TEMPORAL CHANGES IN THE QUALITY OF THE SONG OF A BUSH CRICKET

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Summary

The first songs produced by newly adult *Poecilimon schmidti* (Fieber) are shown to be composed of pure tone bursts. At this time the file is in its pristine condition. After a week of stridulatory activity the songs of the same individual start to be contaminated with anharmonic components, arising from wear damage that occurs to the file teeth and plectrum. The disruption of the pure tone burst adds other elements to the Fourier spectra so that they now become difficult to interpret. The number of plectrum–tooth impacts, normally 2–5, also varies with ageing. Although females responded well to old males there is a possibility that the change in song quality would enable the female to discriminate between males.

Introduction

Acoustic mate-finding requires that the signal emitted by the caller must be identifiable by the receiver as belonging to the right species and that the position of the caller must be determinable, even in a noisy environment. In the Gryllidae it is important for phonotaxis that the song is sharply tuned to a narrow frequency band (Stout *et al.* 1983). In the Tettigoniidae, in spite of a vast amount published on spectral components of their songs, there is very little hard evidence on the parameters responsible for phonotaxis. Many bush crickets produce long songs containing many syllables. Each syllable is composed of many plectrum–tooth impacts in close succession. The consequent convoluted frequency distribution is often extremely complicated. However, there is evidence to suggest that various parts of the call convey information at different distances. For example, in some *Conocephalus* species, females will perform distant phonotaxis on white noise, but at close quarters they depend on modulation patterns within the natural call (Morris & Fullard, 1983). Female *Tettigonia cantans* performed phonotaxis preferentially on songs with enhanced high frequencies, but also responded better to songs with a lower modal frequency of 6·8 kHz rather than 8·8 kHz (Latimer & Sippel, 1987). In these examples it seems that song quality may not be of great

importance, particularly at a distance. Therefore, any wear and tear on the sound-producing apparatus, which could also further contaminate the song, may not matter too much, although this has not been tested.

In contrast, most phaneropterines have a very precise communication system. Here a duet is established between a calling male and a replying female, often using a brief high-frequency song, as in *Leptophyes punctatissima* (Robinson *et al.* 1986). In this species, the male performs phonotaxis on the even briefer female reply which has to arrive within a very precise time window. These songs have a restricted narrow frequency band associated with the modal vibration of the wings, and song quality could be extremely important in avoiding confusion caused by environmental contamination.

Since these sounds are produced by scraping plectrum across file, the structures involved will be subject to wear, as seen for example in *Steropleurus stali* (Hartley *et al.* 1974). Such abrasion should affect the quality of the sound produced. To investigate this we used a bush cricket, *Poecilimon schmidti*, which produced a very simple song composed of a few discrete plectrum–tooth impacts.

Materials and methods

Insects

We used male *Poecilimon schmidti* bred in the laboratory at Nottingham. After the final ecdysis, males were marked individually and kept in separate cages from females. The calling songs of individually identified males were recorded every few days for 5 weeks. The files and plectra of newly ecdysed males and of the experimental males at the end of the 5-week singing period were examined by scanning electron microscopy (SEM).

Sound recording

The recording equipment was a QMC SM1 microphone and a Racal Store 4 direct record tape recorder running at 15 inches s^{-1} (38·1 cm s^{-1}). The songs of the males were recorded as follows. During the period of day when the males were singing, the experimental male was carefully moved from the cage onto a perch, a twig with leaves standing in a pot of water, so that the insect was some 10–20 cm above the bench surface and 10 cm below the microphone. For some recordings a plastic foam mat was placed on the bench under the perch.

Analysis of the song

The songs were analysed, in the Physiology Department at Leicester, on a Bruel & Kjaer 2032 signal analyser. This machine performs a fast Fourier transform (FFT) on single or repetitive signals and other more complex modes of analysis.

Fourier analysis

The songs were played back at one-eighth speed to ensure that all their acoustic

power fell within the spectral range of the analyser (0–25·6 kHz). All songs were contaminated by echoes from objects near the singing insect (see Fig. 3). Since we were specifically interested in the spectral response of the plectrum–tooth impulse (PTI) we analysed calls with a rectangular window of slightly longer duration than the PTI. This windowing isolated the first PTI of any call, ensuring that the spectral analysis was free of contamination arising from the echoes. Since the duration of the window was greater than the duration of the PTI, windowing in no way affected the determination of the Fourier spectra of the PTI.

Measurement of the interval distribution of plectrum–tooth impulses

We measured the statistical distribution of PTIs in the following way. The song was passed through a pulse shaper, which was tuned to give a single transistor threshold logic (TTL) pulse corresponding to each tooth impulse. The resulting train of pulses was passed through a pulse-width demodulator, which gave an output voltage proportional to the pulse width. The probability density and distribution of the demodulated output voltage were determined using the probability density and distribution functions available on the B&K 2032. A block diagram of the demodulator circuit is shown in Fig. 1.

