

Acoustic signals in cicada courtship behaviour (order Hemiptera, genus *Tibicina*)

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Abstract

During pair formation, cicadas produce acoustic signals that allow sexual partners to meet. The male is generally the emitter, producing calling songs at long range and courtship songs at short range, and the female generally the receiver. The male–female courtship behaviour of seven taxa belonging to the Palaearctic genus *Tibicina* is described here for the first time. Male courtship songs consisted of a succession of groups of pulses arranged in two sub-groups. They were short in duration with strong amplitude variations. In all taxa, courtship songs were preceded by a series of 1–5 audible wing-flicks. Differences in courtship song structure between two pairs of sympatric species, respectively *T. corsica corsica*/*T. nigronervosa* and *T. corsica fairmairei*/*T. tomentosa*, suggest that courtship signals could act as distinctive species mating recognition systems. In response to male acoustic signalling, females of *T. c. corsica*, *T. c. fairmairei* and *T. nigronervosa* produced audible wing-flicks such that both sexes established an acoustic duet ending in physical contact. In addition, males and females of *T. tomentosa* produced silent wing-flicks, a previously unknown behaviour, which could facilitate pheromone diffusion. Females did not exhibit a species-specific temporal pattern in acoustic reply to male courtship song and female wing-flick behaviour does not seem necessary for pair formation. Nevertheless, this strategy through male and female signalling ensured a reciprocal phonotactic approach that probably enhanced the likelihood for the two sexes to meet in complex habitats.

Key words: sound communication, courtship, male–female duet, audible and silent wing-flicks, cicadas *Tibicina*

INTRODUCTION

Many insect species use sound communication for pair formation, the male being most often the emitter and the female the receiver (Ewing, 1989; Bailey, 1991; Greenfield, 2002). Two main categories of acoustic mating signals exist in insects: calling songs and courtship songs (Alexander, 1967, 1968). Calling songs are used to attract females at long range, and constitute the first step in pair formation. Courtship songs follow calling songs temporally. They are produced at short range, attracting responsive females before mating and are thought to be a necessary prerequisite for a successful copulation. Calling songs are thought to support species-specific identification and to allow orientation, while courtship songs are used in female choice (Fitzpatrick & Gray, 2001).

In cicadas (order Hemiptera, family Cicadidae), calling and courtship songs are produced by a particular system,

the tymbal. Calling songs, emitted by all species, are often loud and repeated over long time periods. They are relatively easy to record and mainly for this reason have been extensively studied (for a review see Sueur, 2001). Unlike calling songs, courtship songs are probably not produced by all species and are quite difficult to observe under natural conditions. It is also difficult to elicit their production artificially in captivity. Hence, despite their obvious importance in sexual behaviour, there is little information on cicada courtship songs. For example, male courtship songs have only been reported in nine species from the western Palaearctic sub-region (Fonseca, 1991; Boulard, 1992, 1995; Gogala & Trilar, 1998; Puissant, 2001). In this area, species of the Palaearctic genus *Tibicina* produce sustained calling songs lasting from several seconds up to > 10 min. Structure and function of these signals have been studied in detail (Sueur & Aubin, 2002, 2003a, b; Sueur & Puissant, 2003; Sueur & Sanborn, 2003; Sueur, Puissant & Pillet, 2003) while, probably owing to their scarcity, *Tibicina* courtship signals have only been analysed for two species (Fonseca, 1991: *T. garricola* under the name *T. quadrisignata*; Boulard,

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1995: *T. haematodes* and *T. garricola*). On the one hand, calling songs of *Tibicina* show such a striking similarity in structure that it has been argued that they could not act as distinct specific-mate recognition systems (Sueur & Aubin, 2003b). On the other hand, distribution and ecological parameters have been recognized as potential factors that could contribute to species isolation (Sueur & Puissant, 2002). What then are the structure and function of the *Tibicina* courtship signal? Are there any differences in temporal and frequency parameters between the signals of the species? Can these signals play a role in species isolation? How can females signal their presence or willingness to a mate?

During our long-term field work in France, the courtship behaviour in seven *Tibicina* taxa was observed and recorded. These original observations were marked by the recording of male courtship songs preceded by male wing-flicks and by the discovery of a female acoustic response for some species, leading to a remarkable bi-directional acoustic courtship behaviour.

