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ARTICLE

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Sexual coercion does not exclude luring behavior in the climbing camel-spider *Oltacola chacoensis* (Arachnida, Solifugae, Ammotrechidae)

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Abstract Sexual coercion in the form of forced copulation has been used as a typical example to illustrate the conflict of interests between females and males. Among arthropods, forced copulation has been reported for some groups of insects and crustaceans, but not for arachnids. In the present work, we analyse and describe the behavioral patterns of mating behavior of the climbing camel-spider, *Oltacola chacoensis*, relating it to relevant morphological features, In this species, the male forcefully clasps the female's genital region with his chelicerae and locks her fourth pair of legs with his pedipalps. In some cases, the cuticle of the female's abdomen was damaged by this cheliceral clasping. In contrast to other camel-spiders, the female *O. chacoensis* never remained motionless during mating, but continuously shook her body, opening her chelicerae notably towards the male. Despite this coercive context, males performed copulatory courtship (tapping with pedipalps) and females showed an apparent cooperative behavior (they remained still during a short period of the sperm transfer phase). These results strengthen the idea that sexual coercion (in the form of forced copulation) and luring behavior (in the form of copulatory courtship) are not two mutually-exclusive male's strategies during a single copulation.

Key words Sexual coercion · Forced copulation · Sexual dimorphism · Clasping structures · Copulatory courtship · Arachnids · Camel-spiders

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Introduction

Although behavioral biologists accept the existence of a conflict of interest between males and females, there is no consensus on how this conflict could affect intersexual interactions, such as courtship and copulation. Currently, there are two main hypotheses to explain the function and evolution of the sexual traits involved in mating. The "female choice hypothesis" proposes a context of selective cooperation in which females have the chance of choosing between males according to their qualities and/or the female's own sensorial-biased preferences, before, during or after mating (good genes and runaway-process – Andersson 1994; Kokko et al. 2003). This hypothesis predicts that males will lure females by sexual stimulation (rather than physical coercion) to convince females to copulate and/or to influence cryptic female choice (Eberhard 1996). In addition, this hypothesis predicts that female resistance during mating could be discriminated to certain males, acting as a "screening" mechanism to choose the best mate by evaluating endurance/persistence for sexual stimulation (Eberhard 2002a). The female choice hypothesis is criticized by the defenders of the sexually antagonistic coevolution hypothesis (Arnqvist and Rowe 2002; Chapman et al. 2003). It predicts that males evolve coercive adaptations to overcome indiscriminated female reluctance and that, subsequently, females also evolve adaptations to counteract advantages developed by males to control reproductive events (Chapman et al. 2003; Moore et al. 2003). A classical example of this "arms race" (Holland and Rice 1998) is the presence of anticlasper organs in females of the water strider *Gerris incognitos*. These are used to hamper the performance of the corresponding clasping apparatus of males during copulation (Arnqvist and Rowe 1995).

In the context of the later hypothesis, sexual coercion in the form of forced copulation (Smuts and Smuts 1993; Clutton-Brock and Parker 1995) has been documented in many taxa, including some groups of insects (for reviews, see Thornhill and Alcock 1983; Choe and Crespi 1997; Vahed 2002). Although sexual coercion is associated with existence of sexually antagonistic coevolution, its mere presence does not necessarily imply that this type of coevolution occurs (Pizzari and Snook 2003). Traditionally, sexual coercion and luring behavior have been seen as opposing male strategies (Clutton-Brock and Parker 1995; Eberhard 2002a, b). Therefore, it is not expected that males will perform sexual stimulation before or during copulation if they force females to mate. However, both options can occur as alternative male strategies in a single species (e.g., Thornhill 1981 in the scorpion fly *Panorpa*; Sakaluk et al. 1995 in sagebrush crickets; Bissaza et al. 2001 in poecillid fishes; Okada and Hasegawa 2005 in a Japanese stag beetle; Watters 2005 in coho salmon).

The present work focuses on these topics, describing a case in which sexual coercion does not exclude luring behavior during a single copulation in a species of camel-spider (Arachnida, Solifugae). There are available data on mating behavior only for three out of seven families of this amazing group of arachnids: Galeodidae (for three species of *Galeodes* and *Othoes saharae*), Solpugidae (for *Metasolpuga picta*) and Eremobatidae (for four species of *Eremobates*) (Punzo 1998). With exception of some harvestmen (e.g., Edgar 1971; Mora 1990; R.H. Willemart et al., in preparation), courtship includes many behavioral patterns, and females seem to control mating sequences in most arachnids (e.g., Thomas and Zeh 1984; Weygoldt 1990; Eberhard 1996; Elgar 1998; Peretti and Carrera 2005). In camel-spiders, however, previous data on sexual behavior might indicate presence of some coercive traits (Muma 1966a; Punzo 1998; A.V. Peretti and E. Maury, unpublished data). For example, some male camel-spiders quickly and vigorously clasp the female by means of their large chelicerae at the beginning of mating (Punzo 1998). In addition, male cannibalism to reluctant females has been observed in some eremobatid species (Muma 1966a) whereas female cannibalism to courting males is more frequent in scorpions and spiders (e.g., Elgar 1992; Peretti et al. 1999). These results may be an artifact of laboratory confinement, but the animals were well-fed and maintained prior to mating (Muma 1966a, b). Because of the risks of being cannibalized, Thomas and Zeh (1984) concluded that pairing may incur considerable costs in these arachnids. Indeed, this intraspecific cannibalism had been one of the main reasons that have limited observations on mating.

Following the typical sexual pattern described in galeodids (Heymons 1902; Punzo 1998), mating starts when, after approaching cautiously, a male quickly grasps the female with his pedipalps, causing the female to adopt a torpor-like state that lasts the entire mating. The male clasps the female with his chelicerae and massages the ventral region of her body and then inserts the tips of the chelicerae into her genital opening. Apparently, the male opens the female's genital opening by means of a series of chewing motions of his chelicerae (Punzo 1998). He then deposits, on the substrate, a spherical spermatophore, which is picked up with his chelicerae and inserted into the female's genital opening. The male runs off rapidly before the female recovers from her lethargic state. There are some differences from this general pattern depending on the family and species (Punzo 1998). For example, Junqua (1966) observed that in the galeodid *O. saharae*, the male directly grips the female without any prelude, using his pedipalps to tap her body after this initial contact. This author also highlights the existence of cheliceral massages on the female's genital opening before leaving, which may facilitate the release of spermatozoa from the transferred spermatophore.

