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SEISMIC COMMUNICATION DURING COURTSHIP IN TWO BURROWING TARANTULA SPIDERS: AN EXPERIMENTAL STUDY ON *EUPALAESTRUS WEIJENBERGHI* AND *ACANTHOSCURRIA SUINA*

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ABSTRACT. During courtship, males of *Eupalaestrus weijenberghi* and *Acanthoscurria suina* performed body vibrations and palpal drumming after contacting conspecific female silk at the burrow entrance. Receptive females responded by leg tapping. To elucidate the communicatory channels involved in both species, courting males were placed in terraria with females that had burrowed. In the first experiment, the courting male was covered with a glass cup, minimizing airborne acoustic communication but allowing seismic communication. In the second, the male courted without the cup cover. In the third experiment, the male and the female were placed into two separated parts of the terrarium, greatly limiting seismic communication. In the fourth, these last parts were joined. Females of both species responded to the courtship with receptive behavior in all of the experiments except experiment 3. We conclude that male signals produced during courtship in these two species are mainly seismic. Male body vibrations (that would generate seismic signals) as well as female display, are a widespread phenomena in theraphosid spiders.

Keywords: Theraphosidae, seismic signals, male vibration, female sexual display

Spiders use different channels to communicate during courtship: chemical, tactile, visual and acoustic/vibratory (Krafft 1980; Uetz & Stratton 1983). Each channel has advantages and disadvantages in relation to the lifestyle of the animal and its environmental constraints. As a consequence of the potential nuptial cannibalism of spiders and the poor vision in most taxa, pressures of selection may have favored acoustic or seismic species-specific signals during courtship. An advantage of these signals is that they are relatively independent of environmental conditions (light, temperature, humidity) for efficiency of signal propagation (Foelix 1982; Krafft 1982; Redondo 1994). Another advantage is the temporal characteristic of the signal, which can be modified quickly according to the motivational state of the animal. Disadvantages include the short temporal persistence of the signal, and the high cost of production. The advantages could explain why acoustic/vibratory signals are so widespread in Araneae.

Acoustic/vibratory signals in spiders can be produced in three ways, according to Uetz & Stratton (1982): a) stridulation (22 families), b) percussion (six families) and c) vibration of structures (two families). Spiders may use air, water or substrate (ground, leaves, silk threads, etc.) for propagating vibrations. Stridulation and percussion have been studied in some species, but sometimes they are difficult to isolate from one another because a single motion can produce both signals, as happens in male palpal drumming. Some lycosids have a stridulatory organ located at the tibio-tarsal joint of each palp. Rovner (1967, 1975) found that, in some wolf species, palpal movement not only produced acoustic signals but also vibrations, which were transmitted into the substrate by means of specialized spines at the tip of the tarsal palp, a mechanism termed ‘‘substratum-coupled stridulation.’’ Using playback techniques, Rovner discovered that females are capable of perceiving acoustic signals, but their responses are more intense when the speaker is laying on the ground. He concluded that female spiders orient better to substratum vibrations than to airborne sounds.

The third method of sound production, vibration of structures, has been described in two species: by Rovner (1980) in *Heteropoda venatoria* (Linnaeus 1767) (Heteropodidae) and by Barth (1982) and Barth et al. (1988) in *Cupiennius salei* (Keyserling 1877) (Ctenidae). It consists of movements of the legs or abdomen, in such a way that the entire body vibrates. These movements produce vibrations which are transmitted via substrate (seismic communication).

A growing number of studies on sexual behavior of mygalomorphs (Coyle 1985, 1986; Coyle & OShields 1990; Jackson & Pollard 1990; Costa & Pérez-Miles 1998), and in particular from the theraphosid family (Baerg 1958; Minch 1979; Prentice 1992, 1997; Costa & Pérez-Miles 1992, 2002; Pérez-Miles & Costa 1992; Shillington & Verrell 1997; Yáñez et al. 1999) has revealed previously hidden intricacies in the mechanisms of communication employed by this group. As an example, 30 years ago it was believed that tarantula males initiated their courtship only after touching the females (Platnick 1971). Today we know that these males start courtship after detecting tactochemical cues associated with the female silk (Minch 1979; Costa & Pérez-Miles 1992, 2002; Prentice 1997; Shillington & Verrell 1997; Yáñez et al. 1999).