METHODS

Subjects and location

Courtship behaviour was studied in 7 *Tibicina* taxa following: *T. haematodes* (Scopoli, 1763); *T. tomentosa* (Olivier, 1790); *T. corsica* (Rambur, 1840) (sub-species *T. corsica corsica* (Rambur, 1840) and *T. corsica fairmairei* Boulard, 1984); *T. quadrisignata* (Hagen, 1855); *T. nigronervosa* Fieber, 1872 and *T. garricola* Boulard, 1983. The names of taxa follow recent modifications in *Tibicina* taxonomy (Boulard, 2000; Sueur & Puissant, 2003). All observations and recordings were made under natural conditions in France during June and July 1999–2001, except for the pair 'qua51' recorded in captivity in July 1995 by Jacques Coffin (Table 1).

Recording procedure

Recordings were made with a Telinga Pro4PiP microphone (frequency response 40–18 000 Hz \pm 1 dB) connected to a Sony TCD-D8 digital audiotape recorder (sampling frequency: 44.1 kHz, frequency response flat within the range 20–20 000 Hz). The recordings were carried out between 11:00 and 18:00, a period corresponding to the maximal activity of *Tibicina* species. The ambient temperature ranged between 25 and 35 °C with a mean of 29.4 °C.

Signal analysis

The signals from the analogue output of the DAT recorder were digitized at a sampling rate of 32 kHz and then analysed in both temporal and frequency domains with AVISOFT Lab Pro version 4.2 software (Specht, 2002).

In the temporal domain, measurements were made of the call duration (CD), the silent inter-call duration (ICD), the low amplitude part duration (LPD), the high amplitude part duration (HPD) and the number of groups of pulses per second (NGP) (Fig. 1). The number of amplitude variations (NAV) was taken into account. Records were also made of the presence or absence of audible wing-flicks, i.e. the fast wing movements that produced audible clicks, and the presence or absence of silent wing-flicks, i.e. the slow wing movements that did not produce audible sounds, for males and females.

In the frequency domain, the carrier frequency of the low amplitude part (LPF) and the high amplitude part (HPF) on mean spectra of 1 call chosen at random in the courtship sequence was analysed. The spectra were computed using a FFT (fast Fourier transform), with a 512 point Hamming window size ($\Delta f = 62.5$ Hz) and a 50% overlap, at a 32 kHz sampling rate.

Table 1. List of courting pairs of *Tibicina* spp. observed with site of observation (French administrative code number), date, ambient temperature and host plant

Pairs	Site	Date	Ambient Temperature (°C)	Host plant
<i>T. c. corsica</i> (pair 1)	San Vincenzo, Occhiatana, (2A)	9 Jun 2000	32	Undetermined grass
<i>T. c. corsica</i> (pair 2)	San Vincenzo, Occhiatana, (2A)	9 Jun 2000	32	<i>Cistus</i> sp.
<i>T. c. fairmairei</i> (pair 1)	Vendres (34)	15 Jul 1999	31	<i>Atriplex halimus</i> L.
<i>T. c. fairmairei</i> (pair 2)	Vendres (34)	20 Jul 1999	30	<i>Rubus ulmifolius</i> Schott
<i>T. garricola</i> (pair 1)	Domazan (30)	4 Jul 2000	35	<i>Vitis vinifera</i> L.
<i>T. haematodes</i> (pair 1)	Cairanne (84)	28 Jun 1999	25	<i>Vitis vinifera</i> L.
<i>T. haematodes</i> (pair 2)	Cairanne (84)	11 Jul 2001	29	<i>Vitis vinifera</i> L.
<i>T. haematodes</i> (pair 3)	Cairanne (84)	11 Jul 2001	29	<i>Vitis vinifera</i> L.
<i>T. nigronervosa</i> (pair 1)	Santo-Pietro-di-Tenda (2A)	13 Jun 2000	28	<i>Arbutus unedo</i> L.
<i>T. nigronervosa</i> (pair 2)	Santo-Pietro-di-Tenda (2A)	14 Jun 2000	26	<i>Arbutus unedo</i> L.
<i>T. quadrisignata</i> (pair 1)	Notre-Dame des Anges (83)	21 Jul 1999	32	<i>Arbutus unedo</i> L.
<i>T. quadrisignata</i> (pair 2)	Molitg-les-Bains (66)	3 Jul 2000	25	<i>Quercus</i> sp.
<i>T. quadrisignata</i> (pair 3)	Campoussy (66)	18 Jul 2000	25	<i>Pinus</i> sp.
<i>T. tomentosa</i> (pair 1)	Plan-de-la-Tour (83)	29 Jun 1999	28	undetermined Umbellifer
<i>T. tomentosa</i> (pair 2)	Vendres (34)	29 Jun 2000	32	<i>Juncus maritimus</i> Lam.
<i>T. tomentosa</i> (pair 3)	Lespignan (34)	30 Jun 2000	31	<i>Foeniculum vulgare</i> Mill.

