Acoustic communication in the Palaearctic red cicada, *Tibicina haematodes*: chorus organisation, calling-song structure, and signal recognition

J. Sueur and T. Aubin

Abstract: Males of the Palaearctic red cicada, *Tibicina haematodes*, produce calling songs that are attractive to both sexes. For the first time we (*i*) describe the organisation of the chorus formed by aggregating males, (*ii*) analysed the physical characteristics of the calling song, and (*iii*) used playback experiments of natural, modified, and allospecific signals to investigate the signal-recognition process. Males overlap each other's calling song and try to call first and last during a chorus, leading to what we term domino and last-word effects, respectively. The calling song consists of a two-part sequence made up of a succession of pulses. It is characterized by slow and fast amplitude modulations and three frequency bands. The structure of the signal varied among individuals in both temporal and frequency parameters. Our playback experiments showed that males make a rough analysis of frequency and duration features of the signal. They pay no attention to amplitude modulations. Because males are not capable of precise analysis, they reply to various allospecific calling songs. Females' analysis of the calling song being difficult to test, the role of this signal in sexual selection still needs to be documented.

Résumé : Les mâles de la cigale rouge paléarctique, *Tibicina haematodes*, émettent des signaux sonores d'appel qui attirent les deux sexes. Pour la première fois, nous décrivons (*i*) l'organisation des chœurs par les groupes de mâles, (*ii*) la structure acoustique des signaux d'appel, (*iii*) le processus de reconnaissance du signal à l'aide d'expériences de diffusion de signaux naturels, modifiés et allospécifiques. Les mâles superposent leurs signaux d'appel et chaque mâle essaie d'être le premier et le dernier à émettre dans les chœurs, donnant lieu à ce que nous avons appelé les effets « domino » et « dernier mot ». Le signal d'appel comporte deux parties, toutes deux constituées d'une succession d'impulsions. Il est caractérisé par des modulations d'amplitude lente et rapide et par trois bandes de fréquences. Les paramètres de fréquence et de durée diffèrent d'un individu à l'autre. Nos expériences de diffusion indiquent que ces paramètres sont analysés par les mâles de façon peu précise et que les modulations d'amplitude ne sont pas prises en compte. Comme ils n'effectuent pas une analyse acoustique détaillée, les mâles répondent à la diffusion de certains signaux allospécifiques. L'analyse du signal d'appel par les femelles reste difficile à tester et le rôle de ce signal dans la sélection sexuelle demeure inconnu.

Introduction

During pair formation, many animals communicate by means of rhythmic signals. When the calling sex has no other resources but genes to offer to the other sex, callers tend to cluster at a single site (Alexander et al. 1997). In such dense aggregations, calling individuals tend to either alternate or synchronize their advertisement signals. The emergence of synchronization has recently been interpreted as an epiphenomenon created by competitive interactions between males whose signals overlap (Greenfield and Roizen 1993). In many arthropods, signals involved in such collective behaviour are acoustic (Ewing 1989; Bailey 1991). Among acoustic insects, cicadas probably produce the most intense and striking choruses (Alexander and Moore 1958; Young 1981; Williams and Smith 1991; Wolda 1993; Sueur 2001). Emitted only by males, the calling song, termed calling tymbalisation by Boulard (1995), informs conspecific reproductively receptive females of the caller's position (Alexander and Moore 1958). Sound production is mainly due to the high rate of repeated deformations of a pair of tymbals (Pringle 1953, 1954).

In the case of chorusing species, calling males assemble in a specific area where they form chorus centres. They synchronise their songs with greater or less accuracy. The Palaearctic red cicada, *Tibicina haematodes* (Scopoli, 1763), forms such choruses with partially overlapping songs. This large species (body length about 30 mm) mainly inhabits woodlands, gardens, and vines. During summer days, when ambient temperatures reach 23–25°C, males produce an intense burst of song consisting of pulses without frequency modulation. We observed the collective acoustic behaviour of this species under natural conditions and report these behaviours here for the first time. We describe the time and frequency features of the calling song through an audiospectrographic analysis. We investigated whether there were individual signatures in either the temporal or the fre-

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quency domain. Finally, by broadcasting natural, modified, and allospecific signals to caged males, we tried to determine whether certain signal parameters were more critical than others in eliciting male chorus behaviour.

Methods

Subjects and location

Populations of *T. haematodes* are found in the south of France. Seventeen males were recorded from mid-June to mid-July of 1999 and 2000 in the vicinity of Cairanne (Vaucluse), where dense populations inhabit vines. Males were tested in the laboratory from 24 June to 7 July 2000, at the beginning of the emergence period, when they are reported to be highly motivated to call.

Recording procedure

The songs of *T. haematodes* were recorded with an omnidirectionnel Telinga Pro4PiP microphone (frequency response 40 – 18 000 Hz ± 1 dB) connected to a Sony TCD-D8 digital audio tape recorder (sampling frequency 44.1 kHz, frequency response flat within the range 20 – 20 000 Hz). The males were recorded dorsally. The distance between the microphone and the insect was between 0.5 and 2 m, with a mean of 1 m. Males 61 and 62 were recorded when the ambient temperature was 30–32°C, the remaining males were all recorded at 24–25°C. The sound-pressure level (in dB) was measured with a Bruël and Kjaer sound-level meter type 2203 (linear scale, slow setting). These measurements of sound-pressure level were made dorsally at a distance of 0.5 m from the insect.

Acoustic measurements

Signals from 17 males were digitized at a sampling rate of 32 kHz and then analysed in both temporal and frequency domains through the SYNTANA analytical package (Aubin 1994). In the temporal domain we analysed call duration, duration of intercall silence, and number of group of pulses per second. In the frequency domain we analysed the three main bands (F1, F2, F3) on spectra computed with a fast Fourier transformation (FFT), using a window size of 512 points (frequency resolution 62.5 Hz). Because of background noise, analyses of the number in the group pulses per second and the frequency parameters (F1, F2, F3) were available for only 12 and 7 males, respectively. Means, standard deviations, and minimum and maximum values were calculated. For each parameter we calculated the ratio CV_i/CV_b, where CV_i is the within-individual variation and CV_b is the between-individual one, according to the formula $CV = 100 \times (1 + 1/4n) \times SD/X$, where n, SD, and X are the number of calls analysed, the standard deviation, and the mean of the measured parameter, respectively (Scherrer 1984).

