

RELATIVE IMPORTANCE OF SONG PARAMETERS DURING FLIGHT PHONOTAXIS AND COURTSHIP IN THE BLADDER CICADA *CYSTOSOMA SAUNDERSII*

BY JANE M. DOOLAN AND DAVID YOUNG

*Department of Zoology, University of Melbourne, Parkville, Victoria 3052,
Australia*

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Summary

Parameters of the calling song that were necessary to evoke phonotaxis in female bladder cicadas (*Cystosoma saundersii*) were determined for both long-range and short-range communication between the sexes.

1. Females flew to loudspeakers that were broadcasting model calling songs that resembled the natural calling song of the males. They also initiated courtship in response to the model calling songs.

2. When flying females were offered a choice between a model resembling the natural song in all parameters (the control model) and a model in which one of the temporal parameters had been changed (the experimental model), they were attracted equally to the control and experimental models. When the carrier frequency of the experimental model was changed, the females were attracted exclusively to the control model.

3. When the same model calling songs were presented to tethered, flying females in the laboratory, they turned only towards models with a carrier frequency close to that found in the natural song. Changing the temporal parameters of the model did not affect either the turning preferences of the females or their reaction times.

4. When the same series of control and experimental models were played, one at a time, to caged females in the laboratory, courtship responses were elicited only by models with temporal parameters similar to those of the natural song. In contrast, a wide range of carrier frequencies was found to elicit courtship, provided that the temporal parameters were similar to those of the control.

5. It is concluded that, in *C. saundersii*, identification of conspecific males by females is a two-stage process, with the carrier frequency of the male calling song being more important in long-range communication (flight) and the temporal parameters of the calling song being more important in short-range communication (courtship).

Introduction

The males of many insect species produce acoustic signals that attract con-

Key words: cicada, communication, *Cystosoma saundersii*, song.

specific, reproductively receptive females. The females respond by moving towards the sound source (Elsner & Popov, 1978), and this phonotactic response has been used to determine which characteristics of the signal are used in species-recognition by the female. The research has been concentrated on Orthoptera, especially field crickets: most studies have analysed the phonotactic reactions of walking females (Walker, 1957; Zaretsky, 1972; Hoy & Paul, 1973; Hill, 1974; Morris *et al.* 1975; Popov & Shuvalov, 1977; Thorson *et al.* 1982; Stout *et al.* 1983), some have examined the preferences of flying females (Ulagaraj & Walker, 1973, 1975; Popov & Shuvalov, 1977; Moiseff *et al.* 1978; Pollack & Hoy, 1979, 1981; Doolan & Pollack, 1985; Nolen & Hoy, 1986), and a few have compared flight phonotaxis and walking phonotaxis in the same species of field cricket, and similarities have been found (Pollack & Hoy, 1979, 1981; Pollack *et al.* 1984).

In this paper, the characteristics of the song that are necessary to elicit responses from female cicadas are examined for both flight and walking, which represent long-range and short-range communication, respectively. The species used in this study is the bladder cicada, *Cystosoma saundersii*, which occurs along the subtropical coastal fringe of eastern Australia. Males sing only at dusk for approximately 30–40 min (Doolan & Mac Nally, 1981); their calling song consists of regularly repeated sound pulses (40 Hz) having a relatively pure carrier frequency of approximately 850 Hz (Simmons & Young, 1978; Young, 1980).

Field observations show that females fly towards a group of chorusing males and, judging by their flight path, they appear to make the final choice to approach a particular male at a distance of 1–2 m. They then spiral in to land, usually within 0.5 m of the chosen male. Within this sphere, females appear unable to locate the male with any accuracy. Having alighted, the female moves about and begins to flick her wings. The male responds to the wing-flicking by producing a courtship song, which has similar characteristics to the calling song but is quieter and broken into small chirps (Simmons & Young, 1978). The female continues to move about and to wing-flick, usually between the chirps of the male. The male then moves towards the female and mating follows (Young, 1988).

The experiments reported here were designed to extend our understanding of the natural behaviour of *C. saundersii* by examining female preferences with respect to calling song parameters under conditions corresponding to two important stages in the above mating sequence. These are (1) the preferences shown by females flying at distances of more than 1 m from a calling male (long-range communication) and (2) the preferences of females that have alighted at distances of less than 0.5 m from a calling male (short-range communication).

Evidence of female preferences was obtained from three classes of experiment. First, the responses of free-flying females to a series of two-choice experiments involving artificially synthesized, model calling songs were tested in the field. Second, the steering responses of tethered, flying females to the same model calling songs were examined in the laboratory. Third, the song parameters necessary to elicit courtship behaviour were determined by playing back these model calling songs to courting females and measuring their response.

Materials and methods

Specimens of *C. saundersii* were obtained at Port Macquarie in New South Wales. Field experiments were conducted on a coastal farm at Port Macquarie.

Model calling songs were synthesized by using a pulse generator (Tektronix FG 502) and an amplitude modulator to modulate sine waves from a function generator (Tektronix PG 505). The resulting output was stored on tape using a Sony TC-510 tape recorder. The models included a control, which resembled the natural song, and experimental songs in which the parameters of the song were changed (Fig. 1). These parameters included carrier frequency, pulse period, pulse duration and pulse interval. In the natural song, the amplitude of each pulse does not fall to zero before the onset of the next pulse. Therefore, pulse duration is