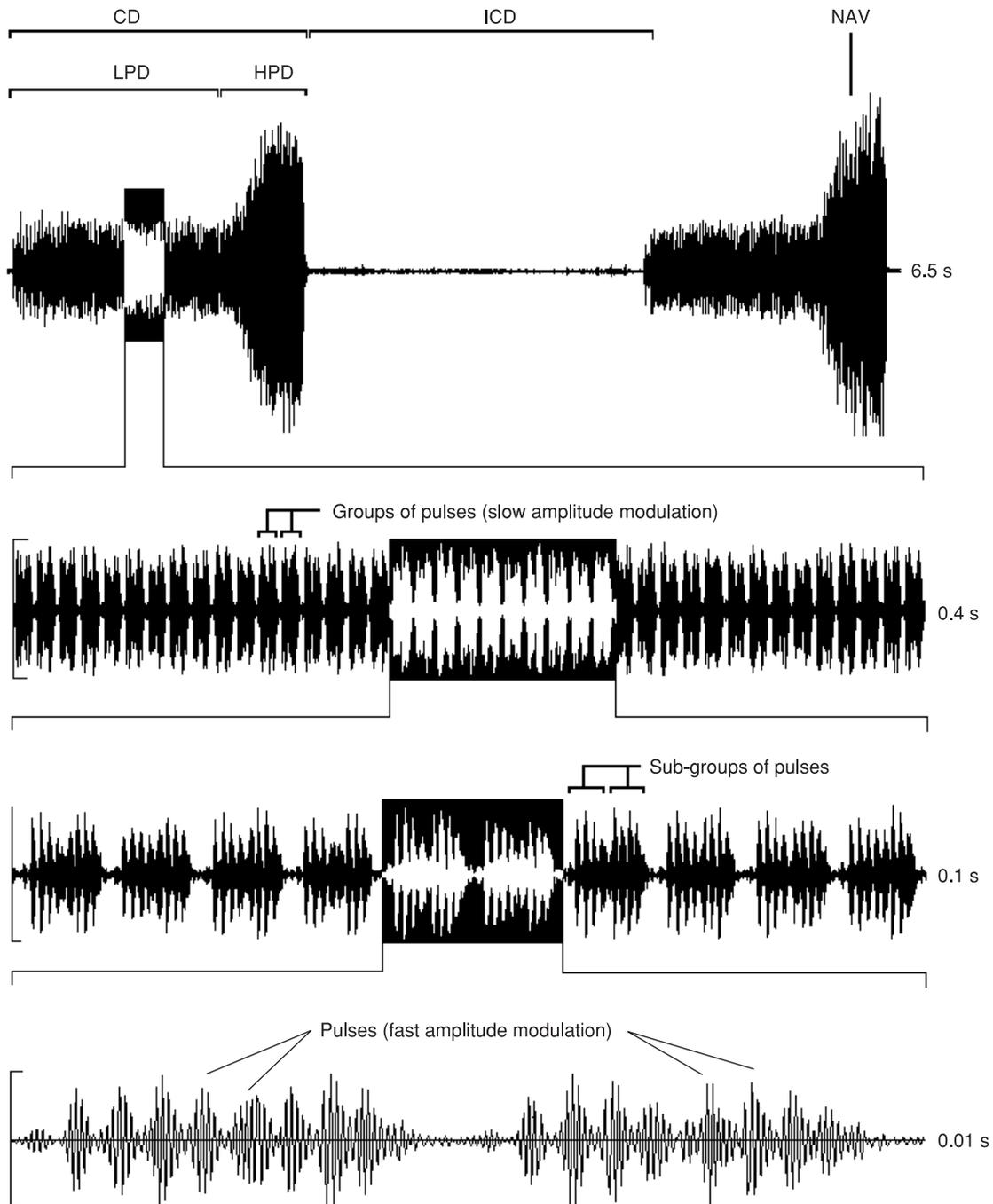


Fig. 1. Two successive courtship songs of *Tibicina haematodes*: oscillograms at different magnifications with indications of time measurements: call duration (CD), inter-call duration (ICD), low amplitude part duration (LPD), number of amplitude variations (NAV). NAV = 1.

