

COURTSHIP AND SPERM TRANSFER IN THE WHIP SPIDER *PHRYNUS GERVAISII* (AMBLYPYGI, PHRYNIDAE): A COMPLEMENT TO WEYGOLDT'S 1977 PAPER

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ABSTRACT. The aim of this study was to provide descriptive and quantitative data regarding behaviors involved in courtship and in sperm transfer of the whip spider *Phrynus gervaisii* (Pocock 1894) in order to complete the previous description for this same species given by P. Weygoldt. The specimens were captured in anthills of *Paraponera clavata*, on Barro Colorado Island, Panama. Ten courtship and five sperm transfer sequences were recorded. Four out of five mating sequences with sperm transfer occurred between adults with similar body size and in the other case the female was smaller than the male. Sexual interactions did not occur between very small adults. Two male behavior patterns that have not been reported were observed during the initial stage of courtship: “pedipalp rubbing” and “female operculum rubbing”. Contrary to Weygoldt’s description, in this study the female never performed “shaking” movements with her antenniform legs. It was observed that the two distal horn-like extensions of the spermatophore facilitate the females movements during the sperm transfer. The distal part of the spermatophore stalk provides a suspension area when the female rests on those horns. It was verified that the female can move the claw-like sclerites of the gonopods in all directions. The male executed copulatory courtship and successfully transferred sperm in five analyzed sequences. The female did not pick up the sperm packages when copulatory courtship was not performed. Males that lacked one antenniform leg were able to mate, however they had to perform vibrations more intensely with their non-injured leg for a longer duration. The data are compared with those previously obtained in other whip spiders. Some functional characteristics of the spermatophore and female genitalia of *P. gervaisii* are also discussed.

RESUMEN. El objetivo de este trabajo es aportar datos descriptivos y cuantitativos sobre patrones de comportamiento que ocurren durante el cortejo y transferencia espermática del amblipígrado *Phrynus gervaisii* (Pocock 1894) con la finalidad de completar la descripción previa de P. Weygoldt para esta misma especie. Los especímenes fueron capturados en hormigueros de *Paraponera clavata*, en la Isla de Barro Colorado, Panamá. Se registraron 10 secuencias de cortejo y cinco de transferencia espermática. Cuatro de las cinco secuencias de apareamiento con transferencia espermática completa ocurrieron entre adultos de tamaño corporal similar mientras que en el otro caso la hembra fue más pequeña que el macho. No se produjeron interacciones sexuales entre adultos muy pequeños. Durante la etapa inicial del cortejo fueron observados dos patrones de comportamiento masculinos que no habían sido citados con anterioridad: “roces de pedipalpos” y “roces al opérculo genital femenino”. Al contrario de la descripción de Weygoldt, en el presente estudio la hembra nunca realizó movimientos de “latigqueo” con sus patas anteniformes. Se observó que las dos expansiones distales con forma de cuerno del espermatóforo facilitan los movimientos de la hembra durante la transferencia espermática. La parte distal del tallo del espermatóforo ofrece un área de suspensión cuando la hembra se apoya sobre estos cuernos. Se verificó que la hembra puede mover los escleritos en forma de uña de sus gonópodos hacia todas las direcciones. El macho efectuó cortejo copulatorio en cinco secuencias analizadas, en ellas la transferencia espermática fue exitosa. Por el contrario, la hembra no recogió los paquetes espermáticos cuando no existió cortejo copulatorio. Los machos que carecían de una pata anteniforme también fueron capaces de aparear. Sin embargo, ellos tuvieron que realizar más intensamente las vibraciones con sus patas no dañadas, y sobre todo durante un tiempo más prolongado para evitar que la hembra se alejara. Se comparan los datos aquí registrados con aquellos previamente obtenidos en otros amblipígrados. Se discuten algunas características funcionales del espermatóforo y genitalia femenina de *P. gervaisii*.

