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SEISMIC SEXUAL SIGNAL DESIGN OF TWO SYMPATRIC BURROWING TARANTULA SPIDERS FROM MEADOWS OF URUGUAY: *EUPALAESTRUS WEIJENBERGHI* AND *ACANTHOSCURRIA SUINA* (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. *Eupalestrus weijenberghi* (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are two fossorial, sympatric, synchronic, and similar-sized species of tarantulas that inhabit the meadows of Uruguay. Both species use seismic signals for communicating during courtship (body vibrations in males, leg tapping in females), but little is known either about temporal and spectral signal characteristics or effective signal range. Males were elicited to court (body vibrations) by exposing them to sexual pheromones in one end of a terrarium, whereas females were successively placed in burrows at different distances from the courting male. Seismic male signals were registered by using a geophone placed near the females. We found that *E. weijenberghi* male signals reach at least 135.75 cm, whereas *A. suina* signals reach at least 110.5 cm. There was no correlation between latency of female response and distances at which the male was courting for either of the spider species. For *A. suina*, a bout of vibration was characterized by two syllables (tucks), followed by a series of syllables (buzz 1 and buzz 2). *Eupalestrus weijenberghi* males show several tucks, followed by buzz 1 and buzz 2. Differences in sexual signals (length of syllables and number of tucks) are assumed to maintain the reproductive isolation between these similar sized, sympatric and synchronic species. Similarities are seen in adaptations to the same environment, allowing effective rates of sexual communication at long distances.

Keywords: Tarantula male signals, seismic signal reach, courtship behavior

Vibratory sexual signals (acoustic and seismic) are frequently used by courting male spiders, including tarantulas (Uetz & Stratton 1982, 1983; Prentice 1992, 1997; Quirici & Costa 2005). As tarantulas are nearly blind, vibratory signals are particularly useful as these signals do not need light to be perceived and they are quite directional (Foelix 1982; Redondo 1994). Long distance communication is particularly important for male spiders due to the cannibalistic lifestyle of females (Krafft 1980; Uetz & Stratton 1983), and, as mentioned by Narins (1990) and by Endler (2000), these signals propagate long distances without loss of effectiveness. Seismic signals generated by male spiders can reach 1 m in ctenids (through leaves, Rovner & Barth 1981; Barth et al. 1988) and 1.20 m in theraphosids (using an artificial substrate Prentice 1997). The usual indicator of effective signals is the behavioral change of the receptive female. The most unambiguous receptive response is a female signal, usually leg waving, leg tapping, or body vibrations. These behaviors have been observed in lycosids (Rovner 1968; Costa 1975), ctenids (Rovner & Barth 1981) and theraphosids (Prentice 1992; Quirici & Costa 2005).

Eupalestrus weijenberghi (Thorell 1894) and *Acanthoscurria suina* Pocock 1903 are two sympatric, synchronic, and similar-sized tarantulas species that inhabit burrows in the meadows of Uruguay. Both species can be found in high densities: *E. weijenberghi* shows a random distribution while *A. suina* shows aggregated distribution (Pérez-Miles et al. 2005). The mating season of these two species is brief and synchronic, starting at the end of the summer (February–March) when a huge number of walking males appear on the

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roads (“road tarantulas”) and ending two month later when all males die (Costa & Pérez-Miles 2002; Pérez-Miles et al. 2005). Adult males live only 2 mo in the wild, but persist in good body condition for 4–5 mo under laboratory conditions (Pérez-Miles et al. 2005); females can live around 8–10 yr (Costa pers. obs.). Females continue molting throughout their lives, so in each molt they become “virgins” (without sperm in the sperm receptacles).

These two species share the same reproductive strategy and behavior. They can be distinguished by color (*A. suina* brown, *E. weijenberghi* black, with pale bands in legs), by conspicuous tibial spurs (only on *E. weijenberghi* forelegs), and by defensive displays (*A. suina* raises forelegs and opens fangs, whereas *E. weijenberghi* raises the abdomen). When the walking male touches the female silk, which has been imbued with sexual pheromone, he courts the female primarily by means of body vibration. Body vibrations generate seismic signals eliciting receptive female behavior (leg tapping), which orients the male toward the burrow entrance (Quirici & Costa 2005). The seismic nature of this system was elucidated by Quirici & Costa (2005) using a discontinuous substrate, but effective signal range and details of their temporal and spectral characteristics were unknown. Our objectives in the present study were to find out the temporal characteristics of the signals of both species, and also to find out how far signals propagate and still elicit female leg tapping displays.