Playback procedure

For playback experiments we used a Sony TCD-D8 digital audio tape recorder connected to a self-powered Audax TWO34XO tweeter (frequency response 2000 – 20 000 Hz ± 2 dB).

Males were caught each day and then carried in a net and kept in cages placed in a garden. The cages measured 0.5 × 0.5 × 0.5 m and were covered with black gauze netting. A female was placed in the cage to stimulate the tested male. The cage used for playback experiments was isolated from the other cage in which the remainder of the collected males were kept. Thus, during playback experiments there were no surrounding males. Playback tests were conducted between 11:00 and 18:00, a period corresponding to the natural sound activity of cicadas. During the experiments the ambient temperature ranged from 22 to 32°C, with a mean at 23°C. The loudspeaker was placed 1.5 m from the centre of the cage and at a height of 0.25 m. Signals were played back at a sound-pressure level of 64 dB, which corresponds to a male calling at a distance of 12 m in an open field with a natural sound-pressure level of 82 dB.

Each experimental signal was broadcast twice with a silent interval of 15 s. This rhythm corresponded to natural sound emission. Then, after a 1-min period of silence, another experimental signal was broadcast twice. The order of presentation of the signals was randomized for the different males tested.

Experimental signals

In animal sound communication, information may be encoded through temporal and frequency parameters (coding process according to Shannon and Weaver 1949). Thus, the experimental signals consisted of natural calling songs modified in either the frequency or the temporal domain. To test the species-specificity of acoustic parameters, we also broadcast allospecific calling songs. The original signal was modified with the SYNTANA analytical package (Aubin 1994).

Control signal

We chose a representative natural calling song of *T. haematodes*. The frequency and temporal values of this call corresponded to the mean values measured for the calling songs of the 17 males recorded.

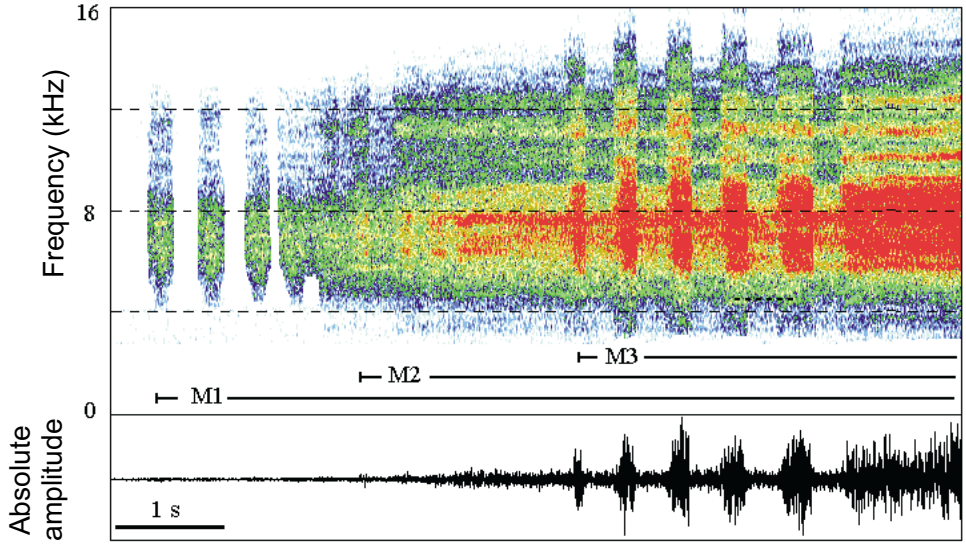
Original signal modified in the temporal domain

We modified either the amplitude modulation or the natural temporal pattern of the signal. (*i*) The amplitude modulations of the original signal were removed but the natural frequency features were kept. To do this we used the analytical signal calculation (Mbu-Nyamsi et al. 1994). The result was a signal with a natural duration and natural frequencies but with no amplitude modulation. (*ii*) To modify call duration we truncated the signal by removing 4- and 6-s bouts (i.e., about one-half and three-quarters of the second part). We also broadcast either the first or the second part of the original signal. (*iii*) To test the importance of the rhythm we built a hybrid signal with the frequency features of the species studied, but with the temporal pattern of another sympatric and syntopic species (*Cicada orni*). The temporal pattern of the signal of the latter species consists of 0.06-s bouts repeated at a regular rate of 7 bouts/s.

Original signal modified in the frequency domain

The natural calling song was shifted linearly up or down in frequency (Randall and Tech 1987). The linear shifts of the spectra were ±5000, ±4000, ±3500, ±3000, ±2500, ±2000, and ±1000. The values of such modified signals fell well outside the natural frequency range of the species. Except for these modifications of the pitch of the carrier frequency,

Fig. 1. "Domino effect": oscillogram (time vs. absolute amplitude) and spectrogram (time vs. frequency) illustrating three distant male *Tibicina haematodes* (M1, M2, M3) whose signals overlapped (sampling rate 32 kHz, FFT window size 512 points, frequency resolution 62.5 Hz).



the temporal and amplitude parameters of the natural calling song were unchanged.

Allospecific signals

Experimental signals are presented in Fig. 6. We chose a representative calling song of 7 cicada species that are also present in the south of France, and thus should be susceptible to acoustic competition with *T. haematodes*. Four species belonged to the same genus: *Tibicina corsica fairmairei*, *T. garricola*, *T. quadrisignata*, and *T. tomentosa*. Three species belonged to other genera: *Lyristes plebejus*, *C. orni*, and *Cicadatra atra*. The duration of the allospecific signals broadcast was adjusted to the length of the original signal of *T. haematodes*.