Keywords: *Phrynus gervaisii*, Amplypygi, courtship, sperm transfer, spermatophore

Whip spiders (Amblipygi) represent an interesting group of arachnids, the biology and natural history of which are still poorly known. Whip spiders have strong, raptorial

pedipalps armed with sharp spines. Since whip spiders continue to molt and grow after reaching sexual maturity, adults of the same species may be different sizes (Weygoldt 1995). The courtship behavior and spermatophore morphology are two of the most fascinating subjects to be analyzed in these animals. Whip spiders use vibration of the “anteniform” first pair of legs during courtship (Thomas & Zeh 1984; Weygoldt 1990). After a prolonged dance, the male turns until facing away from the female and deposits a stalked spermatophore. Then he turns towards the female again and lures her to approach the spermatophore and pick up the spermatozoa (Weygoldt 1990, 1998). Few amblypygid species have been observed (i.e., Weygoldt and others have studied the courtship of 19 out of approximately 125 described species). Although the literature contains general descriptions of the mating, we lack many descriptive and quantitative details of behaviors involved in each stage of the courtship and sperm transfer. In fact, the elaborate displays involved in the courtship and spermatophore deposition of whip spiders show the importance of more detailed observations not only to increase our general knowledge but also to lend insight into the sexual selection that shaped the displays.

Spermatophore morphology and sperm transfer mechanisms vary among genera and families and provide useful characters for systematics (Weygoldt, 1998). One of these families, the Phrynidae, contains medium to large-sized whip spiders and occurs in tropical and semitropical areas of the Americas (Quintero, 1981). The spermatophores of phrynids are large and have triangular, heavily sculptured heads (Weygoldt 1969, 1974, 1977, 1990, 1999). The female genitalia are characterized by the existence of two gonopods, each equipped with a claw-like sclerite that is used to pick up the small sperm packages from the spermatophore (Weygoldt 1990, 1999). It is currently unclear how these claw-like sclerites come into contact with the sperm packages. Similarly, it would be of interest to understand the behaviors, such as copulatory courtship, that occur during and after the sperm transfer. In arachnids copulatory courtship has been observed in spiders (Eberhard 1994), scorpions and solpugids (Peretti 1997, pers. obs.). Although in whip spiders Wey-

goldt (1990, etc.) has mentioned the presence of antenniform tapping along with other male-female contact during the sperm pick-up, it is necessary to add more details to increase our knowledge of this behavior (e.g., do all the males of a same species always perform copulatory courtship?, can any male traits, such as body size, affect copulatory courtship behavior?).

The aim of this study was to provide descriptive and quantitative data regarding behaviors involved in courtship and in sperm transfer of the whip spider *Phrynus gervaisii* (Pocock 1894) in order to complement the previous general description given by Weygoldt (1977) for this species. Weygoldt studied the mating behavior and spermatophore of *Tarantula palmata* Kraepelin 1899, using adults specimens captured in Santa Martha, Colombia. Quintero (1981), in the important revision of the amblypygid genus *Phrynus* in the Americas, synonymized this species with *Phrynus gervaisii*. Thus, in this study Weygoldt's observations are adopted as the most important and direct antecedents, comparing the data with those published by this author and, mainly, adding new details to that general description, in particular with respect to behavioral variation.

METHODS

Capture site and laboratory conditions.—Twenty females and 13 males of *P. gervaisii* were collected in October, 1996 in Barro Colorado Island (Smithsonian Tropical Research Institute -STRI), Panama, where the observations were carried out under laboratory conditions (see details below). The specimens were captured in the morning and in the early afternoon in anthills of *Paraponera clavata* (Hymenoptera, Formicidae) inside the parcel of 50 hectares that STRI has on the island. Externally, these anthills consist of excavations at the base of a tree. *Phrynus gervaisii* lives inside galleries of the anthills, going out at night to feed (Pérez Mendieta 1996; Peretti, pers. obs.). In order to capture specimens I hit the base of a tree containing anthills several times with a metal rod. This made many ants to run out very quickly and made some whips spiders leave the anthills and climb the tree; immediately afterward the specimens were captured (by covering them with plastic containers 9.6 cm in diameter).

The animals were housed individually in cages of different sizes, all furnished with a piece of tree bark set vertically so that they could climb. They were fed crickets and locusts once a week. Moist cotton balls were used to maintain high humidity and the temperature varied from 24–32 °C. Following Weygoldt & Hoffmann (1995), all animals were kept under a light/dark cycle of 12:12 hours. In the present work the dark phase started at 1100 h. This synchronized the activity rhythms of the animals with each other and with our activity.