Eremobatid species differ from the described pattern (Muma 1966a, b; Punzo 1998), in that the male emits a droplet of seminal fluid from his genital opening directly onto the female's genital opening. Thereafter, the male thrusts his chelicerae into her genital opening with a series of chewing movements, apparently to force the sperm into a storage area (Muma 1966b; Punzo 1998). In addition, female lethargic state is less notable in this family. Muma (1966a) identified three main phases associated with mating behavior in eremobatids: (1) initial attack phase, which includes all activities of males and females prior to sperm transfer, (2) contact phase, which includes their actions during sperm transfer, and (3) release phase, comprising their actions following sperm transfer. This operational division of the mating is useful and can be applied, with their respective particularities, for other species of families of solpugids.

Even though earlier descriptions of the main characteristics of sexual behavior in camel-spiders have been valuable, there are many aspects that were not examined. For example, whether the male forcefully uses the chelicerae to open the female's genital opening prior to sperm transfer remains unclear. Apparently, in *O. saharae* the male might force the female's genital opening (Junqua 1966) while in *Galeodes granti* the female lifted her abdomen allowing him to grasp her genital area with his jaws (Cloudsley-Thompson 1967). Furthermore, there are no published data quantifying patterns of female resistance prior to and during mating, and it is not known whether male clasping can damage the female.

The present study has three objectives: (1) to describe the mating behavior of the climbing camel-spiders *Oltacola chacoensis*, a species belonging to Ammotrechidae, a family that has not been studied, (2) to examine in both sexes the morphology of the principal traits involved in the mating, and (3) to identify behaviors and traits that indicate either presence of sexual coercion or luring behavior during mating, and interpreting the data in the light of current hypotheses on this topic.

Material and methods

Study species: collection and rearing

Oltacola chacoensis is a nocturnal camel-spider that inhabits Argentina from Patagonia to the "Salinas Grandes" region of the Province of Córdoba (A.V. Peretti and E. Maury, unpublished data). Typically, the individuals climb shrubs and remain motionless on the tip of the branches waiting for prey such as beetles and moths (A.V. Peretti and

C. Mattoni, unpublished data). The mating season is limited for 2 months (November and December). During this period, males show a high locomotory activity, searching for adult females that usually are motionless on the branches. Oviposition occurs in January (A.V. Peretti and C. Mattoni, unpublished data).

Males and females were collected as adults during the years of 1999, 2000, 2001 and 2004 near San José de las Salinas, Córdoba, Argentina (64°48′S 30°02′W). We used a UV-light portable lamp to detect individuals during the night (they show a light-blue fluorescence under this light). Animals were kept individually in cages of different sizes, all of which were furnished with a piece of tree bark. *Blaptica dubia* (Insecta, Blattodea, Blaberidae) nymphs and *Tenebrio molitor* (Insecta, Coleoptera, Tenebrionidae) larvae and adults were provided as food twice a week. Moist cotton balls were used to maintain humidity, and the temperature varied from 23 to 32°C. All animals were kept under a light:dark cycle of 12:12 hours. We began our observation approximately at 2000 hours, in the first hours of the dark phase.

Data collection and analysis of behavior

We placed male–female pairs in mating arenas ($60 \times 22 \times 35$ cm) with a substrate of soil, stones and pieces of tree bark from the capture sites, and observed sexual interactions using two 40-W red lamps. We conducted observations during three mating seasons, from 1999 to 2003. We recorded the behavior of both sexes, paying special attention to the occurrence of cannibalism and the percentage of complete and incomplete mating sequences. We recorded verbal descriptions of six sexual interactions (three incomplete and three complete matings) on audiocassettes, noting the timing and frequency of all behaviors. Seven sequences (four incomplete and three complete matings) were recorded on video, using a digital video-camera (SONY DCR-TRV 351) equipped with +4 close up lenses and the "night shot" function. In summary, the description of mating in *O. chacoensis* was based on the observation of 13 mating attempts (that involved 13 different pairs), 6 of which were complete and 7 of which were incomplete (the pair interrupted the contact prior to sperm transfer).

Careful positioning allowed close-up views of movements of males and females, in particular of both of the male's chelicerae in the female's genital opening. Events were transcribed from videotapes and audiocassettes using the program for the analysis of behavior JWatcher 0.9 (©2000 D.T. Blumstein, C.S. Evans & J.C. Daniel). Behavioral patterns were identified following the literature on camel-spiders, adapting the terminology for mating phases from Muma (1966a, b). Complementary to general ethological analysis, we examined all the videotaped sequences of mating on computer, frame-by-frame, using the Adobe Premier and Video Analysis for Windows (version 2) programs. This step was important in order to detect – once the female was clasped by the male – subtle details in movements or positions that could indicate cooperative or forced acceptance to mate. Mean values are presented ± one standard deviation. We used parametric (for data which fulfilled the requirements without transformation) and nonparametric tests for comparisons between quantitative data of behavior and morphology. Tests were two-tailed with α set to 0.05. Both in females and males, willingness to perform a new courtship with a new male (i.e., different from the previous male) was observed daily.

External morphological traits associated with mating

Before and after mating we also examined both the morphology and conditions of the female's genital area (operculum, genital opening), and the parts of the male's chelicerae used to clasp the female and to transfer sperm (fixed and mobile fingers and flagellum). In addition, we also measured, in males and females, other traits involved in body contacts during mating, such as sizes of pedipalps, forelegs and raquet organs (a series of triangular malleoli placed on the ventral surface of the hind legs that function in chemoreception – Punzo 1998). For all the sequences, body size of the male and the female were estimated using the combined length of the chelicerae and propeltidium referred to as the "CP index" (Brookhart and Muma 1981). All the materials were preserved in ethanol (70%). We used a SONY DSC-40 CyberShot camera for photography of these dissected specimens under a stereomicroscope. Two voucher specimens (one male and one adult female) have been deposited at the Arachnological Scientific collection of the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina.

Results

Reproductive status and mating

Males only gripped mature females that were in reproductive condition (with the abdomen repleted of eggs) (see Fig. 4). Both sexes ran quickly away, in opposite directions, if the female was not mature. Out of 40 male–female encounters observed, 11 resulted in cannibalism (against males in six cases).