RESULTS

Courtship sequence

Courtship behaviour of *Tibicina* taxa followed the same general pattern. Stationary singing males switched from calling song production to courtship song production as soon as a female approached to within *c.* 1 m. Courtship songs were mainly characterized by short duration (CD < 10 s) and by strong amplitude variations (NAV). The

latter were correlated with vertical oscillations of the abdomen, which was at rest during low amplitude parts of the courtship call and vertically raised during the high amplitude parts. During courtship song production, wings were not lifted on the body as occurred during calling song production. A series of audible wing-flicks preceded each courtship song sequence. In *T. tomentosa*, audible wing-flicks were also produced during the courtship song. In *T. c. corsica*, *T. c. fairmairei* and *T. nigronevosa*, the female produced audible wing-flicks between the male

courtship songs and male and female, thereby establishing an acoustic duet. In *T. tomentosa*, males and females produced silent wing-flicks. During these interactions, the female came closer to the male by short flights or by walking on branches. When the female and male were at a close range (< 30 cm), both sexes searched for each other, the male then becoming mobile. Males and females that produced audible wing-flicks exchanged acoustic signals until physical contact occurred. At contact, the male seized the female laterally with his fore and middle legs, and ensuing copulation lasted 20–30 min.

Additional observations

Two males of *T. c. corsica* were observed producing courtship songs in the absence of any obvious female. Two other males of the same species produced courtship songs and attempted to copulate with a dead female of *T. nigronervosa* fixed at the apex of a 50 cm rod and slowly moved towards the male. Courtship songs of a male of *T. c. fairmairei* were elicited by artificial clicks produced by the observer. Two males of *T. nigronervosa* produced courtship songs when the observer slowly extended his thumb which the two males each tried to grasp.

Male courtship song pattern

For each species, oscillogram and spectrogram of example courtship songs are represented in Fig. 2. Temporal and frequency parameters of male courtship songs are given in Table 2.

Tibicina courtship songs showed a common general design: a succession of groups of pulses arranged in two sub-groups. Two categories of amplitude modulations were distinguishable: a slow amplitude modulation distributed within groups of pulses and a fast amplitude modulation at the level of each pulse (Fig. 1).

In the frequency domain, the mean spectrum of the signals of all species was characterized by three main peaks. These frequency peaks were a by-product of the fast amplitude modulation detected in the pulses. The first and third frequency peaks corresponded to the two lateral bands, and the second frequency peak to the carrier frequency (LPF or HPF), as illustrated in Fig. 3 for the *T. tomentosa* courtship song. For the male courtship song, no difference exists for the values of the frequencies between the low amplitude part and the high amplitude one. As a consequence, it can be stated that the courtship song presented no frequency modulation.

The courtship song of *T. tomentosa* differs greatly from those of all other species in its long duration (CD) and the great number of amplitude variations (NAV) produced concomitantly with audible wing-flicks. Unfortunately, the number of specimens recorded per taxa (Table 1) was too low to undertake a precise statistical comparison between the different parameters of the courtship songs of the species studied.

Audible and silent wing-flicks

The occurrences of audible wing-flicks or of silent wing-flicks produced by males and females during courtship interactions are summarized in Table 3. The sound structure of wing-flicks is a very short impulse of *c.* 1 ms duration, with a wide frequency band indistinguishable between species and between sexes. Audible male wing-flicks were produced before tymbal activation except for *T. tomentosa*. For this species, audible wing-flicks were emitted before and during tymbal activation, the rhythm of audible wing-flicking following approximately the rhythm of song amplitude variation. Audible wing-flicks were produced by females of *T. c. corsica*, *T. c. fairmairei* and *T. nigronervosa* between two successive male courtship songs. No regular response latency was detected between the end of the male courtship song and the female wing-flicks and consequently no specific rhythm could be noted for courtship song/wing-flick production. Silent wing-flicks produced between call production were noted only for *T. tomentosa* courtship.

DISCUSSION

Our study on the courtship behaviour of *Tibicina* cicada taxa has revealed an acoustic system more elaborate than that usually described in cicadas. Courtship behaviour in *Tibicina* is characterized by two main features: (1) the males produce short songs with large amplitude variations preceded by audible or silent wing-flicking; (2) the females of some species were able to signal by audible or silent wing-flicking. Alternation of male and female signals led to an alternation of sender/receiver roles, unusual in cicadas.