Mode of song generation

It was shown by Heller (1984) that *Poecilimon schmidti* only generates sound on the closing stroke of the wings, and a single wing movement generates the complete chirp. This can also be observed directly in the singing insect, as the wing movement is relatively slow. Heller also showed that the movement is not a simple smooth flowing closure but one that is broken up into a series of jerks. Each jerk corresponds with a single plectrum–tooth contact. The whole chirp is made up of only 2–5 plectrum–tooth impulses. Because of the slow wing movement the sound is generated principally by vibrations set up as the plectrum springs free of the file tooth. For convenience we call this the plectrum–tooth impulse (PTI).

Results

The first part of the Results is based on one particular male (male A) initially chosen at random. All observations were corroborated by sequential studies on a number of other individually identified males.
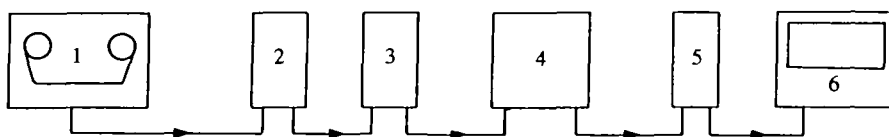

Fig. 1. Block diagram of the demodulator circuit used to obtain the PTI interval distributions. (1) Racal Store 4 recorder (direct record); (2) level trigger; (3) pulse width unit; (4) AIM 65 micro; (5) D–A convertor (Analog Devices AD574); (6) Bruel & Kjaer 2032.
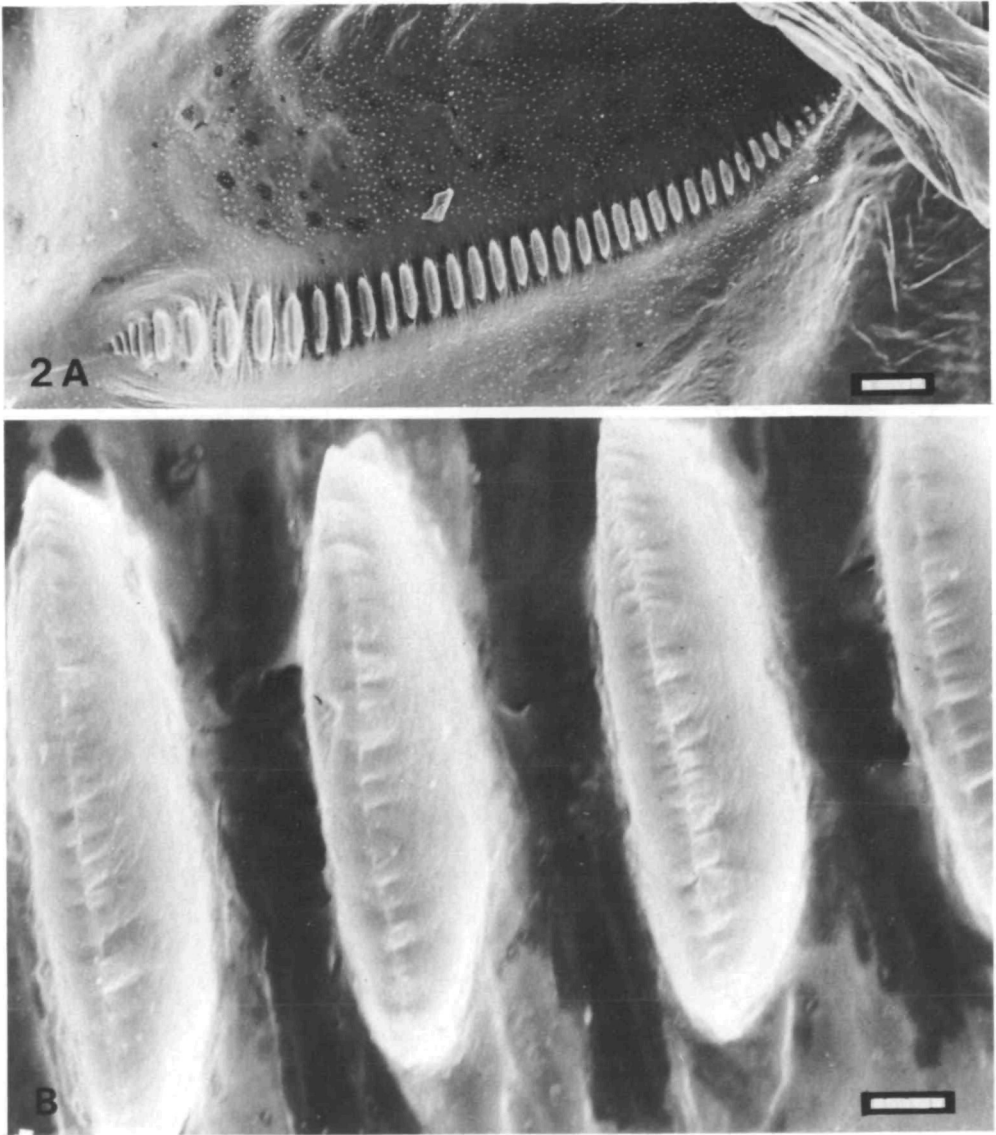
Fig. 2. Scanning electron micrographs of the file and file teeth of *Poecilimon schmidti*.
(A) The entire file, distal end borne on inflated vein to the right. Scale bar, 100 μm.
(B) Detail of teeth in newly matured adult. Scale bar, 10 μm.