Attack phase of mating

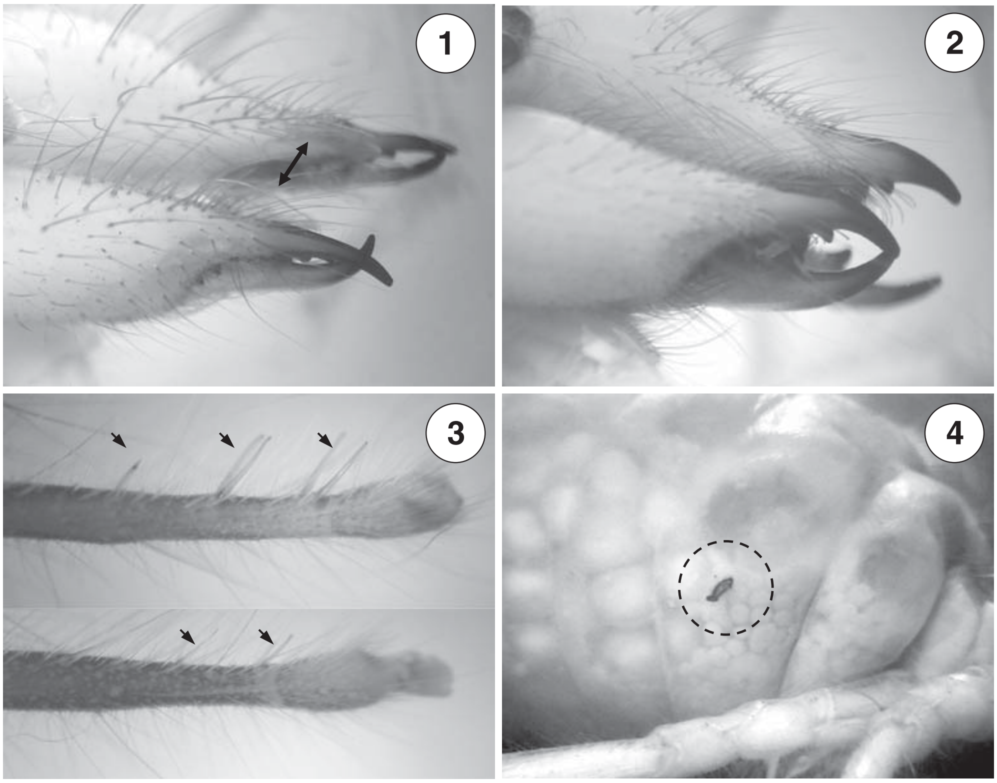
This phase started when the male gripped the soft cuticle of the female's abdomen with his chelicerae, and ended when he clasped her genital operculum with them. Mean duration of this phase was 4.75 ± 1.78 s (range 2.45–7.16 s, $n = 13$). The male uses the chelicerae like a pair of pincers. Sexual dimorphism associated with this function is evident, because not only is a spoon-like flagellum present in the internal face of each male's chelicera (a typical character of the family Ammotrechidae), but males also have large chelicerae (Table 1) showing their tips very curved and crossing one another (Figs. 1, 2). Sexual dimorphism was also

Table 1. Measures of some body traits of adult males and females involved in the mating of *Oltacola chacoensis*

Traits	Mean (± SD)		Test	P
	Male ($n = 20$)	Female ($n = 20$)		
Body size (CP index)	9.75 ± 1.37	10.31 ± 2.28	$U = 27.5$, $z = -0.472$	0.32
Chelicerae				
Total length (fingers + hand)/hand width	2.93 ± 0.26	2.73 ± 0.48	$U = 46$, $z = 2.083$	0.018
Fixed finger length/hand length	0.70 ± 0.05	0.59 ± 0.09	$U = 52$, $z = 2.78$	0.003
Distance from first tooth to the tip of fixed finger/fixed finger length	0.32 ± 0.03	0.33 ± 0.04	$U = 34$, $z = -0.695$	0.26
Pedipalps				
Absolute length	27.85 ± 2.97	21.56 ± 2.10	$t = 4.876$	0.0001
Relative length (absolute length/body size)	2.87 ± 0.18	2.14 ± 0.31	$U = 64$, $z = 3.360$	0.0004
Forelegs				
Absolute length	20.4 ± 2.19	16.33 ± 1.65	$t = 4.182$	0.0005
Relative length (absolute length/body size)	2.10 ± 0.12	1.61 ± 0.19	$t = 5.969$	0.00004
Raquet organs[a]				
Absolute length	3.52 ± 0.34	2.04 ± 0.27	$t = 12.515$	0.0000001
Relative length/body size (propeltidium length)	2.10 ± 0.12	1.61 ± 0.19	$t = 5.969$	0.00001

t Student-two samples test, *U* and *z* Mann–Whitney *U* test

[a] For this comparison the data used correspond to the distal raquet organ (the other four raquet organs present the same morphometric pattern)

