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Communication during copulation in the sex-role reversed wolf spider *Allocosa brasiliensis*: Female shakes for soliciting new ejaculations?

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ABSTRACT

Traditional studies on sexual communication have focused on the exchange of signals during courtship. However, communication between the sexes can also occur during or after copulation. *Allocosa brasiliensis* is a wolf spider that shows a reversal in typical sex roles and of the usual sexual size dimorphism expected for spiders. Females are smaller than males and they are the roving sex that initiates courtship. Occasional previous observations suggested that females performed body shaking behaviors during copulation. Our objective was to analyze if female body shaking is associated with male copulatory behavior in *A. brasiliensis*, and determine if this female behavior has a communicatory function in this species. For that purpose, we performed fine-scaled analysis of fifteen copulations under laboratory conditions. We video-recorded all the trials and looked for associations between female and male copulatory behaviors. The significant difference between the time before and after female shaking, in favor of the subsequent ejaculation is analyzed. We discuss if shaking could be acting as a signal to accelerate and motivate palpal insertion and ejaculation, and/or inhibiting male cannibalistic tendencies in this species.

1. Introduction

Intersexual communication, defined as behaviors performed by one sex designed to induce responses in the other sex that are favorable to the signaler (Williams, 1966), has traditionally focused in the exchange of signals during courtship (Guilford and Dawkins, 1991; Endler, 1992; Andersson, 1994; Peretti and Aisenberg, 2011). However, gradually more studies evidence the occurrence of communication between the sexes during and after copulation (Eberhard, 1991, 1996 Edvardsson and Arnqvist, 2000; Tallamy et al., 2002; Ortíz, 2003; Ramírez, 2004). In insects, duetting, or consecutive signal exchange between the sexes, has been cited for Orthoptera, Plecoptera, Hemiptera, Neuroptera, Coleoptera (Bailey, 2003). Duetting during courtship, copulation and after copulation can play essential roles in species recognition and female choice (Bailey, 2003; Cocroft and Rodríguez, 2005).

Several studies indicate that male signaling during copulation through chemical or vibratory signals could serve as an inhibitor of female aggressiveness, and/or elicitor of female sexual receptiveness, affecting cryptic female choice by favoring males that emit more intense signals or respond to female signals more promptly (Eberhard, 1996; Rodríguez, 1998; Becker et al., 2005; Bloch-Qazi, 2003; Sirot et al., 2007; Aisenberg, 2009). In contrast, female signaling during copulation has been much less reported and possibly overlooked mainly due to the historical focus on male sexual performance (Eberhard 1996, 2004 Uhl and Elias, 2011). Examples of this kind have been cited for insects and spiders (see reviews by Eberhard, 1994; Rodríguez, 1998). In spiders, through signals emitted during copulation, females can potentially provide information about their sexual reluctance and try to suspend mating or end male palpal insertions (Peretti et al., 2006), or they can motivate males for further palpal insertions and sperm ejaculation (Ferretti et al., 2011). Under extreme sexual conflict, females can potentially provide information about their resistance to mating by exposing their fighting abilities and showing possible punishments to their mating partners (Rodriguez, 1998 Crudgington and Siva-Jothy, 2000; Aisenberg and Barrantes, 2011).

Allocosa brasiliensis (Petrunkevitch) is a nocturnal wolf spider that inhabits the sandy coasts of rivers, lakes and of the Atlantic Ocean along Argentine, Brazil and Uruguay (Capocasale, 1990). Individuals become most active during summer nights and they construct burrows in the sand where they stay during daylight and

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Table 1
Pre-copulatory, copulatory and post-copulatory behavioral patterns performed by *A. brasiliensis* during the sexual interactions with their corresponding descriptions.

