

SHORT COMMUNICATION

Description of the sexual behavior of the Neotropical wolf spider *Pavocosa gallopavo* (Araneae: Lycosidae), with comments on sexual cannibalism

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Abstract. We describe for the first time the sexual behavior of *Pavocosa gallopavo* (Mello-Leitão, 1941) (Lycosidae), analyzing encounters between 25 pairs of virgin adult individuals. Both courtship and copulation were brief, averaging 3.66 min and 1.74 min respectively. Males showed a very conspicuous and vigorous courtship, with Leg Shaking and Palpal Drumming as the most noticeable displays. Females were also active during courtship, performing Leg Waving as well as showing some level of aggression by displaying Cheliceral Opening and Pushes against males. The males mounted the females in the typical position of wolf spiders, and females initially performed intense body shakes (Bucking). The copulatory pattern consisted of alternating single insertions of both palps, with a unique hematochoal expansion by insertion. Females cannibalized males three times, two of them before copulation and the third after copulation. Copulation was brief with respect to other wolf spiders, and females were unusually active during copulation. The species would be suitable for further studies of multimodal communication and the sexual inhibition of female aggression.

Keywords: Courtship behavior, copulatory pattern, Uruguay

Sexual behavior is largely unknown for Neotropical spiders. Moreover, in small countries like Uruguay, with a long tradition of ethological studies of wolf spiders, sexual behavior has been described for only six of the thirty species recognized by Castro-O'Neil (2010) in the country. These six species belong to three subfamilies: *Schizocosa malitiosa* (Tullgren, 1905), *Lycosa thorelli* (Keyserling, 1877), and *L. carbonelli* (Costa & Capocasale, 1984) to Lycosinae; *Allocosa brasiliensis* (Petrunkevitch, 1910) and *A. alticeps* (Mello-Leitão, 1944) to Allocosinae; and *Aglaoctenus lagotis* (Holmberg, 1876) to Sosippinae (Costa 1975, 1979, 1991; Costa & Capocasale 1984; Aisenberg & Costa 2008; González et al. 2013, 2014). Here we present data on *Pavocosa gallopavo* (Mello-Leitão, 1941), a medium-sized Lycosinae occurring in southern Brazil, northern and central Argentina and throughout Uruguay (Murphy et al. 2006; Aisenberg et al. 2011b; World Spider Catalog 2015). The species is characterized by moderate sexual dimorphism, with an average body length of 11.3 mm in males and 15.1 mm in females. Males have a whitish ventral surface, whereas females may be whitish or have a small or large dark pigmented area on their venters.

The taxonomic status of the species is in doubt. For example, Castro-O'Neil (2010) examined the taxonomy and distribution of Uruguayan wolf spiders and considered *P. gallopavo* as a junior synonym of *Molitorosa molitor* (Bertkau, 1880). The genus *Pavocosa* (Roewer, 1960) is also controversial because it has only five species living in countries far from one another: Argentina, Brazil, Uruguay, Thailand, and the Caroline Islands. Murphy et al. (2006) included Brazilian specimens of *P. gallopavo* in their comprehensive phylogenetic analysis of wolf spiders and found affinities between the species and an Australasian clade of species, suggesting a Gondwanan origin of the group. Piacentini (2014), using morphological characters, found significant support for the hypothesis that *P. gallopavo* specimens from Argentina form a single clade with the Nearctic burrowing species *Geolycosa missouriensis* (Banks, 1895).

Until recently, *P. gallopavo* had been found only in very low density in Uruguay, preventing quantitative studies of its reproductive behavior. However, in 2014 we found high density populations in two open areas of the Departments of Canelones and San José. Using molecular techniques based on individuals from San José (close to our site of collection), Lacava (2014) found that this spider consumes

mainly crickets, lepidopterans, and ants. Murphy et al. (2006), in a phylogenetic study of wolf spiders, considered *P. gallopavo* as a permanent inhabitant of burrows. However, nothing else is known about the biology of the species, and little is known about the entire genus. Our study of the reproductive behavior of *P. gallopavo* will provide new taxonomic characters useful for constructing the phylogeny of wolf spiders and will form the foundation for future behavioral studies.