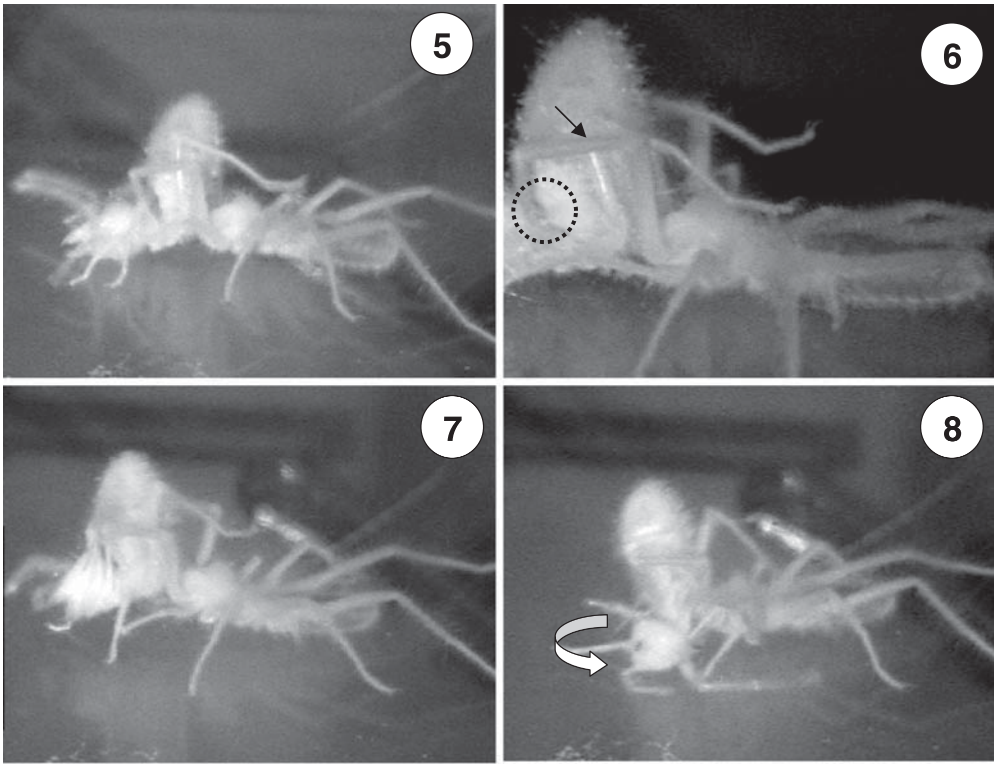


Figs. 1–4. Sexual dimorphism in chelicerae and pedipalps. **1** Male's chelicerae. **2** Female's chelicerae. **3** *Arrows* indicate the large spines on the ventral region of pedipalps in males (*above*) and homologous spines in females (*below*). **4** Cuticular damage in female's abdomen caused by male's palpal spines during the behavioral pattern "encircling" (see also Fig. 6). Note the eggs in the female's abdomen (on the *left*). More explanations in the text

observed in the density and shape of the setae of the dorsal portion of the chelicerae; they are less abundant but larger and harder in males (Figs. 1, 2). Interestingly, these hard setae remain strongly pressed against the female's perigenital region during the contact phase of mating.

Males were able to grip females with the jaws by the anterio-lateral portion of the abdomen (46.15% of sequences, $n = 13$) or the last abdominal tergite (53.85%). There were no significant differences between these two types of grasping, even when sperm transfer occurred later (Fisher's exact test: $P = 0.395$). There were no lesions of the cuticle of the female's body when she was clasped by the end of the abdomen. However, the cuticle was damaged in three out of six cases in which the female was clasped by the soft abdomen pleura. Males were able to hold the genital region faster, starting the contact phase (see below) when the female was initially gripped by the tip of her abdomen (3.5 ± 1.8 s vs 6.1 ± 2.3 s of lateral grasping; Mann–Whitney *U* test: $U = 43$, $z = -2.953$, $P = 0.002$)

.During the attack phase, while keeping the female grasped, the male performed two behavioral patterns: encircling and tapping. During encircling, he used his pedipalps



Figs. 5–8. Digital video images showing male cheliceral clasping of female genitalia. **5**, **6** Male pedipalps locking of the female's fourth pair of legs (*arrow*). The *dotted circle* shows the place where the spines of male's pedipalps anchor against the female's abdomen. **7**, **8** Sequence of a female shaking: **7** The female opens her chelicerae and starts to curve her body; **8** She tries to grasp a male's leg with her chelicerae at the end of this behavioral pattern

to clasp her abdomen and to lock her hind legs (Figs. 5, 6) so that she was not able to rest the racquet organs and tarsus of these legs on the ground. The distal spines of the male's pedipalps remain pressed against both sides of the female's abdomen, injuring the cuticle in some cases (detected in six females) (Fig. 4). The male's pedipalps are adapted to this complementary clasping function: they are larger than the female's pedipalps (Table 1) and have larger distal spines (Fig. 3). The male performed tapping of the female's body with his forelegs (sometimes the second pair of legs participated but more slightly). Tapping continued during all the mating, being interrupted only when the male deposited the sperm drop on the substrate. Body parts involved in encircling and tapping behaviors show sexual dimorphism in size: male's pedipalps and legs are significantly larger than those of the females (Table 1). The male then started to redirect his chelicerae until reaching the female's genital region (Fig. 14), never stopping encircling the female. During all this phase the female shook her body sideways.