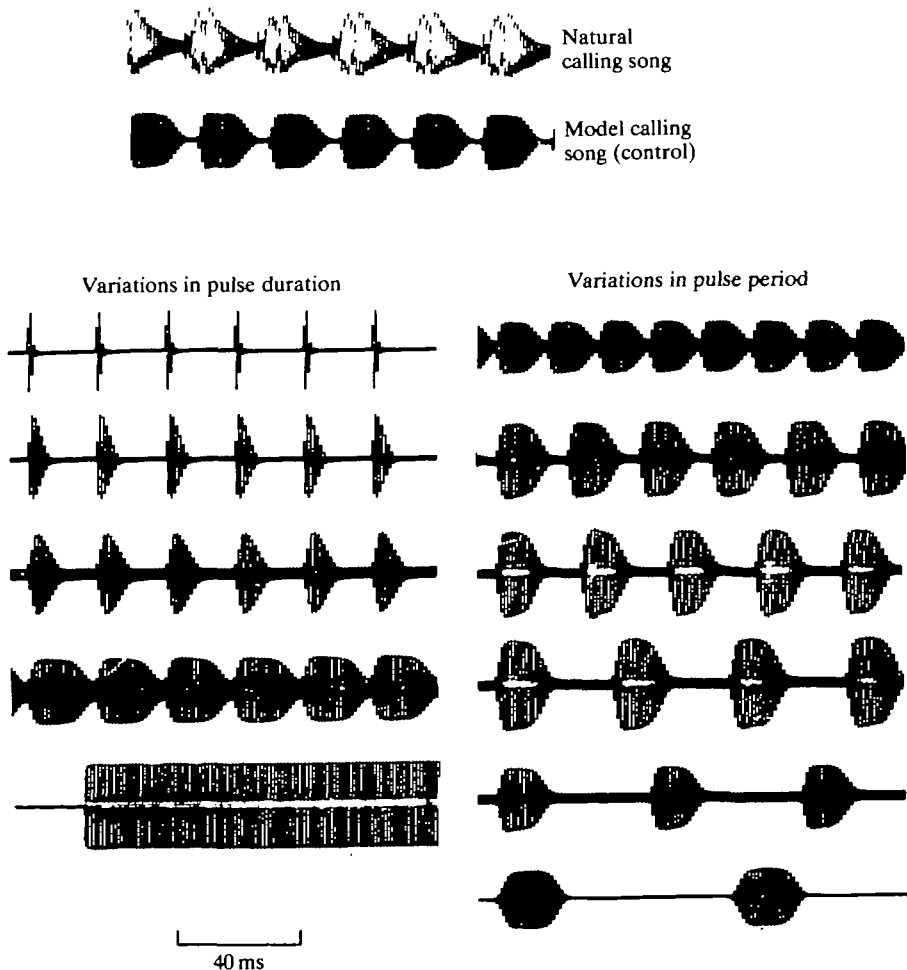


Fig. 1. Oscillograms of model calling songs that were used in both field and laboratory experiments. The songs in which the carrier frequency was varied had the same temporal parameters as the control song.

defined as the time during which the sound amplitude is at or above half its maximum value, and the pulse interval as that period during which the sound amplitude falls below half its maximum value. All models had short breaks of about 0.5 s incorporated at approximately 10-s intervals, in imitation of the natural song, in which such breaks occur irregularly.

Throughout these experiments, all measurements of sound pressure levels (SPL) were made with a Bruel & Kjaer type 4121 microphone connected by a 3 m long cable to a Bruel & Kjaer type 2203 sound level meter, displaying root mean square pressure. The frequency response was linear, i.e. without weighting or octave filters, and the response time was set on fast, the duration of which (125 ms) is sufficient to include several cycles of both natural and model calling songs. The SPL meter was calibrated using a noise source, Bruel & Kjaer type 4240. Measurements are expressed in dB re 20 μ Pa.

Flight analysis

Field experiments

Model calling songs were broadcast using a battery-operated tape recorder, a battery-operated audio-amplifier and a loudspeaker (Auratone 5RC super road cube). Two such systems were used simultaneously, with the speakers situated 7.5 m apart and facing an area of bushland inhabited by *C. saundersii*. Each speaker was placed on a stand 0.7 m high, which is within the normal range of heights used by singing males (Doolan & Mac Nally, 1981). A sheet of white plastic was placed beneath each speaker so that it was easy to see insects as they landed near the speakers. Females would fly to loudspeakers without the white sheets, as well as to tethered singing males, and since some broadcast models did not attract any insects (see Results), there is no reason to suppose that the white plastic sheets played any role in attracting females. The songs were broadcast at 105 dB, measured at 30 cm from the loudspeaker, which is much higher than the output of a single singing male (Mac Nally & Young, 1981) but has the advantage of attracting a greater number of cicadas (Doolan, 1981). Since the SPL meter averages root mean square pressure over several cycles of the song, all the broadcast models were of similar sound power per unit time.

Broadcasting began at dusk approximately 5 min after the onset of the natural chorus and was continued until the end of the chorus. Only one experiment was attempted each night. In each experiment, one loudspeaker always played the control song, and the other loudspeaker played an experimental song. Animals were collected as they flew in to the loudspeakers. The position of the control loudspeaker was alternated on successive nights to avoid any position effects. Each experimental song was tested against the control on three occasions and the total numbers of females and males attracted to each were recorded.

Laboratory experiments

These experiments investigated the steering responses of individual tethered,

flying females to the same model calling songs (Fig. 1). They were carried out within an acoustic chamber, insulated with 35 mm thick rockwool (Bradford R4 Type A duct-liner), which has absorption coefficients of 0.95–1.0 in the frequency range used. The loudspeaker was situated 0.9 m from the insect to ensure that the sound waves reaching the animal were planar (Michelsen & Nocke, 1974). Sound pressure level was measured using a microphone placed close to the position of the animal and connected to the SPL meter.

Each animal was secured by the pronotum to a holder and suspended in an airstream. This procedure induced most female cicadas to fly. The airstream was generated by an electric fan situated outside the acoustic chamber and was passed through a tube, 7 cm in diameter, containing approximately 100 drinking straws. The length of these straws (21.0 cm) was at least 50 times their diameter (0.4 cm), which ensured that the airstream passing the animal was of laminar flow.