We collected fifty juveniles of *P. gallopavo* during March 2013 and 2014, in the Department of Canelones, Uruguay (34°48'50.52"S, 55°58'16.18"W) and in the Department of San José, Uruguay (34°19'13.4"S, 56°43'06.5"W). All the spiders were collected at night, using headlamps. The habitat where *P. gallopavo* was found is open dry areas, with soil as substratum, small stones, and little or no grass. In the laboratory, the spiders were housed individually in Petri dishes (diameter 9.5 cm, height 1.5 cm) with a thin layer of sand as substrate, and a piece of cotton embedded in water. We fed all of the individuals twice a week with a mixed diet of mealworm larvae, *Tenebrio molitor* Linnaeus, 1758 (Coleoptera; Tenebrionidae), and juvenile stages of cockroaches, *Blattica dubia* Serville, 1839 (Blattodea; Blattellidae). The individuals were monitored daily to determine the exact date that they reached adulthood. We used only virgin males and females of three or more days after last molt and did not reuse individuals. Room temperature and humidity averaged 21.6 ± 3.7 °C (mean ± SD) and 67.4 ± 10.4 %, respectively, and the photoperiod was 12:12 h light:dark.

Thirty-two trials were conducted during April and May of both 2013 and 2014. We used cylindrical glass arenas of 20 cm diameter and 10 cm height, with sand as substrate with very small pebbles (≤ 1 cm) to recreate the microhabitat where they were collected and to provide potential refuges. Females and males were randomly selected and males were removed after 30 min if they did not copulate. Females were placed in the arenas 48 hours before each trial for the deposition of draglines. Males were carefully placed in the arena on the opposite side from the females. Because this species is most active at night (Lacava 2014), all trials were performed at night, between 20:30 and 22:00. We illuminated the test arena from above with a 40-watt red light located 50 cm away. We video-recorded all the trials with a Sony DCR-SR45 video camera with a night shot mode. The

Table 1.—Description of the behaviors performed by *Pavocosa gallopavo*, during courtship and copulation.

Behavior	Description
<i>Male behaviors</i>	
Locomotion	Slow walking movements, with forelegs raised or directed forward, and palps contacting the substrate. Locomotion alternates with being motionless.
Palpal drumming	Quick and alternate pedipalps knocking on the substrate. Initially the drumming is of low intensity, but intensifies when approaching the female.
Leg shaking	Sudden and simultaneous movements, backward and forward, of both extended forelegs, creating an approximate angle of 45°–80° with respect to the substrate surface, usually with short advances. When the male is near the female, forelegs shake in vertical position and the second pair of legs can also raise and shake. When walking, one or few shakes occur consecutively, but near the female, the male performs a series of intense shakings (up to five times). In this last case, the male accompanies shakings with forward and backward movements, as well as with palpal drumming.
Rubbing	Alternate scraping of one leg against another ipsilateral leg, usually the first against the second leg, or the second against the third.
Tapping	Vibration of the extended first and second pair of legs on the frontal area of the carapace and forelegs of the female, with the concomitant raising of the male body when extending third and fourth legs. Simultaneously, he tries to separate the female's forelegs.
Retreat	Backwards movements of the male without stopping courting, when the female pushes him.
Mounting	Male climbing on the female's back, placing himself in the typical copulatory position of wolf spiders. It occurs when the male separates the raised forelegs of the female and achieves the simultaneous hyper-flexion of his palps against the clypeus.
Palpal insertion	Introduction of the embolus of one palpal bulb into one of the female genital openings. During each insertion, the hematodocha of the used palp expands once (ejaculation) and the leg spines become erect.
Side change	Change of the male position, allowing alternate palpal insertion. When inserting left embolus, male leans towards his right side, surrounding the female abdomen with his left foreleg and separating female fourth leg with the other foreleg. When inserts the right embolus, the reverse arrangement occurs.
Dismounting	Descent of the male from the female's back, followed by a quick escape.
<i>Female behaviors</i>	
Locomotion	Slow walking movements, in alternation with motionless.
Turn	Female rotation towards the approaching male.
Leg raising	Foreleg elevation (the first and sometimes also the second pair) facing the male, exposing to him the fully pigmented ventral surface of legs.
Cheliceral opening	Exposure of the dark opened chelicerae (basal segments and fangs) to the male. This behavior usually occurs during Leg raising.
Pushes	Shoving the male with forelegs with the front part of the body raised, when the partner is facing her.
Leg waving	Alternate movements of forelegs towards the courting male.
Lowering body	Female lowers her body and touches the substrate, allowing the male to mount.
Abdominal twists	Rotations of the abdomen side to side. These twists occur both during courtship (when the male shakes close to the female and touches her) and during copulation (accompanying male side changes).
Bucking	Intense body shaking during mounting, apparently trying to dislodge the male.
Attack and cannibalism	Attacks and attempts to kill the male, when male and female are facing or when the male dismounts.