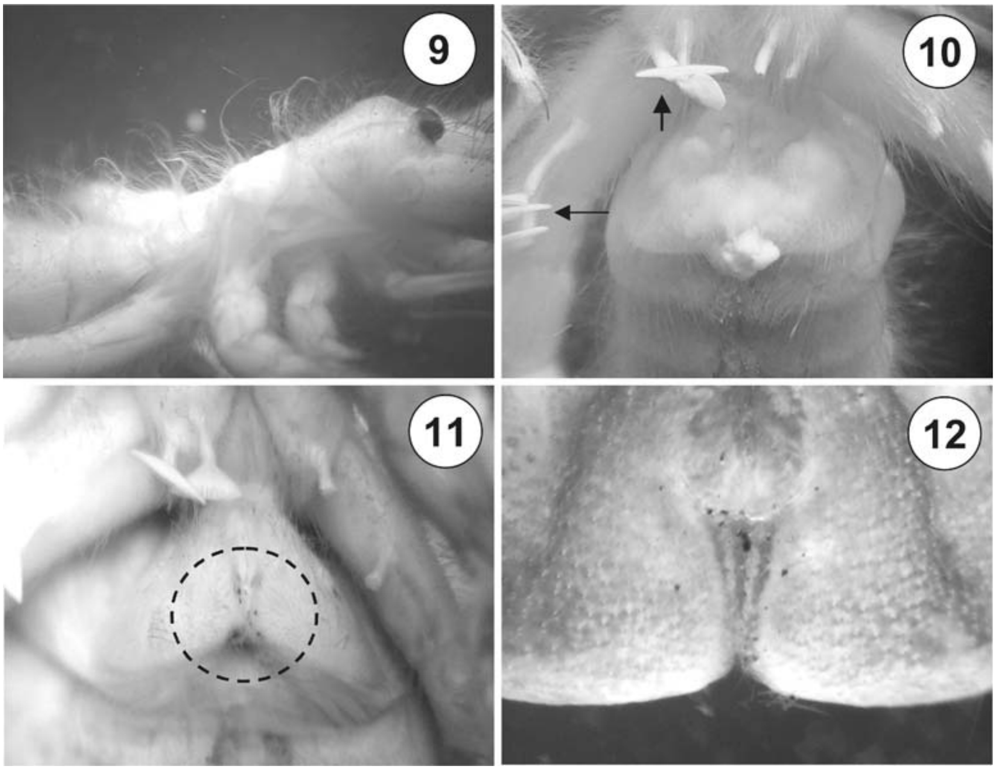
Contact phase of mating

Pre-sperm deposition behavior

During this phase, the male pushed the female continuously in a perimeter of approximately 4–7 cm^2. The male used the mobile fingers of his chelicerae to clasp the female's genital operculum, whereas the fixed fingers were inserted into the genital opening. Males gripped the operculum by its medial triangular depression, a characteristic present only in females (Figs. 10, 11, 12). During the initial stage of this genital clasping, the male pulled the female forwards, which facilitated a rapid intromission of the cheliceral fixed fingers into her gonopore. Fine analyses of the digital videos allowed us to determine that the female never opened her genital opening (e.g., by moving her operculum forwards) before the genital clasping by the male took place. It was observed that the back of the male's mesopeltidium and metapeltidium is covered by a dense layer of thin and long hairs (Fig. 9), a characteristic never previously reported for camel-spiders. It was on this region where the ventral part of the female abdomen rested during the contact phase.

Not all male–female interactions that completed the contact phase resulted later in sperm transfer because 7/13 (53.85%) sequences were interrupted during this phase, parting both sexes in opposing directions. Apparently, this interruption occurred because of intensive female shaking (see below). Male–female size ratio was not different between complete (0.79 ± 0.14, $n = 6$) and interrupted matings (0.72 ± 0.12, $n = 7$) (Mann–Whitney U test: $U = 25$, $z = 1{,}121$, $P = 0.26$). Mean duration of interrupted matings was 46.57 ± 16.60 s, which is significantly lower (Student-two samples test: $t = -5.770$, $P = 0.00012$) than the entire duration of complete matings (144.33 ± 41.34 s) but longer than the pre-sperm deposition stage of the contact phase of complete matings (26.0 ± 5.93 s) (Student-two samples test: $t = 3.058$, $P = 0.0081$)

All females vigorously shook their bodies during this and the other phases. Indeed, this was the most conspicuous female behavior. In complete matings this behavior occurred more frequently after the sperm deposition phase



Figs. 9–12. **9** Lateral view of male's prosoma showing the dense layer of thin and long hairs covering the mesopeltidium and metapeltidium. **10**, **11**, **12** Sexual dimorphism in genital operculum. **10** Male's operculum. Note the sperm extruded in the genital opening (produced by fixation in ethanol) and some raquet organs on the *left* (male's right side, *arrows*) (those on the *right*, that is, male's *left side*, were removed for measurement); **11** General view of the female's operculum; **12** Details of the *dotted* area of **11** showing the medial cavity of the operculum where the male anchors the mobile fingers of his chelicerae during mating

(Fig. 13). While shaking, the female curved the prosoma towards the male, opening her chelicerae to his position (Figs. 7, 8). The male then prevented being gripped by pushing the female forwards and curving his body laterally to place his legs distant to the female. Shaking rate (absolute number of shakings/duration of mating phase) was significantly higher in interrupted matings than in the entire duration of complete matings (Mann–Whitney *U* test: $U = 39$, $z = -2.571$, $P = 0.004$) (Fig. 13). Furthermore, all mating interruptions were always preceded by a vigorous shaking.

Sperm-deposition and pre sperm-transfer behavior

Emergence of the sperm drop from the male's gonopore (Fig. 15) and its subsequent deposition on the substrate lasted less than a second. The male then released the female's operculum to pick up the sperm drop (Fig. 16). Typically, after a short backward movement, the male picked the sperm up with the tarsae of his forelegs and placed it between the flagella of the cheliceral fixed fingers. During this action, the male continued to encircle and tap the female. In addition, the male moved his pedipalps vigorously upwards and downwards on the female so that her body was rotated sideways. During all this rotation, and until the reinsertion of chelicerae took place, the female continued to shake her body, always opening notably her chelicerae (see Fig. 16). She never closed her genital opening during this brief non-clasping stage. All these mentioned actions occurred in a short period that, from sperm deposition until chelicerae reinsertion, lasted only 2.26 ± 0.25 s (data from three videotaped sequences).

Sperm-transfer behavior

Sperm transfer began 23 ± 2.7 s after the start of contact phase in the six complete matings. Simultaneously to the cheliceral reinsertion into the female's genital opening, the male stopped abruptly the rotation of the female and intensified the tapping on her second and third pair of legs (Fig. 17). The male then started to move intensely the fingers of chelicerae. Mobile fingers were alternately moved from the middle to the lateral side of the external cavity of the female's operculum. The male and the female stopped almost all the movements (except for male chelicerae) 5.0 ± 0.15 s after the start of the reinsertion. This motionless stage lasted 17.6 ± 2.08 s.

Post-sperm transfer behavior

The male restarted the movements by tapping the female again during approximately 30 s. In contrast to the sperm transfer stage, male cheliceral movements were less evident, almost null, during this last mating phase. Progressively, the female shook her body more intensely, turned her prosoma back, towards the male, and opened her chelicerae. Female shaking was a very characteristic behavior of the post-sperm transfer phase. Indeed, on average, 88.4 ± 5.2% of all the shakings of a complete mating appeared during this phase ($N = 233$ shakings from seven matings) (Fig. 13). The female moved continually during this phase, and pulled the male, that continued clasping her genitalia with the chelicerae. She also tried to grapple branches or stones with her chelicerae, possibly to perform a better traction.