Criteria of responses

In natural conditions, male *T. haematodes* are static singers. They stay at the same place and reply acoustically to calls emitted by individuals belonging to the same species. When they are grouped, their calling songs tend to overlap. On the basis of these observations, we used a five-point scale to evaluate the intensity of response of tested males to playback signals. This scale was ranked as follows: 0 (none): no reaction; 1 (weak): agitation, movement; 2 (medium): calls after the second broadcast; 3 (strong): calls after the first broadcast at the end of the playback signal; 4 (very strong): calls after the first broadcast, just at the beginning of the signal played back. Points 3 and 4 were pooled for signals truncated in duration.

For clarity of representation, the intensity of response for each signal played back was calculated by adding the levels of response observed for each individual and dividing this sum by the theoretical maximal response. The results obtained are provided as percentages.

Statistical analysis

The sign test (Scherrer 1984) was used to compare two-by-two the response to experimental signals and the response to the control signal. One-tailed sign tests were computed using Statistica Version 1–5 software, with a significance level of $p < 0.05$.

Table 1. Identification of the leader in chorusing pairs of male *Tibicina haematodes*.

Male pair	*N*	Male 1 began to call (%)	Male 2 began to call (%)
A	7	100	0
B	5	100	0
C	8	87.5	12.5
D	6	50	50
E	4	75	25
F	9	100	0
G	12	75	25

Note: *N* is the number of chorus sequences recorded.

Results

Collective sound behaviour: "domino" and "last-word" effects

Within a population at high density, males sang in chorus. As a general rule, one male began to call and then the surroundings males followed. Thus, the signals were not produced in phase but with a short time delay (Fig. 1). Except in one case (pair D), the observation of seven pairs of chorusing males showed that one of the two males called preferentially before the other (Table 1). Bouts of collective singing alternated with silent periods of roughly equal duration. Collective singing suggested a group of four to five males. The sound activity of one chorus group could stimulate that of another male positioned at a greater distance, and also that of another group. Such stimuli have been observed between two groups more than 50 m apart in open fields. Thus, one male can stimulate the activity of a great number of individuals, producing a "domino" effect on the following individuals. Furthermore, it seems that males' calling songs tend to overlap the end of the calling song of their neigh-

Fig. 2. "Last-word effect": oscillogram and spectrogram illustrating two distant males whose signals overlapped at the end of a collective calling bout. The parameters of acoustic analysis are given in Fig. 1.

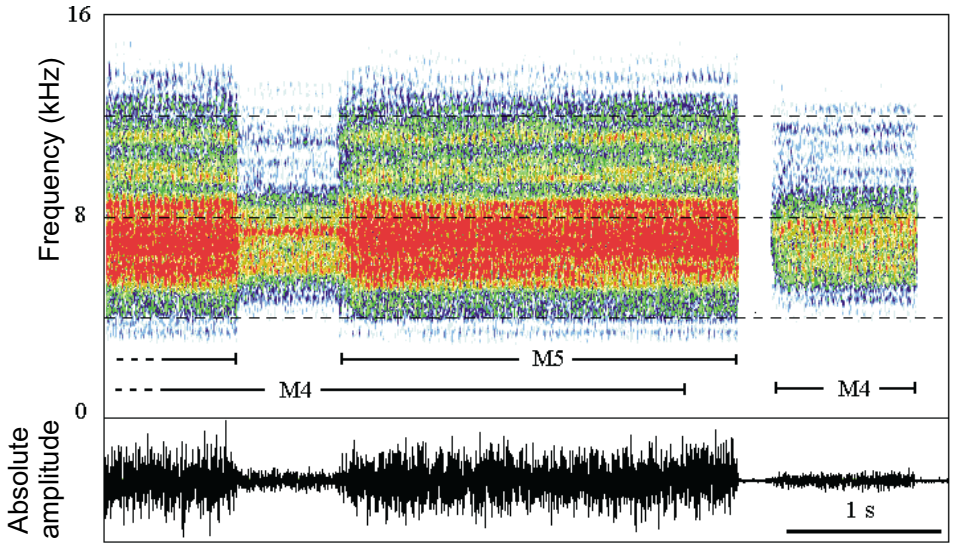


Table 2. Time parameters of the *T. haematodes* calling song.

Individual ID No.	DC	CV_i	CV_i/CV_b	DIS	CV_i	CV_i/CV_b	GPS^{-1}
61	16.7 ± 1.5 (15)	9.1	0.55	9.2 ± 4.8 (12)	53.3	0.81	98
62	17.3 ± 3.4 (21)	19.9	1.19	11.4 ± 8.2 (19)	72.9	1.09	98
91	13.0 ± 1.6 (8)	12.7	0.76	9.5 ± 4.6 (8)	49.9	0.75	98
93	11.4 ± 1.1 (5)	10.1	0.61	13.4 ± 5.7 (5)	44.7	0.67	—
95	15.1 ± 1.7 (12)	11.5	0.69	42.4 ± 85.9 (11)	207.2	3.11	102
96	18.3 ± 3.0 (7)	17.0	1.01	16.3 ± 7.5 (6)	48.1	0.72	—
910	14.7 ± 0.9 (7)	6.3	0.38	6.3 ± 2.4 (8)	39.3	0.59	98
911	13.8 ± 4.1 (6)	30.9	1.85	22.5 ± 26.7 (6)	123.6	1.86	100
912	16.8 ± 1.7 (4)	10.8	0.49	20.3 ± 27.5 (3)	146.8	2.20	—
913	12.9 ± 1.5 (9)	12.0	0.65	10.6 ± 8.3 (9)	80.5	1.21	98
914	15.8 ± 1.7 (4)	11.4	0.70	11.5 ± 12.4 (4)	114.6	1.72	—
915	14.5 ± 1.2 (12)	8.6	0.52	6.0 ± 1.8 (11)	30.7	0.46	96
916	14.1 ± 1.1 (10)	8.0	0.48	5.5 ± 1.1 (8)	20.6	0.31	—
921	11.8 ± 1.6 (8)	14.0	0.84	6.3 ± 2.3 (8)	37.7	0.57	98
923	12.0 ± 2.1 (6)	18.2	1.09	13.0 ± 7.7 (5)	62.2	0.93	98
925	10.0 ± 1.6 (4)	17.0	1.01	9.0 ± 0.8 (4)	9.4	0.14	97
927	12.0 ± 2.1 (24)	17.7	1.06	16.2 ± 31.1 (24)	194.0	2.91	99
	DC	CV_b		(DIS)	CV_b		GPS^{-1}
Between individuals	14.1 ± 2.3 (17)	16.7		13.3 ± 8.7 (17)	66.6		98

Note: Mean ± standard deviation, with the sample size in parentheses, and within and between variation coefficients (CV_i and CV_b, respectively) were calculated for duration of call (DC) and duration of intercall silence (DIS). The number in the group of pulses per second (GPS^{-1}) was stable within individuals.