trials ended after the male dismounted. We used JWatcher software (Blumstein et al. 2000) to analyze the occurrences and durations of the behavioral units. The male age during the trials averaged 10.8 ± 8.7 days (mean \pm SD) after last molt, whereas the corresponding female age was 13.9 ± 11.0 days; the room temperature averaged 20.5 ± 1.5 °C and humidity 72.5 ± 9.7 %. We registered courtship latency (period from male deposition to first courtship unit), courtship duration (from first courtship behavior to mounting), copulation duration (from mounting to dismounting), number of palpal insertions and number of side changes. We immediately removed the male when the female attacked him. Voucher specimens were deposited at the Arachnological Collection of the Facultad de Ciencias, Montevideo.

We performed 32 trials and observed 25 copulations. Four trials ended after 30 min without mounting, and three led to cannibalism. We analyzed the sexual behaviors of the 25 successful couples and recognized 19 behavioral units. A catalog of the most relevant units is shown in Table 1, and an ethogram of sexual behavior of *P. gallopavo* is shown in Fig. 1.

The sexual behavior of *P. gallopavo* was very brief (5.41 ± 4.18 min, mean \pm SD, range 1.34–21.47 min) and was divided into courtship (3.66 ± 3.88 min, range 0.69–18.49 min) and copulation (1.74 ± 0.82 min, range 0.40–3.07 min). During the copulation, males of *P. gallopavo* performed on average 12.56 ± 3.88 palpal insertions (range: 3–17) and 12.04 ± 3.87 side changes (range: 3–17). Once inside the arena, males usually remained stationary for several minutes (Motionless) prior to initiating Locomotion. In all trials, males began courtship after finding female draglines and touching them with their legs or palps. Females appeared able to perceive the male's display at a distance of 5–6 cm, when they turned and usually slowly walked towards the males. Males oriented towards females only after they perceived female movements. Some females (7 in 25 cases) performed Leg Waving. When the male was close to the female, she could stay still or performed short Pushes against the male, raising her forelegs. Female Leg Raising was accompanied by Cheliceral Opening in half of the cases. Once the males assumed the copulatory position, all females shook their bodies intensely up to nine times

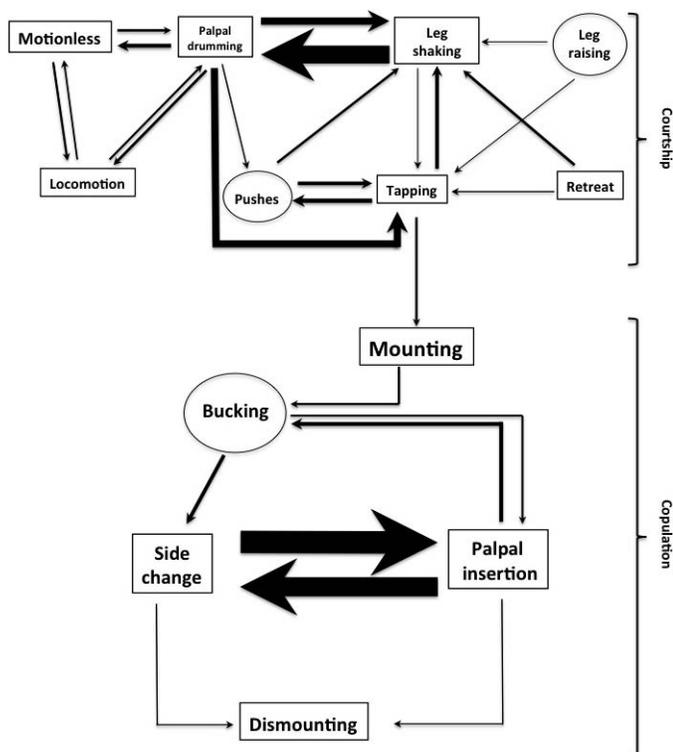


Figure 1.—Ethogram of courtship and copulation behaviors in *Pavocosa gallopavo*. Males performed the behavioral units within boxes and females performed the behavioral units within ovals. Behavioral acts that occurred less than ten times were not included in this diagram.