The holder, to which the animal was waxed, was a swivel that allowed movement horizontally, i.e. in the yaw plane (Fig. 2). A wind vane was placed at its distal end to provide a restoring force that would keep the animal in the centre of the airstream. The width of the wind vane could be varied to overcome any variation among animals.

Females of *C. saundersii* are capable of flying for only 2–3 min at a time and do not recover quickly. The short flying time reflects the natural situation, in which females need to make only short flights to find the relatively sedentary males during the dusk chorus. Consequently, it was possible to test each female with a model calling song only twice each day. However, females that responded phonotactically did so reliably. Therefore, at the start of their experimental series, females were required to turn towards the control song played first from the right and then from the left. Any females that did not respond or had a bias towards one side were discarded. Thereafter, experimental songs were presented from the right side only and at a sound pressure level of 74 dB, except in threshold determi-

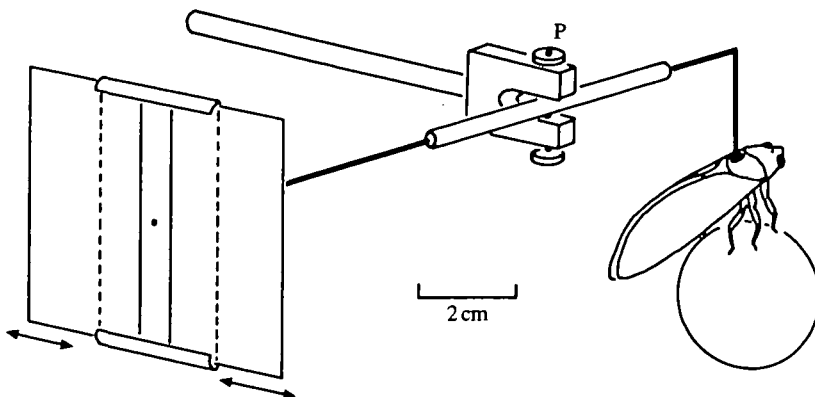


Fig. 2. Diagram of the pivot that was used in the flight steering experiments. The pivot swivels in the yaw plane around point P. The width and weight of the wind-vane were increased or decreased to overcome variation among animals.

nations. This value was chosen because it represents the sound pressure level likely to be experienced by a female between 1 and 2 m from a calling male, which typically generates 90 dB at 20 cm (Mac Nally & Young, 1981), and a distance of 1–2 m is that at which a female appears to make the decision to approach a particular male (see Introduction and Young, 1988).

For each experimental song, females were required to fly straight in the absence of sound for 10–15 s. The sound stimuli were then presented for 30 s and the presence or absence of steering behaviour was noted. Females were then required to fly straight for another 10 s in the absence of sound. Positive responses to experimental songs were counted only if the female moved the pivot at least 20° in the yaw plane and exhibited at least one of three behavioural characteristics associated with steering (these are described in Results and Fig. 3). Angles of steering were judged by viewing the animal from above, with a large protractor placed under the pivot. Negative results were counted only if a female, which had not responded to two successive sound stimuli, subsequently responded to the control song. A female that failed to respond to the control in these circumstances was withdrawn from further experiments.

Using this procedure, there were three different groups of seven females that remained responsive throughout their experimental series. One group was tested with stimuli in which the frequency was varied; a second, with stimuli in which the pulse period was changed; the third, with stimuli in which the pulse duration was changed. Five females of this last group remained responsive after having finished the experimental series and these were then tested with variations in pulse period. Thus five females were tested against a wide range of varying ratios of pulse interval to pulse duration, i.e. the duty cycle.

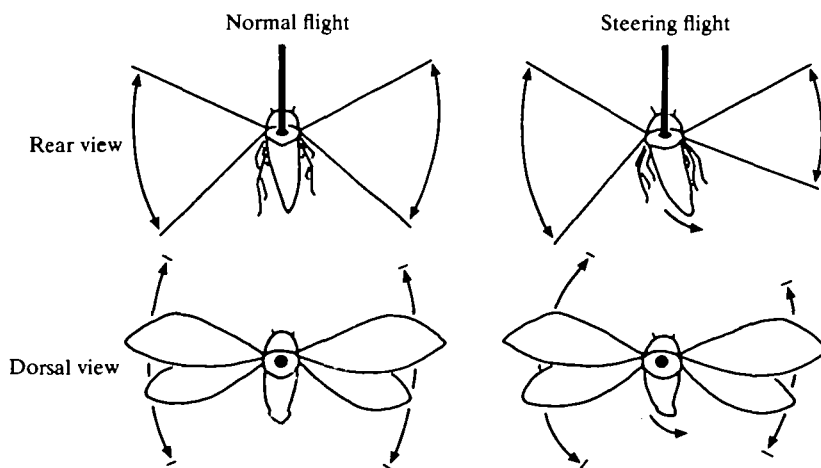


Fig. 3. Behavioural characteristics associated with flight steering (in this case, to the right). Rear view (top) shows the displacement of the abdomen and the decreased wing swing on the side to which the animal turns. Dorsal view (bottom) shows the increased wing sweep on the wide opposite to the turning direction.

In the two experimental series involving variations in pulse period and pulse duration, the reaction times of females that turned towards the sound source were noted. The means and variances of these reaction times were calculated for each test call and the control. Variances were compared using Cochran's test and where they were heterogeneous, were log-transformed. Then the means were compared within each experimental series using the Student–Neumann–Keul's test (Sokal & Rohlf, 1969).

Within the group that was tested against variations in frequency, behavioural thresholds were calculated for each frequency. Thresholds were determined by presenting stimuli at subthreshold levels and increasing the sound pressure level by 2 dB steps until the individual exhibited some behavioural steering characteristics and some movement of the pivot in the direction of the sound source (i.e. $>10^\circ$).