Please note that the parentheses around "(DIS)" will be removed at the next stage.

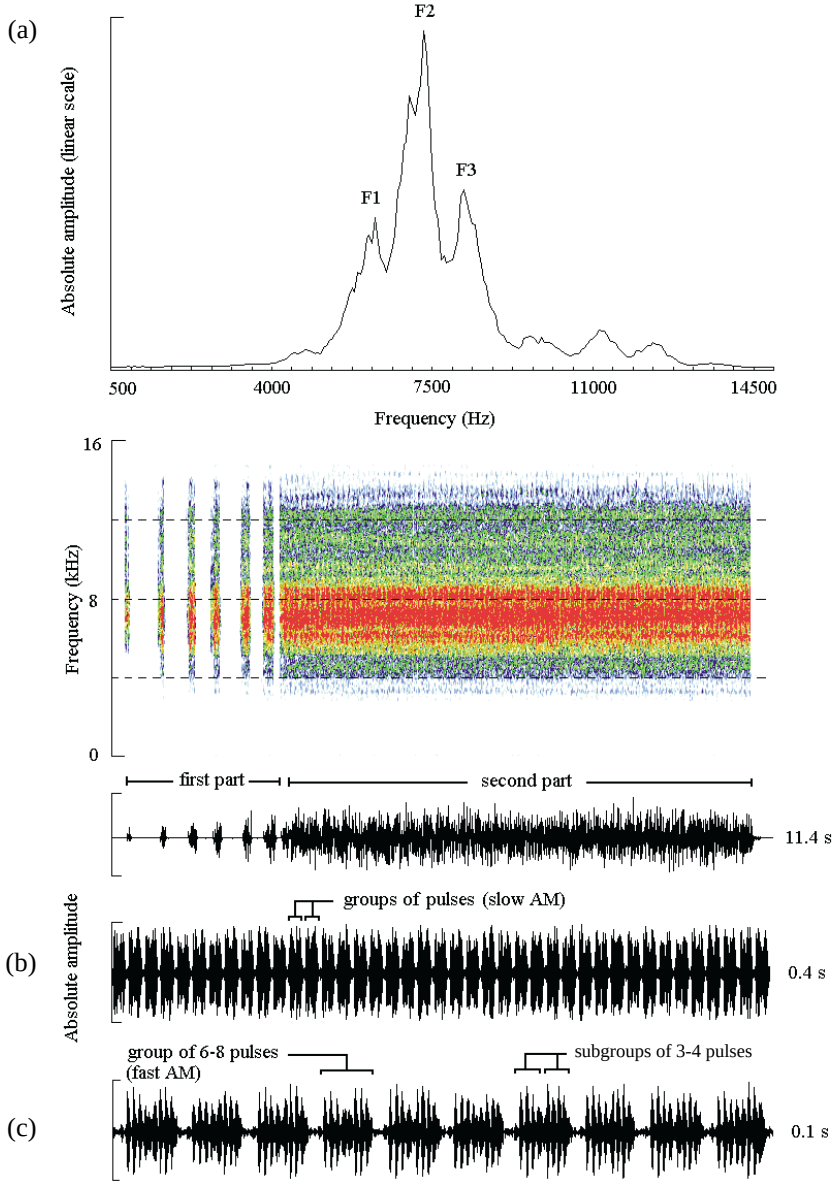
bours (Fig. 2). At the end of the chorus, a "last-word" phenomenon resulted in competition between males to sing last.

Song pattern

The song pattern of *T. haematodes* is represented in Fig. 3. At a distance of 0.5 m and at 32°C, sound-pressure levels were 82.17 ± 1.29 dB (mean ± SD) (range 80–83.5 dB, $n = 6$). An oscillogram showed that signals consisted of a succession of groups of pulses.

A typical song sequence was composed of two parts (Fig. 3*a*). The first part was composed of 3.64 ± 1.56 (range 1–8, $n = 141$) successive short trains of pulses and the second part of a sustained train of pulses. Within and between individuals the coefficients of variation (CV_i and CV_b, respectively) and their ratio for the main temporal parameters are presented in Table 2. Except in two cases (males 62 and 911), CV_i of the duration of call appeared to be lower than or equal than CV_b ($CV_i/CV_b = 1$). For the duration of intercall silence, CV_i was lower than CV_b for 10 males and higher for 7 males. The number in the group of pulses was stable within and between individuals. The group of pulses generated a large amplitude modulation (AM1) at an average rate of about 98 Hz (Fig. 3*b*). A group of pulses was made up of 6–8 pulses arranged in two subgroups containing 3–4 pulses

Fig. 3. Calling song of *T. haematodes*. (*a*) Spectrum (frequency vs. absolute amplitude), spectrogram, and oscillogram (from top to bottom) of an entire sequence with the first rhythmic part and the second sustained part. (*b*) Detailed oscillogram showing groups of pulses. (*c*) Detailed oscillogram showing groups of pulses, subgroups of pulses, and slow and fast amplitude modulations (AM). The parameters of acoustic analysis are given in Fig. 1.



(Fig. 3*c*). Each subgroup should be attributed to one muscle contraction, since the analysis of another signal of the species (distress song) after the inactivation of one tymbal showed that the tymbals contracted alternately (J. Sueur, unpublished data). Each tymbal consists of a membrane bearing 7–8 long ribs alternated with 6–7 short ribs (Fig. 4). The succession of 3–4 pulses in subgroups should thus be correlated with the successive buckling of the first 3–4 of the 7–8 long ribs. The pulses lasted approximately 1 ms and generated a fast amplitude modulation (AM2) at a rate of about 1000 Hz.