Male courtship behaviour

Once a female *Tibicina* arrives in the proximity of a calling male, the latter switches from calling to courtship song. Courtship songs differ mainly from calling songs by their short duration, by their large amplitude variations and usually by following audible wing-flicking. The fine structure of the courtship songs is similar to those of the calling songs (Sueur & Aubin, 2003b): both consist of a regular succession of groups of pulses generating three frequency bands. This similarity of the fine structure is probably the result of an identical activation of the tymbal mechanism (for a description of the tymbal mechanism, see Sueur & Aubin, 2002, 2003b). Small differences in the number of groups of pulses per second and in the carrier frequency were mainly identified between *Tibicina* calling songs previously described in Sueur & Aubin (2003b). In spite of the lack of statistical analysis, similar differences seem also to be found between courtship songs. As these differences are small, we suspect that fine temporal and frequency parameters of courtship songs do not play an important role in species-specific identification and consequently in species isolation between

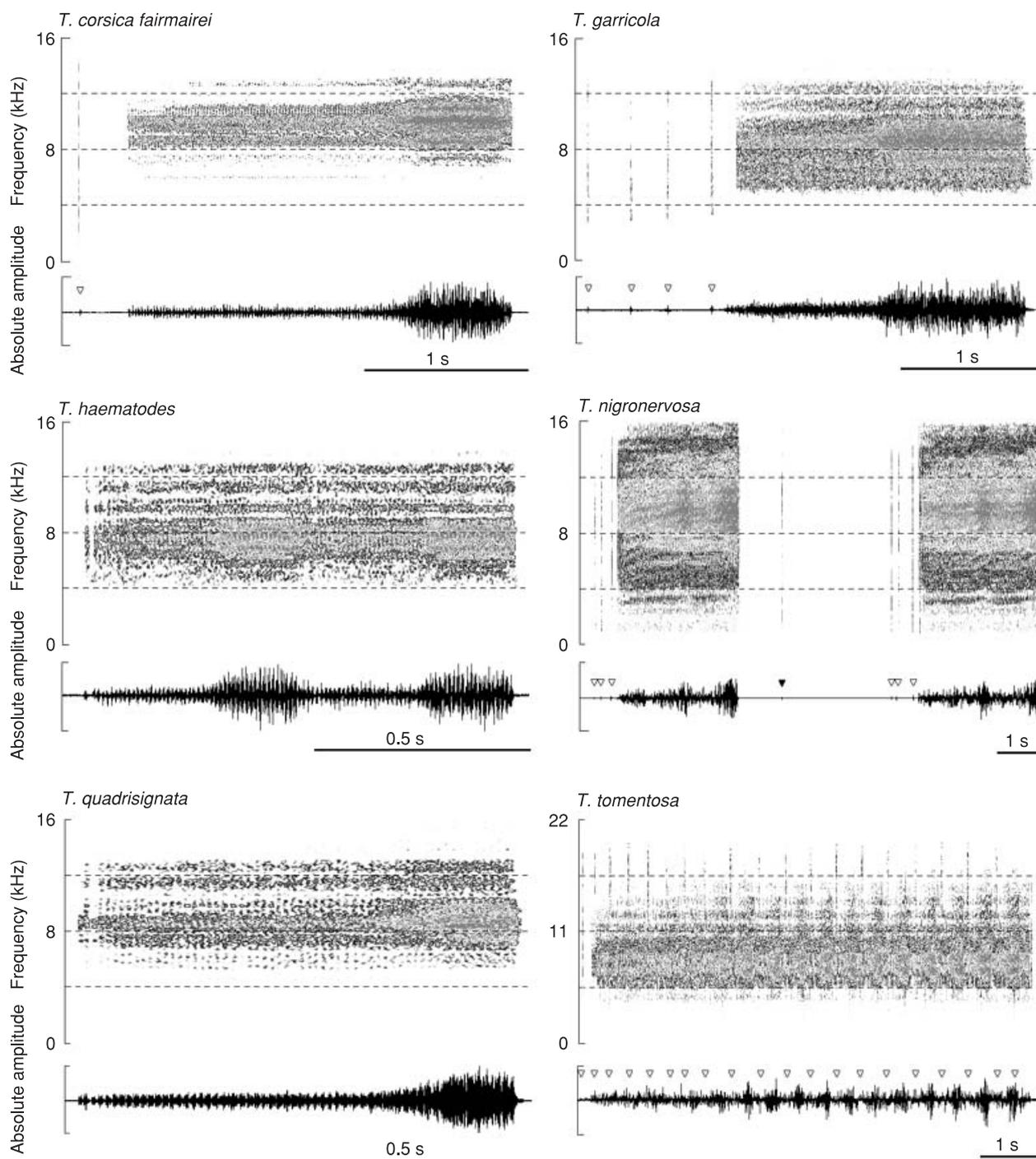


Fig. 2. Oscillographic (absolute amplitude vs time) and sonographic (frequency in kHz vs time) representation of courtship call in *Tibicina* taxa. Note the change of frequency scale for *T. tomentosa*. White inverted arrows, male audible wing-flicks (not available for all species); black inverted arrow, female audible wing-flick (only for *T. nigronervosa*).

Tibicina taxa. Another parameter that could potentially act as a species-specific acoustic marker in the courtship song is the number of amplitude variations (NAV) that coincided with abdomen raising as observed and analysed previously in an Australian cicada species (Young, 1990). The sympatric *T. c. corsica* and *T. nigronervosa* differ in this amplitude pattern, the former producing a maximum of two amplitude variations and the latter producing

systematically more than two amplitude variations. Similarly, *T. c. fairmairei* and *T. tomentosa* were sometimes found at the same site, but these two species produce courtship songs that differ greatly in the number of amplitude variations. *Tibicina tomentosa* also produces audible wing-flicks before and during singing while *T. c. fairmairei* only emits these signals before the tymbal courtship song. In these cases, such acoustic features could