Eupalaestrus weijenberghi (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are burrowing theraphosids that have a widespread distribution in Uruguay. They are frequently sympatric, syntopic and synchronous, presenting a similar reproductive strategy (Costa & Pérez-Miles 2002). Their sexual periods occur during March and April, at the end of summer and beginning of autumn in the southern hemisphere (Costa & Pérez-Miles 2002). Mignone et al. (2001) and Costa & Pérez-Miles (2002) observed males of both species courting outside female burrow entrances after contacting conspecific female silk. Mignone et al. (2001) reported that females of *E. weijenberghi* responded to male courtship by displaying foreleg waving at the burrow entrance. Male courtship, either for *E. weijenberghi* or *A. suina*, was mainly characterized by Mignone et al. (2001) and Costa & Pérez-Miles (2002) as bouts of body vibrations while the male grasps the substrate with its legs. These vibrations apparently originate in the third pair of legs (unpublished data from restraining each pair of legs). According to these authors, courting males also perform palpal drumming, that can produce acoustic signals (airborne) as well as seismic signals (substrate borne). Theraphosid spiders possess stridulatory organs (Legendre 1963). Moreover, *A. suina* has stridulatory setae located retrolaterally at the trochanter of the palps (Pérez-Miles et al. 1996). Acoustic and or vibratory signals were suggested by Costa & Pérez-Miles (1992, 2002) as species-specific isolating mechanisms in theraphosids, as previously tested among Mesothelae species by Haupt & Traue (1986).

Our main objective was to find whether acoustic, seismic or both channels are involved in the courtship of *A. suina* and *E. wejenberghi*. Moreover, we described and analyzed elements of courtship by males and females for the two species.

METHODS

Materials.—Males were collected in the provinces of Canelones (Solymar Norte, 34° 45′ S, 56° 00′ W and Salinas Norte, 34° 45′ S, 55° 50′ W) and Montevideo (Melilla, 34° 45′ S, 56° 20′ W),Uruguay, during March 2002. For all experiments we used females of known reproductive history, which were collected from the same localities, between 1996 and 1999. As is well-known for Theraphosidae, adult females continue molting throughout their lives, so in each molt they become ‘‘virgin’’ (without sperm) again. All the females molted in the laboratory between December 2001 and January 2002. We used a total of 20 females and 20 males from each species. They were housed in glass jars of 9.5 cm diameter and 15 cm height, with soil as substrate and water provision. They were fed cockroaches (*Blaptica dubia*, Blattaria, Blaberidae) ad libitum. Voucher spiders specimens of both species were deposited in the entomological collection at the School of Sciences, Universidad de la República, Montevideo, Uruguay.

Experiments were carried out in glass terraria of 30cm x 16cm base x 20cm height, containing 6 cm of soil as substrate or, in the case of the third experiment, the aquaria were 15cm X 16 cm X 20cm. Females inhabited burrows in these terraria, which were constructed by us against the glass wall, allowing our observations. Each female walked along the soil at night, so the silk with pheromone was widely released on the soil surface. We carried out experiments during March–May 2002, in coincidence with the reproductive period of these species in natural populations. All terraria were placed over polyurethane blocks in order to isolate animals from ground vibrations. Distances between males and females varied between 10–25 cm. For experiment three, ten glass terraria were built as two separated parts; one part contained the female burrow and the other only substrate. These ‘‘separated blocks’’ were later put together using an iron clamp, then being similar to an unitary block, contacting both soil and glass walls. In other experiments we used a thick glass cup, of 10 cm diameter and 10.5 cm height, which covered the courting male. For video recording, a Super VHS video camera was used. Sexual encounters were analyzed with a frame-by-frame video recorder in the Ethology Laboratory of the School of Sciences (Universidad de la República), Montevideo, Uruguay. The experiments were carried out at an average environmental temperature of 25.13 °C ± 1.05 SD.