File structure

Fig. 2A–D shows SEM pictures of the file in a recently moulted adult male (not
male A) and of male A after 5 weeks of singing. In the newly moulted male, the
file and plectrum are smooth with clean surfaces. After 5 weeks of singing, both
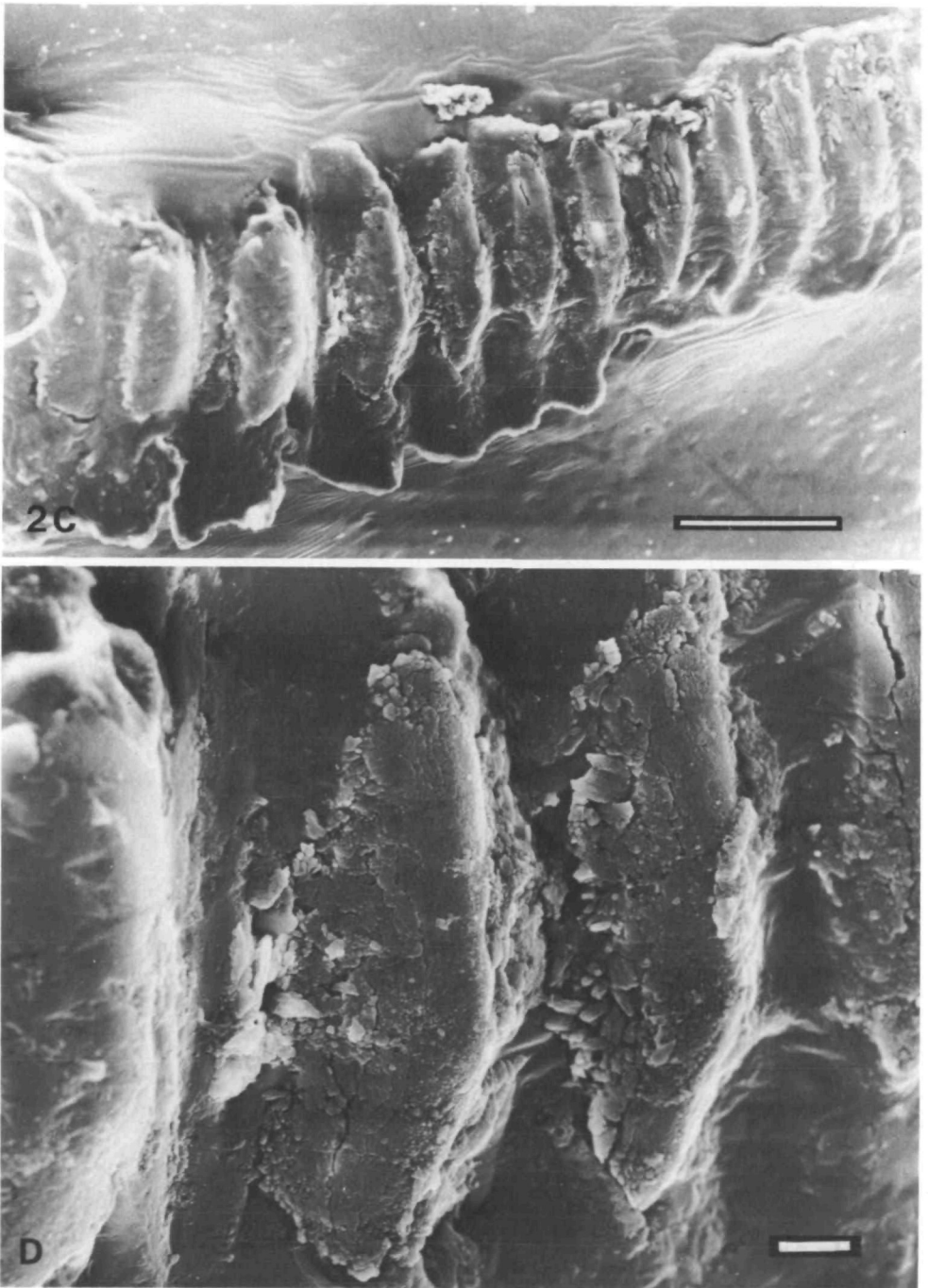file and plectrum show significant wear. Both have rough surfaces and parts of the