Courtship behavioral patterns	Descriptions
Pre-copulatory phase	
Female waves	The female performs bursts of tapping on the sand with forelegs and palps
Male shakes	The male performs bursts of body shakes
Female enters	The female enters male burrow
Male waves	The male performs bursts of tapping on the sand with forelegs and palps
Female exits	The female turns and leaves the male burrow
Female–male exchange	Male and female exchange positions inside the burrow and the male moves to the top while the female moves to the base of the burrow
Female approaches	The female gets close to the male
Female touches	The female touches with legs 1 and 2, the corresponding forelegs or carapace of the male
Male touches	The male touches with legs 1 and 2, the corresponding forelegs or carapace of the female
Copulatory phase	
Mounts	The male mounts the female in the typical lycosid mating position, with the male on top of the male looking in opposite directions
Male explores	The male contacts the epigynum with the palp
Male inserts	The male performs the palpal insertion with one palp at the time
Female shakes	The female performs bursts of body shaking
Male vibrates	The male performs bursts of abdominal vibrations, moving up and down his abdomen
Male taps	The male performs bursts of touches on the female carapace while inserting the palp
Male ejaculates	The male ejaculates several times during each palpal insertion
Male grooms	The male cleans his palps and forelegs by taking them to the mouth
Post-copulatory phase	
Male exits	The male leaves his burrow
Male covers	The male covers the burrow entrance from outside the burrow transporting sand with his chelicerae and palps
Female releases silk	The female stays inside the burrow and lays silk around the burrow entrance

in winter (Costa, 1995). This species shows a reversal in typical sex roles and sexual size dimorphism expected for spiders (Aisenberg et al., 2007; Aisenberg, 2014). Males are larger than females and females are the mobile sex that search for male burrows and initiate courtship. The copulation takes place inside male burrows (Aisenberg et al., 2007). Both sexes are selective when making mating decisions: females prefer males that build larger burrows and males prefer virgin females in good body condition. Rejected females can be cannibalized (Aisenberg et al., 2011).

Copulation includes approximately nine mounts and dismounts (Aisenberg et al., 2007). After the final mount, the male exits and blocks the burrow entrance before leaving. The female stays inside, oviposits there and emerges for spiderling dispersal (Postiglioni et al., 2008), carrying the progeny on top of the dorsum as is typical for wolf spiders (Foelix, 2011). Previous observations of the copulatory sequences in *A. brasiliensis* (Aisenberg and Peretti, unpublished data) showed that females performed body shakings during the mount and in inter-mount periods, what could indicate the occurrence of copulatory communication. The objective of the present study was to analyze if female body shaking is associated with male copulatory behavior in *A. brasiliensis*, and discuss the functions of copulatory signaling in this sex role reversed species.

2. Material and methods

2.1. Collecting and rearing

We captured 38 adult males and 93 juveniles of *A. brasiliensis* between October 2008 and April 2009, at the coastlines of rivers Río San Antonio, Río Anisacate and Río La Suela, Córdoba Province, Argentine. Each spider was individually raised in plastic transparent boxes (length 9 cm, width 5 cm, height 2 cm), with a layer of approximately 2.0 cm of sand as substrate and a piece of cotton embedded in water. To obtain virgin females, we collected and kept penultimate females under laboratory conditions until they molted to adult.We fed the spiders twice a week with *Tenebrio* sp. larvae (Coleoptera, Tenebrionidae) and monitored them daily for recording molting occurrence and determining the exact date of reaching adulthood.

2.2. Observation and analysis of behavioral sequences

The average temperature during the experiments was (mean ± SD) 23.0 ± 3.0 °C, range: 20–26. All the trials began after dusk coinciding with the period of activity reported for the species (Costa, 1995). We used glass cages for the trials (length 30 cm, width 16 cm, height 40 cm) with a layer of 15 cm of sand as substrate and a piece of cotton embedded in water. We moistened the first 5 cm layer of sand placed at the base of the glass cage to provide humidity.

We randomly assigned females and males to the experimental pairs. Virgin females were used 7–20 days post adult-molt, coinciding with the sexual receptivity period reported for females of this species (Aisenberg, 2014). Males were used five days after their capture at the field. We did not reuse individuals.