Courtship analysis

These experiments investigated the responses of courting females to a series of model calling songs in which one of the call parameters had been varied. The wing-flicking response of the courting female, measured as the number of flicks female⁻¹ min⁻¹, was used as a quantitative estimate of the willingness of a female to mate. These experiments were performed in the evening as the courtship responses of the female could be elicited only after dusk. Up to three females were tested at a time but rates of wing-flicking were measured separately for each individual. The females were placed in a small container made from mosquito netting, 45 cm from the loudspeaker. At this distance and at the frequencies used, there would have been no near-field effects from the loudspeaker (Michelsen & Nocke, 1974; Doolan, 1981).

The model calling songs were presented at a sound pressure level of 92 dB measured at the position of the females, except in threshold determinations, because this value represents the sound pressure level likely to be experienced by a female that is within a few centimetres of a calling male (Mac Nally & Young, 1981). The responses of the females were measured, first to the control song, then to a series of four different experimental songs followed by another control song. If a female's response to the second control song was reduced or absent, the preceding sequence was discarded.

For each sequence, the wing-flicking rates of each female to both controls were averaged. The response to an experimental song within each sequence was then calculated as the ratio of the experimental wing-flicking rate to the average control rate. Females generally flick their wings in the short breaks occurring in the natural song of the male. Therefore, periods of measurement always began at a break in the model calling song and ran for 1.5 min, with nine song-breaks occurring during each test period.

Three groups of 12 females were tested with songs in which temporal parameters had been varied – the first group with songs in which the pulse period was changed, the second with songs with variations in pulse duration, the third with songs in which both the pulse period and pulse duration were changed. In the second

group, eight females remained responsive after finishing the series. These were then tested with the songs in which pulse period was varied, thus providing responses to a wide range of duty cycles.

Lastly, a group of 10 females was tested with models in which the frequency was varied but the temporal parameters were kept constant at the control values. For each female, behavioural thresholds were calculated for each frequency. Thresholds were determined by presenting stimuli at subthreshold levels and increasing sound pressure level by 2 dB steps until the individual began wing-flicking.

Results

Flight analysis

Field experiments

Both males and females responded to songs broadcast from the loudspeakers by flying towards a speaker and landing nearby, usually on the white sheet beneath the speaker. Females appeared to locate a loudspeaker with about the same accuracy as they locate a calling male. The numbers of individuals attracted to each of a pair of loudspeakers playing model calling songs are given in Table 1. Where temporal parameters were varied in the experimental songs, there was no significant difference between the experimental and control speakers in either the total number of attracted individuals or the total number of attracted females. In three trials, a pure tone of 850 Hz was compared with the control song and again there was no significant difference in the total number of individuals or number of females attracted to either loudspeaker. These results suggest that changes in the temporal structure of the song are of little importance to flying individuals of *C. saundersii*, and that amplitude modulation is not an essential feature of the song at this stage.

In trials where the frequency parameter of the song was changed, there were significantly fewer females and males attracted to the experimental loudspeaker than to the control. In nine trials in which the frequency component of the call was varied, not one individual of either sex was attracted to the experimental call (Table 1). This result suggests that carrier frequency is important in evoking phonotaxis in flying individuals of *C. saundersii*.

Laboratory experiments

Three behavioural characteristics were observed during flight steering in *C. saundersii*: (1) movement of the abdomen downwards and in the direction of the turn, (2) a decreased wing swing in the vertical plane on the side of the turn, (3) increased wing sweep in the horizontal plane on the side opposite to the turn (see Fig. 3). These characteristics have been associated with turning in flight in other insects, e.g. locusts (Camhi, 1970; Zarnack & Möhl, 1977; Baker, 1979; Cooter, 1979), crickets (Moiseff *et al.* 1978) and moths (Roeder, 1967).

All experimental songs, in which the temporal parameters were changed whilst

Table 1. *Results of two-choice field experiments with model calling songs of Cystosoma saundersii*

Model characteristics			Females attracted			Total attracted			No. of trials
Frequency (Hz)	Pulse duration (ms)	Pulse period (ms)	Experiment	Control	Probability	Experiment	Control	Probability	
<u>500</u>	17	24	0	10	0.001	0	13	0.0001	3
<u>1600</u>	17	24	0	6	0.016	0	10	0.001	3
<u>3000</u>	17	24	0	10	0.001	0	11	0.0004	3
850	<u>Pure tone</u>		2	4	0.344	9	9	0.593	3
850	<u>5</u>	24	3	7	0.172	4	9	0.133	3
850	<u>11</u>	24	7	4	0.726	10	5	0.849	3
850	<u>17</u>	<u>40</u>	5	5	0.623	5	8	0.291	3

The control is a model that resembles the natural song in all parameters.

The model characteristic that has been changed in each experiment is underlined.

The total number of cicadas attracted is the total number of males and females attracted to that loudspeaker.

Probabilities given are exact probabilities calculated from a one-tailed binomial distribution.

