figure 6 (a–b) Calling song of *Platypleura maytenophila.* (a) Sonagram of transition between parts A and B, (b) power spectrum. (c–d) Calling song of *Platypleura hirtipennis.* (c) Sonagram, (d) power spectrum.

and separated by 70 ms. The pulses are double.

Platypleura zuluensis. Villet (Figures 4, 7a–d; Table 1)

Frequency range: 8,0–16,0 kHz; emphasized frequency: 11,6 kHz; pulse rate: 240–300 pulses/s.

Two parts alternate roughly every 6 s in this call. In the first (part A, Figures 4, 7a), about 30 groups/s of 13 pulses each are produced, each overlapping its neighbours and producing a hissing sound. Half this number of groups are found in the second section (part B, Figures 4, 7c), creating a slightly quieter, rattle-like sound. The pulses contain three subpulses.

Oxypleura lenihani. Boulard (Figures 8a–d; Table 1)

Frequency range: 4,0–11,0 kHz; emphasized frequency: 6,9 kHz; pulse rate: 350–450 pulses/s.

As in the previous species, two phrases alternate to create this song. They are each 10–25 s long. One consists of some 30 groups/s of 12 pulses each. The groups are 25 ms long, and around 8 ms apart (part A, Figure 8c), giving the phrase a slightly rattling quality to the human ear. In the other (part B, Figure 8a) there are about 60 overlapping pulse groups, the pulses of which appear to overlap exactly with those in the next group, creating an uninterrupted train of sound which is slightly louder than the rattling phrase. Each pulse has two subpulses.

Munza basimacula. Walker (Figures 9a–d)

Frequency range: 7,0–14,0 kHz; emphasized frequency: 10,1 kHz; pulse rate: 460–490 pulses/s.

This call is unusual for a platypleurine in that it consists of a number of very narrow, discrete frequency bands, rather than a more characteristic broad spectrum (Figure 9b). The first segment of the call (part A, Figure 9a) consists of a series of pulse groups produced at a rate of 50 groups/s, and lasts 9 s. The other (part B, Figure 9c) is 1 s long, and contains half the number of groups. Part A is some 3 dB louder than part B. The pulse groups are 30 ms long, with 10 ms pauses, and their pulses overlap exactly in part A.

Pycna semiclara. Germar (Figures 10a–d; Table 1)

Frequency range: harmonics of 800 Hz from 4,0 kHz up to 16,0 kHz; emphasized frequency: 4,8 kHz; pulse rate: 730–850 pulses/s.

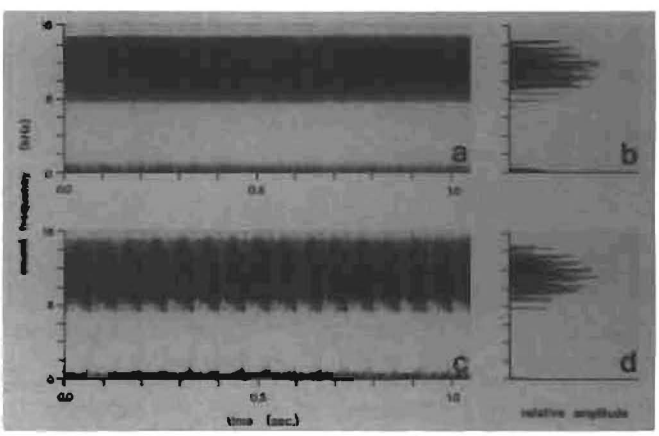

Figure 7 Calling song of *Platypleura zuluensis*. (a–b) Part A. (a) Sonagram, (b) power spectrum. (c–d) Part B. (c) Sonagram, (d) power spectrum.

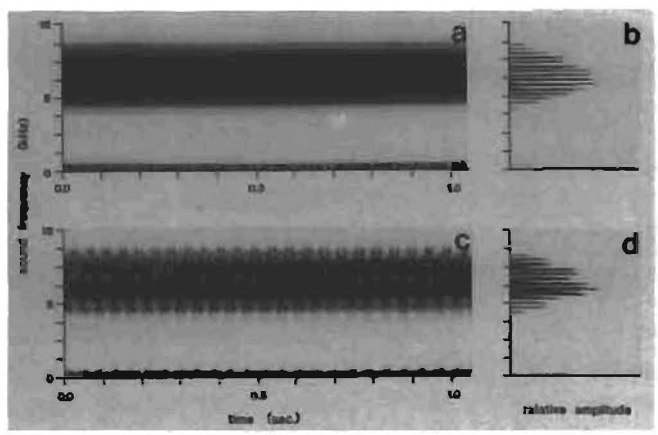

Figure 9 Calling song of *Munza basimacula*. (a–b) Part A. (a) Sonagram, (b) power spectrum. (c–d) Part B. (c) Sonagram, (d) power spectrum.