Each male was placed in the glass cage 48 h before the trial to allow burrow construction. Individuals usually construct their burrows against the glass walls, allowing the observation of their behaviors when they are inside the burrows (Aisenberg et al., 2007). The trial began when we introduced the female to the experimental cage and finished after the male exited the burrow and covered the burrow entrance in the case of mating; when mating did not occur, trials finished after 30 min without courtship, or after one hour with female and/or male courtship. We performed the trials in total darkness and recorded the sexual interactions with a digital video camera Sony Handycam DCR-SR65E with night-shot function and equipped with +6 close-up lenses.

We obtained a total of 15 copulations of *A. brasiliensis* ($N = 20$). We analyzed the video recordings with JWatcher software (Blumstein et al., 2000). We named behavioral courtship and copulatory characteristics in agreement with Aisenberg et al. (2007). We recorded the number and duration of courtship and copulatory behavioral units. The number of ejaculations was recorded indirectly through the erection of spines on male legs, as has been previously applied for this species (Aisenberg et al., 2007) and as has been reported for other wolf spider species (Costa, 1979; Foelix, 2011). We performed Markov analysis for determining the sequential associations between the behavioral units. We considered as female body shaking when the female performed

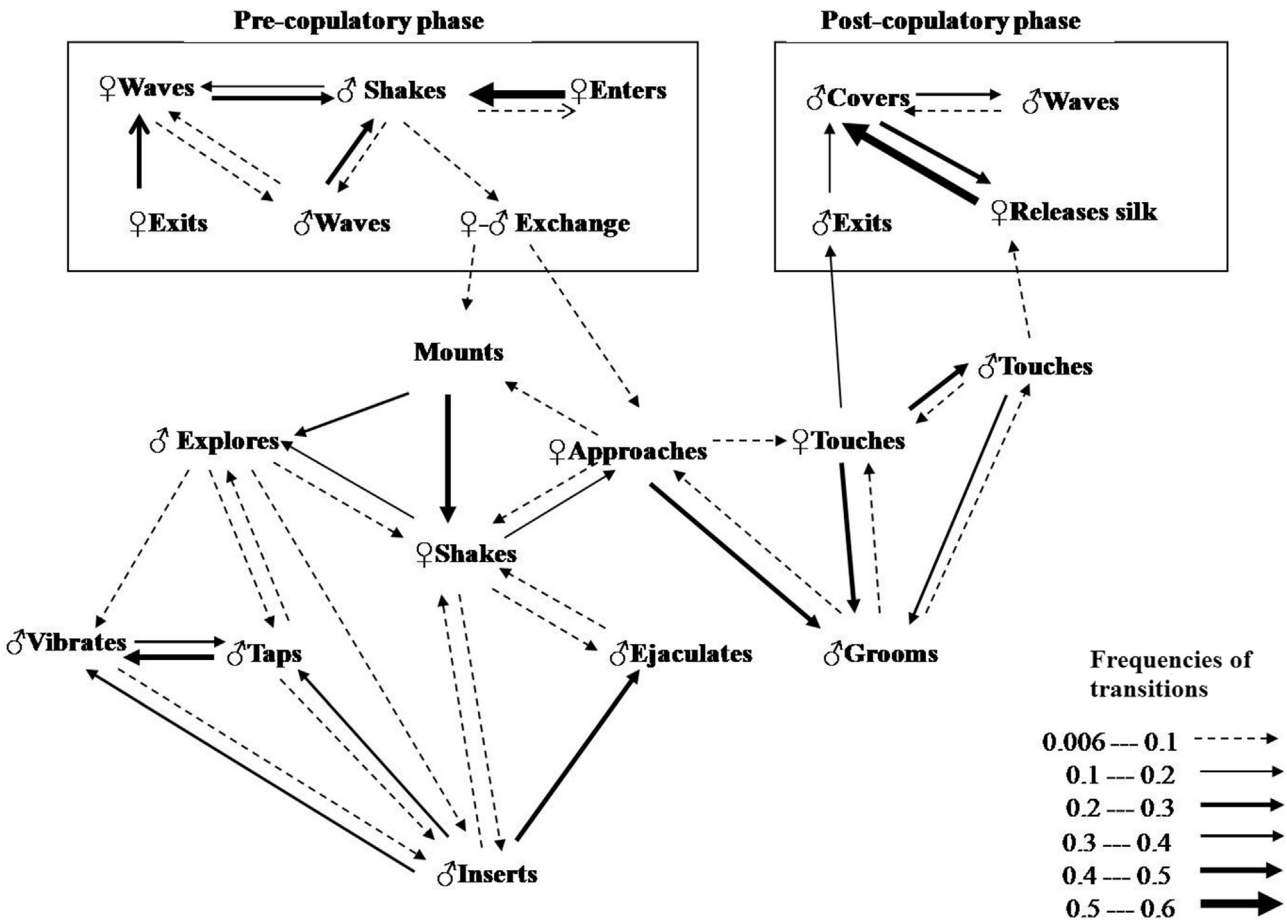

Fig. 1. Flow diagram summarizing the transitions among the behavioral patterns of courtship, copulation (not framed) and post-copulation in *Allocosa brasiliensis*. Frequencies of transitions were obtained from the transcriptional matrix of the Markow's sequential analysis. The maximum value is 1. This diagram – as all flow diagram – does not analyze the time elapsed between behavioral acts (for this purpose see the analysis of the time included in the text).
Note: The female enters the burrows but she can exit momentaneously and enter again. The flow diagram only shows higher frequencies of transitions, and for this reason there is not an arrow toward the behavioral act named "exit" (i.e., due to its very low frequency – see Fig. 2).