(Bucking). Males usually resisted being dislodged, but in two cases they were displaced, although were able to re-mount.

The copulatory pattern consisted of a strict alternation of a single insertion of each embolus of the palpal bulb, with a single hematodochal expansion (ejaculation) per insertion. Meanwhile, the female rotated her abdomen allowing embolus introduction into each genital opening of her epigynum (right embolus into the right female genital opening, and the left into the left). Initially, the male changed sides several times before performing the first insertion with sperm transfer. Palpal insertion was evidenced by the expansion of the hematodocha and by the erection of spines of male hind legs, both due to the increase of hemolymph pressure. Each insertion was mediated by a change in the use of each palp (Palpal Change). Ending copulation, the male touched the female abdomen alternately with his forelegs and quickly dismounted.

Females cannibalized males three times in 32 trials, twice before copulation and once after copulation. In the first two cases, males performed courtship after contacting female silk and females approached them. When they faced each other, the males performed Leg Shaking and Palpal Drumming but immediately tried to mount instead of continuing with courtship while the female gave threat displays. In the postcopulatory case, the male reached the typical copulatory position but could not perform palpal insertions, failing several attempts (flubs) in one or the other side. When the male tried to dismount, the female immediately attacked and cannibalized him.

Pavocosa gallopavo females were active during courtship, performing their own receptive display but simultaneously showing clear symptoms of aggression. While the copulatory position was typical of wolf spiders, intense female mobility and brief copulation were atypical (Stratton et al. 1996; González et al. 2013; García-Díaz et al.

2015). The observed copulatory pattern (alternated single insertions of both palps, performing a unique hematodochal expansion by insertion) was also infrequent for the family (Stratton et al. 1996).

The meeting of both sexes seems to be mediated by female contact sex pheromones, because males initiate searching and courtship behaviors prior to locating the female but after finding female silken threads. This type of chemical communication is well known in other wandering wolf spiders (Tietjen & Rovner 1982; Gaskett 2007; Baruffaldi et al. 2010; Uhl & Elias 2011; Dolejš et al. 2012). The conspicuousness of male Leg Shaking in *P. gallopavo* is extreme for the family, involving not only the first pair of legs raised but also frequently the second pair when the male is facing the female; we did not find in the literature other lycosids that shake their front four legs. This striking display may have increased energetic costs and predatory risks for the male. Furthermore, Leg Shaking involving four legs also implies that all the legs are in good condition because the remaining four hind legs must firmly maintain the male equilibrium during the display. In other words, it seems to be an honest display (Zahavi 1975). Considering that *P. gallopavo* is a nocturnal species (Lacava 2014), we suggest that the conspicuousness of this display allows the male to compensate for the difficulties of visual communication under low light conditions.

As occurs in other Lycosinae (Hebets et al. 1996; Foelix 2011), small stridulatory organs are present at the tibiotarsal joint of the pedipalps of *P. gallopavo* males (Piacentini, pers. comm.). Males articulate this joint during palpal drumming, and they also hit the palps with intensity on the substrate, generating small holes in the sand surface. These observations suggest the occurrence of both stridulation and percussion during sexual communication (Uetz & Stratton 1982). These types of signal production could involve both acoustic and seismic channels, which seem to be particularly useful to communicate at short distances and during the nighttime. We are now studying these behaviors in more detail.

When a male and a female were facing each other, and the male increased the courtship intensity, we observed that the female always pushes the male, simulating attacks. A similar behavior (“lunge”) was usually performed by unreceptive female wolf spiders, according to Hebets et al. (1996), Scheffer et al. (1996) and Brown (2006) in *Schizocosa retrorsa* (Banks, 1911), *S. ocreata* (Hentz, 1844), and *Rabidosa sanrita* (Chamberlin & Ivie, 1942), respectively. These pushes suggest that the female is testing the male’s abilities. The female may also test male vigor and persistence by rejecting several male mount attempts, maintaining both the body and the forelegs raised. However, this hypothesis remains to be tested.