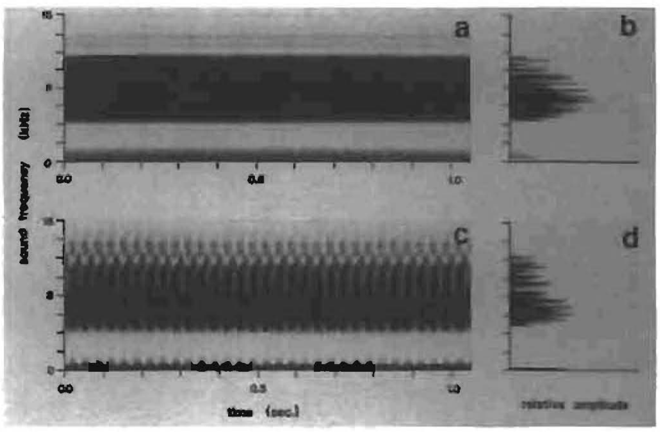

Figure 8 Calling song of *Oxypleura lenihani*. (a–b) Part A. (a) Sonagram, (b) power spectrum. (c–d) Part B. (c) Sonagram, (d) power spectrum.

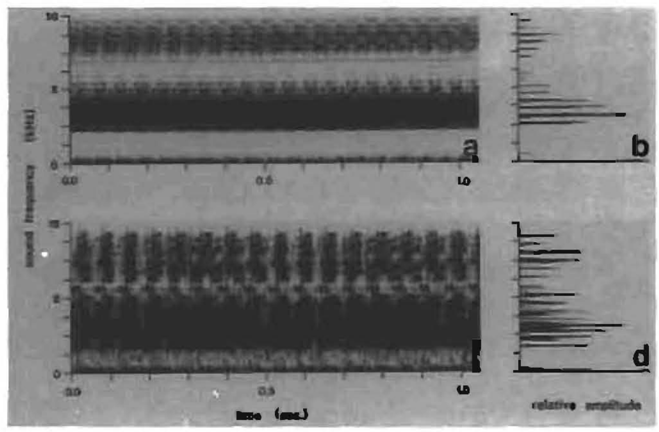

Figure 10 *Pycna semiclara*. (a–b) Calling song. (a) Sonagram, (b) power spectrum. (c–d) Encounter call. (c) Sonagram, (d) power spectrum.

A sustained hum (Figure 10a), composed of a harmonic series of very narrow frequency bands which give this calling song a very shrill, piercing quality. The first four harmonics appear to be absorbed by the resonating system. Slight frequency modulations occur 20 times per second.

P. semiclara has a second song (Figure 10c) made up of 20-ms long groups of pulses produced at a rate of 20 groups/s, at the same sound frequencies as its usual call. The intervals are filled by a fainter, frequency-modulated group of pulses. The increase in the modulation angle of this element of the call at higher sound frequencies confirms the interpretation of the call's structure as a harmonic series. It is an overture to the first call, but is also made when the insect detects a conspecific nearby, and may therefore be termed an 'encounter call' (*cf.* Wells 1977).

A third call, sounding like a brief 'zeep', is voiced sporadically. It was too infrequent to record, but often was followed by a 'zeep' from one or two of the neighbouring males.

Behaviour during calling

Calling males generally remained stationary, except when approached by other males or females. On seven occasions males were seen feeding when they began to sing. Six of these soon removed their mouthparts from the plant and continued singing; the other ceased calling and carried on feeding. No other specimens were found calling and feeding.

In all of the species examined, males spread their wings (Figure 11a) and arched and extended their abdomens (Figure 11b) when they called. However, during the 'encounter' call of *Pycna semiclara*, the abdomen is relaxed and near its resting position. Manual manipulation of freshly dead specimens showed that arching the abdomen increases the tension in the folded membrane which lies anterior to the tympana. Modulations in the songs of *Platypleura divisa*, *P. argentata*, and *P. maytenophila* were synchronized with a wagging of the abdomen in the sagittal plane. Their songs were quietest when the abdomen was unarched, and loudest when it was held flexed (Figure 11b), e.g. during the sustained part of the call. A similar habit has been noted in some Sri Lankan and Australian species (Pringle 1954b).