Experimental design.—To test for the occurrence of acoustic (airborne) communication, a series of two consecutive experiments (A & B: see below) were carried out using the same ten pairs of female/male individuals of both species. For testing the occurrence of seismic (substrate borne) communication, another series of two consecutive experiments (C & D: see below) were carried out using a different set of ten pairs of female/male spiders of both species. Each pair of spiders was reused 1–7 days after the first experiment. Individuals were randomly assigned to pairs and experimental series. This design allows us to avoid the influence of individuality and/or subtle differences in the terraria (cut blocks, humidity). The observational time began when the male was placed in the terraria until female sexual display, or until 30 min, if there were no female response.

In the experiment A, or ‘‘cup block’’, a male was placed into a confined sector which occupied one third of the total surface of the terrarium, whereas a female inhabited her burrow in the other sector. A metallic grid with vertical bars separated 6mm from one another, impeded the access of the male to the female burrow. The male was covered with the glass cup, minimizing any possible acoustic communication. The experiment B, or ‘‘unitary block’’, was similar to A but no glass cup was used. In the experiment C, or ‘‘separated blocks’’, each terrarium was built as two separate parts: one containing the female in her burrow, the other, the confined male. The two parts, separated from each other by three millimeters, were set on polyurethane blocks, with each part located on separated tables, eliminating any possible seismic communication between male and female. During the night prior to the test, another female was located in the smaller container for depositing silk and pheromone. This female was removed before the trial. In this way when the male contacted the silk and pheromone during the trial, he responded with courtship. The experiment D, or ‘‘joined blocks’’, was similar to C, but in this case the two parts were pushed together, eliminating the gap, and joined with an iron clamp (Fig. 1).

Description and analysis.—The observed behavior of both females and males during the experiments was described and analyzed. The courtship behavioral units of males and females were described from the experiment B for both species, because this group best reflected what occurs in nature. Normality and homogeneity of variance of continuous variables (durations of the behaviors) were tested using the Kolgomorov- Smirnov and Cochran C-test, respectively. Non parametric Mann-Whitney U-test, the one sample and two samples Chi-square tests were used for frequencies and non- parametric durations. The McNemar test for the significance of changes was used for dependent samples (A vs. B and C vs. D), but when the expected frequency was less than 5, the Binomial test was used. All statistical analyses were performed using free software programs (http:/www.r-project.org).

RESULTS

Courtship.—Male courtship of both species was characterized by the alternation of periods of activity and inactivity. Activity consisted mainly of body vibrations and palpal drumming. Male body vibrations were caused by spasmodic contractions of legs, apparently by the third pair. During vibrations, tarsal claws were fixed to the ground. Vibration was complex, its intensity was very var-