consecutive bursts of vibrations of the whole body, with open legs pressed against the substrate and producing quick movements similar to body trembling. We analyzed during each mount and in inter-mount period the number of occurrences and durations of each female body shake and male responses to this behavior. For this purpose, we examined the chronological association between palpal insertions and female body shakings. We analyzed the presence–absence of both behavioral acts together during the mounts and examined whether female shook her body before or after the males performed palpal insertions. Subsequently, we analyzed the elapsed time between ejaculations and female body shaking. In ejaculations with female body shaking, we measured the time interval from the last ejaculation to the beginning of the first female body shake and the time from the end of the shake to the next ejaculation. We measured carapace width of each individual as an estimator of body size in spiders (Eberhard et al., 1998; Moya-Laraño and Cabeza, 2003), and recorded burrow dimensions (length and width of the burrow entrance) in each case.

We analyzed the results using Past Palaeontological Statistics version 1.18 (Hammer et al., 2003) and NCSS 2001 (Copyright 2000, Jerry Hintze). Variables were checked for normal distribution (Shapiro–Wilk test) and homogeneity of variances (Levene's test). We used the non-parametric Kruskal–Wallis test for comparing the occurrence of female body shaking, palpal insertions and ejaculations, along the consecutive mounts. We used Student's *t*-test for paired samples (parametric test), or Wilcoxon matched-pairs sign test (non-parametric test) for determining possible associations between female body shaking and palpal insertion, and female body shaking and elapsed time to ejaculation.

3. Results

3.1. Fine-scale analysis of copulatory behavior

We summarize courtship and copulatory behavioral patterns and their corresponding descriptions in Table 1. From the Markov analysis, we developed a flow diagram (Fig. 1) of the mating behavior of *A. brasiliensis*. This diagram shows the sequence of behavioral patterns (see also Fig. 2) of the three principal mating phases: pre-copulatory (from female leg waving to exchange of positions), copulatory (mount and associated behavioral acts), and post-copulatory (the male covers the burrow entrance with the help of the female from inside the burrow).

