

## Temporal patterns in the vibratory courtship signals of the wandering spider *Cupiennius salei* Keys.

Wolfgang Schüch and Friedrich G. Barth

Gruppe Sinnesphysiologie, Zoologisches Institut der Johann Wolfgang Goethe-Universität, Siesmayerstrasse 70, D-6000 Frankfurt am Main 1, Federal Republic of Germany

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**Summary.** The vibratory courtship signal generated by abdominal and leg movements of male *Cupiennius salei* on plants consists of impulses, which in groups of about ten form syllables. A syllable together with the preceding “silent” pause is called a sequence. Up to 50 sequences chained together form a series. A series together with the preceding silent period is called an interseries. A complete courtship is built up from a row of successive interseries. An additional signal produced by palpal drumming only occurs between syllables. Females respond to ca. 40% of the male signal series with a single irregular signal produced by leg oscillations and lasting for 113–1790 ms. Their response reduces the duration of the male interseries significantly from an average of 27.9 s to 20.6 s. The female signal follows a male signal series within a narrow time frame of  $0.89 \pm 0.53$  s. Analysis over long periods of time and of complete courtships showed the male signalling to be highly structured in the time domain and to contain many cues potentially usable by the female for both such precise timing and conspecific recognition: (1) On average, the interval between the last two syllables is significantly longer than the preceding ones. (2) During the course of a series, syllable durations increase nearly linearly from 93 ms to 123 ms. (3) The twelfth sequence (T-12) prior to the final one (T) is outstanding since here, roughly 4 s before the end of a series, the duration of sequences and pauses, the signal amplitudes and the occurrence of palpal drumming abruptly start to increase. Also, the frequencies contained in the syllables shift to higher values. (4) Between sequences T-4 and T-6 pause duration and sequence duration reach their minimum whereas the values for signal acceleration and the occurrence of palpal drumming are highest.

### Introduction

*Cupiennius salei* is a tropical wandering spider that lives on banana plants (*Musa sapientum*), agaves, and bromeliads near the tropical rain forest in the highlands of Central America (Barth and Seyfarth 1979). Like many other spiders *C. salei* uses vibratory communication during courtship. The vibratory signals conveyed between male and female spiders are transmitted through their host plants and ensure finding of the mate and species-specific copulation (Rovner and Barth 1981).

The male starts vibrating upon exposure to a pheromone previously deposited by a mature female onto the plant. Its display is immediately followed by a brief vibratory response of the female, produced by rapid oscillation of her legs (Rovner and Barth 1981). The response of the female often follows the male courtship signal after a time interval shorter than that between two signals within the male's display, and still it never overlaps any of the male's signals (Rovner and Barth 1981). Such precise timing implies that the female knows about the end of the male signal.

In the present paper we look for the clues in the vibratory signal which might contain such information. It was suggested that the interval between the last two male signals, which is on average significantly longer than the preceding ones, may trigger the female response (Rovner and Barth 1981). Since the responses of some females showed the same precise timing, even in cases when the terminal interval in the male series was not longer than the previous ones, we investigated the male courtship series within a broader time frame. It turned out that several parameters of the male signal consistently change over longer periods of time in a typical way. These changes may serve not only to help the female recognize the end of a male

vibratory courtship series, but also to ensure conspecific recognition and mating.

## Materials and methods

Four adult males (A, B, C and D) and two adult females (X and Y) of the spider *Cupiennius salei*, all reared in the laboratory, were used for the present study. A female *Cupiennius* was allowed to move freely on an agave (*Agave americana*) for about one day. During this time it was confined to one of the leaf blades which was covered with a plastic bag for this purpose. When the female was replaced by a male the next day the male usually started courting in response to the pheromone secreted by the female (Dumpert 1978; Rovner and Barth 1981). In 8 out of 13 courtships the female was sitting on another leaf blade when it responded to the courtship signals of the male with its own vibratory signals. Signals from both female and male spiders were measured with different types of vibrometers (see below) from a third leaf. All experiments were conducted on the same plant, using the same leaf blades for female and male spiders and for the measuring sensors.

Vibrations were mainly measured with an accelerometer (B and K 4339, sensitivity 9.86 mV/g, weight 16 g). The accelerometer was waxed onto the mid region of the leaf at about 5 cm from the "stem". Its output signal was fed into a measuring amplifier (B and K, 2606) through a preamplifier (B and K, 2625). Signal transmission characteristics of the agave leaf will be slightly changed by the accelerometer's mass but this is tolerable with respect to the temporal parameters studied here. Furthermore, these were also measured with non-contact devices (see below), where the problem of added mass does not exist at all.