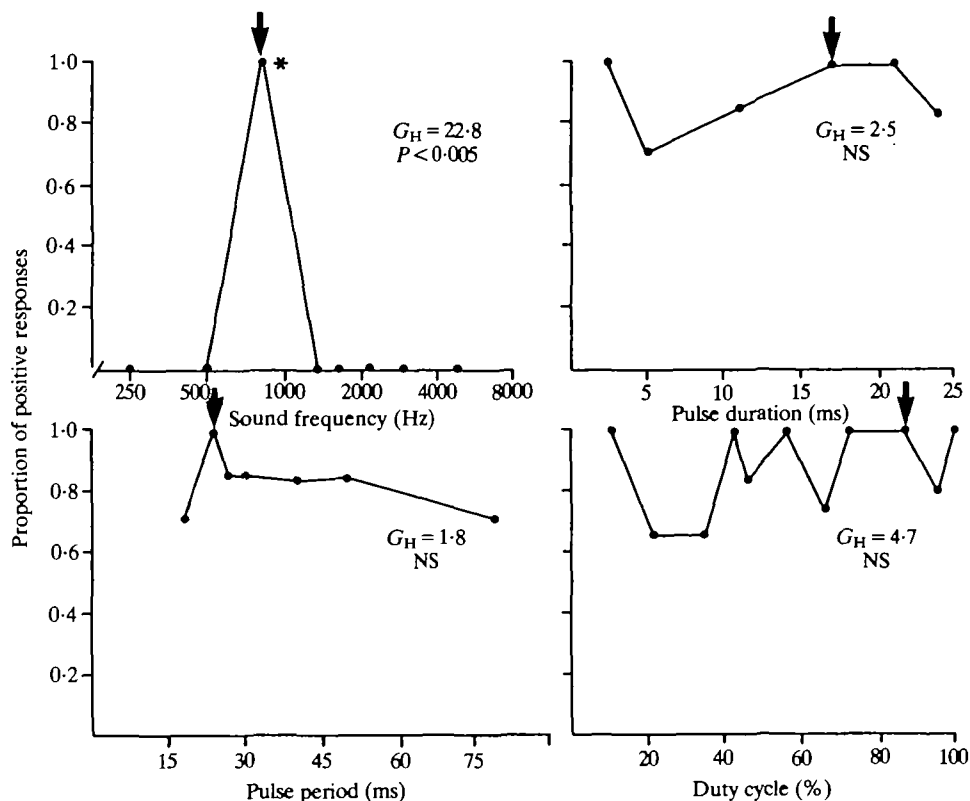


Fig. 4. The proportion of positive steering responses by seven females to model calling songs. In each plot, one song parameter has been varied whilst the others were maintained at the control values. The control value in each plot is indicated by an arrow. Heterogeneity in data sets was examined by using the G -test (Sokal & Rohlf, 1969), and the asterisk denotes a value that is significantly different from expected ones (partitioning of G).

the frequency was held constant at the control values, induced positive turning responses in females (Fig. 4). Although there was some variation in the degree of response, all pulse periods consistently elicited steering responses towards the loudspeaker. Similar results were obtained where the pulse duration of the song was varied and where the duty cycle was changed. Comparisons between the number of females that showed positive steering responses and those that did not were made for the entire range of pulse periods, pulse durations and duty cycles. In each of the three experimental series, there was no heterogeneity in the data (Fig. 4). This implies that the number of positive responses elicited by any one of the models, in which one temporal parameter was varied, was not significantly different from the number of positive responses evoked by the control.

The reaction times of females that turned towards the sound source were noted in the experimental series involving variations in pulse period and pulse duration (Fig. 5). In the series of songs in which the pulse duration was varied, no mean

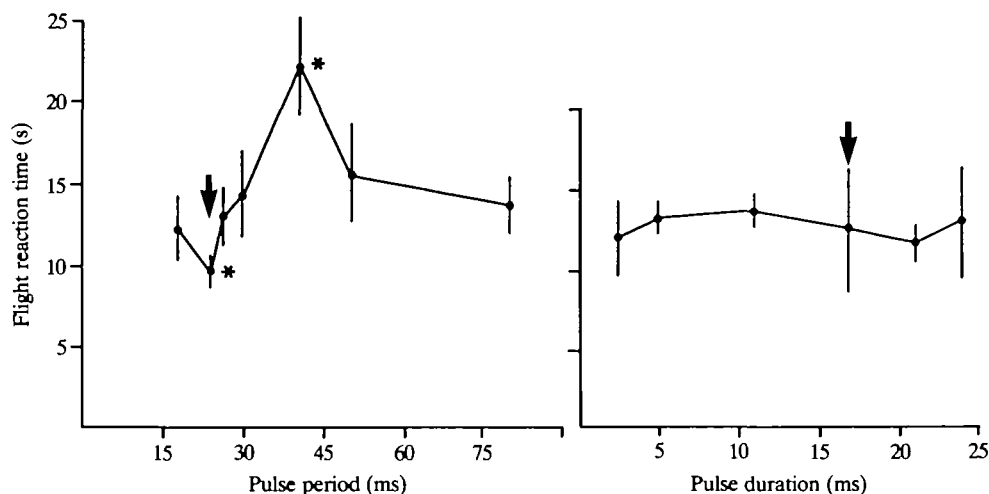


Fig. 5. Reaction times of females to variations in pulse period and pulse duration (means and standard errors). Means that are significantly different, using the Student–Neumann–Keul's simultaneous test procedure (Sokal & Rohlf, 1969), are indicated by asterisks. Arrows denote control values.

reaction time was significantly different from any other. In the series in which the pulse period was varied, only two mean reaction times were significantly different, the smallest and the largest.

These laboratory results suggest that changes in the temporal parameters of a call do not affect either the steering preferences of flying females or their reaction times, i.e. the time taken to make the decision to turn.

Seven females were tested with a series of models in which the carrier frequency was varied (Fig. 4). Seven frequencies were used in the range 250–3000 Hz, including the control value of 850 Hz. The control frequency was the only frequency to induce flight phonotaxis towards the sound source and accounted for most of the heterogeneity observed in the data. It would appear that carrier frequency is critical in stimulating turning responses in flying females.

Behavioural thresholds were measured at each frequency and the mean threshold for each frequency was calculated by converting to a linear scale. At several frequencies, the behavioural thresholds of some individuals were higher than the loudest intensity available (these individuals are indicated by arrowheads in Fig. 6). In these cases the mean threshold was calculated from the sample in which behavioural thresholds were measurable and thus underestimates the true population mean. The shape of the sensitivity curve derived from steering behaviour closely corresponds to that of the hearing sensitivity curve (Fig. 6). Both are sharply tuned to the carrier frequency of the calling song near 850 Hz.