In the frequency domain the power spectrum was characterized by a frequency bandwidth of about 2000 Hz with three main peaks: one band of higher energy at about 7400 Hz and two lateral bands at around 6400 and 8400 Hz. In almost all cases CV_i was lower than CV_b for the three frequencies measured (Table 3).

Responses to playback signals

Modification in the temporal domain (Fig. 5)

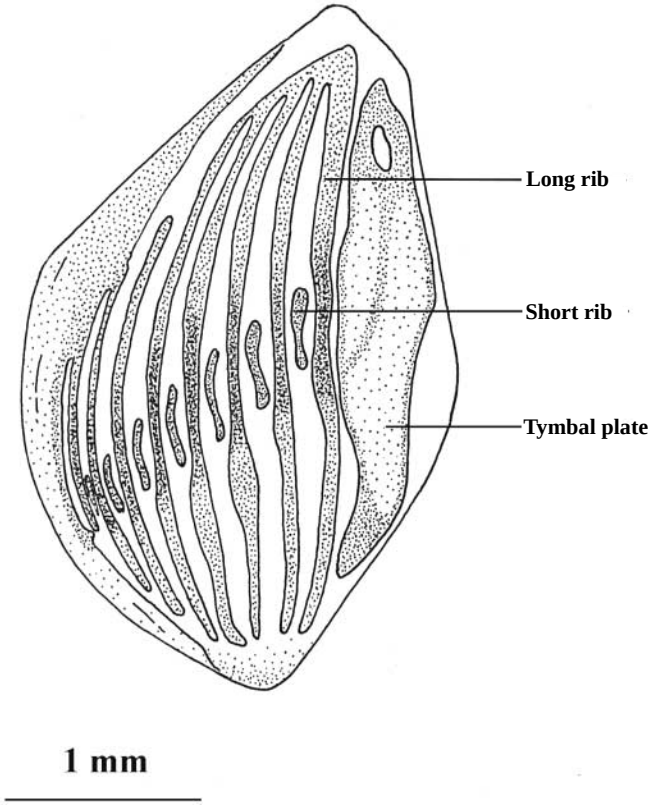
Signals without amplitude modulation clearly elicited a response. Although we observed lower responses to the broadcast of experimental signals with 6 s removed, with the first or second parts removed, no statistical difference ($p > 0.05$) were found with the responses to the control signal. Although the response was higher than for the *C. orni* song playback (see below), there was a significant difference between the control signal and the signal that was built with

Table 3. Frequency parameters of the *T. haematodes* calling song.

Individual ID No.	F1	CV_i	CV_i/CV_b	F2	CV_i	CV_i/CV_b	F3	CV_i	CV_i/CV_b
62	6797 ± 197 (8)	2.99	0.71	7889 ± 22 (18)	0.29	0.07	8640 ± 119 (8)	1.42	0.61
95	—			7151 ± 78 (12)	1.11	0.28	8286 ± 142 (12)	1.75	0.75
910	6625 ± 239 (7)	3.74	0.88	7473 ± 157 (7)	2.18	0.55	8351 ± 231 (7)	2.87	1.22
911	6837 ± 56 (5)	0.86	0.20	—			8187 ± 40 (6)	0.51	0.22
915	6896 ± 51 (6)	0.77	0.18	7700 ± 81 (5)	1.11	0.28	8637 ± 326 (5)	3.96	1.69
925	6425 ± 69 (5)	1.13	0.27	7363 ± 67 (5)	0.96	0.24	8375 ± 88 (4)	1.12	0.48
927	6207 ± 99 (22)	1.61	0.38	7233 ± 119 (22)	1.66	0.42	8204 ± 125 (22)	1.54	0.66
	F1	CV_b		F2	CV_b		F3	CV_b	
Between individuals	6631 ± 269 (6)	4.23		7468 ± 282 (6)	3.93		8382 ± 187 (7)	2.34	

Note: Mean ± standard deviation, with the sample size in parentheses, and within and between individual variation coefficients (CV_i and CV_b, respectively).

Fig. 4. Lateral view of a left tymbal of *T. haematodes*, showing 8 long and 7 short ribs.



the temporal parameters of *C. orni* and the frequency characteristics of *T. haematodes* ($p < 0.05$). This indicated that 0.06-s bouts repeated at a rate of 7 per second were not sufficient to elicit a good response. Nevertheless, this signal elicited more responses than the natural signal of *C. orni*.

Modification in the frequency domain (Fig. 6)

In the case of the frequency-shift series, significant differences appeared, from a positive frequency shift of 2500 Hz or more and from a negative frequency shift of 2000 Hz or more.

Response to allospecific signals (Fig. 7)

There was no statistical difference between the response to the control signal and the response to the signals produced by the species belonging to the same genus. The songs of *Cicatra atra* and *C. orni* did not trigger any response ($p < 0.05$). However, male *T. haematodes* clearly replied to the songs of *L. plebejus*.