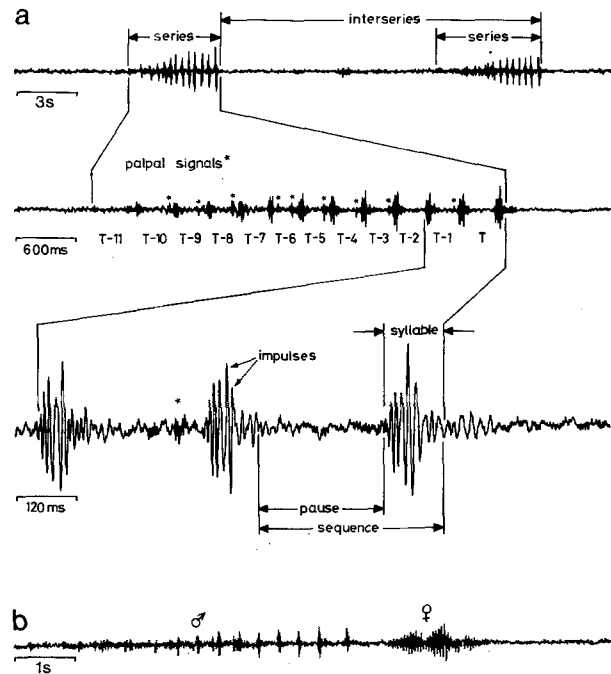
Leaf displacement was measured with a non-contact, displacement-sensitive system (Multi Vit KD 2300, 0.5 SU, micro epsilon; sensitivity: 2 mV/ $\mu$ m) and a laser vibrometer (Klärner and Barth 1982). The output signals of the different measuring systems were monitored by an oscilloscope (Philips, PM 3211), recorded with a frequency-modulated tape recorder (Bell and Howell, CR 3000) at a speed of 19 cm/s, and printed by a thermo-pen-writer (Watanabe, LINEARCORDER MARK V). Using a digitizer (Kontron, MOP) the values for the different signal parameters were fed into a computer (digital, MINC-11) for storage and statistical evaluation. Analysis of variance was computed by an F-test (Linder and Berchtold 1979). The Fast Fourier Transforms (FFT) were carried out with another computer (Nicolet MED-80) using the signal analysis software package MED-80.

High-speed cinematography was performed with a high-speed camera (Weinberger AG, STALEX WS-2) and its control units, at 200 frames/s. A camera triggered stroboscope (Orthotron, Strobohertz) was used to provide optimal light flashes for each frame. Film data were acquired by using a 16 mm film projector (L-W International, Photo Optical Data Analyzer MARK V).

## Results

### Overall signal structure

**Male.** The male courtship signal consists of abdominal movements transmitted to the substratum through the legs and of palpal drumming against the plant. Its basic element is a package of 6–12 regularly spaced impulses which result from the



**Fig. 1 a, b.** Courtship signal of *Cupiennius salei* recorded with an accelerometer. **a** Structure of male courtship signal. *T* terminal sequence; *T-n* "n"th sequence before end of series. **b** End of a male signal series and female response

up and down movements of the abdomen. This package we call a syllable (Fig. 1a). Subsequent syllables are separated from each other by pauses. One pause and the following syllable together form a sequence. Finally, a train of sequences, sometimes up to 50, constitutes a courtship series.

After completing a courtship series the male stays motionless as if avoiding the production of vibratory noise while expecting a female's response. Irrespective of the female's response, however, the male starts the next courtship series after a certain period of time (approx. 8–10 s if a female is present). At the beginning of a courtship series the syllables are of very low amplitude, which, however, increases towards the end of the series. Palpal drumming occurs exclusively between two syllables. It results in vibrations shorter in duration and of higher frequency than those contained in the syllables and due to abdominal oscillations. There are 0–4 palpal signals within one pause.

In the time domain the male courtship signal is characterized by the durations of the interseries, pauses, syllables, and sequences. In addition the frequency content and amplitude of the syllables, as well as the number of palpal signals per sequence, are potentially important features. Except for the duration of an interseries, all other parameters refer to particular individual sequences. So we adjoined the measured values of the different pa-