3.2. Association between female body shaking and male copulatory behavior

We analyzed in each mount, the number of the palpal insertions, ejaculations and female body shaking behavior. In overall, when we compared the different mounts along copulation (Table 2), we did not find significant differences in the number of insertions, female body shaking, or ejaculations (Table 2, see Supplementary

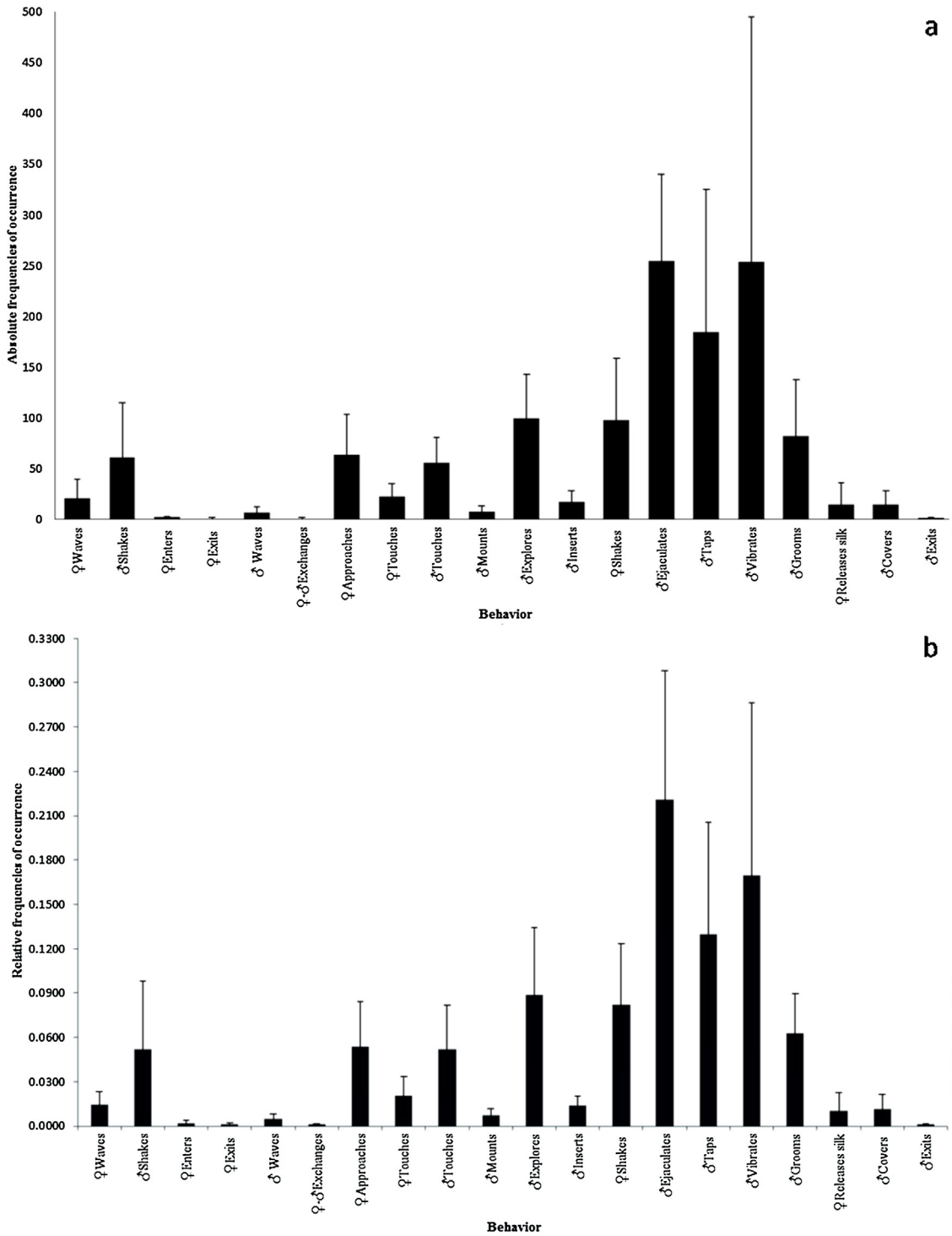

Fig. 2. Average occurrence of the behavioral acts of the mating in *Allocosa brasiliensis*: (a) absolute frequencies of occurrence, (b) relative frequencies of occurrence.

figure). By comparing the first vs. the last mount, we did not find significant differences in the time between insertions (Table 2). In contrast, elapsed time was significantly different between ejaculations (Table 2).