Courtship analysis

The courtship responses of females to model calling songs were measured as the

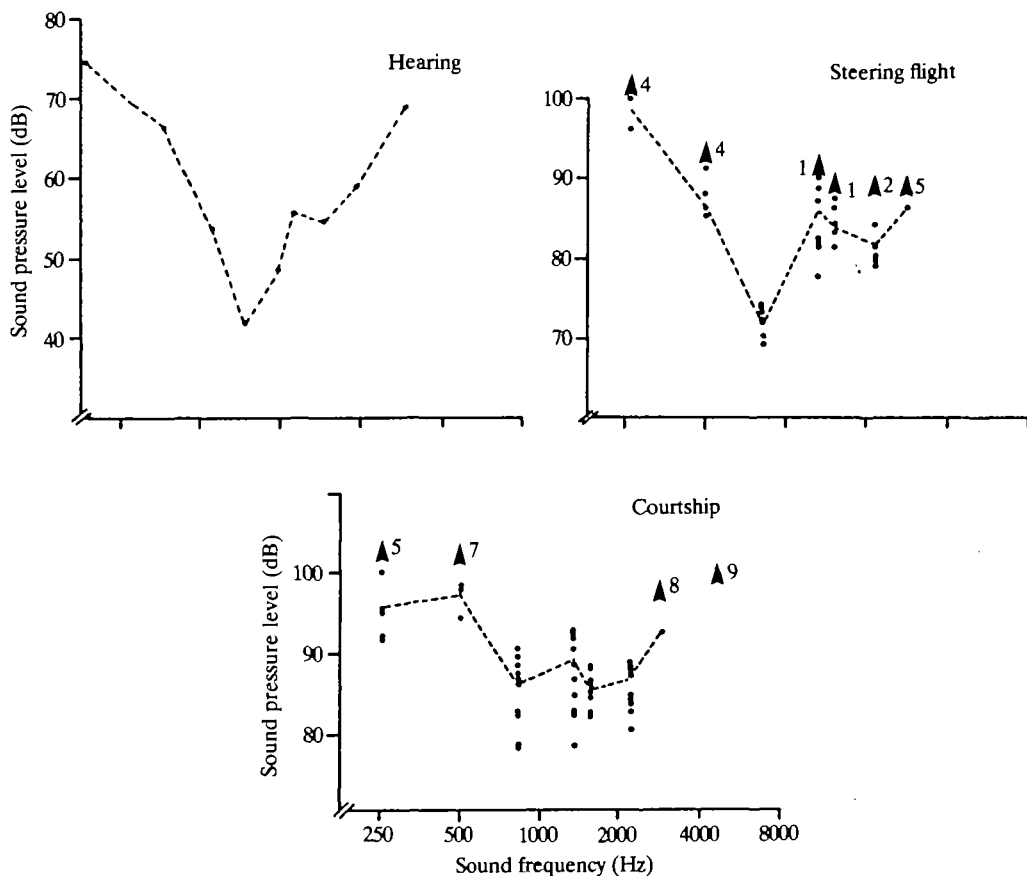


Fig. 6. Threshold curves for hearing, flight steering and courtship. Individual thresholds are plotted in the behavioural curves. Arrowheads indicate thresholds that were greater than the highest available sound pressure level. Numbers indicate how many cases exhibit such an electrical threshold. Dashed lines join the mean values calculated from those females for which thresholds were determined. The hearing curve is redrawn from Young & Hill (1977).

ratio of the wing-flicking rate in response to the test call to the average wing-flicking rate in response to the control.

Responses of two groups of females to songs, in which the various temporal parameters were changed, showed a sharp peak when each temporal parameter approached the value found in the natural song (Fig. 7). In each of the experimental series, the 95 % confidence limits of the mean wing-flicking ratios were calculated for each experimental call. If these overlapped 1.0 (the mean wing-flicking ratio of the control), the experimental song was judged to be not significantly different from the control song in apparent attractiveness to females. In the series in which pulse period was varied, only two of the experimental songs, with pulse periods of 18 ms and 26 ms, had 95 % confidence limits that overlapped