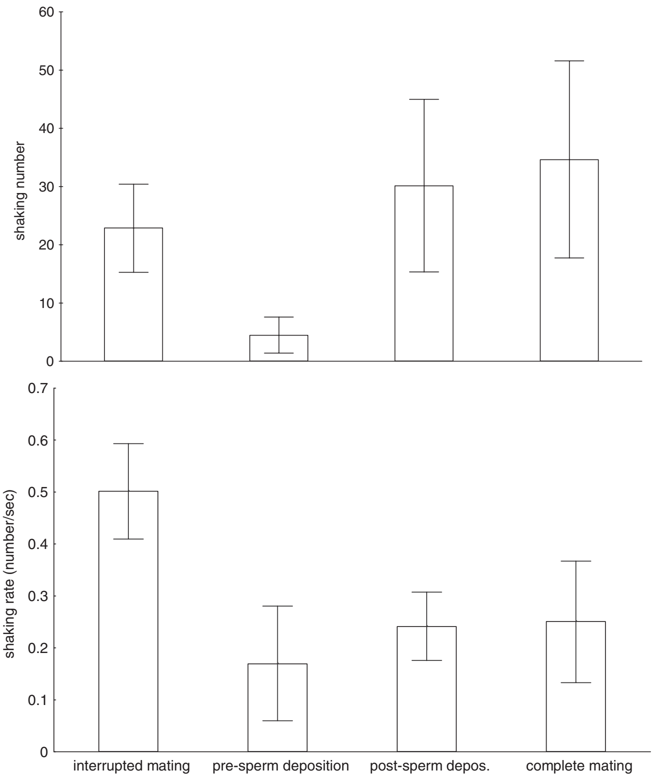


Fig. 13. Absolute number (*above*) and rate (*below*) of shaking behavior of females *O. chacoensis* during interrupted and complete matings (pre-sperm and post-sperm deposition are also shown). Vertical axes: *above* absolute shaking number; *below* shaking rate (shaking number per second). *Bars* represent mean values with standard deviations

Release and subsequent events

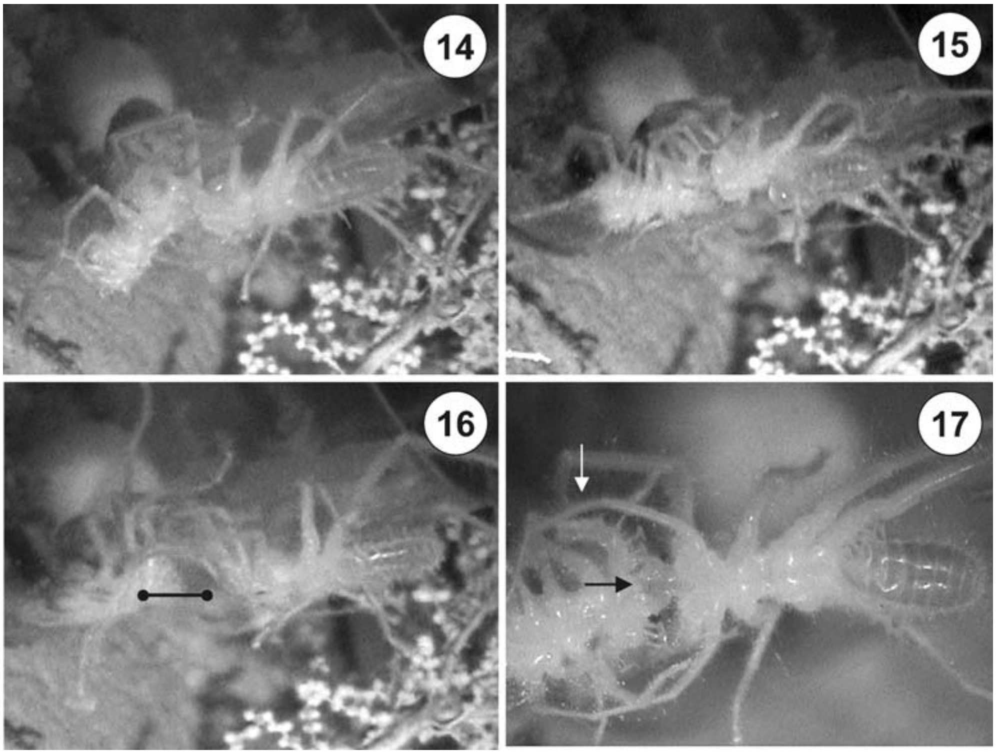
Finally, the male released the female genital area and then both individuals ran off rapidly in opposite directions. Post-sperm transfer cannibalism was never observed. Only 1/6 of the inseminated females were sexually receptive for a new mating, whereas 2/6 of males mated again from 1 day after a previous sperm transfer. Of the six inseminated females, two died before oviposition. They presented damage in the cuticle of the operculum and in the abdominal pleura, both produced by male clasping. Indeed, these two females had initially been grasped by the pleura. It is important to point out that the lesions had not been observed during examination of the individuals under light microscope before mating. The mean time from the mating to the oviposition was 21.4 ± 6.3 days. All the females laid the eggs on the sand, and remained near them during 2 or 3 days. The clutch size was of 36.8 ± 12.8 eggs ($n = 4$ females). All the females died within approximately 2 weeks.

Discussion

Evaluation of the principal coercive traits

The mating of *O. chacoensis* appears as the most vigorous among the species of camel-spiders studied to date. In addition to the strong and continuous male cheliceral clasping of the female's genitalia, *O. chacoensis* mating shows at least four principal characteristics that were not observed in other species, and that indicate presence of sexual coercion:

Figs. 14–17. Digital video images showing the sperm-deposition and sperm-transfer phases (in this sequence copulation occurred on the glass wall of terrarium, so in these pictures the pair is viewed from the ventral face of body). **14** The male keeps the female grasped by her genitalia with his chelicerae before sperm deposition. **15** Sperm deposition (*arrow* indicates the sperm drop emerging from the male's genital opening). **16** The male picks the sperm up and the female starts shaking (the *line* shows the interdistance between male's chelicerae and the female genital area. The female was released by the male for less than a second in order to pick the sperm up. **17** Sperm transfer. The male has restarted cheliceral clasping of female genitalia (*black arrow*), anchoring the mobile fingers in the medial groove of her operculum. Note that the male's forelegs (*white arrow* indicates the left foreleg) are tapping the female's body from both sides