Table 2. Time and frequency parameters in *Tibicina* courtship songs: call duration (CD), inter-call duration (ICD), low amplitude part duration (LPD), high amplitude part duration (HPD), number of amplitude variations (NAV), number of groups of pulses per second (NGP), low amplitude part frequency (LPF), high amplitude part frequency (HPF). When available values are given as average $x \pm SD$ (sample size)

Individual	CD (s)	ICD (s)	LPD (s)	HPD (s)	NAV	NGP	LPF (Hz)	HPF (Hz)
<i>T. c. corsica</i> (pair 1)	1.99 ± 1.15 (61)	4.29 ± 2.19 (61)	1.25 ± 0.25 (63)	0.68 ± 1.16 (63)	1.03 ± 0.18 (61)	60	9812	10000
<i>T. c. corsica</i> (pair 2)	2.43 ± 2.72 (155)	9.87 ± 15.60 (155)	1.20 ± 0.236 (156)	1.20 ± 2.84 (156)	1.00 ± 0.08 (155)	59	9750	9812
<i>T. c. fairmairei</i> (pair 1)	5.49 ± 16.48 (122)	5.79 ± 4.93 (122)	0.79 ± 0.44 (194)	2.66 ± 13.20 (194)	1.55 ± 0.73 (122)	61	10062	10187
<i>T. c. fairmairei</i> (pair 2)	2.80 ± 6.55 (185)	3.33 ± 2.57 (185)	1.19 ± 0.42 (191)	1.51 ± 6.49 (191)	1.03 ± 0.19 (185)	61	10062	10000
<i>T. garricola</i> (pair 1)	3.40 ± 2.30 (27)	5.39 ± 4.18 (25)	1.21 ± 0.53 (25)	2.23 ± 2.12 (25)	0.94 ± 0.27 (27)	68	8625	8625
<i>T. haematodes</i> (pair 1)	0.33 ± 0.40 (113)	0.70 ± 0.79 (113)	0.22 ± 0.18 (70)	0.14 ± 0.07 (70)	0.62 ± 0.49 (122)	98	7375	7500
<i>T. haematodes</i> (pair 2)	0.47 ± 1.23 (113)	1.11 ± 2.34 (113)	0.09 ± 0.58 (207)	0.34 ± 0.97 (207)	0.95 ± 0.75 (113)	98	7187	7187
<i>T. haematodes</i> (pair 3)	0.91 ± 5.60 (367)	0.60 ± 0.76 (367)	0.19 ± 0.12 (320)	0.30 ± 0.42 (320)	0.87 ± 0.82 (367)	98	7500	7500
<i>T. nigronervosa</i> (pair 1)	2.90 ± 0.43 (7)	—	0.63 ± 0.21 (18)	0.43 ± 0.06 (18)	2.57 ± 0.53 (7)	105	9812	9687
<i>T. nigronervosa</i> (pair 2)	3.52 ± 1.48 (39)	5.47 ± 4.02 (39)	0.77 ± 0.45 (107)	0.51 ± 0.15 (107)	2.74 ± 1.39 (39)	106	9812	9812
<i>T. quadrisignata</i> (pair 1)	0.61 ± 0.28 (65)	1.39 ± 2.86 (65)	0.43 ± 0.27 (65)	0.19 ± 0.03 (65)	1.00 ± 0 (65)	78	8312	8312
<i>T. quadrisignata</i> (pair 2)	0.57 ± 0.40 (120)	0.67 ± 1.65 (120)	0.31 ± 0.35 (128)	0.23 ± 0.10 (127)	1.05 ± 0.29 (120)	76	8562	8750
<i>T. quadrisignata</i> (pair 3)	0.80 ± 0.33 (42)	0.33 ± 0.16 (42)	0.45 ± 0.22 (45)	0.27 ± 0.09 (45)	1.07 ± 0.34 (342)	74	8687	8687
<i>T. tomentosa</i> (pair 1)	7.59 ± 4.79 (8)	5.28 ± 2.43 (8)	0.27 ± 0.36 (103)	0.32 ± 1.26 (101)	12.63 ± 4.17 (8)	164	8500	8500
<i>T. tomentosa</i> (pair 2)	3.83 ± 1.57 (3)	4.93 ± 1.62 (3)	0.34 ± 0.44 (20)	0.24 ± 0.12 (20)	6.67 ± 3.51 (3)	160	8812	8812
<i>T. tomentosa</i> (pair 3)	10.43 ± 15.21 (23)	74.55 ± 120.70 (23)	0.31 ± 0.47 (281)	0.89 ± 7.26 (274)	12.35 ± 3.70 (23)	154	8562	8562