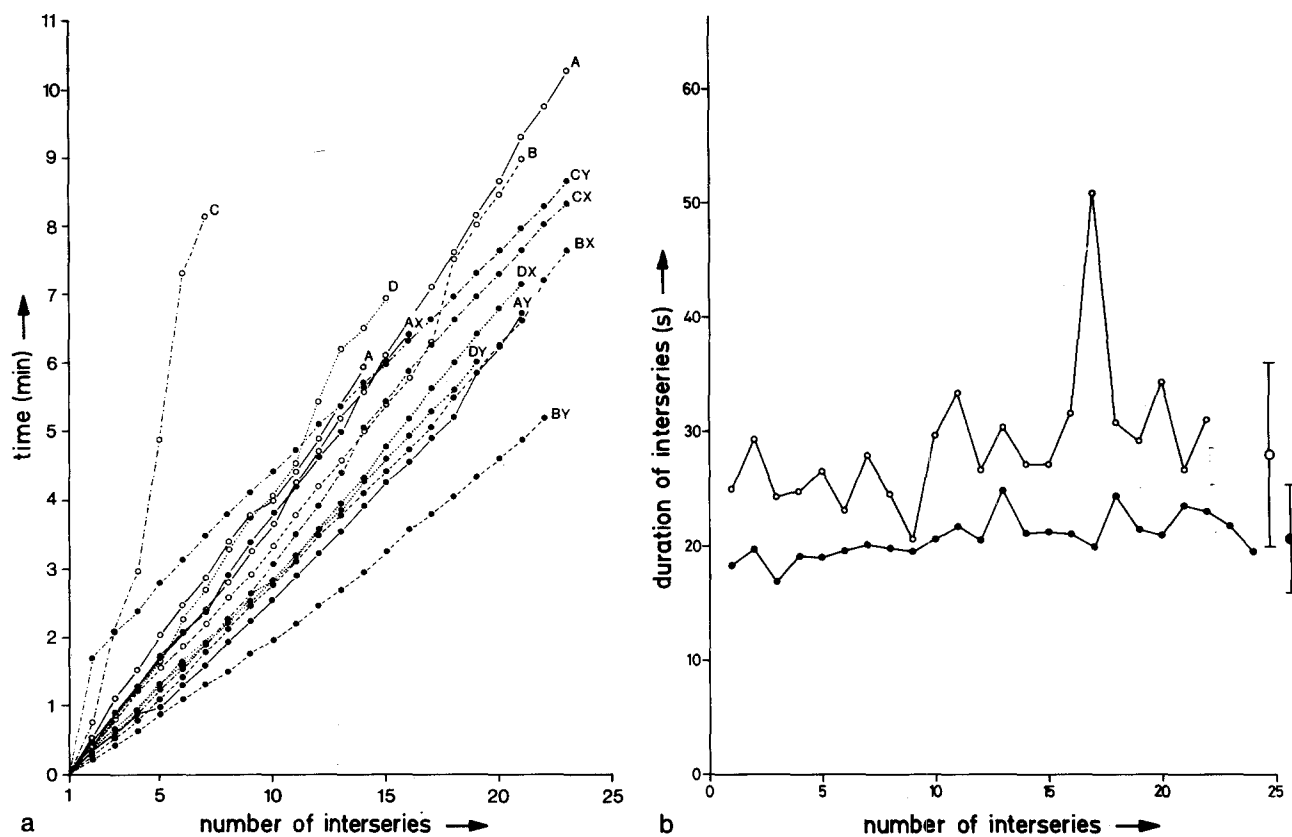


Fig. 2a, b. Interseries in four males (A, B, C, D) with (●) or without (○) a responding female (X, Y). a Time courses of 13 courtships. b Average duration. On the right are the mean values with standard deviation

rameters to their respective sequence and numbered all sequences of every courtship series. All terminal sequences within the series are marked T for "terminal sequence" and the preceding sequences are numbered T-1, T-2, T-3, ... etc. This permits statistics on the level of single sequences and avoids obscuring the general progress of the parameters over the whole series.

*Female.* The courtship signal of the female is less regular than that of the male. It is produced by movements of all except the third legs and contains a mixture of several frequencies of different amplitudes (Figs. 1 b and 7b). Depending on the degree and duration of the leg movements the duration of the response varies between 0.1 and 1.8 s. The time span between the end of a male courtship series and the beginning of the female response varies between 0.0 and 1.5 s and is remarkably short. Apart from its duration and the time span between its onset and the end of a male courtship series the parameters used to describe the female vibratory signals are its peak amplitude and the two main frequencies contributing the highest relative amplitudes in the frequency spectrum (Fig. 7).

#### *Parameters in the male signal*

*Duration of interseries.* The series of a particular courtship are repeated at regular temporal intervals (Fig. 2a). Once a certain repetition rate is initiated it is kept remarkably constant throughout the whole courtship. The average duration of the first 24 interseries of all courtships observed is  $22.8 \pm 6.7$  SD s ( $n=232$ ). The differences among the individual values are not significant ( $F=0.93$ ,  $n1=23$ ,  $n2=208$ ,  $P<0.05$ ;  $n1$ ,  $n2$ : 1st and 2nd degree of freedom). If a responding female is present during the male courtship the average duration of the interseries ( $20.6 \pm 4.7$  s,  $n=163$ , eight courtships) is significantly shorter than without the female ( $27.9 \pm 8.0$  s,  $n=69$ , four courtships) ( $F=76.9$ ,  $n1=1$ ,  $n2=230$ ,  $P>0.05$ ) (Fig. 2b). Evidently the courtship behavior of the male is influenced by the presence of a responding female (Rovner and Barth 1981). The differences in the duration of interseries between single courtships of the same spiders or different individuals are small (Fig. 2a). This parameter may well serve intraspecific recognition.