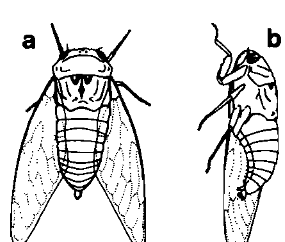

Figure 11 Posture of male cicadas during calling song, illustrated by a specimen of *Brevisana brevis*. (a) Dorsal view, (b) lateral view with nearside wing omitted for clarity.

Variation within populations

Coefficients of variation, derived from data gathered from populations at Mtunzini, range from 2,2–8,1% for spectral parameters, and from 16,4–50,4% for temporal parameters (Table 1). Band-width, which is partially related to loudness, is generally intermediate between these two groups. These figures indicate that the spectral properties of a species' call differ little between individuals within these populations, while the temporal properties show less constancy.

During oscillographic analysis, the pulse repetition rate of individuals was found to rise and fall in an irregular way within the same bout of calling. When a recording was viewed on an oscillograph screen, the wave form would move backwards and forwards across the screen, i.e. along the time axis, as the pulse rate increased and decreased respectively.

Geographic variation

The calls of five species were sampled at more than one site (Table 2). In all cases, the variation in the measured parameters of the smaller samples falls within that of the largest conspecific sample, except in *P. haglundi*, where there is a great deal of overlap instead.

Discussion

As in previous studies, the calling songs described above are characteristic of the species producing them. Even in species which produce a simple, sustained train of pulses, e.g. *B. brevis*, *P. haglundi*, and *P. semiclara*, the calls are easily distinguished by their spectral features. Furthermore, all of the calls described to date, including

Table 2 Characteristics of conspecific calling songs from the widely separated localities shown in Figure 1

Locality	*n*	Emphasized frequency (kHz)	Pulse repetition rate (pulses/s)	Phrase duration (s)
Platypleura haglundi				
Dunstable Farm	2	12,3 – 12,5	330 – 360	–
Northam	4	11,8 – 13,6	320 – 345	–
Mkuzi	10	12,7 – 14,0	330 – 350	–
Platypleura divisa				
Mkuzi	2	10,9 – 11,0	380 – 430	23 – 30
Mtunzini	10	10,5 – 11,0	360 – 445	14 – 35
Dunstable Farm	2	10,8 – 11,3	395 – 460	25 – 29
Illfracombe	1	10,9	410	27
Platypleura hirtipennis				
Grahamstown	3	7,5 – 8,0	255 – 305	0,5 – 0,8
Broederstroom	7	7,2 – 8,0	240 – 300	0,5 – 0,7
Nyala Park	2	7,25	230 – 240	0,6 – 0,7
Oxypleura lenihani				
Mkuzi	3	6,5 – 6,8	355 – 380	?
Mtunzini	20	6,0 – 7,5	350 – 450	24 – 39
Pycna semiclara (full call)				
Grahamstown	3	4,6 – 4,9	780 – 850	–
Dunstable Farm	2	4,7 – 4,8	770 – 820	–
Mtunzini	57	4,4 – 5,3	730 – 850	–

those reported in this study, are unique to their species. Such evolutionary divergence is not surprising, considering the number of variables involved and the forms they can assume.

The calling songs of cicadas are involved in the attraction of mates (Alexander & Moore 1958; Doolan & Mac Nally 1981), and appear to be an integral part of their fertilization mechanisms (Claridge *et al.* 1979). Fertilization mechanisms serve to bring the sexes together for reproduction, and to function successfully, the mechanisms of the two sexes must be closely co-adapted (Paterson 1978, 1985). For this reason they can be expected to fall under strong stabilizing selection, and therefore to show little geographic variation (Lambert & Paterson 1984).

The greater variation in spectral than in temporal parameters may arise because the sound frequencies of the calls are strictly constrained by the physics of the sound-producing organs, while the temporal patterns are under the control of the neuromuscular system (Pringle 1954b). Pulse repetition rates vary greatly, even within the calls of individuals, and are probably not resolvable to the tettigonian ear (Huber *et al.* 1980; Popov 1981). This implies that they do not carry information to the receiver, and are not under stabilizing selection in this regard. In species which exhibit gross temporal modulations of the amplitude of their calls, e.g. *P. hirtipennis*, *P. divisa*, and *P. argentata*, the modulations make these calling songs very distinctive, despite their variability. Environmental temperatures do not appear to affect the call parameters of platypleurine cicadas (Villet 1986).

The posture of the abdomen appears to increase the loudness of the call. Arching of the abdomen could reduce damping caused by slackness in the folded membrane. The wings might act as baffles during singing, but this remains to be tested.

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