Fig. 2. (C) Appearance of file after 5 weeks of singing, note deposits around file. Scale bar, 100 μm. (D) Detail of damage to teeth near distal end of file as in C. Scale bar, 10 μm.
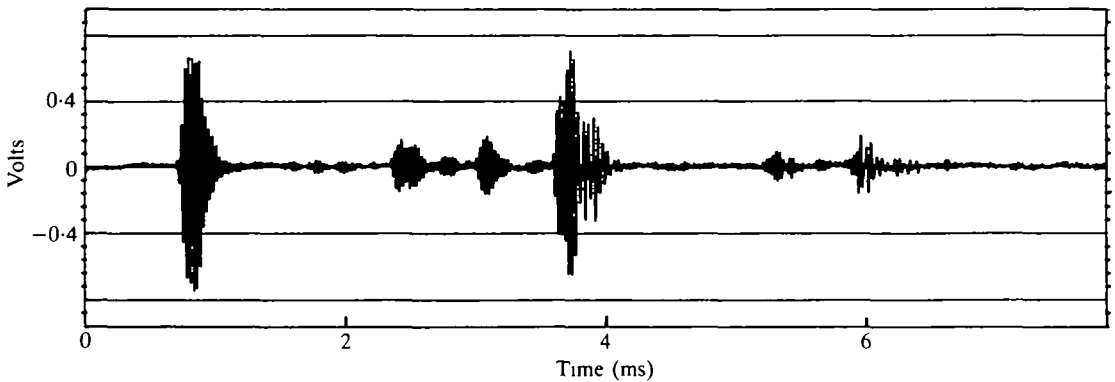
Fig. 3. Oscillogram of entire song of a male *Poecilimon schmidti* recorded soon after it became adult.

file teeth are missing. There is also a fair amount of debris in the form of a waxy deposit around the teeth. In the worn files only a short length of the file shows abrasion, although the deposit is smeared over a greater part. The vein bearing the file is strongly inflated towards its distal end. Judging by the wear, it is only the teeth on this part and a few on the descending slope that are struck during stridulation.

The song

The call of *P. schmidti* recorded during the first week of adult life is shown in Fig. 3. The song of male A usually consisted of 2–3 transient coherent pulses of sound each less than 0·3 ms in duration, each arising from a single PTI, separated by intervals of 2–3 ms. The first PTI is followed by a series of small sound pulses at 0·3, 0·6, 0·8 and 1·1 ms. Altering the nature of the perch, or placing a foam mat under it, changed these smaller pulses, clearly showing them to be echoes. The second PTI occurs some 2 ms after the first. It is slightly longer than the first and is not quite as clean. This probably results from the double action of the plectrum, as it first strikes and then springs free of the second tooth.

Fig. 4A is an expanded oscillogram of the first PTI. This has the appearance of a gated pure tone burst lasting 0·25 ms with a carrier frequency, determined from the periodicity of the oscillations, of 36 kHz. The Fourier spectrum calculated for the first PTIs of 25 consecutive calls is shown in Fig. 4B. The spectrum does not immediately appear to reflect the simple structure observed in Fig. 4A, because it is now a convolution of the carrier frequency and pulse envelope. The effects of such convolutions are illustrated in Fig. 5. Fig. 5A shows the Fourier spectrum of a continuous pure tone of 4·75 kHz (one-eighth of the song carrier frequency and therefore comparable with the song frequency analysed at one-eighth speed. Gating this tone to produce a rectangular tone burst of 1 ms duration produces the
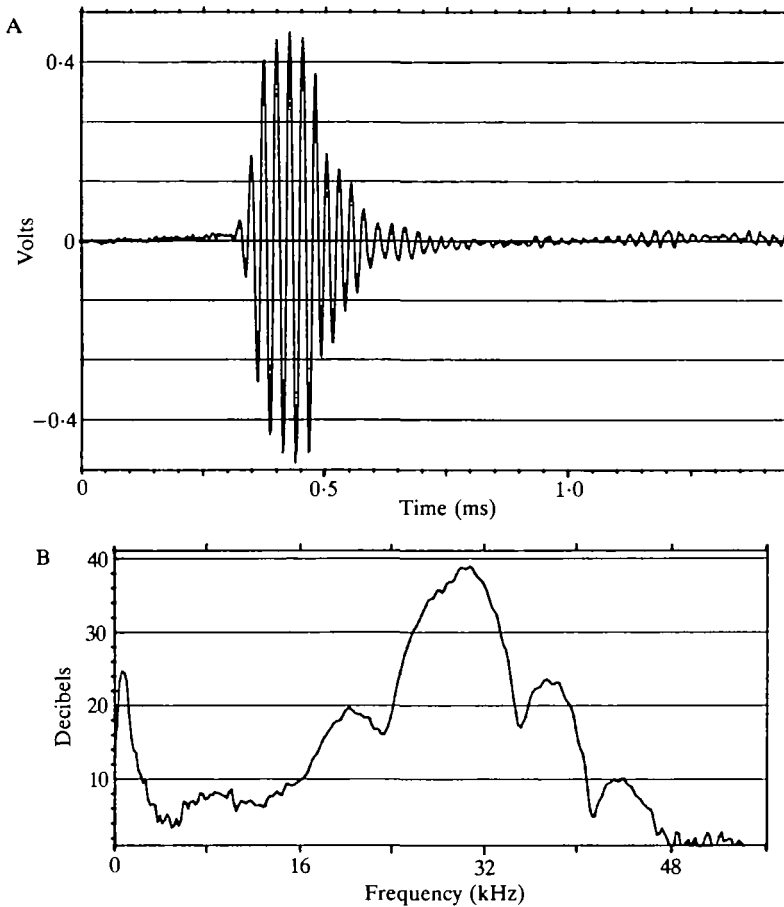
Fig. 4. (A) Expanded oscillogram of a first plectrum–tooth impulse similar to that in Fig. 3. (B) Fourier spectrum of first PTI of 25 successive songs similar to that shown in Fig. 3.

convoluted spectrum shown in Fig. 5B. For an impulse of duration T the spectrum of the envelope, $W(f)$, is given by:

$$W(f) = \frac{T\sin(\pi Tf)}{\pi Tf}$$

(Randall, 1977).