METHODS

Materials.—Spider males of both species were collected during March 2004 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, with the maximal distance among captures being 40 km. For all experiments, females of known reproductive history were used. They were collected from the same localities between 1996 and 1999 and raised under laboratory conditions. All females used in the study molted in the laboratory between December 2003 and January 2004. A total of 10 females and 25 males for each species were used in this study. They were housed in glass jars of 9.5 cm diameter and 15 cm height, with 5 cm of soil as substrate and water provision, and were fed live cockroaches (*Blaptica dubia*, *Blattaria*, Blaberidae) provided ad libitum. Voucher specimens of both species were deposited in the entomological collection at the School of Sciences, Universidad de la República, Montevideo, Uruguay.

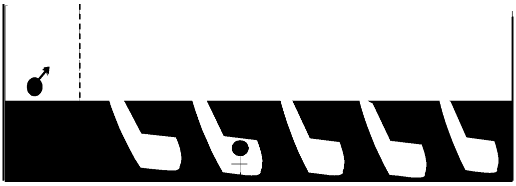

Figure 1.—Schematic representation of the experimental design used for the two theraphosid species. Broken vertical lines represent the metallic grid separating the male from the female. Males were placed on the soil, in the same place, while females remained inside the burrows that were chosen by us at random.

Spiders were kept in captivity for at least two weeks before being tested. Experiments were carried out in four long glass terraria of 20 cm width and 20 cm height containing a 7 cm thick layer of soil as a substrate (collected from their natural habitat). For *E. weijenberghi*, the length of the two terraria used was 170 cm; for *A. suina*, the two *terraria* measured 120 cm length because preliminary observations had suggested that *E. weijenberghi* signals reached farther than those of *A. suina*. In each terrarium, five burrows were constructed in a line against the glass wall, allowing visual observations of female behavior inside burrows. The distance between two consecutive burrows was 30 cm for *E. weijenberghi* and 25 cm for *A. suina* (Fig. 1). Each terrarium was placed on an anti-vibratory table (weighty wood plate placed on four inflated bicycle tires) in order to minimize ground vibrations and to prevent seismic signals from passing between terraria (in a preliminary study without the anti-vibratory table a female responded to a courting male in an adjacent terrarium). A geophone with vertical polarization (Geospace industries, model GS 20-DX, damping resistor = 1000 ohms) was used to collect substratum-coupled vibratory signals. To test if signals would pass to an adjacent terrarium, the geophone was placed in one terrarium and a courting male in the

Table 1.—Experimental design for each of the four terraria used in this study (two for *A. suina* and two for *E. weijenberghi*). Each male group was composed of five individuals, and each of them was used once with one female for each of the two terraria. The five females (A, B, C, D, and E) were located in each burrow, avoiding repeated encounters with the same male. A total of 50 trials were performed for each spider species.

Males	Burrow 1	Burrow 2	Burrow 3	Burrow 4	Burrow 5
Group 1	A	B	C	D	E
Group 2	E	A	B	C	D
Group 3	D	E	A	B	C
Group 4	C	D	E	A	B
Group 5	B	C	D	E	A

other, and any courting signals could be registered by the geophone. Data were recorded on an analog recorder UHER 4200, at a speed of 9.5 m/s (frequency band of 20 Hz to 16 kHz). Experiments were carried out from 16 March to 16 April 2004, synchronously with the reproductive period of these species under natural conditions. During the experiments, mean room temperature was 24.96° C (±2.05 SD).

Experimental design.—Preliminary experiments analyzing the duration of bouts of vibrations produced by males prompted the use of the two step sample method in this study (Snedecor & Cochran 1984). Primary sample units were the species and the secondary samples units were the individuals within each species. Variance components were examined throughout one-sample two-step ANOVA (hierarchical ANOVA), following Sokal & Rohlf (1979). The experimental design is shown in Table 1. The order of consecutive burrows, where females were located one a time, is indicated in Arabic numbers (1 to 5). Individual females are identified by capital letters (A to E). All burrows were tested with a female inside, perceiving male vibration bouts at all the experimental distances. Each group (1 to 5) was composed of five different males. All the males used, as well as the male-female pairs and the female burrow locations, were randomly assigned but repetition was avoided. Since two terraria were used for each species, each male courted two different females during the entire experimental period, one in each terrarium. Consequently, each female was exposed to two different males. Only one experiment was conducted per day.