Mutual presence of palpal insertions and female shaking during a mount was statistically significant (Fisher exact test, $p = 0.00001$) (Table 3). Interestingly, female body shaking principally occurred prior to palpal insertion (Fisher exact test, $p = 0.01$) (Table 3).

In general, we did not find differences between times to ejaculations with or without shaking (Table 4). However, through a fine-scale analysis of the chronological associations of copulatory behaviors, we detected that female body shaking was closely associated to the subsequent occurrence of a new ejaculation (Fig. 3). Indeed, the time from a female shaking to the next ejaculation was lower than the time between ejaculations without shaking (Table 4). In addition, the time from female shaking to the next ejaculation was lower than the time from the last ejaculation to shaking (Table 4).

We did not find a significant correlation between the number of female body shaking behaviors and burrow length ($R = 0.10$, $F = 0.12$,

Table 2
Results of the Kruskal–Wallis analysis of variance of the frequencies of occurrence of sexual behavioral acts during the mounts. This is a comparison of mounts within a single male–female pair, across a single "copulation" event. For this, we calculated a mean value of each act per mount for each copulation.

	H	*p*
Palpal insertions	2.66	0.9
Ejaculations	9.70	0.2
Female body shaking	4.06	0.8
Time between insertions (first vs. last mount)	5.28E–02	0.8
Time between ejaculations (first vs. last mount)	16.72	0.00004

$p = 0.7$), male or female body size ($R = 0.12$, $F = 0.04$, $p = 0.9$), or male body size in comparison with female body size (male size/female size) ($R = 0.11$, $F = 0.09$, $p = 0.8$).

4. Discussion

Cooperation involves communication, and communication implies a dynamic bidirectional flow between the signaler and the receiver (Harper, 1993; Bradbury and Vehrencamp, 1998). In our observations on *A. brasiliensis* copulations, the basic concept was reflected in the relationship between a particular female behavior, body shaking, and the subsequent male's response, ejaculations. In fact, female body shaking associated positively with the occurrence of ejaculations. The significant difference between the elapsed time before and after the shaking, in favor of the subsequent ejaculation may support the idea that through body shaking behavior, the female may be requesting a new ejaculation. However, why would females need solicit additional ejaculations? According to preliminary studies, males have very small testes in this species, compared to other wolf spiders of similar size. Also, according to Aisenberg et al. (2011) they are choosy when taking mating decisions. So, males of this species and their sperm are the scarce resource for which females compete. Once the females have accepted a male, through their body shaking during mating and in the inter-mating period, females could be transmitting their high sexual receptivity and motivating their partners to inseminate them. For animals with scarce vision and mating under the ground and one on top of the other, vibrational signals are possibly a good choice for communicating this message.

Another alternative explanation is that the female performs body shaking to communicate her intention to interrupt copulation. In this case, the male may respond with ejaculations in order to transfer a larger amount of sperm before the sexual interaction ends, thus, representing an example of sexual conflict over copulation duration (Chapman et al., 2003; Arnqvist and Rowe, 2005). This alternative explanation involves a prediction. For example, we would expect that the female after making a certain amount of shaking, with or without the corresponding response of the male, should interrupt copulation. However, we did not observe such interruptions in this as well as other studies (Aisenberg et al., 2007; Aisenberg et al., 2011). Male sexual cannibalism can occur in this species (Aisenberg et al., 2009; Aisenberg et al., 2011). Therefore, considering that males are larger than females, it seems that females would rarely tend to terminate unilaterally copulation simply because of the potential risk of being attacked and cannibalized. Furthermore, we observed females approaching males and performing body shaking behaviors between dismounts, while the male was grooming his palps.

Table 3
Association between female body shaking (SHAKES) and palpal insertions (INSERTS) during the mount, showing combinations of frequencies of occurrence of both behavioral acts (top) and analysis of the precedence of female body shaking and palpal insertions (bottom).