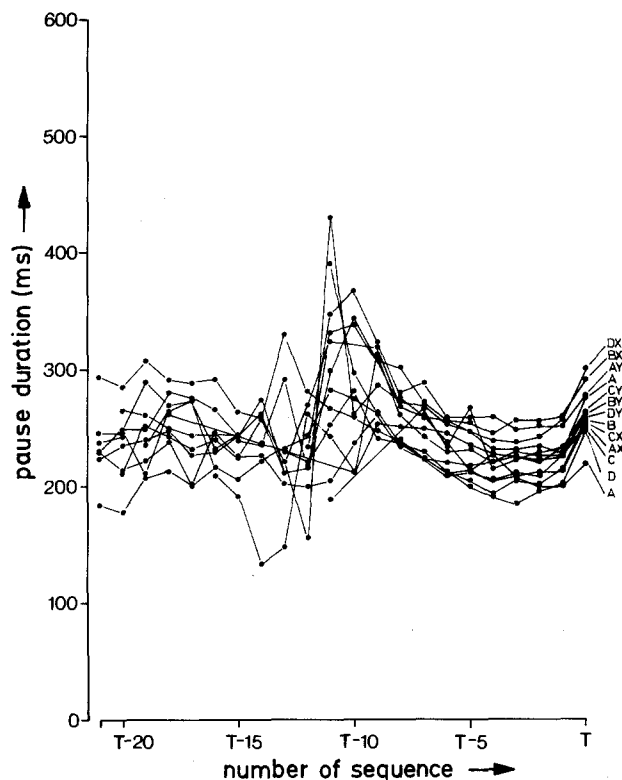


Fig. 3. Duration of succeeding pauses during the final phase of a male courtship series. Mean values from 13 courtships in the presence and absence of responding females. A, B, C, D males. Double characters indicate courtships with responding females, X and Y

*Duration of pause, syllable, and sequence.* During a male courtship series the durations of pause, syllable, and sequence change in a characteristic way and the last 13 sequences of every courtship series have special significance in this respect. At the beginning of a courtship series the duration of the pauses is 230–240 ms. In the sequence T-12 this value abruptly increases to sometimes more than 400 ms (Fig. 3). Often this effect is due to a decrease of the time taken by the pause relative to the previous one. Pause duration will again diminish continuously beyond the sequence of maximum pause duration, reach a minimum in the sequence T-4 ( $222 \pm 20$  ms,  $n = 164$ ) and then again increase continuously. In one third of all series the final pause in the sequence T lasts up to 400 ms and its average value increases to  $263 \pm 21$  ms ( $n = 175$ ) (Fig. 3). In contrast to the pauses, the duration of the syllables within a series changes only slightly, starting at approximately 100 ms and increasing to about 120 ms towards the end of the series. Both pause and syllable together make up one sequence (Fig. 1 a). Since the syllable duration rises only slightly during the course of a series, the characteristic change in sequence duration is

mainly due to the change in the duration of the pauses. It increases significantly during sequence T-12 from about 340 ms to over 500 ms. After that it invariably decreases continuously down to a minimum of  $334 \pm 29$  ms ( $n = 164$ ) in sequence T-4 and again increases towards the end of the series. According to measurements taken of 175 courtship series the course taken by the duration of pause, syllable, and sequence always has the same characteristic shape. The presence or absence of a female responding to the male's courtship vibrations has no significant influence on this (*F*-test,  $P < 0.05$ ).

*Amplitude of syllables.* Mechanical signalling on a plant, such as that produced by spiders during courtship, causes high amplitude (mm-range) and low frequency displacement of the leaves around their resonance frequency, which is 8–9 Hz in the case of the *Agave* plant used, and depends on the leaf length (McMahon 1975). Tests with four different-sized *Agave* plants concerning their resonance frequency showed them to have on average 8.1, 8.7, 11.2 and 13.2 oscillations per second with leaf lengths of 41, 37, 28 and 18 cm respectively (Schüch 1983). These basic oscillations are overlaid by the courtship signals proper, which are of much lower amplitudes ( $\mu\text{m}$ -range), higher frequency, and emphasized in recordings using an accelerometer instead of a displacement receiver (Fig. 1).

The acceleration amplitudes gradually increase within a male courtship series from its beginning towards its end, with the last 5 or 6 sequences of the series showing the highest values. There are big differences in the maximum acceleration reached at the end of each series, even within a single courtship (Fig. 4a). When considering a complete courtship series, one sees that the acceleration amplitudes of the syllables abruptly start to increase at sequence T-12. This is particularly prominent in plots of relative acceleration (Fig. 4b), which reaches its maximum in sequence T-4 after having increased by a factor of 2 to 2.5 within these 8 to 9 sequences. The course taken by this increase is similar in all cases, however. Again, the presence or absence of a female during signalling by the male has no significant influence on this (*F*-test,  $P < 0.05$ ).