Trials in each terrarium were carried out for ≥24 h, allowing each female to adapt to the burrow (acclimatization period). This time period also allowed another female to release sex pheromones at the end of the terrarium where the males were located to help elicit male courtship. At approximately 19:00 h this last female was removed and a male was located in the same place. The time of each experiment was recorded from the start of male courtship until completion of female sexual response or until 30 min after courtship if there was no female response. The geophone was located each time near the entrance of the occupied burrow. Distance from males to the geophone vary from 21.5 cm, 50.5 cm, 75.5 cm, 110 cm and 134.75 cm for *E. weijenberghi*, and 15.25 cm, 37.25 cm, 60.25 cm, 84.75 and 110.5 cm for *A. suina*, which correspond to the burrow location. A total of 50 trials was recorded for each species.

Data analysis.—The temporal characteristics of male courtship signals were analyzed using the software, Sound Ruler (0.9.4.0), which allows the visual and acoustic identification of pulses and accompanying silences. We analyzed a total of 47 male courtship signals for *E. weijenberghi* and 67 for *A. suina*, belonging to 15 males from each species.

The Fisher two tailed exact probability test (Siegel 1956) was used to compare the occurrence of female response among burrows for each species. The latency of female response was used as an estimate of female receptivity (defined as the time period from the end of the first male bout of vibration until the first female leg tapping, according to Quirici & Costa 2005). Simple linear regression was used to examine a relationship between the latency of female response (dependent variable) and the distance between male and female (as an independent variable). Previously, regression analysis residues were plotted in order to remove outliers and assess normality. Analyses of variance were used for testing significance of the regressions (Daniels 1989).

When assumptions of normality or variance homogeneity were not confirmed, non-parametric tests (Mann-Whitney U-test and Kruskal-Wallis) were used. All statistical analyses were performed using the software program, Rproject (http://www.r-project.org).

Table 2.—Occurrence frequency of leg tapping from 10 different females located in the five burrows. Distances between vibrating male and each female burrow were: 1 = 21.5 cm, 2 = 50.5 cm, 3 = 75.5 cm, 4 = 110 cm and 5 = 134.75 cm for *E. weijenberghi*, and 1 = 15.25 cm, 2 = 37.25 cm, 3 = 60.25 cm, 4 = 84.75 and 5 = 110.5 cm for *A. suina*.

	Burrow				
	1	2	3	4	5
E. weijenberghi	10	9	10	9	9
A. suina	8	8	6	7	8

RESULTS

Female responses.—In 94% of the trials with *E. weijenberghi* and 74% of the trials with in *A. suina*, females responded to courtship at all distances, including cases at the maximal possible distance for *E. weijenberghi* (135.75 cm) and also for *A. suina* (110.5 cm) (Table 2). No statistical differences were found using the Fisher exact test when comparing the occurrence of female response of each species in each of the five burrows (P = 0.474 for burrow 1, $P = 1$ for burrow 2, P = 0.086 for burrow 3, $P = 0.582$ for burrow 4, and $P = 1$ for burrow 5).

Table 3 shows the recorded values of latency of female calls for both species and for each burrow. The latency was highly variable in both species, with all the obtained variation coefficients higher than 60%. When comparing latency values across all five burrows, we found no statistical differences either for *E. weijenberghi* ($H_{4,47} = 1.192$, $P = 0.879$) or for *A. suina* ($H_{4,37} = 1.032$, $P = 0.905$).

Simple linear regression analyses showed no significant correlation between distance and latency of female response, neither for *E. weijenberghi* ($F_{[calculated]} = 0.479$, $F_{[critical]}$ = 0.492, $n = 44$, $P = 0.09$) nor for *A. suina* ($F_{[calculated]} = 0.257$, $F_{[critical]} = 0.614$, $n = 35$, $P = 0.37$). Moreover, distance explained less than 2% of variation in female behavior in both species.