	With SHAKES	Without SHAKES
With INSERTS	60.65 ± 29.81	0
Without INSERTS	30.33 ± 48.02	9.02 ± 22.17
	Preceded by SHAKES	Not preceded by SHAKES
INSERTS begins	34.48 ± 32.78	11.86 ± 17.08
INSERTS ends	9.11 ± 10.28	8.13 ± 10.26
After INSERTS	30.17 ± 24.59	6.21 ± 4.99

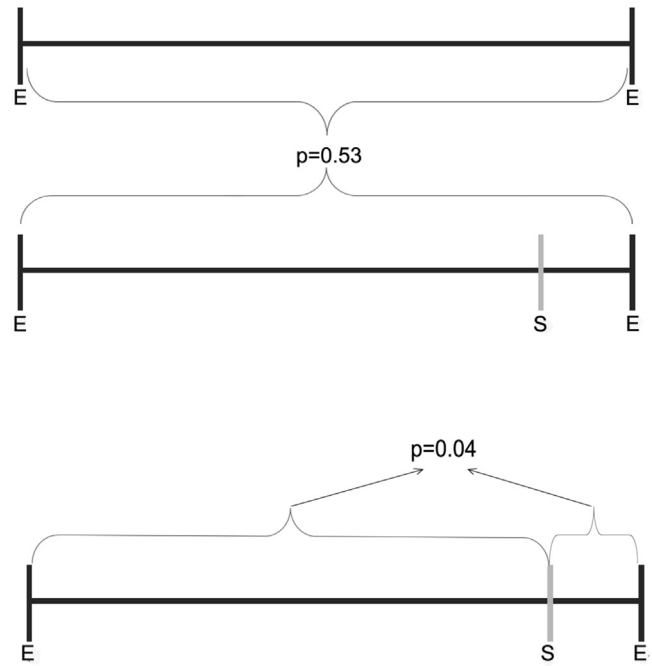

Fig. 3. Diagrammatic representation of the time periods elapsed between two successive ejaculations with and without female shaking (top). There were no significant differences in both cases. However, the time between female shaking and the subsequent ejaculation was shorter than the time elapsed from shaking to the previous ejaculation (bottom). Abbreviations: E: ejaculation, S: female shaking.

Males that adjust sexual responses according to female sexual feedback have been reported in the wolf spider *Schizocosa rovneri* (Sullivan-Beckers and Hebets, 2011). These authors found that males receiving visual and/or seismic feedback cues from puppet females increased their overall signaling effort during courtship. To our knowledge, copulatory communication is not common within the Lycosidae family, in which the female usually remains still, and sometimes is quiescent during mount (Costa, 1979; Stratton et al., 1996; Foelix, 2011). As far as we know and until now, only three burrowing lycosids are known to mate inside their burrows: *A. brasiliensis* (Aisenberg et al., 2007), *Allocosa alticeps* (Aisenberg and Costa, 2008) and *Tricca lutetiana* (Dolejš et al., 2010). Conspicuous female body shakes could be possible due to the secure mating place. Though there are no reports of female body shakes in *A. alticeps* or *T. lutetiana*, similar body shakes have been cited for *Aglaoctenus lagotis*, the only web building wolf spider whose copulation occurs in a refuge, inside the web tube (González et al., 2013). It is evident that presence and characteristics of communication during copulation has been, with some few exceptions, little studied in wolf spiders as well as in other families (Eberhard, 2004, 2009). However, the few studies in this field suggest that many forms of copulatory communication could potentially occur among spiders. For example, in the Pholcidae *Physocyclus globosus*, the females stridulate during copulation in order to modulate the duration of male's palpal insertion (squeezing) (Peretti et al., 2006). Interestingly, the female in this last species uses stridulation to request that the male stops momentarily deep insertion. Copulatory communication apparently also occurs in some basal groups of

Table 4
Fine-scale analysis of the chronological associations (elapsed time) between female body shaking (SHAKES) and ejaculations during the mounts.