*Frequencies contained in syllables.* Compared to the parameters just discussed the frequencies contained in the syllables (number of syllable impulses divided by syllable duration) change little. Centering at around 75 Hz they increase slightly towards the end of the series (Fig. 5). The presence or absence of a female response has no significant influence on this (*F*-test,  $P < 0.05$ ). Frequency spectra

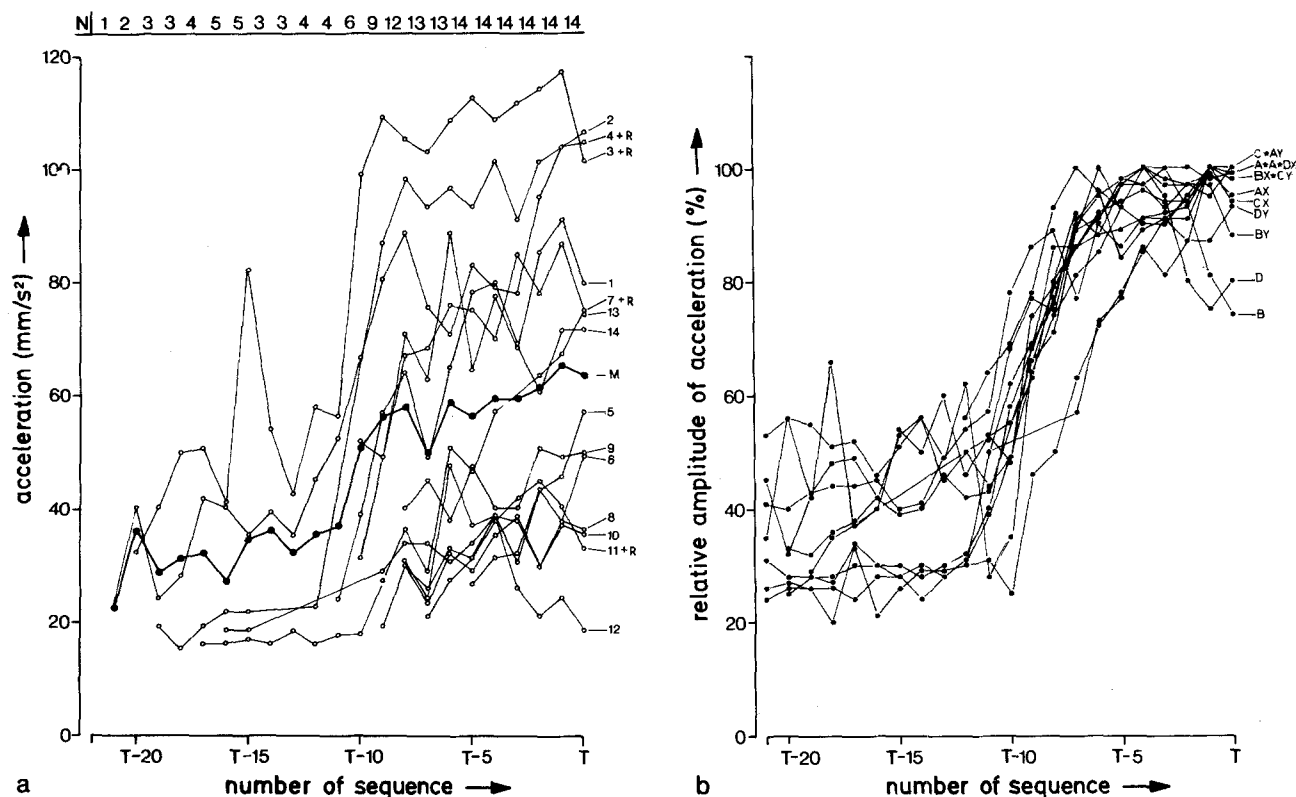


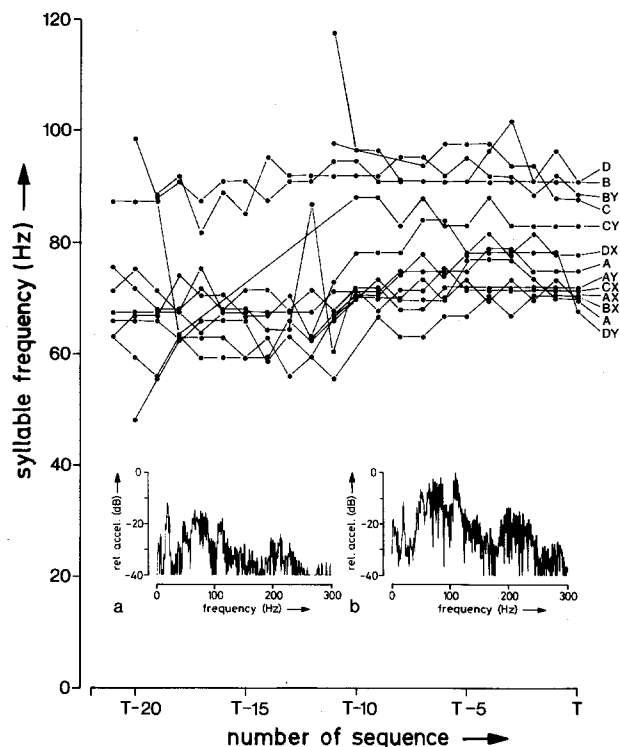
Fig. 4a, b. Amplitudes of succeeding syllables during the final phase of a male courtship series. *A, B, C, D* males; *X, Y* females. **a** Absolute values of acceleration from 14 series in the courtship *BX*. 1–14 number of succeeding series; *R* series answered by a female. **b** Relative amplitudes; syllables with the highest average acceleration arbitrarily defined as 100%. Different courtships which reached the same value at the end are divided by an asterisk

taken from the last nine sequences of a male courtship series (Fig. 5, inset: b) and the preceding 8 (Fig. 5, inset: a) also show that there is little frequency shift in the course of a series. In addition, they underline the drastic amplitude increase towards the end of a series pointed out above.