***Acanthoscurria suina*: description of male courtship signal.**—The set of consecutive male body vibrations separated by pauses, or ‘‘bouts,’’ was characterized by two temporal components. A first component included a single syllable, identified as ‘‘tuck,’’ whereas a second component involved a series of syllables, referred to as ‘‘buzzes’’ (terms were chosen to resemble the sounds made by the spiders) (Fig. 2). A typical male vibration bout was composed of two consecutive ‘‘tucks’’ (tuck 1 mean duration = 0.100 s, SD = 0.113, n = 22; tuck 2 mean duration = 0.064 s, SD = 0.025, n =25) followed by two consecutive ‘‘buzzes.’’ (buzz 1 mean duration = 0.55 s, SD = 0.34, n = 63; buzz 2 mean duration = 0.745 s, SD = 0.237, n = 54). Periods of silence between tucks, between tuck 2 and buzz 1 and between buzz 1 and buzz 2, were called ‘‘interpulses’’: I1 (mean duration = 0.282 s, SD = 0.14, n = 16), I2 (mean duration = 0.414 s, SD = 0.382, n = 24) and I3 (mean duration = 0.589 s, SD = 0.184, n = 52), respectively.

There were no significant differences between the duration of tuck 1 and tuck 2 (U = 148, $P = 0.429$, n = 14, 25). When comparing all interpulse periods, significant differences were found (Kruskal-Wallis test: $H_{2,92}$ = 23.44, $P < 0.001$). Interpulse 3 (I3) had the longest mean value. Buzz 2 had a greater duration than buzz 1 (two-tailed t-test, $t = -4.5$, $df = 115$, $P < 0.001$).

***Eupalaestrus weijenberghi*: description of male courtship signal.**—As in *A. suina*, male

Table 3.—Latency (s) for female response (leg tapping behavior) for both tarantula species and for each burrow. Values shown are means, standard deviations (SD) and coefficients of variation (CV).

	Eupalaestrus weijenberghi			*Acanthoscurria suina*		
Burrow	Mean	SD	CV	Mean	SD	CV
1	172.33	245.27	142%	246.97	188.3	76%
2	80.5	76.1	95%	321.13	468.98	146%
3	104.96	68.78	66%	366.9	236.65	65%
4	79.82	47.5	60%	456.27	518.63	114%
5	127.63	193.89	152%	288.5	311.28	108%

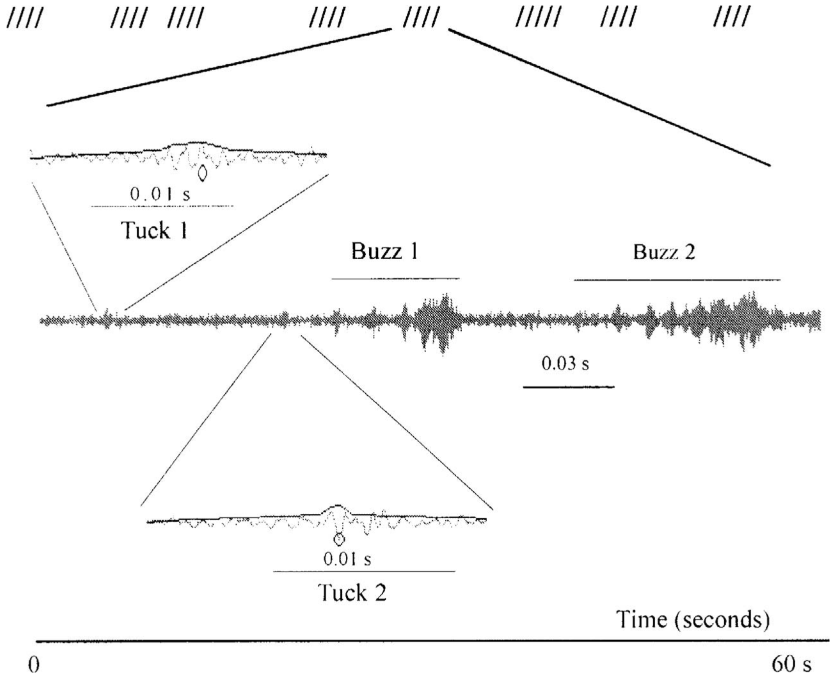

Figure 2.—Above: schematic drawing of male *A. suina* courtship through time. Oblique lines represent a "bout" of vibration produced by the male. Entire sequence corresponded to one minute. Bellow: oscillogram of a single bout of vibration. All the components are indicated (tucks, interpulse periods, and buzz). Tuck 1 and tuck 2 were amplified.