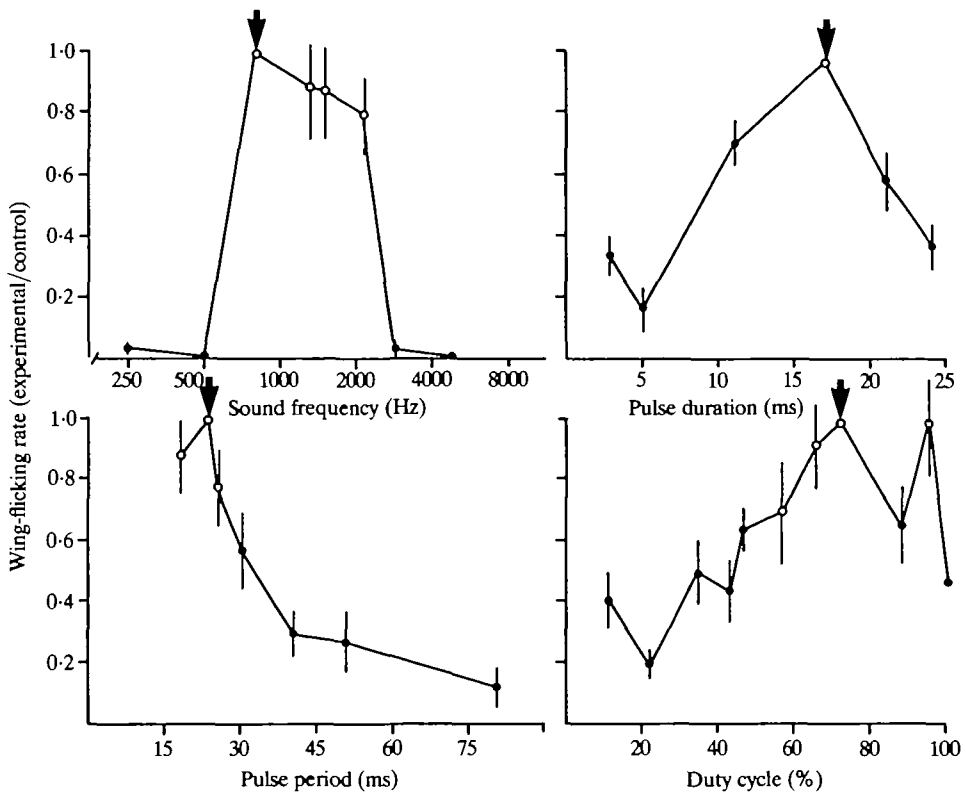


Fig. 7. Responses of courting females to model calling songs, expressed as the ratio of wing-flicking rate in response to the experimental song to the wing-flicking rate in response to the control song (means and standard errors). In each plot, one song parameter has been varied whilst the others were maintained at the control values. The arrow in each plot indicates the control value for the parameter being varied. Open circles indicate mean responses whose 95 % confidence limits overlap the response to the control (i.e. 1.0). Closed circles indicate mean responses whose 95 % confidence limits do not overlap 1.0.

1.0. These pulse periods are close to the control value of 24 ms and occur naturally in the population range of the calling song. In the pulse duration series, no test call had 95 % confidence limits that overlapped 1.0 and thus all elicited responses were significantly less than that evoked by the control song (Fig. 7). In the series in which the duty cycle was varied, there were three test calls with 95 % confidence limits that overlapped the control value (Fig. 7). Again, these were very close to that found in the natural song and are included in the population range of the calling song.

The above results indicate that changes in the temporal parameters of a song affect the preferences of courting females. Only songs with temporal parameters that are similar to those found in the natural song will evoke wing-flicking behaviour in a female.

Table 2. *Characteristics of threshold curves, obtained from laboratory experiments with females of Cystosoma saundersii*

	Flight	Courtship	Probability
<i>N</i>	7	10	
Frequency of peak sensitivity (Hz)	850 \pm 0	1625 \pm 483	<0.001
Bandwidth 3 dB above peak (Hz)	192 \pm 49	888 \pm 360	<0.005
Q value	4.65 \pm 1.09	2.43 \pm 2.17	<0.005

Values of each characteristic are means and standard deviations measured from individual threshold curves.

All characteristics calculated from courtship-threshold curves are significantly different from those calculated from flight-threshold curves (Wilcoxon two-sample test; Sokal & Rohlf, 1969).

The responses of 10 females to a series of models in which the carrier frequency was varied, were investigated. Mean wing-flicking ratios and 95 % confidence limits were calculated for each of eight frequencies. Three frequencies had 95 % confidence limits that overlapped 1.0 and thus were not significantly different from the control in apparent attractiveness to the female. These were 1400 Hz, 1600 Hz and 2200 Hz, all of which are minor components of the natural calling song (Young, 1980). Thus, a wide range of song frequencies will elicit courtship responses from females.

Mean behavioural thresholds were measured for each frequency, using the same procedure as in the flight experiments (see above). The threshold curve calculated for courtship has a peak which is broadly tuned in the range 850–2200 Hz (Fig. 6). This is in contrast to the threshold curve for flight, derived from the laboratory experiments, which is sharply tuned around 850 Hz. A measure of the sharpness of tuning (*Q*) is obtained by dividing the peak frequency by the bandwidth 3 dB below the peak. *Q* values were calculated for the threshold curves of each of the individuals in the flight and courtship experiments. *Q* values calculated from courtship curves were significantly smaller than those calculated from flight curves (Table 2). Thus, song frequency appears to be less important to courting females than to females in flight.

Discussion

Species recognition in *C. saundersii* appears to take place in two stages, which are distinguished by the distance between the receiver (the female) and the sound source (the male). The relative importance of song parameters in contributing to species specificity differs between the two stages. The first stage is flight phonotaxis (long-range communication), during which the carrier frequency of the song seems to be of greater importance in species recognition and the temporal parameters are unimportant. The second stage is courtship (short-range communication), which begins after a female has landed near a calling male. At this stage, the temporal parameters of the male's calling song become important in species

recognition and the carrier frequency of the song becomes much reduced in importance.

These results contrast with the situation in field crickets, the group of insects in which acoustic communication has been studied most intensively. Where phonotaxis has been studied in one species during both flight and walking, the responses of the females during walking are similar to those during flight (Moiseff *et al.* 1978; Pollack & Hoy, 1981; Pollack *et al.* 1984). Hence the relative importance of the calling song parameters in eliciting phonotaxis does not differ between flight and walking, with the exception that the temporal parameters of the calling song are of reduced importance in flight phonotaxis when the intensity of the song is only just above threshold (Doolan & Pollack, 1985). During both flight and walking, the carrier frequency of the calling song contributes to species recognition in field crickets (Hill, 1974; Oldfield, 1980; Pollack *et al.* 1984; Nolen & Hoy, 1986), but the temporal parameters of the song are of overriding importance provided the intensity of the song is well above threshold. Normally, a sound of the correct carrier frequency will not elicit phonotaxis in females unless it is also subdivided into syllables (pulses) having the species-specific syllable period (Pollack & Hoy, 1981; Thorson *et al.* 1982; Stout *et al.* 1983; Nolen & Hoy, 1986).