**Palpal signals.** As a rule palpal drumming occurs during the last 13 sequences of a signal series but rarely before (Figs. 1 a and 6). The highest percentage of palpal signals is found in sequence T-6 (i.e. the sixth preceding the last one); more than 80% of this sequence ( $n=157$ ) contained palpal signals. Towards the end of a series the percentage of sequences containing palpal signals decreases again; in only every tenth series did the last sequence contain at least one palpal signal ( $n=175$ ). Sequences containing one palpal signal are most frequently found. Despite the similarity in the distribution of the palpal signals over the last 13 sequences of a series, the absolute number of palpal signals varies considerably among the series even of a single courtship. There are series without a single palpal signal.

### The female signal

The female response occurs after the end of a male courtship series without overlapping the male's signal. It usually follows within a narrow time frame of  $0.89 \pm 0.53$  s after the end of a male courtship signal (Rovner and Barth 1981). In a few cases the duration between the end of the male courtship signal and the beginning of the female response is even below the duration of a single syllable. We therefore conclude that the temporal cue triggering the onset of the female response is contained within the male courtship signal series. The average of the duration between the end of the male signal series and the beginning of the female response was  $972 \pm 365$  ms ( $n=32$ ) for female X and  $525 \pm 274$  ms ( $n=25$ ) for female Y. This difference between the two individuals is statistically significant ( $F=26.0$ ,  $n_1=1$ ,  $n_2=55$ ,  $P>0.05$ ). Not every male courtship series is followed by a female response. From a total of 200 courtship series (with responding females) we registered 80 responses (40%). The duration of the female courtship signal varied between 113 and 1790 ms. Obviously there

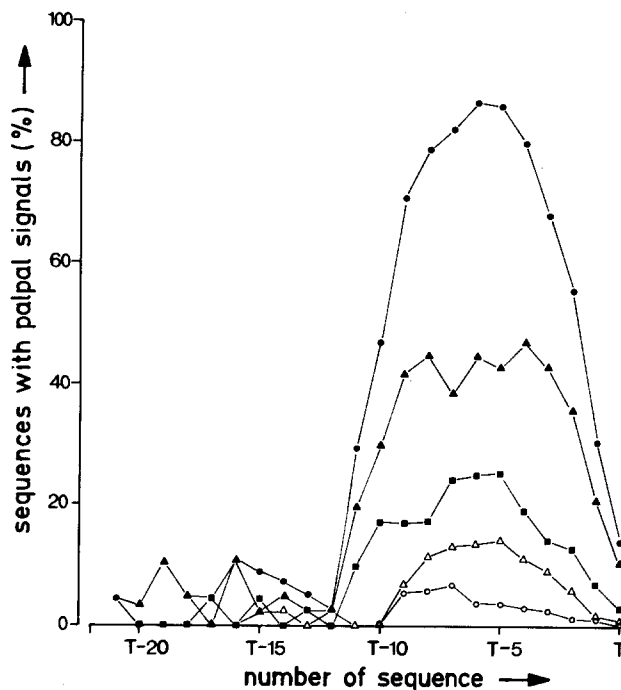


**Fig. 5.** Frequency (syllable impulses divided by syllable duration) of succeeding syllables during the final phase of a male courtship. Mean values from 13 courtships with and without responding females. *A, B, C, D* males; *X, Y* females. *Insets:* Frequency spectra of a single male courtship series. **b** The last 9 sequences with high syllable amplitudes; **a** the previous 8 sequences with lower syllable amplitudes. The scale of relative acceleration in spectrum (**a**) is referenced to that in spectrum (**b**)

is a relationship between its duration and its intensity. The responses with the longest durations usually exhibit the highest acceleration amplitudes (Fig. 7a).

As shown by high-speed cinematography (200 frames/s) courting females only move their leg pairs 1, 2 and 4 when producing their vibratory signal, not their third legs (Fig. 7b, inset). During a response the female slightly flexes and extends these 6 legs about 5 to 9 times ( $6.6 \pm 1.52$ ;  $n = 5$ ). On average the duration of one such movement takes  $49.2 \pm 8.40$  ms ( $n = 33$ ). Between every movement there is a pause of  $80.9 \pm 39.96$  ms ( $n = 28$ ). In addition the intensity with which these movements are performed increases from the first to the last movement within every response.

The frequency spectrum of the female courtship signal shows that there are main peaks at 20 Hz and at 40–50 Hz (Fig. 7b). Possibly the peak at 20 Hz is directly related to the leg movements of the female performed during her response, which have a very similar frequency.