bout vibrations of *E. weijenberghi* presented single syllables or tucks (tuck 1 mean duration = 0.066 s, SD = 0.034, n = 33; tuck 2 mean duration = 0.088 s, SD = 0.049, n =33) and sequences of syllables or buzzes (buzz 1 mean duration = 0.871 s, SD = 0.238, n = 46; buzz 2 mean duration = 0.812, SD = 0.183, n = 45). Separately by a serious of interpulses: I1 (mean = 0.391 s, SD = 0.289, n = 33), I2 (mean = 0.504 s, SD = 0.3, n = 33) and I3 (mean = 0.459 s, SD = 0.159, n = 45). However, vibrations in *E. weijenberghi* differed from *A. suina* signals in the number of tucks preceding buzzes, from six to eight. Figure 3 shows a schematic representation of a male vibration bout throughout time and an oscillogram of a bout of *E. weijenberghi*.

There were no statistical differences in the duration of the tucks before buzz 1 (U = 398.5, P = 0.062, n = 33, 33), or among silences (Kruskal-Wallis test, $H_{2,110}$ = 5.92, P = 0.06). Contrary to *A. suina*, no differences between buzz 1 and buzz 2 were found (t = 1.3, df = 89, P = 0.194).

Male sexual signal vibrations: comparing both spider species.—When signal components were compared, buzz 1 of *E. weijenberghi* showed a longer duration than *A. suina* (t = 7.067, $P < 0.001$, df = 107), whereas interpulse duration between buzz 1 and buzz 2 was longer in *A. suina* (t = −3.667, P = 0.004). No significant differences were detected in any of the other parameters; durations of tuck 1 (U = 339.5, P = 0.505, n = 33, 23), interpulse (U = 176, P = 0.08, n = 32, 16), tuck 2 (U = 316, P = 0.129, n = 33, 25), interpulse (t = 1.005, P = 0.319, df = 55, n = 33, 24) and buzz 2 (t = 1.569, P = 0.119, df = 97, n = 45, 54). Considering all parameters measured, *E. weijenberghi* signal bouts were twice as long as *A. suina* ones (3.82 s versus 1.902 s) (taking into account all tucks that precede buzz 1 in *E. weijenberghi*) and were statistically significantly different (Mann-Whitnney U-test U = 175, $P < 0.001$, n = 46, 67). So, differences between species were in the duration of buzz 1 and in the duration of I3 (*A. suina* showing higher values) and in the number of tucks that preceded buzz 1 in *E. weijenberghi* (from six to eight).

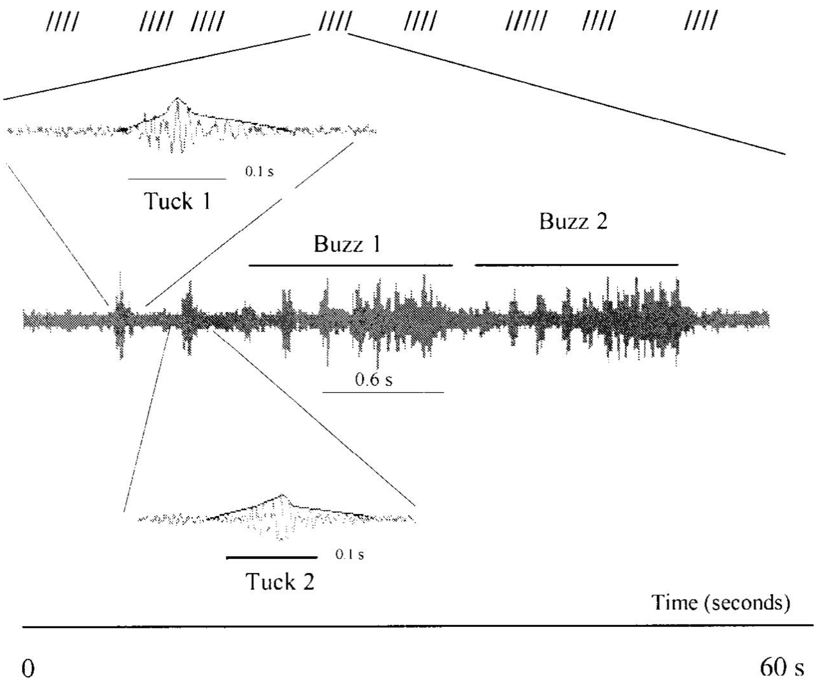

Figure 3.—Above: schematic drawing of male *E. weijenberghi* courtship through time. Oblique lines represent a "bout" of vibration produced by the male. Entire sequence corresponded to one minute. Bellow: oscillogram of a single bout of vibration. All the components are indicated (tucks, interpulse periods, and buzz). Tuck 1 and tuck 2 were amplified.