The convolution produces minima on either side of the main peak at frequencies of $f_0-1/T, f_0-2/T$, etc. and $f_0+1/T, f_0+2/T$, etc. where f_0 is the tone frequency (4·75 kHz). This is just what is found in Fig. 5B. The minima on either side of the main peak are the predicted 1 kHz apart.

The spectrum, shown in Fig. 5C, is of the same tone burst (Fig. 5D) now with a shape approaching that of the observed PTI and lasting just under 1 ms at half-maximum amplitude. It resembles that of Fig. 5B but with minima slightly further apart. The PTI shown in Fig. 4A has, at the one-eighth playback speed, a duration
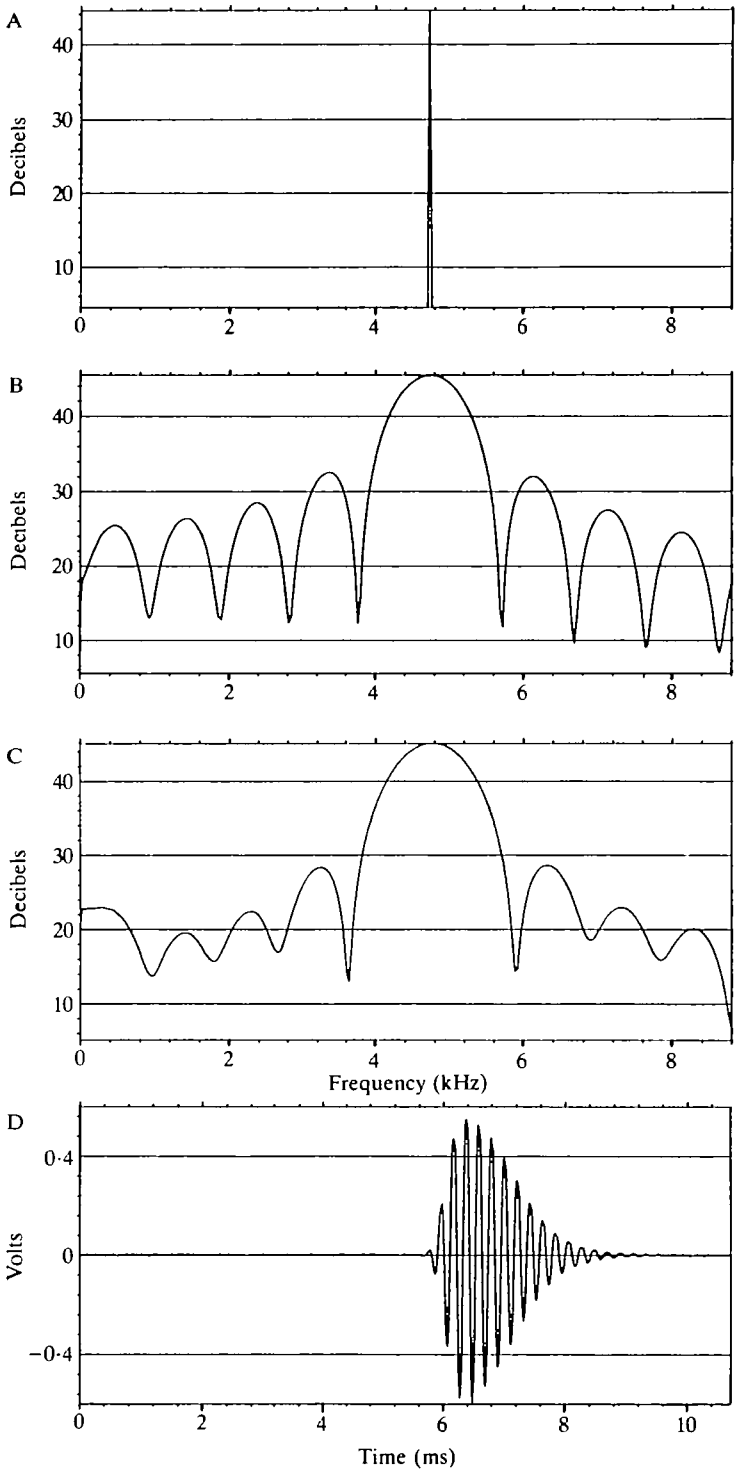
Fig. 5

Fig. 5. (A–C) Fourier spectra of a pure tone of 4·75 kHz; (A) for a continuous tone; (B) for a rectangularly gated tone burst of 1 ms duration; (C) for the more naturally shaped tone burst shown in the oscillogram (D).

of approximately 1 ms (0·125 ms actual) at half amplitude, producing a convoluted spectrum (Fig. 4B) with minima at 3·6 (= 28·8) and 5·5 (= 44·0) kHz. These are approximately 1 (= 8) kHz either side of the mean 4·5 (= 36·4) kHz, as predicted for a gated tone burst. The frequency thus determined is very close to that measured from the periodicity of the oscillations above.

