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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