**Fig. 6.** Mean distribution of palpal signals over the last 22 sequences of a male courtship series. Sequences containing one palpal signal (▲) are most often seen, while the occurrence of sequences containing 2 (■), 3 (△), and 4 (○) palpal signals decreases in this order of succession. The four types of sequences thus distinguished have their maximum between T-5 and T-6. (●) indicates the percentage of sequences that contain at least one palpal signal (sum of sequences containing 1, 2, 3, or 4 palpal signals)

## Discussion

In arthropods, vibratory communication during courtship is widespread, and courtship signals have been described in many species (Markl 1969, 1973; Michelsen et al. 1982; Keuper and Kühne 1983). In spiders, vibratory signals are of great importance (Barth 1982), and the use of vibrations during courtship is known in almost every group (Robinson 1982). In a few cases vibratory signals have been recorded (Krafft 1978; Rovner and Barth 1981). So far, however, there has been neither a full analysis of courtship signalling, nor an adequate study of the behavioral effects of a change in the signal parameters. Most parameters of vibratory signals of *Cupiennius salei* have previously been described as mean values calculated for many sequences (Rovner and Barth 1981). This is common practice but does not consider potential changes of a parameter within a broader temporal frame. So far two such changes were known in the male courtship signal of *Cupiennius salei*

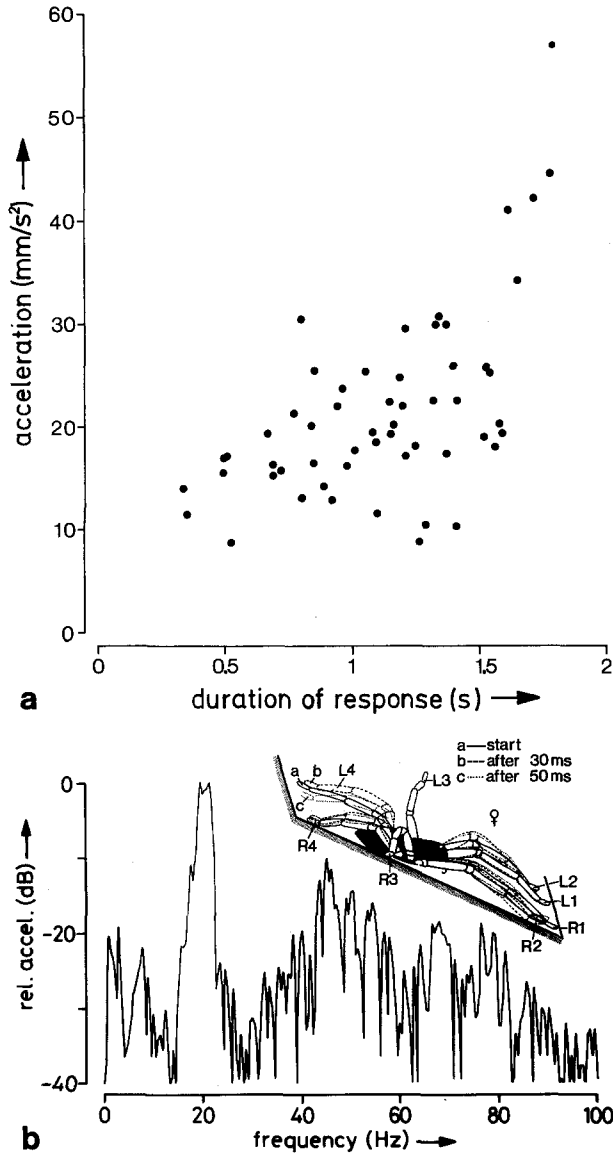


Fig. 7. **a** Dependence of the duration of the female's signal on the response amplitude. Data from 55 responses in 8 different courtship combinations with the males *A*, *B*, *C*, *D* and the females *X* and *Y*. **b** Frequency spectrum of a female courtship signal. *Inset*: Female leg movements during a response, based on high-speed cinematography. While performing her response all tarsi remain in contact with the ground

(Rovner and Barth 1981): (1) syllable amplitudes reach their highest values in the last 8–10 syllables of every male signal series; (2) the mean duration of the last pause is significantly longer than that of the previous four within the series.