Lack of pre-clasping courtship and lethargic state in females

Male *O. chacoensis* did not perform any courtship behavior before clasping the female. In contrast, in all the studied species of Gaelodidae, Solpugidae and Eremobatidae males initially touch or stroke the female with the pedipalps before clasping her abdomen with their chelicerae (Punzo 1998). Furthermore, female *O. chacoensis* never ceased all bodily movements. She did not become lethargic after clasping, and shook her body energetically during the entire mating bout. In contrast, this torpor-like state is the typical behavioral pattern that females adopt after being initially touched by the male in the above mentioned families (although the lethargic state is less pronounced in Eremobatidae), and persists during the entire mating. The female recovers from her lethargic state immediately after the male moves quickly away. Cloudsley-Thompson (1961) suggested that in the female of *Galeodes arabs*, the lethargic state might be induced by the palpal stroking performed by the male during courtship. Punzo (1998) summarized previous ideas on the torpor-like state adopted by females, indicating that a complete induction of a lethargic state in the female (and prevention of her counter-attack) is dependent upon a combination of the initial contact of her body with his pedipalps and the rapidity by which the male then clasps the female with his chelicerae. In *O. chacoensis*, however, male clasping did not induce the female to adopt a lethargic state. Interestingly, in a species of *Nothopuga* (Ammotrechidae), in which the male performs a pre-clasping courtship, the female becomes lethargic once she is tapped by the male's pedipalps (A.V. Peretti, unpublished data). Therefore, whereas male *O. chacoensis* exhibit the most direct and forceful clasping among camel-spiders, females show the most conspicuous resisting behavior.

Continuous clasps of the female's hind legs

Among camel-spiders, only in *O. chacoensis* the male maintain a tight and constant grip of the female with his pedipalps, seizing her hind legs off the ground. What is the function of leg locking in *O. chacoensis*? Combined to cheliceral clasping, palpal clasps may function as a complementary male device to prevent the female fleeing during mating. Although in other species male pedipalp clasp of the female body was observed, this behavior was never performed on the hind legs, which are the most robust and locomotory legs. For instance, in the galeodid *O. saharae* the male surrounds the female body slightly, only touching her pedipalps and thin forelegs, whereas her last two pairs of legs rest freely on the substrate. In eremobatid species, the male only surrounds the third pair of legs of the female during the position "A" of the mating of this family (Muma 1966a, b; Muma and Muma 1988), but never taking it away from the substrate. Perhaps the most similar pattern to that observed in *O. chacoensis* appears in the gaelodid *G. arabs*, where in Fig. 2 of his work Cloudsley-Thompson (1961) illustrated a male lifting the second, third and female's hind legs. However, this behavior occurred after the female became completely lethargic and, as a result, showed her legs very relaxed. In contrast, male *O. chacoensis* locked the female's legs strongly to prevent her from escaping and, additionally, to avoid being injured. This is because by means of this behavior he might limit her cheliceral movements towards him during her continuous shaking. The locomotory limitation imposed on the female by this firm leg-locking was clearly observed during the post-sperm transfer stage, when she moved very slowly and heavily because lack of the propulsion of her last pair of legs. Indeed, this inhibited a rapid separation from the male, who remained with his chelicerae anchored to her genitalia. Leg-locking behavior was structurally similar between interrupted and non-interrupted mating. In both groups, separation took place not because the female was able to put her fourth pair of legs down but because the male released her genital operculum due to her continuous shaking. Interestingly, mating leg-locking behavior seems to be a typical camel-spider feeding behavior: both male and female *O. chacoensis* use their pedipalps to encircle and fasten the prey immediately after capturing (Punzo 1998; A.V. Peretti, unpublished data).

Intense female shaking

This behavioral pattern has never been observed in other camel-spiders. Even though we cannot discount the fact that this behavior could have been overlooked by previous authors (e.g., because they rarely filmed mating sequences) it seems logical that the widespread presence of a lethargic state in females during mating in the other camel-spider species indirectly suggests lack of any type of female resistance such as this shaking behavior. The principal characteristics of the shaking behavior (i.e., vigorous turning of the body with chelicerae wide opened towards the male) may indicate that females performed it as an attempt to grasp the male and/or to modulate the cheliceral pressure on her genitalia. At least in the studied sample, the male avoided being grasped by moving his body laterally just when she approached her chelicerae to his legs. That the male may control, at least partially, female shaking became evident when, prior to sperm transfer, he released her body for a few milliseconds to pick up the sperm with his chelicerae, a period during which the female performed the most vigorous shaking observed, almost reaching the male's legs with her opened chelicerae.

Interestingly, the male performed a forceful side-to-side semirotation of the female's body during this non-cheliceral clasping phase. Males may use this behavior to disturb the female, preventing her running away. Although it cannot be stated that the female shook her body to interrupt mating attempts, it seems possible that this could have been her purpose in many cases, just as after the sperm-transfer stage of complete sequences. Indeed, the shaking rate was very high in the interrupted mating sequences and during the post-sperm transfer stage of complete matings. Therefore, by means of this behavior, and in combination with forced locomotion, females may be able to indirectly reject some males and modulate, at least partially, mating duration.

Cuticular damage caused by male clasping

This phenomenon had not been reported before for camel-spiders. The presence of injuries was not related to whether the matings were complete or interrupted. We did not detect, in the laboratory, that injured females died before the non-injured females. However, mortality of camel-spiders, including *O. chacoensis*, is very high in captivity (Punzo 1998; A.V. Peretti and E. Maury, unpublished data), a fact that may make it difficult to detect differences between the two groups. We cannot discount the fact that cuticular damage may have negative effects on the reproductive lifetime of females in the field. More studies are needed to explore the potential costs that females may incur.

Thus the results of our observations of *O. chacoensis* are evidence of the existence of a coercive context during mating, in which males force females to copulate and females continuously try to break the grip of such coercive males. In contrast to this type of intersexual interaction, males of other well–studied arachnids, such as spiders (e.g., Andrade 1996; Elgar et al. 2000; Eberhard 2004; Persons and Uetz 2005; Snow and Andrade 2005; Peretti et al. (2006) and scorpions (e.g., Polis and Sissom 1990; Benton 2001; Tallarovic et al. 2000; Peretti and Carrera 2005; Contreras et al. 2006), usually show elaborated luring behavior during courtship, and females clearly control events during copulation. However, upon re-review of videotapes from previous studies of mating in the wolf-spider *Schizocosa ocreata*, Johns and Uetz (2005) have recently found that forced copulations sometimes occur (13% of mating trials) in this species. Subsequent examination also revealed cuticular wounds oozing hemolymph, which were not seen in consensual matings (Johns and Uetz 2005). Also, coercive behaviors apparently occur during copulation in some harvestmen (Edgar 1971; R.H. Willemart et al., in preparation) and during a part of the sperm-transfer phase in some scorpions (Peretti 2003, unpublished data). Therefore, male coercive behavior during mating in arachnids may appear more frequently than was previously estimated. In particular, *O. chacoensis* mating is similar to that of some species of insects in which forced copulation occurred in all of the mating trials (Clutton-Brock and Parker 1995). For example, Arnqvist (1997) and Hosken et al. (2003), observed, in water striders and sepsid flies respectively, forceful male clasping on females that indiscriminately always resisted mounting males by shaking the body vigorously during the entire copulation. In a bushcricket species, Vahed (2002) highlighted the lack of precopulatory courtship in all of the mating sequences, and presence of cuticular damage of the female's abdomen caused by male clasping. Crudgington and Siva-Jothy (2000) analyzed the causes and consequences of cuticular damage in female genitalia of the beetle *Callosobruchus maculatus*, and observed that the female tried to control copulation duration by continuously kicking her body.