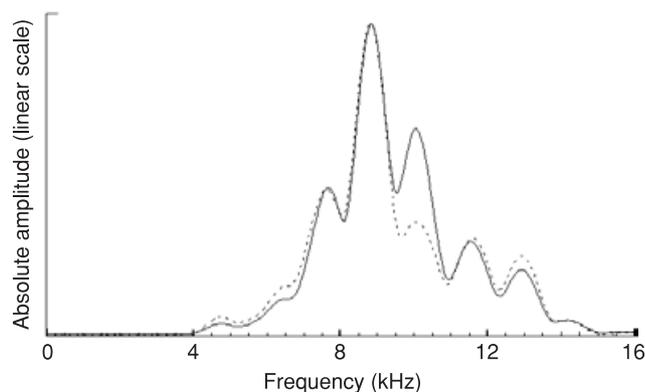


Fig. 3. Mean spectrum of low amplitude part (dotted line) and high amplitude part (solid line) in a *T. tomentosa* courtship call.

act as distinct species mating recognition systems, but this still needs to be tested through playback experiments.

Another remarkable feature of the behaviour is the male audible wing-flicking. The mechanism of such sound production in cicadas is still debated (Popov, 1981; Boulard, 1992). In *Tibicina*, Boulard (1995) has proved that wings do not touch the substrate (plant) and therefore that sound is not produced by substrate percussion. We then suggest that the clicks could be produced in *Tibicina* by buckling stiff mechanically bi-stable portions of the wings, as has been proposed in some butterflies (Yak *et al.*, 2000) and very recently in other cicada species (Gogala & Trilar, 2003).

Our study reports for the first time the existence of male silent wing-flicking in *T. tomentosa*. Communication by pheromones has never been clearly proven in cicadas but is widespread among other Hemiptera (Aldrich, 1996). Such remarkable behaviour could be related to the dispersion of

Table 3. Male and female audible wing-flicking during courtship interactions. ‘Audible’ refers to fast wing-flicks producing audible clicks. ‘Silent’ refers to slow silent wing-flicks. (+) observed, (–) never observed, (?) not observed but low number of observations

	Male		Female	
	Audible	Silent	Audible	Silent
<i>T. c. corsica</i>	+	–	+	–
<i>T. c. fairmairei</i>	+	–	+	–
<i>T. garricola</i>	+	–	?	–
<i>T. haematodes</i>	+	–	–	–
<i>T. nigronervosa</i>	+	–	+	–
<i>T. quadrisignata</i>	+	–	?	–
<i>T. tomentosa</i>	+	+	–	+

a chemical signal, and also to the production of a visual or vibratory signal. *Tibicina* courtship communication could then be multi-modal, a system that increases communication efficiency (Endler, 1993; Rowe, 1999).