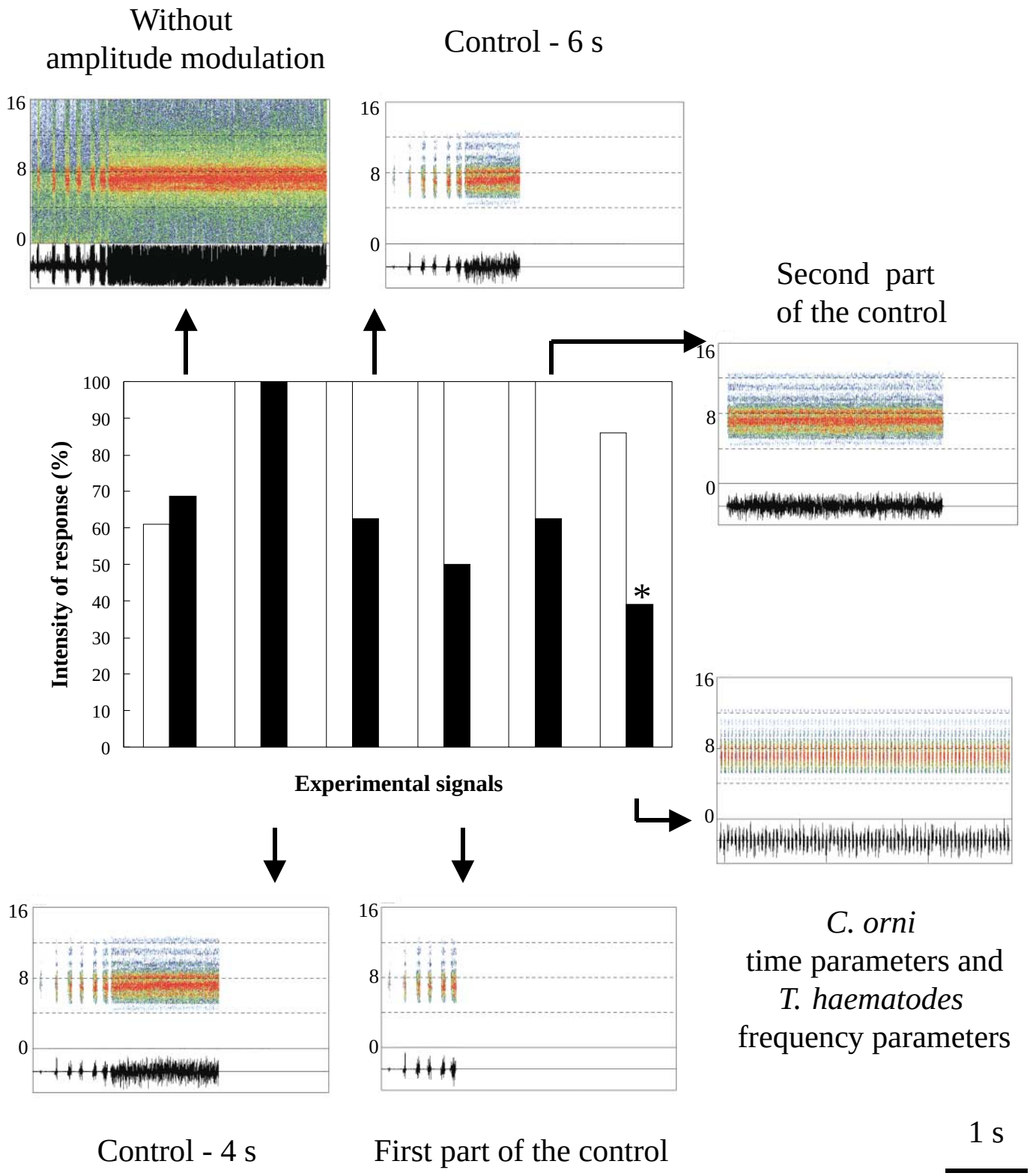
Discussion

Chorus organisation

Greenfield (1983) distinguished between two kinds of aggregations: active aggregation, when males exhibit positive phonotaxis to conspecific song, and the passive aggregation caused by an unequal spatial distribution of resources. *Tibicina haematodes* has invaded agricultural vines, where it is now commonly found. Vines provide profitable food resources for both larvae and adults and good oviposition sites for adult females. Thus, aggregation seems to be passive. Nevertheless, males are also clearly attracted by conspecific songs. Thus, we can suppose that active aggregation occurred first and was secondarily followed by passive aggregation when a reliable habitat was found. Identification of the leading male in a pair of chorusing males shows that in the majority of cases one male began, and thus a sequence was common. Furthermore, we often observed silent males located close to calling ones, which suggests the existence of satellite males. These two observations indicate that a "dominant" role in chorus organisation should be attributed to some males.

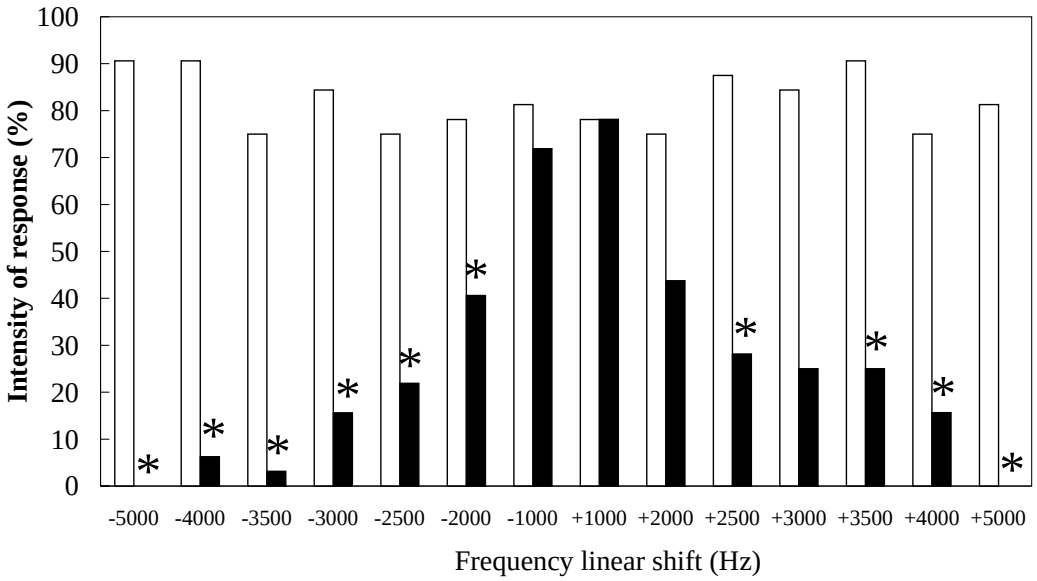
Two main categories of temporal interaction in chorus organisation have been described: synchrony and alternation (Otte 1977; Greenfield 1994*a*, 1994*b*). Synchrony never seems to be perfect: there is always a time shift between two calling neighbours, and consequently one is a leader and the other a follower. In various species of chorusing anurans and insects, females turn preferentially towards the leading signal and thus select "acoustic leader" males (for a review see Greenfield and Rand 2000). This preference, known as the precedence effect in psychoacoustics, is supposed to enhance acoustic competition between males (Greenfield et al. 1997). Thus, synchrony is now interpreted as an epiphenomenon created by competitive interactions between males whose signals overlap (Greenfield and Roizen 1993). Although the precedence effect is still experimentally untested, this interpretation is in agreement with our preliminary observations of sound-social organisation in *T. haematodes*. Males tend to jam the calls of neighbouring males, but we have shown that broadcast of the first part of the specific tymbalisation was enough to stimulate the response. Competition between males leads to a domino effect similar to the "chain-reaction effect" already evoked for katydids (Greenfield 1983; Greenfield