Changes in song structure with time

The first PTI of the song of the newly matured male (Fig. 4A) is a simple clean tone burst. The first PTI of all later songs was observed to vary in structure over the 5-week period (Fig. 6A–D). It also varied from pulse to pulse during a single period of singing. Initially the PTI generated a brief 0·25 ms tone burst, whereas 5 weeks later the duration of the impulse has almost doubled. In Fig. 6D the impulse
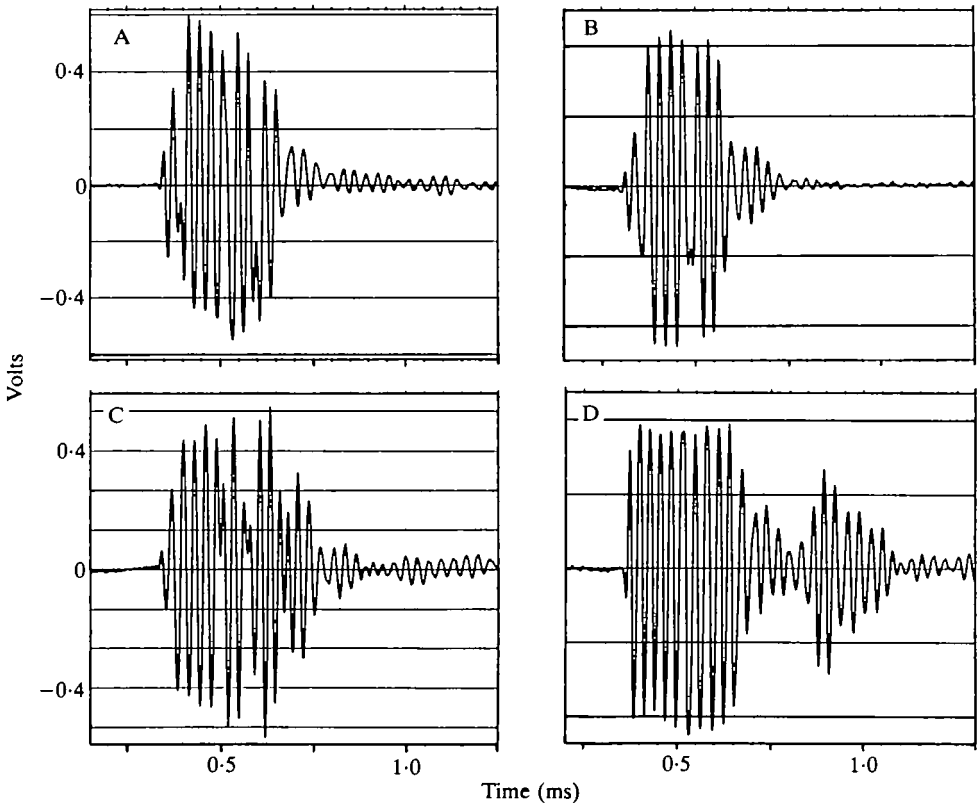

Fig. 6. (A–D) Expanded oscillograms of the first PTI of songs, randomly chosen, at successive weekly intervals. (A) At the beginning of the second week of singing; (B) third week; (C) fourth week; (D) fifth week.

Table 1. *Calculated frequency from initial four oscillations of the PTIs shown in Figs 5A, 6A–D*

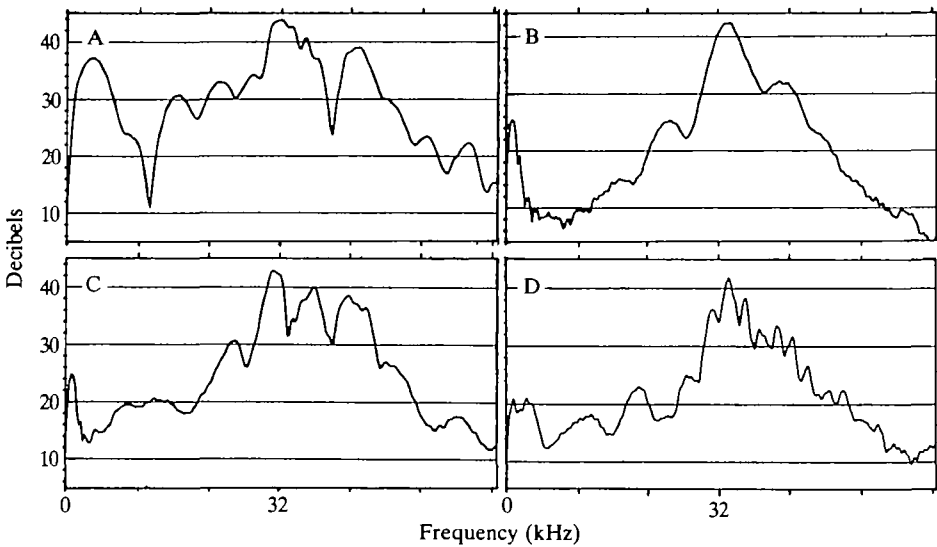| Week of singing	Oscillogram figure	Calculated frequency (kHz)
1	5A	36
2	6A	33
3	6B	33
4	6C	32
5	6D	29