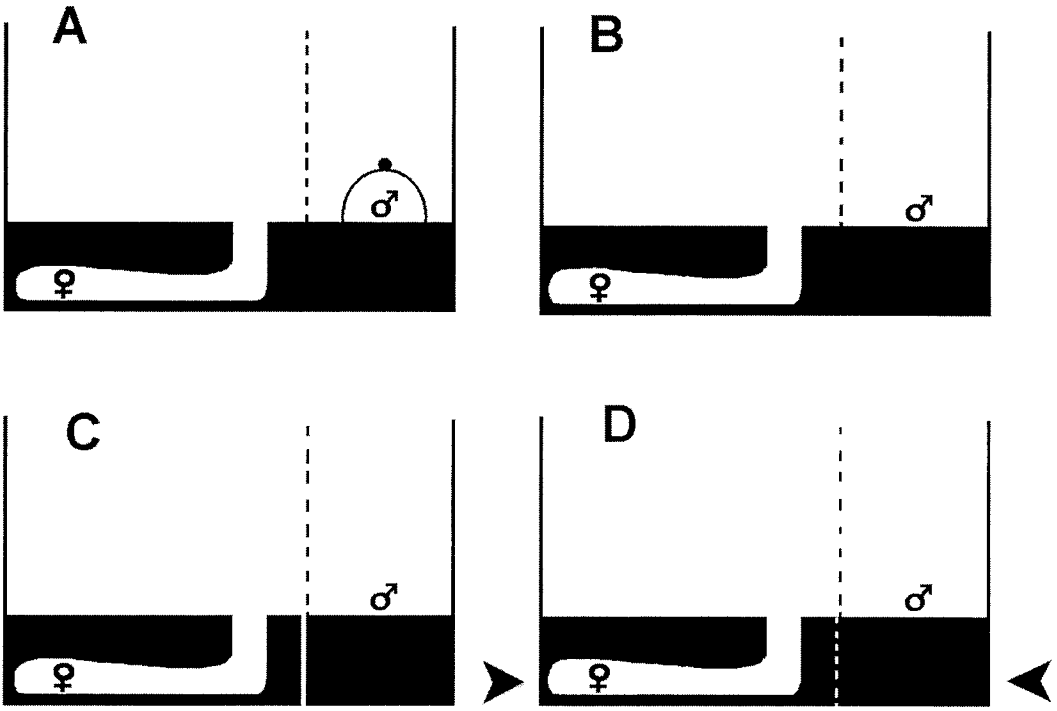

Figure 1.—Schematic drawings showing the experimental design used for the two Theraphosidae species. Broken vertical lines represent the metallic grid separating the male from the female. Each male was placed on the soil, while each female remained inside her burrow. Experiment A = cup block, experiment B = unitary block, experiment C = separated blocks, experiment D = joined blocks.

iable, and could not be quantitatively described using the video register because it was not possible to observe male movements in detail. However, vibrations seem to be of low frequency. Palpal drumming consisted of alternative, soft ‘cycling movements’ of the palps on the substrate. Both body vibrations and palpal drumming, in general, were alternated but sometimes they took place synchronously, mainly when the body vibrations were of low intensity. Bouts of vibration and drumming were considered together when analyzing the durations of active courtship periods of males. Tables 1 & 2 show the mean durations of these bouts until female response for the two species. Mean duration of bouts of vibration and drumming was approximately seven seconds for both species.

Females of both species showed their characteristic sexual display inside the burrows, tapping vigorously with the first and second pair of legs against the substrate, immediately after a male bout. In frame-to-frame video analyses, females of both species showed the following displays: leg flexing, lifting and lowering, contacting the ground. In some cases, the percussion was audible to the observer. Two latencies were considered: Latency 1 was from the end of the last male signal bout until female leg tapping, and Latency 2 from the end of the first male bout until female leg tapping. Some females responded immediately after the first bout; thus, these two latencies are equal (Tables 1 & 2). Mean number of leg movements during the first bout of female leg tapping, as well as the number of female bouts of leg tapping during the whole experimental period, are shown in Tables 1 & 2. After female responses, males frequently changed their behavior. In *E. weijenberghi,* 6 of 10 males oriented to the female burrow, 2 of 10 increased their locomotive rate without orientation and 2 of 10 showed no response to the female call. In *A. suina,* 8 of 10 females responded to male courtship. Two of 8 males oriented to the female burrow, 2 of 8 increased their locomotive rate and 4 of 8 showed no responses.

Table 1.—Courtship characteristics of *Eupalaestrus weijenberghi* (experiment B). Male courtship duration includes both vibrations and palpal drumming until female response. Latency 1 = latency from the end of the last male signal to the first leg tapping of the female. Latency 2 = latency from the end of the first male signal to the first leg tapping of the female. Leg movements = number of movements of one leg during female leg tapping. Leg tapping = number of female bouts performed during the whole experiment.

Pair	Courtship (sec)	Latency 1 (sec)	Latency 2 (sec)	Leg movements	Leg tapping
1	9	1	1	15	4
2	15	1	4	21	2
3	11	0	6	13	4
4	2	1	1	14	2
5	5	3	53	5	7
6	9.5	1	83	14	4
7	4	1	1	22	3
8	5.75	3	53	11	2
9	4	1	22	15	1
10	2	1	53	16	3
Mean ± SD	6.7 ± 4.3	1.3 ± 0.9	27.7 ± 30.2	14.6 ± 4.8	3.2 ± 1.7

When comparing mean durations of male signaling bouts (vibration + drumming) between species, both before first female response, no significant differences were found using the Mann-Whitney test ($U = 30.5$, $P = 0.397$). No statistical differences were found either when comparing the latency of female response to the last bout of a male ($U = 20.5$, $P = 0.083$), or when comparing latency to the first male bout ($U = 34$, $P = 0.60$). The number of movements during female leg tapping was greater in *E. weijenberghi* than in *A. suina* ($U = 17. 5$, $P = 0.04$); the number of bouts of female leg tapping was also higher in *E. weijenberghi* ($U = 15$, $P = 0.03$).