Fig. 5. Intensity of responses to signals modified in the temporal domain. Open bars denote response to control signals and solid bars denote response to experimental signals (*, $p < 0.05$). The sample size was eight males. The units on the *y* axes of the spectrograms are kilohertz.



and Shaw 1983). In addition, we witnessed overlap at the end of the calling song as each male tried to be the last caller. Female orientation towards a male should be confused by a great number of surrounding calling songs. Therefore, being the last, and finally alone, to sing should be advantageous for a male. Precedence and last-word effects

Fig. 6. Intensity of responses to signals modified in the frequency domain. Open bars denote response to control signals and solid bars denote response to experimental signals (*, $p < 0.05$). The sample size was eight males.



would lead to positive selection of males that both begin and finish chorus bouts.

Song pattern

The songs of *T. haematodes* have already been described, but briefly and for only one specimen (Boulard 1990, 1995; Boulard and Mondon 1996). Thus, this is the first time that several male *T. haematodes* have been used to describe and analyse the calling song in detail.

We have documented variation in time and frequency parameters among several individuals. These differences are not linked to an effect of ambient temperature, since almost all recordings were done at similar temperatures. If we consider that a CV_i/CV_b ratio inferior or equal to 1 indicates that this parameter may serve as individual marker, then the duration of a call potentially encodes individual information. Similarly, the three frequency bands (F1, F2, F3) that have very low CV_i/CV_b ratios might act as parameters for an individual signature.

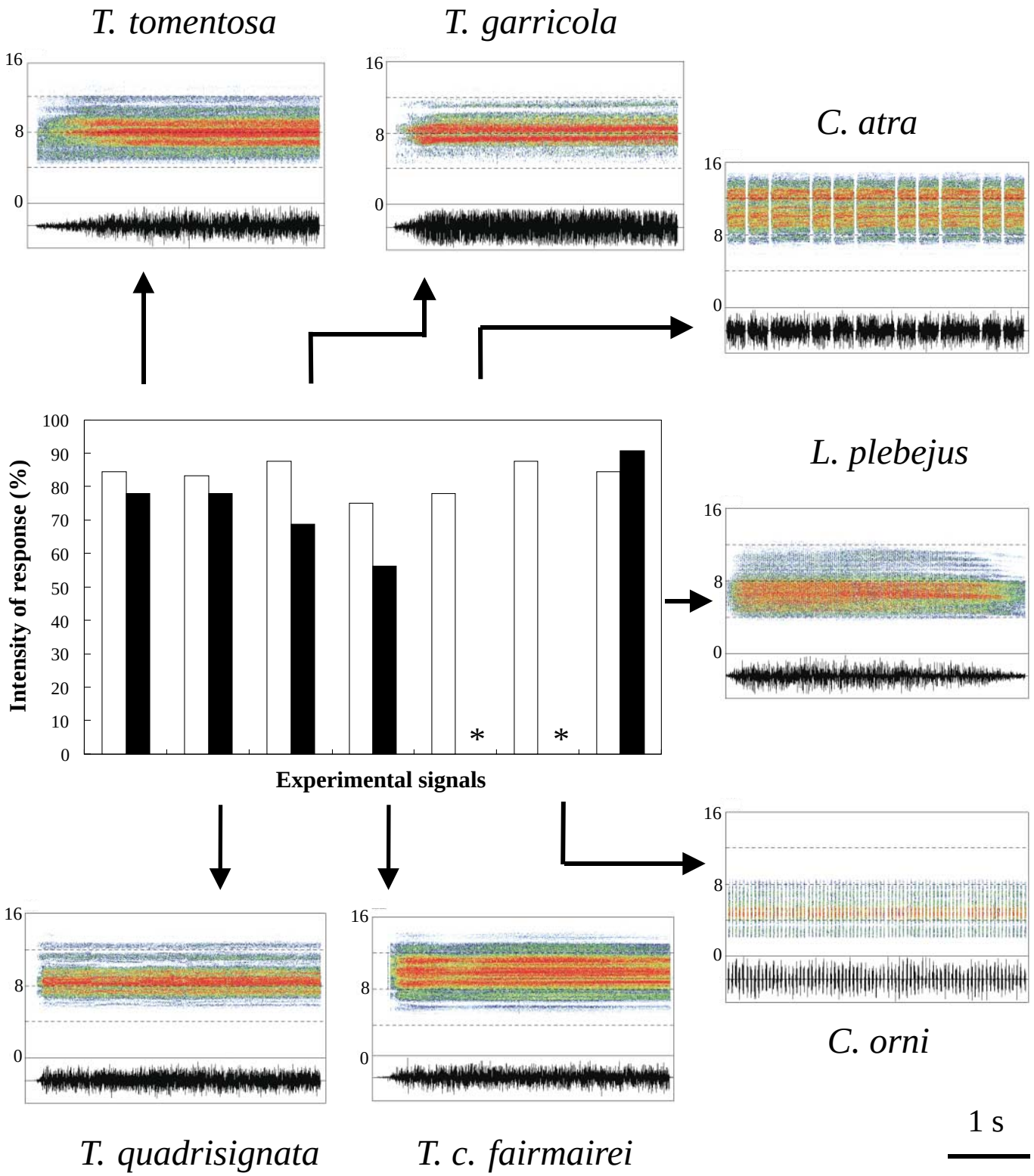
Calling songs were also characterized by slow amplitude modulation around 98–100 Hz (AM1). This value is higher than the values mentioned for *T. quadrisignata* from Portugal (49–58 Hz; Fonseca 1996) and two other cicada species, *Magicicada cassini* and *M. septendecim* (90 and 68 Hz, respectively; Young and Josephson 1983) but lower than that for *Okanagana vanduzeei* (550 Hz; Josephson and Young 1985). The tymbal muscle frequency contraction that generates a slow amplitude modulation seems to be different, even between species belonging to the same genus. Thus, slow amplitude modulation could encode specific information. In the case of the second amplitude modulation at about 1000 Hz (MA2), it appears that this fast amplitude modulation is generated by successive pulses occurring approximately every millisecond. This is confirmed by spectrum analysis: the three main peaks (F1, F2, F3) are a by-product of the pulse structure with two lateral bands (F1, F3), one on each side of the carrier frequency (F2).