Fig. 7. (A–D) Fourier spectra of 25 successive first PTIs measured at weekly intervals as indicated in the legend to Fig. 6.

seems to contain three separate contact events as the worn plectrum rubs different parts of the abraded tooth. Anharmonic components are clearly present in all later oscillograms.

This is to be expected from the wear damage we found. The plectrum no longer slides smoothly over the tooth, but catches on the abraded tooth in a slightly different way each time. Close examination of the oscillograms (Fig. 6) also indicates that the harmonic frequency of the pulse changes irregularly with time. In Table 1 the basic harmonic frequencies from the initial oscillations are shown. The reasons for such variations are not clear. Accumulation of the deposits shown in Fig. 2C,D could account for a decrease in frequency. Changes in humidity in the greenhouse where the insects were kept might also be a factor.

Fig. 7A–D shows the Fourier spectra averaged for 25 similar pulses for each of

the series shown in Fig. 6. These Fourier spectra bear little clear relationship to the oscillograms. The spectra now show many separate peaks (16 in Fig. 7D). It is clear that each peak cannot be associated with a harmonic frequency in the PTIs shown. Most of these peaks are generated by different events, some of which can be seen in the individual oscillograms. When the pulse is a simple tone burst (as in Fig. 4A), the Fourier spectrum (Fig. 4B) has a simple relatable structure. When the PTI has a more complex structure, caused by interference in the oscillation pattern and changes in the duration and shape of the impulse envelope, and also varies from PTI to PTI, the resulting Fourier spectra become extremely difficult to interpret in any meaningful way.

Plectrum–tooth impulse distribution

The PTI interval distribution was also measured for the calls. The results are shown in Fig. 8. Fig. 8A shows the distribution over 60 consecutive calls of male A. Initially, this male produced a call consisting entirely of chirps with just two PTIs. The interval is remarkably constant at a mean of 2·66 ms. Over the 5-week period the distribution became more variable until finally the call reduced to a single PTI.

Observations on other males

The principal difference between the calls of male A and those of other males was the number of PTIs per call. Most other males produced 3–5 impulses, separated by similar time intervals, all in the range 2·0–2·7 ms. The form of their oscillograms and autospectra were indistinguishable from those of male A.

Female response

Unmated females replied to the calls of males regardless of male age. However, they were not given a choice of young and old males in close succession. They were certainly able to identify and respond to the contaminated call of the old male.

Discussion

Phonotaxis in *P. schmidti*, like that in many other phaneropterine bush crickets, is initiated in the male as the result of a duet between male and female. The male call initiates a female response call and the male performs phonotaxis on the reply. In *Leptophyes punctatissima*, which has a similarly brief high-frequency call, communication distances of up to 5 m have been observed (Hartley & Robinson, 1976). There, as here, all the information required to initiate a female response is contained within a single male chirp. In *Leptophyes* this can be a synthetic chirp consisting of a 10 ms 40 kHz tone burst (Robinson *et al.* 1986). Extending this argument to the real song, it is likely that the necessary information is contained in the pure tone modal frequency alone and not in frequency components arising from pulse length, shape or inter-pulse interval.

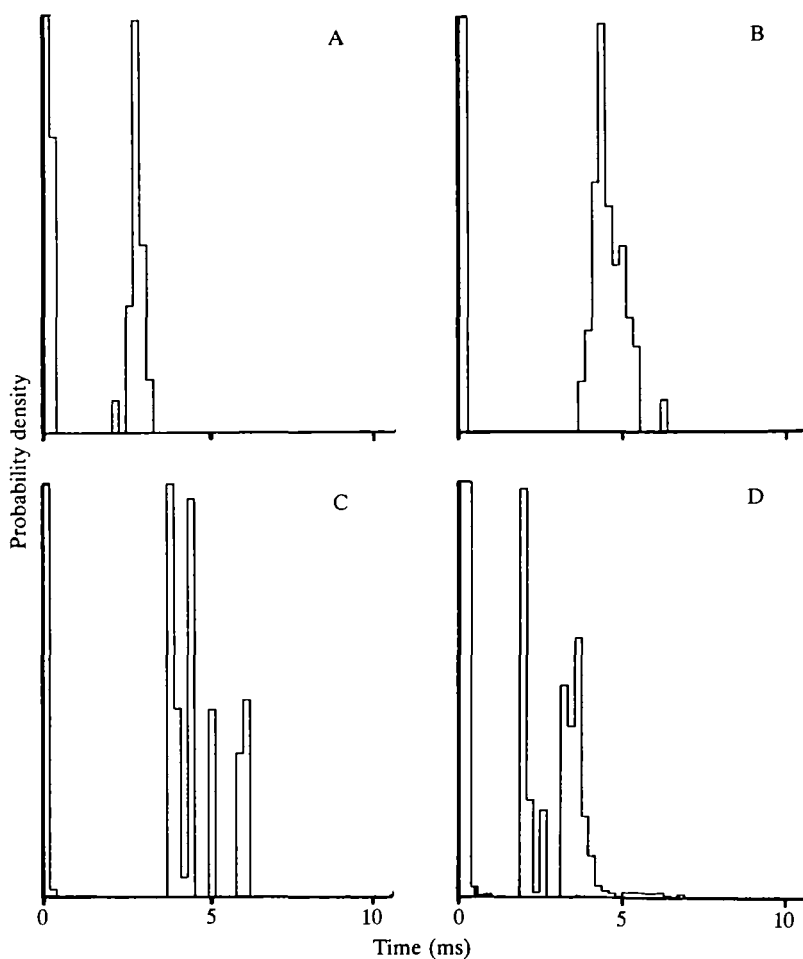The autospectrum of the plectrum–tooth impulse is a convolution of the