Communicatory channels.—The number of female responses from the four experiments are given in Table 3. All the females of *E. weijenberghi* belonging to experiments A, B and D responded to male courtship. On the other hand, in *A. suina* 7 of 10 responded to male courtship in experiment A, 8 of 10 in B, and 4 of 10 in D. In separated blocks (experiment C), none of the *E. weijenberghi* nor *A. suina* females showed responses to male courtship. Observed versus expected Chi-

Table 2.—Courtship characteristics of *Acanthoscurria suina* (experiment B) corresponding to the eight cases where females responded. Male courtship duration includes both vibrations and palpal drumming until female response. Latency 1 = latency from the end of the last male signal to the first leg tapping of the female. Latency 2 = latency from the end of the first male signal to the first leg tapping of the female. Leg movements = number of movements of one leg during female leg tapping. Leg tapping = number of female bouts performed during the whole experiment.

Couple	Courtship (sec)	Latency 1 (sec)	Latency 2 (sec)	Leg Movements	Leg tapping
1	7	0	0	6	1
2	11.3	0	0	8	1
3	7	0	21	6	2
4	7.3	3	26	14	4
5	6.1	1	436	19	2
6	5	0	38	10	1
7	7.3	1	67	5	1
8	8	0	110	6	1
Mean ± SD	7.4 ± 1.8	0.6 ± 1.1	87.3 ± 145.6	9.3 ± 4.9	1.6 ± 1.1

Table 3.—Number of females that performed leg tapping in response to the male courtship in the four experimental groups.

	E. weijenberghi		*A. suina*	
	Leg tapping	No leg tapping	Leg tapping	No leg tapping
Cup block (A)	10	0	7	3
Unitary block (B)	10	0	8	2
Separated blocks (C)	0	10	0	10
Joined blocks (D)	10	0	4	6

square test among the four experiments (assuming 50% as expected value) showed significant differences for *E. weijenberghi* ($\chi^2 = 10$, $P < 0.019$, df = 3) and also for *A. suina* ($\chi^2 = 8.16$, $P < 0.043$, df = 3). The female response in experiment C is significantly different from response in B for both species (for *E. weijenberghi*, $\chi^2 = 16.20$, $P = 0.0001$, df = 1; for *A. suina* $\chi^2 = 10.21$, $P = 0.0014$, df = 1). In *E. weijenberghi*, experiments A and B were identical ($P = 1$, Binomial test), but significant differences were found between C and D ($\chi^2 = 10$; $P < 0.001$) with the McNemar test. Experiments B and D were identical ($\chi^2 = 0$, $P = 1$, df = 1) using the Chi-square test in this species. In *A. suina*, there were no significant differences between A and B ($P > 0.31$) with the Binomial test, nor between C and D ($P = 0.16$). There were no differences between B and D ($\chi^2 = 1.880$, $P = 0.17$, df = 1) using the Chi-square test.

DISCUSSION

Our main objective was to determine experimentally what communicatory channel is mainly used during courtship for the focal species. Rado et al. (1989) demonstrated, using a similar experimental design, that the Mole Rat, *Spalax ehrenberghi*, communicates by seismic signals. In *E. weijenberghi* the results clearly showed that separated blocks (experiment C) prevented the transfer of seismic signals between the sexes, whereas communication was unimpeded in the other treatments.

The females which showed no response in separated blocks, all responded to male courtship once these blocks were joined (experiment D). Thus, we conclude that communication through the substrate (seismic communication) is present during courtship. Moreover, the absence of female response in separated blocks also indicate that airborne acoustic communication, is not important; at least at the experimental distances used in this study. Absence of acoustic communication is also supported by the lack of differences between unitary and cup blocks. Hence, seismic signals are sufficient to elicit a complete female response during the courtship of *E. weijenberghi*.