As suggested by Forrest (1994), the selective forces acting on signal characteristics and influencing signal evolution can be due to phylogenetic, morphological, physiological, or environmental constraints, as well as to sexual selection and predation pressure. Based on previous work and the results of our study, rhythms of groups of pulses produced, both amplitude modulations and general frequency structure, can be explained by morphological, physiological, and environmental constraints rather than by selective forces.

Signal recognition

To understand the signal-recognition process used by male *T. haematodes* during acoustic chorus activity, we broadcast several experimental signals to caged males. The calling song of *T. haematodes* contains two parts: a rhythmic part followed by a sustained part. The playback of the signal with 6 s removed or with one part removed induced lower responses than playback of the control signal or the signal with 4 s removed. Thus, it seems that males need to hear a minimum signal duration to react. The first part, which lasts only 2.5 s, elicits a good response compared with the second part, which lasts 8.5 s. The first part seems to have a high stimulating value during chorus activity. In the North American periodical cicada *Magicicada cassini*, the initial part of the song stimulates males to synchronize their songs, while the final "buzz" part attracts females (Alexander and Moore 1958; Huber et al. 1990; Moore et al. 1993). *Tibicina haematodes* might follow the same process: the first part probably acts as a stimulus for males and the second part may stimulate females. This suggestion is supported by the fact that the remaining species of the genus *Tibicina*, which do not aggregate at high density and exhibit less chorus activity, do not produce the rhythmic part of the song. In addition, by exposing *T. haematodes* to a calling song manipulated to the rhythm of another species (*C. orni*), we primarily changed the rhythm of the first part of the signal. This modification, inducing a lower response, suggests that the stimulus value of the first part had been lowered.

Fig. 7. Intensity of responses to allospecific signals. Open bars denote response to control signals and solid bars denote response to experimental signals (*, $p < 0.05$). The sample size was eight males. The units on the *y* axes of the spectrograms are kilohertz.



With regard to fine temporal structure, the calling song of *T. haematodes* is made up of groups of pulses generating two amplitude modulations. However, the males tested replied to the signal without amplitude modulation. Thus, they paid no attention to the slow amplitude modulation, contrary to our previous hypothesis, which suggests that this parameter might be species-specific. In the same way, female periodical cicadas (*Magicicada* spp.) reply to artificial signals

without pulse structure (Marshall and Cooley 2000). For these two taxa (i.e., *T. haematodes*, *Magicicada* spp.) at least, amplitude modulation do not seem to be used to encode species-specific identity. However, we cannot rule out the possibility that amplitude modulation generated by pulse structure might transmit information such as the estimated distance of the emitter, since a strongly modified amplitude modulation may indicate a distant source.

To evaluate the frequency-discrimination process of male *T. haematodes*, we broadcast experimental signals with large frequency shifts. Our experiments showed that the male's response decreased as the frequency shift of the broadcast signal increased. These results could be first interpreted as a simple measure of the sensitivity of the auditory system. However, Popov et al. (1992) presented the audiogram of the eastern species *Tibicina intermedia*. In this species, which is very similar to *T. haematodes*, the tympanal organs are finely tuned to 4 kHz. They have high sensitivity at this frequency, which is, surprisingly, outside the frequency range of the call of the species. Moreover, it has recently been documented that the thoracic nervous system of the small Iberian cicada *Tettigetta josei* has higher frequency discrimination than was first predicted from audiograms (Fonseca et al. 2000). Therefore, it is probable that *T. haematodes* is sensitive to the frequencies of our experimental signals and that our results do not only reflect their auditory capacities. We showed, significantly, that males stopped responding when the signal was shifted down or up by 2000 Hz. This frequency shift corresponds to the signal-frequency bandwidth. It appears that no responses are observed when the sound broadcast is completely outside the limits of their own frequency production. Thus, frequencies are analysed, but not precisely.

We previously argued that small differences in time and frequency among individuals may encode individual information. Nevertheless, according to the results of our playback experiments, males probably do not use the signal for individual recognition, being unable to discriminate these small differences.

Response to the broadcast of allospecific calling song agrees with our interpretation of signal recognition. Male *T. haematodes* did not reply to the songs of *C. orni* and *C. atra*. This is probably linked to the fact that the frequency bandwidths for these two species are well outside that of *T. haematodes* (Boulard 1995). However, they clearly react to the song of *L. plebejus*, a species producing frequencies matching those of *T. haematodes* but with a completely distinct temporal pattern (Boulard 1995). This is again in agreement with reactions to the calling songs of other *Tibicina* species, which have spectra overlapping that of *T. haematodes* (Boulard 1995). Such responses to allospecific signals suggest that acoustic interference may occur in multispecies populations.

Do females analyse the acoustic signal as males do? Female Australian bladder cicadas, *Cystosoma saundersii*, react to the songs of conspecific males by wing-flicking (Doolan 1981; Doolan and Young 1989). Unfortunately, female *T. haematodes* in captivity do not respond to broadcasts by wing-flicking or other visual displays, and thus experimental investigations are limited to males. Therefore, whether the calling song of male *T. haematodes* is used by females for species recognition and sexual selection remains unresolved.

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