DISCUSSION

Male signal characteristics.—Since the polarization plane of the geophone was vertical, and seismic signals generated by the courting males were well perceived by the apparatus, these signals would correspond to the kind of seismic signals called "Rayleigh waves" (Narins 1990). However, the co-occurrence of signals called "Love" waves (Narins 1990) can not be discounted in *E. weijenberghi* and *A. suina*. A geophone with horizontal polarization would be required to record them and this was not available for this study. For example, the fiddler crab *Uca pugilator* use both kinds of waves for communicating (Aicher & Tautz 1990).

Three interspecific differences were found in the temporal structure of the signal: in the length of buzz 1, in the length of interpulse period between the two buzzes, and in the number of tucks that precede buzz 1. Divergence in sexual signals among sympatric and synchronous species would be an indicator that natural selection is acting on the signal design, favoring species recognition (see Dobzhansky 1940; Greenfield 1997). For example, the sympatric species of the ctenid spider *Cupiennius* diverge in their courtship signals, mainly in the temporal structure (Schüch & Barth 1990).

Female latency and signal efficacy.—Regression analyses showed no differences in the latency of female response as a function of male-female distances. We conclude that courtship signals were above the response threshold of females, and that signal features that elicited female responses were unchanged (until 135.75 cm in *E. weijenberghi* (135.75 cm) and 110.5 cm in *A. suina*). However field experiments would be necessary to confirm these data. For example Elías et al. (2004) found that in the salticid spider, *Habronattus dossenus* Griswold 1987 the effectiveness of male courtship seismic signal appears to be strongly constrained by the available substratum resource. Seismic signals reaching long distances were extensively reported in scorpions (Brownell & Hemmen 2001), crickets (Hill & Shadley 2001), amphibians (Lewis & Narins 1985), fossorial rodents (Heth et al.

1987, 1988; Randall 1989, 1993, 1995; Rado et al. 1989; Narins et al. 1997; Mason & Narins 2001), and spiders (Rovner & Barth 1981; Barth et al. 1988; Prentice 1997). Therefore, we can make a prediction about what could occur in open grasslands. Given that female burrows are in high densities (from 0.07 individuals/m^2 to 0.65 individuals/m^2) with distances between burrows entrances ranges from 8.0 cm to 36 cm (Pérez-Miles et al. 2005), many females could respond to male seismic signals and compete among themselves, performing leg tapping to orient the male towards each burrow entrance. This scenario is plausible principally in *A. suina* where female burrows showed an aggregated distribution.

The use of seismic signals.—Sharing the same spatial and temporal characteristics, both species would converge towards similar seismic signal characteristics. As mentioned by Greenfield (1994), the environmental and physical conditions that determine the reproductive period would be some of the pressures that determine the sexual signal design through selection of signal efficacy. Due to the fact that *Eupalaestrus weijenberghi* and *Acanthoscurria suina* inhabit the same habitat and microhabitat, it was expected that they would use the same communicatory channel. Secondarily, both species are fossorial, and as some authors have postulated (Heth et al. 1988; Hill 2001; Mason & Narins 2001), the use of this kind of signal could be due to convergence because of signal efficacy and efficiency of propagation in this subterranean environment.

On the other hand, following Greenfield (1994) and Endler (2000), the concentration of males in a brief reproductive period would be an indicator that those males take advantage of singular environmental conditions when the physical conditions for transmission and reception of signals are favorable and a huge concentration of receptive females is present. The ‘‘road tarantula’’ males appear in large numbers during cloudy and warm days in which the relative humidity is high (Perez-Miles et al. 2005). Substrate proprieties (compaction, moistening, and humidity) determine the signal speed transmission of the signal (Narins 1990; Endler 2000). Since a humid solid is a better conductor than a dry soil (Narins 1990), we propose that males of both species have been selected to take advantage of this meteorological condition that characterizes the reproductive period of both these species.

From this present study we conclude that there exists convergence and divergence in the temporal signal characteristics between these species and that the signals produced by males are propagated long distances. In addition males appear to be taking advantage of the climatological conditions of the reproductive period when the signals transmission efficiency is high.

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