	Time ejaculations without SHAKES	Time ejaculations with SHAKES	Time from last ejaculation to SHAKES	Time from SHAKES to next ejaculation
Time ejaculations without SHAKES	**5.52 ± 2.59**	$Z = -0.07$ $p = 0.5$	$Z = 3.06$ $p = 0.001$	$T = 6.38$ $p = 0.0001$
Time ejaculations with SHAKES		**5.22 ± 2.01**	$Z = 3.05$ $p = 0.001$	$T = -8.65$ $p = 0.00001$
Time from last ejaculation to SHAKES			**2.53 ± 0.83**	$T = 2.02$ $p = 0.04$
Time from SHAKES to next ejaculation				**2.22 ± 1.23**

spiders such as mygalomorphs. In the Nemesiidae *Acanthogonatus centralis*, females remain active during copulation by making body jerks and struggling. The body jerks of females could be stimulating the male to perform new palpal insertions (Ferretti et al., 2011).

There are other female behaviors in *A. brasiliensis* that may indicate an active role for this sex during courtship and mating. After each mount, the female tends to approach the male and touches him with her forelegs. This female behavior could represent another way of request, in this case to persuade the male to make a new mount. It could also be a case of female choice where the female corroborates male quality based on male response. There are reports of similar behaviors in other species, such as orb-web spiders (*Leucauge mariana*) (Eberhard et al., 1998; Aisenberg, 2009), and wolf spiders (*Schizocosa malitiosa*) (Aisenberg and Costa, 2005). In wolf spiders, there is evidence of co-evolution between male signals and female responses during courtship (Hebets and Uetz, 1999). Female approach to males and leg contact during inter-mount periods could also be related with inhibition of male aggressiveness, considering that males of this species can perform sexual cannibalism (Aisenberg et al., 2011). All these hypotheses require further experimental testing.

Finally, during the post-copulatory phase, another cooperative behavioral pattern was the association between the acts "covering burrow entrance" of the male and "silk deposition" of the female. In fact, this is one of the strongest behavioral associations during mating. Blocking the burrow entrance appears to be essential for the events that follow copulation since, in the two cases when the male did not cover the burrow entrance, the female did not oviposit (V. García, personal communication). By means of this behavioral association, both sexes may ensure a better camouflage of the burrow that could protect them from parasitism by *Anoplius* wasps (Stanley et al., 2013). In addition, for the male it could be a mechanism to ensure paternity, preventing detection of the copulated female by other vagrant males (Aisenberg et al., 2007). Further studies will explore more spider groups in order to analyze possible patterns of convergence at the structural (i.e., types of behavioral acts) and functional levels with regard to female copulatory communication.

5. Limitations

It is extremely difficult to demonstrate a communicative function of a behavior that takes place in the middle of a complicated sequence of reproductive events. We tried to do a thorough job of dissecting apart, and quantifying, the reproductive behavior of this species and in the end, find an association between female body shaking and male insertion/ejaculation. On this point, one could argue that this association could simply be a physiological byproduct of the mating behavior. It may be an external manifestation of a physiological response by females that males could potentially be using as a cue (not a signal) for subsequent ejaculations. However, the typical occurrence of female shaking behavior and, above all, its link with some male behavioral acts seem not be explained by this "neutral" argument. Although an association between two behaviors in their occurrence and their timing is not sufficient to demonstrate communication, is certainly suggestive of communication. Our paper was predominantly descriptive and we tried to use our observations to put forth hypotheses regarding the function of the female shaking. Therefore, from the base offered by the present study is that new studies on specific experiments could be performed such as manipulation of female shaking or male insertion/ejaculation. For example, by obliterating artificially the spermathecae or male palps in order to evaluate how female shaking is influenced by the lack of receiving sperm. Thus, it could be expected that females should increase the frequency of occurrence of shaking if this behavior is really used to request new a ejaculation. These kind of experiments could offer valuable information in this interesting scenario of male–female sexual interaction.

6. Conclusions

There is an association between female body shaking and male ejaculation in *A. brasiliensis*. From fine-scaled observations of behavior we discussed some possible explanations, including the possibility that female shaking could be a positive signal to induce new palpal insertions and ejaculations. New studies should examine the effects of this female sexual behavior and male responses on female sexual receptivity to new matings and male paternity in this wolf spider species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2015.05.005.

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