According to the present study the time courses taken by several additional parameters of the male signal seem to contain information excellently suited to serve species recognition, and to tell the female exactly when a male's series will stop a long time before it actually does (Fig. 8). These are the

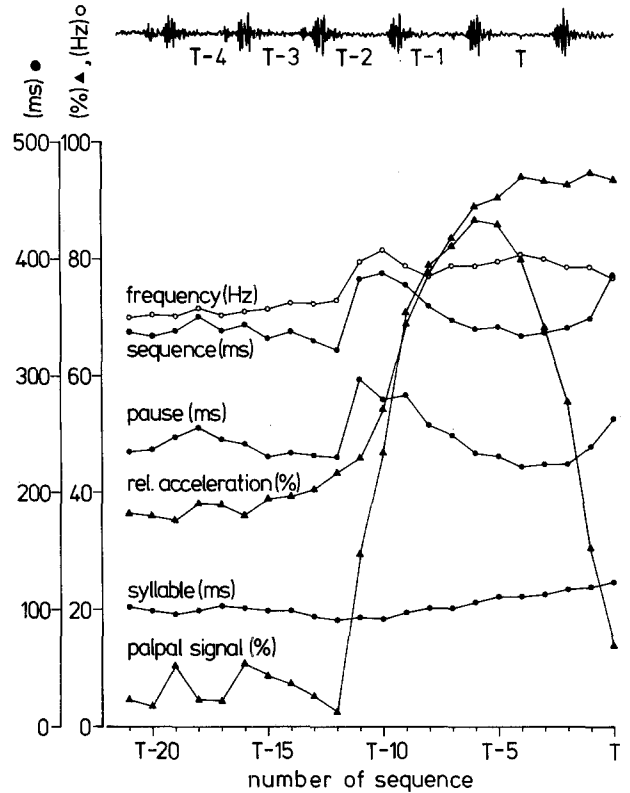


Fig. 8. The time course taken by all six parameters investigated, as recorded during the last 22 sequences of a male signal series (means of single parameters derived from 13 courtships)

duration of sequences and pauses, syllable amplitudes, and the distribution of palpal drumming. There are two outstanding sequences during the final phase of each series with respect to these changes: (1) at sequence T-12, all the above parameters quite abruptly start to increase; (2) at sequence T-4, both the pause duration and the sequence duration reach their minimum, whereas the strength (acceleration) of the signals and the probability of occurrence of palpal signals reach their maximum.

The idea that the female knows the maximum pause between syllables and simply answers whenever the male has been silent for a longer time is attractive. There are two arguments against this, however: (1) the gap between the end of a male series and the beginning of the female's response was less than the duration of a male pause in 14% of the cases studied; (2) the pause at sequence T-11 ( $297 \pm 76$  ms,  $n=41$ ) is on average longer than the last pause ( $263 \pm 39$  ms,  $n=175$ ); there is never a response at T-11, however.

An evaluation of such temporal changes in other animals has rarely been done, although in many cases they may well be present. This applies even to such well-known cases of vibratory court-

ship communication as that of ghost and fiddler crabs (Salmon 1965; Altevogt 1970; Horch and Salmon 1971). Exceptions are *Isoperla grammatica* (Plecoptera) (Rupprecht 1968) and *Melanogryllus desertus* (Gryllidae) (Popov and Shuvalov 1977), where changes in temporal parameters are suggested to be important for species-specific recognition.

We do not know yet which are the important parameters in the courtship signal of *C. salei*, but there are indications in other arthropods as to which parameters might be good candidates to test. The following are known to play an important role in species-specific recognition:

1. *Repetition rate*: in courtships of stoneflies (Rupprecht 1968), waterbugs (Theiß 1983; Theiß et al. 1983), ghost and fiddler crabs (Salmon 1965; Altevogt 1970; Horch and Salmon 1971) and crickets (Popov and Shuvalov 1977; Weber et al. 1981; Thorson et al. 1982).

2. *Ratio of syllable and pause*: in courtships of a grasshopper (von Helversen 1972), but not in the cricket *Gryllus campestris* (Weber et al. 1981; Thorson et al. 1982).

3. *Increasing pulse intensity*: in the calling song of the cricket *Melanogryllus desertus* (Popov and Shuvalov 1977); *sound intensity*, however, is considered not important in *Gryllus campestris* (Weber et al. 1981; Thorson et al. 1982).

Some other parameters such as the carrier frequency (Zaretsky 1972; Weber et al. 1981; Thorson et al. 1982), the duration of verses and their temporal distance (von Helversen 1972), and the number of syllables per chirp (von Helversen 1972; Weber et al. 1981; Thorson et al. 1982) seem to be of minor importance in species-specific recognition of various crickets and grasshoppers.

In *Perla marginata* (Plecoptera) and *Sialis lutaria* (Megaloptera) both the duration of the female's response and the interval between the male courtship signal and the female response (if it is within 0.0 and 0.1 s in *Perla* and within 0.3 and 0.5 s in *Sialis*) are known to be important for conspecific recognition (Rupprecht 1968, 1975). The same may apply to *Cupiennius*, where the female signal invariably follows the male series very closely.

According to what we know from the rather scarce literature about various other arthropods, both syllable repetition rate and the ratio of syllable and pause may be important clues for the female *Cupiennius* in helping it to recognize the conspecific male. At this early stage of experimenta-

tion the relevance of other parameters such as carrier frequency and syllable duration cannot be excluded. Orientational responses of female *Acheta domestica* (Gryllidae) to artificial calling songs show all tested parameters (syllable period, syllable duration, number of syllables, chirp rate, frequency and intensity) to be used by the female for successful tracking (Stout et al. 1983).

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