Female courtship behaviour

Our observations report for the first time a female behaviour pattern in response to the male courtship song: the production of audible wing-flicking, observed in *T. corsica corsica*, *T. c. fairmairei* and *T. nigronervosa* and of silent wing-flicking observed in *T. tomentosa*. In contrast, this behaviour seems to be absent in *T. garricola* and *T. quadrisignata*, but observations were too few (a single observation for *T. garricola* and only two observations in poor conditions for *T. quadrisignata*) to conclude with certainty the absence of such behaviour in these two species. According to our numerous

observations of *T. haematodes* courtships, it seems clearly established that females of this species do not wing-flick.

The mechanism of female wing-flicking is still unknown, but is probably analogous to that of the male wing-flicking mechanism. Audible or silent female wing-flicking could also be linked to a chemical diffusion as has been reported for the audible wing-flicking of the Australian bladder cicada *Cystosoma saundersii* (Doolan, 1981; Doolan & Young, 1989; D. Young, pers. comm.). Female audible wing-flicking has already been observed in other cicada species, but to our knowledge, this is the first time that female silent wing-flicking is reported in cicadas. As with male silent wing-flicking, female silent wing-flicking occurred only in *T. tomentosa*. Such behaviour could also facilitate pheromone diffusion.

Differences in the female courtship behaviour of the various *Tibicina* species studied were not identified. In particular, audible wing-flicks seemed similar, and therefore it is highly improbable that they carry any species-specific information. Female courtship signals do not seem necessary for pair formation. Our complementary observations suggest that males were not selective. In particular, males of *T. nigronervosa* tried to mate with anything that approached them slowly, and males of *T. c. fairmairei* emit courtship songs in the absence of a female. Such non-specificity of female signals and non-selectivity of males are in agreement with the theory of sexual selection and asymmetrical parental investment patterns (Trivers, 1972; Alexander, Marshall & Cooley, 1997). Indeed, sexual acoustic signals are mostly less differentiated in females than in males, and the ability to discriminate between potential mates is less developed in males than in females (Booij, 1982).

Male–female acoustic duet

Male–female acoustic duets have been previously described in a great number of insects, including Coleoptera (e.g. Goulson, Birch & Wyatt, 1994), Plecoptera (e.g. Stewart, 1997), Neuroptera (Wells & Henry, 1992), Megaloptera (Ruprecht, 1975), Orthoptera (e.g. Spooner, 1968) and Hemiptera other than cicadas (Claridge & Vrijer, 1994). Such alternation in signal production has been reported previously in detail for the following cicadas: *Cicadetta quadricincta* (Gwynne, 1987), *Kikihia* and *Amphisalta* (Lane, 1995), *Magicicada* species (Cooley & Marshall, 2001), *Okanagana canadensis* and *O. rimosa* (Cooley, 2001). In all these species, acoustic duets only occur at close range. Males of *C. quadricincta* engage a ‘call-fly’ behaviour while males of other species, including *Tibicina*, are static singers. Females of *C. quadricincta*, *Kikihia*, *Amphisalta* and *Magicicada* species exhibit species-specific temporal patterns relative to the male courtship call. Such a specific time delay of female response could encode species-specific information as found in bushcrickets (Robinson, 1990). Nevertheless, in *Okanagana* – a closely related genus showing striking similarities to *Tibicina* in morphology, ecology and behaviour – female response

does not seem to have a specific relationship to male courtship songs (Cooley, 2001). As first hypothesized by Cooley (2001), such a lack of specificity does not mean that female audible wing-flicking does not act as a sexual signal. It can (1) alert the male to the presence of a female, (2) stimulate the male to produce courtship songs, (3) test male quality through the emission of courtship songs, and (4) elicit searching behaviour by the male.

The microhabitat where *Tibicina* courtship behaviour occurs can be complex in structure (Sueur & Puissant, 2002). Crossing trunks, branches, leaves of trees and bushes constitute an environment where orientation may be difficult and where sound degradation could be important, significantly reducing communication efficiency. Even if not implicated in the species-specific recognition process and unnecessary to pair formation, a bi-directional strategy through male and female signalling does ensure a reciprocal phonotactic approach that probably enhances the likelihood of meeting a mate in such difficult environmental conditions.

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