During mount attempts, females usually perform abdominal twists, which are similar to the ones performed by other wolf spider females during copulation, facilitating palpal insertion (Rovner 1971; Stratton et al. 1996). Rovner (1971) mentioned that abdominal rotation in *Rabidosa rabida* (Walckenaer, 1837) was experimentally elicited by touching the carapace of females that were in a cataleptic state. In *P. gallopavo*, this rotation is the rule and apparently is elicited by the male tapping on the forelegs and the front of the carapace of the female. Abdomen rotation seems to be a clear indicator of female receptivity (all females that performed abdominal shift mated). This receptive behavior contrasts with her threatening displays with raised body and forelegs as well as Cheliceral Opening, which the female displays simultaneously. More studies are needed to understand these behaviors.

During mounting, the male hyper-flexes his palps, suggesting that at the time of maximum danger he moves away his copulatory organs to avoid being bitten by the female. Female Bucking, which occurs with the male in copulatory position, is other behavior may be a test of male quality. Shakes of females in copula were observed in some wolf spiders such as *Aglaoctenus lagotis*, *Allocosa brasiliensis*, and *Hogna vittata* Yin, Bao & Zhang, 1995, which are restless during copulation (González et al. 2013; García-Díaz et al. 2015; González

pers. comm.). However, the body shakes of those species are not as violent as in *P. gallopavo*, where the female can force the male to dismount.

Stratton et al. (1996) state that a few species of wolf spiders (in the genera *Arctosa* C.L. Koch, 1847 and *Geolycosa* Montgomery, 1904) mate for a few seconds or minutes, whereas the majority mate for several minutes up to eight hours. In contrast, copulation duration of *P. gallopavo* (1.7 min) is relatively brief, and is the shortest known in the wolf spiders of Uruguay. Accordingly, palpal insertions (12.6 in average) are few despite the intense male activity. Brief copulation with few insertions would be frequent in burrowing wolf spiders according to Stratton et al. (1996) and Dolejš et al. (2010). We hypothesized it is possible that predation avoidance determines these short copulations because generally mating takes place at the burrow entrance where they are exposed to this danger. On the other hand, the copulatory pattern of *P. gallopavo* (alternation of single insertions with a unique hematodochal expansion) occurs only within Lycosinae subfamily and was described for many species of *Rabidosia* Roewer, 1960 and for some species of *Hogna* Simon, 1885, *Gladicosa* Brady, 1897, *Arctosa*, *Pardosa* C.L. Koch, 1847 and *Geolycosa* (see Stratton et al. 1996 for review). Finally, *P. gallopavo* also shows other copulatory singularities; males do not perform either abdominal vibrations or palpal moistening, two maneuvers which are usual during copulation of wolf spiders.

Sexual cannibalism is infrequent in wolf spiders, perhaps due to their moderate sexual dimorphism and their secure copulatory position. However, high rates of sexual cannibalism have been indicated by Rabaneda-Bueno et al. (2008, 2014) for females of *Lycosa hispanica* (formerly *L. tarantula*) (33% of the cases). In addition, males in the sex-role reversed lycosid *Allocosa brasiliensis* frequently cannibalize females (30% of interactions) (Aisenberg et al. 2011a). In comparison, despite the aggressive behavior of females, *P. gallopavo* has a moderate rate of sexual cannibalism (9%). This rate is comparable to that performed by *Schizocosa ocreata*, according to Scheffer et al. (1996) and Persons & Uetz (2005) (between 5–11.5%), but higher than the sporadic cases observed in *S. malitiosa*, *L. thorelli*, and *L. carbonelli*, according to Costa (1979) and Costa & Capocasale (1984). The single case of postcopulatory cannibalism we observed in this study coincided with the occurrence of frequent flubs of the male intromittent organ when he tried to insert.

This species is well suited to further studies of multimodal communication during sexual encounters and the inhibition of female aggression. These would provide useful new characters in phylogenetic studies of the family.

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