Copulatory courtship and possible cooperative traits

In *O. chacoensis*, sexual coercion did not involve lack of some forms of female cooperation and male luring behavior during a single copulation. For instance, all females stopped shaking when males were transferring the sperm to their genital openings with the chelicerae. Indeed, it was only during this period of the mating that females were completely still. From a simplistic perspective, this behavior may be viewed as an obvious basic cooperation if females want to get enough sperm supply for their eggs. Another non-exclusive explanation is that the female remained motionless to prevent damage to her genitalia by the intense movements of the fixed fingers of the male's chelicerae. However, females restarted shaking before the chewing movements of male's chelicerae ended, so both behaviors co-occurred during the final part of the contact phase. Some results may support an alternative explanation: females might remain motionless during sperm transfer as a result of sexual stimulation by male cheliceral massaging movements. If we compare with other arachnids and insects, chewing movements of the male's chelicerae inside the female's genital opening could be interpreted as genitalic copulatory courtship (Eberhard 1996, 2001; Peretti 2003). However, male cheliceral movements would have influenced the female during a very short time, since they lasted many seconds whereas the female's motionless period occupied less than 1 s. Additional sexual stimulation could come from the male's pedipalps that sporadically rubbed the sensorial raquet organs (probably chemoreceptors – Brownell and Farley 1974) of the female during the palpal clasping of her fourth pair of legs.

The most evident copulatory courtship behavior of male *O. chacoensis*, which co-occurred with sexual coercion, was the tapping performed with the first and, more sporadically, the second pair of legs. This behavioral pattern began immediately after the female was gripped and continued during the sperm transfer phase. It is important to highlight the fact that the tapping of male *O. chacoensis* was detected after analyzing the digital videos of mating sequences in detail. Otherwise, we could have overlooked this behavior, since movements of the male's palps during tapping occurred at high speed. This copulatory tapping may influence the female to modulate, at least partially, her resistance. Also, males of other groups of arachnids and insects frequently use tapping or rubbing with legs as typical behavioral patterns during copulatory courtship (e.g., Eberhard 1991, 1994, 1996; Peretti 1997) and to influence cryptic female choice (Eberhard 1996; Edvardsson and Arnqvist 2000; Tallamy et al. 2002a, b; Bloch-Qazi 2003).

Interestingly, copulatory courtship can also occur during a single copulation in other animals in which sexual coercion has been reported. For example, Vahed (2002) observed that even though the copulation is clearly coercive in the bushcricket *Anonconotus alpinus*, males also perform copulatory and post-copulatory stridulation. This author suggests that stridulation might be expected to influence cryptic female choice in this species. Therefore, our results and these examples indicate that sexual coercion (in the form of forced copulation) and luring behavior (in the form of copulatory courtship) are not two mutually exclusive male strategies. Co-occurrence of these apparently opposing strategies in a single mating have not been explored in depth, and may suggest the possible occurrence of mixed behavioral evolutionary patterns in some groups, considering both a single species and different species (Peretti 2003). Indeed, this subject still awaits an integrative approach from both the sexually antagonistic hypothesis and the female-choice hypothesis (Chapman et al. 2003; Cordero and Eberhard 2003). In addition, an involuntary bias could have often occurred in our previous investigations on this subject, showing with more detail principally the more conspicuous behavioral and morphological data that are commonly associated with forced copulation or luring behavior, depending on the behavioral pattern and species. For instance, in some groups (e.g., winged insects, ducks, etc.) coercive behaviors could have attracted our attention more because they generally involve typical clasping organs in males and notable behaviors in females, such as shaking, kicking or stroking (Thornhill and Alcock 1983; Eberhard 1996). In addition, some male non-coercive patterns like slight male tapping or vibrations could be overlooked if they are performed at high speed. However, the opposite situation (conspicuous luring traits and slight coercive traits) may occur, and affect our perception and interpretation of the facts as well. For both cases, more fine-scaled behavioral observations of male–female interactions may help us to get more complete descriptions, useful to achieve a better understanding of the sexual behavior of our study animal.

Another trait that might indicate the existence of intersexual cooperation is the form of the external female genitalia. The female genital operculum does not show any type of anticlasper structure, but a shape (e.g., presence of a medial groove) that seems to facilitate male clasping with the chelicerae. However, this might reflect a "forced cooperation" that could have been developed to decrease the probability that male grasping damages the female genitalia (Chapman et al. 2003). The injuries observed in some females seem to support this possibility. But in another Ammotrechidae species in which the mating is not coercive (there is a pre-copulatory courtship and females adopt a lethargic state), *Nothopuga* sp., the morphology of the female's genital operculum is also complementary with the male's cheliceral fingers (A.V. Peretti, in preparation). Evidently, data on sexual behavior of more species of Ammotrechidae are needed to explore these alternative options. Finally, sexual dimorphism in raquet organs may be related to searching for mates, since a larger size of male raquet organs could optimize the ability to detect sexual pheromones produced by females to facilitate the encounter (Wharton 1987). Indeed, this was observed for the sexual dimorphism in sensorial structures of other arachnids (e.g., chemosensory sensilla in scorpion pectines and spider pedipalps – Tietjen and Rovner 1982; Gaffin and Brownell 2001). However, as for many other biological aspects, chemical communication is a very unexplored area in this amazing but neglected animal group.

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