The results of *A. suina* were similar to those of *E. weijenberghi*, indicating that they also use the seismic channel for communicating during courtship. The main difference in the *A. suina* was in the non–significant differences between separated and joined blocks (experiments C & D). This could be explained by a lower intensity of the male vibration in *A. suina* (Quirici, unpub. data) and/or less responsiveness from conspecific females than those of *E. weijenberghi*. Acoustic communication in *A. suina* seems not to have an important role in sexual communication, as in *E. weijenberghi*, results from unitary and cup blocks were similar. Due to the presence of a putative stridulatory organ on the palpal trochanter of *A. suina*, the occurrence of acoustic communication would appear reasonable. However, occasional observations in the field showed that males spend a long time performing palpal drumming at the burrow entrance. Acoustic communication could be possible when males reach the burrow entrance, thus avoiding possible obstacles that could deform or interrupt a delicate acoustic signal. Therefore, an acoustic channel of communication could be functional at short distances.

Male vibrations in courtship appear to be a widespread behavior observed in many Theraphosidae spiders, first reported by Gerhardt (1929). Minch (1979) described this behavior as body oscillations; Shillington & Verrell (1997) called it ‘‘quiver’’; Yáñez et al. (1999) called it ‘‘shaking’’; Costa & Pérez-Miles

(1992, 2002) and Pérez-Miles & Costa (1992) named it ‘‘body vibrations’’. Prentice (1992, 1997) termed the behavior ‘‘stridulating vibration’’ and found that the signals could be perceived by the female up to 1.2 m distance on a heterogeneous substrate. Moreover, he reported that stridulation was audible by the observer under laboratory conditions in *Aphonopelma joshua* Prentice 1997. However, these vibrations remind us of the third method of sound production postulated by Rovner (1980), ‘‘vibration of structures’’, but not the stridulatory method. Some tests (unpub. data) in which we tied the third pair of legs and in others tied the second pair of legs (control), showed that the third pair would be responsible of the vibrations (a geophone did not register vibrations when the third pair was tied). According to our findings, the Theraphosidae would communicate by ‘‘vibration of structures’’. All authors postulate a communicative role for this behavior, alerting the female of male presence. The possible function of the vibration as a way of transmitting a species-specific signal through the ground was postulated by Haupt & Traue (1986) for Mesothele, and by Costa & Pérez-Miles (1992, 2002) for Mygalomorphae. Preliminary observations, however, have shown some degree of confusion in sexual communication between *E. weijenberghi* and *A. suina* in the laboratory. This opens an exciting field of research because, as was previously mentioned, these species are sympatric and synchronous and share similar reproductive strategies.

Leg tapping of burrow-occupying females was observed only as a response to male courtship, indicating a receptive state. It was first observed by Prentice (1992) in three species of *Aphonopelma*, who called it ‘‘drumming’’. We found that both *E. weijenberghi* and *A. suina* respond to male courtship from inside their burrows. Female leg tapping would not only inform the male about her willingness to copulate, but also help the male to orient towards the burrow entrance. *Eupalaestrus weijenberghi* males seem to orient more easily than *A. suina* males for the calling female, probably due to the vigorous *E. weijenberghi* female responses. This behavior is possibly more widespread than previously supposed, since female behavior is often unobservable inside the burrow. For example, Prentice (1997) reported females of another *Aphonopelma* species performing leg tapping, and Yáñez et al. (1999) observed females of *Brachypelma klaasi* (Schmidt & Krause 1994) shaking.

Burrowing tarantulas share similarities with other subterranean species in some of their ways of communication, independent from phylogenetic constraints. Compared to acoustic signals, seismic signals have the advantage of propagating through long distances and at speed two–five times faster than the acoustic signals, depending on the type of soil and degree of soil moisture (Rado et al. 1989). Taking into account the advantages of seismic signals, the widespread occurrence of male body vibration, the probable female seismic response, and the absence of costly specialized emission organs, we suggest that seismic signals are the main communicatory channel used by burrowing Theraphosidae during courtship.

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