Thus the relative importance of song parameters in field crickets is generally similar to the situation at the initiation of courtship in *C. saundersii*. The differences are that the temporal parameters of the calling song are unimportant during flight phonotaxis in *C. saundersii* and the carrier frequency is of particular importance at that stage. However, field crickets also have a courtship song in their repertoire, which is used during short-range communication between the sexes. Where it has been studied, the courtship song has been found to differ from the calling song in both temporal and frequency parameters. Hence it is possible that the relative importance of these cues may change between long-range and short-range communication in other acoustically active insects, and this phenomenon may not be unique to *C. saundersii*.

Long-range communication

The laboratory experiments on female steering behaviour demonstrate the importance of carrier frequency in flight phonotaxis. All the model songs, even those with small duty cycles, elicited female responses providing they were of the control frequency. Differences in pulse duration or pulse period had no effect on either the positive steering responses or the reaction times of the females (Figs 4, 5). These results are consistent with natural phonotactic behaviour of flying females, studied in the field experiments (Table 1). However, it does not necessarily follow from these results that female preferences are based on a frequency analysis of the song. Given the sharp tuning of the ear in *C. saundersii*, the observed results would be obtained if the females were simply flying towards the loudest sound that they can hear. If this were so, it might be possible to change the female's frequency preferences by greatly increasing the apparent loudness of the experimental frequencies, as judged by the threshold curve of the female's ear

(Fig. 6). But in nature females are hardly likely to be attracted to the songs of other species calling at different frequencies since these other frequencies will not normally be loud enough to mislead the females. Certainly, flying females of *C. saundersii* are never seen to approach males of any other insect species.

The importance of frequency in long-range communication, as indicated by these experiments, may represent an adaptation to the chorusing behaviour of the males. *C. saundersii* males aggregate in relatively dense choruses and frequently share bushes (Doolan & Mac Nally, 1981). At some distance from a bush in which several males are singing, the temporal parameters of the calling songs will not be discernible. Unless all the songs are perfectly synchronized, which seems impossible, the amplitude modulation of the resultant signal will be constantly changing. Therefore, long-range recognition of conspecific males based on the temporal parameters of their song is not feasible in a species such as *C. saundersii*. But the carrier frequency of the signal emerging from the chorus will be clearly discernible over large distances, and so is suitable for long-range species recognition. In keeping with this, there are some chorusing species of cicada in which the calling song consists of a pure tone, not subdivided into pulses, with only slight amplitude modulation (Young & Josephson, 1983).

Another factor that makes temporal parameters less suitable for species identification during long-range communication is the degradation of the song characteristics, which increases with distance from the sound source. Wiley & Richards (1978) and Richards & Wiley (1980) have shown that low-frequency amplitude modulations, due to nonstationary heterogeneities in the atmosphere, will be superimposed on the original signal. Songs with rates of amplitude modulation below 50 Hz, such as the song of *C. saundersii* with a pulse repetition rate of 40 Hz, are especially liable to be masked by amplitude fluctuations caused by atmospheric turbulence. Consequently, the original pulse structure of the song would often not be perceived by a female flying a long distance from a singing male. Atmospheric fluctuations have no significant effect on the carrier frequency of the song (Richards & Wiley, 1980). Hence the carrier frequency is a more effective vehicle by which species-specific information can be communicated over long distances.

Since field crickets rely on the temporal parameters of the calling song for recognizing conspecific males during flight phonotaxis, they must avoid one or both of the above drawbacks. Although male crickets are aggregated on a broad scale, singing males are actively spaced out within these aggregations by means of aggressive encounters between singing individuals (Heiligenberg, 1966, 1969; Cade, 1981; Evans, 1983). In the field, Cade (1981) found a mean nearest-neighbour distance of about 3.5 m between singing males of *Teleogryllus oceanicus* and Campbell & Shipp (1979) found a mean nearest-neighbour distance of about 8 m for *T. commodus*. Thus the information contained in the temporal parameters of the calling song should not be affected so seriously by the songs of near neighbours in these species. For most species of field cricket the calling song has a syllable (pulse) repetition rate that is even lower than that of *C. saundersii*, and so

the temporal parameters of their songs are just as liable to degradation through atmospheric turbulence as in the case of *C. saundersii*. This tends to confirm the idea that the importance of frequency in long-range communication in *C. saundersii* may be primarily an adaptation to the chorusing behaviour of the males.

Short-range communication

During courtship, females of *C. saundersii* respond to the temporal parameters of the calling song and frequency becomes less important. At this short range, the temporal pattern of the song should reach the receiver intact. The only major source of interference would be other males singing close by. Courting females do not respond to a male unless his song is at least 9 dB louder than that of his nearest neighbour (Doolan, 1981). This failure to respond may well be due to acoustical interference between two neighbouring songs that renders the temporal parameters of the resultant signal unrecognizable. Thus, if two males are singing close to one another, neither will be identified by the female as a conspecific male and courtship will not be initiated. Certainly, males in close proximity (<0.5 m) actively avoid each other and so increase their separation (Doolan, 1981).

Spacing between singing males has often been described in anuran amphibians and insects (Emlen, 1968, 1976; Whitney & Krebs, 1975; Otte & Joern, 1975). In some bushcrickets, it has been shown that the spacing behaviour of males is dependent on their ability to hear the songs of neighbouring males (Bailey & Thiele, 1983); intermale distance appears to be maintained by the sound pressure level of the song received at the ear, and this value is in turn mapped in this male's central nervous system (Römer, 1987; Römer & Bailey, 1986). One of the probable functions of spacing behaviour is to reduce the acoustic interference caused by nearby calling males (Littlejohn, 1977). It is possible that spacing among males occurs generally in species which rely, at some stage, on the temporal parameters of the song for species identification. Conversely, it may be necessary for species that sing in dense choruses to rely on some simple feature other than the temporal parameters of the song for species recognition at long range, with a change to reliance on temporal parameters occurring only at short range. It has been suggested that such a change occurs in snowy tree crickets (Alexander, 1975) and also in the visual displays of fireflies (Lloyd, 1973).

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