Fig. 8. (A–D) Interval distributions of the PTIs in entire songs, measured at weekly intervals. (A) Initial period of singing, as Fig. 3; (B) at beginning of the second week; (C) third week; (D) fourth week. In the fifth week the song had degenerated to a single PTI so there was no interval distribution.

envelope of the impulse and the spectrum generated by the vibration of the wings. In *Poecilion schmidti*, our results show that, shortly after ecdysis, the wings generate what appears to be, from the oscillogram trace and the form of the autospectrum, a pure 36 kHz tone burst. The remaining spectral power in the impulse can be accounted for in the $\sin x/x$ spectral distribution of the envelope of the impulse. At this time the first inter-impulse interval for male A was 2·66 ms; it was between 2·0 and 2·7 ms for other males with almost no variation. Since all males, young or old, elicited female responses, neither the inter-pulse interval nor pulse shape seem to be of importance.

It seems unlikely that the spectral power in the envelope of the impulse contain much useful behavioural information. It is therefore highly likely that all

the information required to stimulate a response call is in the first tone burst generated by the wings. Whether the subsequent pulses matter is not known; they may be purely incidental. Male *P. schmidti*, like *L. punctatissima*, then perform phonotaxis on the single impulse response of the female.

As the male ages there appears to be a slight decrease in the modal frequency of the call. The spectral composition changes with the introduction of components not harmonically related to the modal vibration. This is caused by the accumulation of debris around the file as well as by tooth and plectrum wear. Thus the oscillogram after 5 weeks is no longer just the pure tone burst produced by a single clean tooth–plectrum impulse, but is now contaminated by multiple impulses produced by a roughened plectrum scraping over the damaged surface of the worn tooth. This extends the duration of the impulse as the time to clear the tooth is increased, and it may also affect the overall rate of wing movement, thus altering the inter-pulse interval.

In terms of information entropy, the total entropy of the call is minimal when the insect first sings. The total entropy then increases as the insect ages, owing to the generation of harmonically unrelated frequencies caused by wear. This increase in entropy means that some aspects of the message contained in the call become progressively more garbled as the insect ages. It could, therefore, be possible for a female to discriminate between males of different age. It remains to be seen whether the ability to perform phonotaxis is impaired by the song degradation, though in the female this is likely to be less than in the male, since she only stridulates in response to the male call and only when receptive.

The nature of the damage (Fig. 2D) and the trace pattern shown by Heller (1984) suggest a substantial energy input into the stridulatory movement. Although this could be a reason for the brevity of the song, a more important reason for an insect living in a leafy environment is the problem of echoes. Since the reflectivity of these ultrasonic pulses from small nearby objects can lead to rapid distortion of the envelope of the sound pulse, the briefer the call, the less the possibility of contamination. The even briefer female reply will be even less liable to contamination and echo distortion, but the male will have to be highly attuned. This could help explain the shortness of the acceptable time window found in other phaneropterines such as *Leptophyes punctatissima* (Robinson *et al.* 1986) and *Poecilimon* species (Heller & von Helverson, 1986). Also, since high-frequency sounds (>20 kHz) have only short transmission distances, because of rapid attenuation, there is little reason for the time window to be much longer.

A quite different bush cricket with a very brief, very high-frequency song is described by Gwynne & Bailey (1988). This an Australian zaprochiline in which the male produces a song of two pairs of pulses, each pulse apparently produced by a single PTI, separated by 56 and 130 ms and producing a pure tone burst of 50 kHz asting little more than 1 ms. They give evidence of mate selection by the females and discrimination between songs of this sort would be very sensitive to their gradation from tooth wear.

In other Tettigoniidae with long calling songs made up of many PTIs where

there will be generation of other frequencies arising from pulse length and interval, the effect of wear on the call may be of lesser importance, since these insects do not necessarily need the same precision in their acoustic interactions.

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