Analysis of mating and genitalia.—Observations of the mating sequences were made in a 40x30x30 cm mating arena that was furnished with a vertical piece of tree bark from the capture site. The substrate consisted of soil, bark and some stones. All the elements of the arena were replaced with fresh materials prior to each use. A 40 W red lamp allowed observation without disturbance. Oral recordings of 10 mating sequences were made on audio cassettes; seven were described in more detail and five had complete sperm transfer. These matings were always performed using different males and females. The female was introduced first into the arena and 10–15 min later, the male was introduced. Three males lost the distal part of one of their antenniform legs due to the ant attacks observed in the field. These males were useful in determining whether the amputation could affect their ability to perform courtship and sperm transfer. Timing and frequency of behaviors were recorded. Behavior patterns were identified following Martin & Bateson (1993), Weygoldt (1977) and Weygoldt & Hoffmann (1995). In all the specimens prosoma length was used as an index of body size (Quintero 1981).

Every male-female interaction was recorded, with details of the sperm transfer phase. Two matings were interrupted in order to obtain fresh spermatophores still containing spermatozoa. All the spermatophores were preserved in 70% alcohol. One day before and immediately after a mating I observed in a stereomicroscope if the female had sperm under the claw-like sclerites by slightly opening the genital operculum. Approximately eight hours after a complete sperm transfer, three females were sacrificed and dissected to locate spermatozoa in the spermathecae. The contents extracted from each spermatheca were

stained with methylene blue and examined with a light microscope. Genitalia of live and fixed (in alcohol) females were compared and fit with unused spermatophores in order to determine the correspondence among the structures that are closely in contact during the sperm transfer. Finally, each individuals willingness to perform a new mating was observed daily.

One preserved individual has been deposited as a voucher specimen at the Arachnological Scientific Collection of the Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba and one additional specimen was deposited at the Smithsonian Tropical Research Institute, Panama.

RESULTS

Body size and mating.—In the anthills containing individuals of *P. gervaisii* ($n = 28$ of 37 anthills checked) there were one or two adult whip spiders (five cases), but they were never of the same sex. These individuals varied in size, but all of them were sexually mature (e.g., large and small females with offspring were collected). The individuals mated in the lab with others captured in either the same anthill or elsewhere. In all the sequences the female was smaller than the male (Table 1); in four out of five matings with complete sperm transfer the male:female size ratio was 1.08 ± 0.05 (mean \pm SD) and in the other case it was 1.61. The size ratio was 1.04 for another sequence where the female did not pick up the sperm packages. The duration of the courtship was only 9.10 ± 3.10 min when males were smaller than females (size ratio: 0.78 ± 0.20 ; $n = 3$); in two sequences the male moved away first. Sexual interactions did not occur between very small adults (i.e. prosoma length less than 4.3 mm), and in 100% of the trials ($n = 9$) they moved away from each other after a brief contact with their antenniform legs. The mean duration of the complete matings was 3.20 ± 0.73 h; range = 2.22–4.46 h. Males were larger than females (ratio 1.14) in the two shortest matings while the body size ratio was lower in the two longest sequences (Table 1).

Courtship.—This stage represented $92.12 \pm 2.27\%$ (mean \pm SD) of the duration of an average complete mating. In seven out of 10 courtship sequences males remained motion-

Table 1. Main features of seven mating sequences in *Phrynus gervaisii*. Latency is the time from the beginning of the courtship to the onset of the first occurrence of the behavior pattern. Frequency refers to the total number of occurrences of the behavior pattern per mating. (a): the female did not pick up the sperm packages; (b): this sequence was interrupted to obtain a fresh spermatophore.

| Sequences | Prosoma length (mm) | | Mating duration (h, min) | Grasping with unfolded palps | | Female operculum rubbing | | Pedipalp rubbing | | Spermatophore deposition | | Sperm packages uptaking | | Copulatory courtship |
|-----------|---------------------|--------|--------------------------|------------------------------|-----------|--------------------------|-----------|------------------|-----------|--------------------------|-----------|-------------------------|-----------|----------------------|
| | Male | Female | | Latency (min) | Frequency | Latency (min) | Frequency | Latency (min) | Frequency | Latency (h, min) | Frequency | Latency (h, min) | Frequency | |
| 1 | 8.3 | 8.0 | 4h 28' | — | 0 | — | 0 | 53.2 | 1 | 4h 13' | 4h 22' | 1 | Yes | |
| 2 | 8.8 | 7.7 | 2h 53' | 8.6 | 5 | 24.5 | 3 | 32.3 | 3 | 2h 41' | 2h 50' | 3 | Yes | |
| 3 | 8.7 | 7.6 | 2h 13' | 13.5 | 2 | 18.6 | 2 | 29.1 | 1 | 1h 57' | 2h 8' | 1 | Yes | |
| 4 | 7.8 | 7.5 | 3h 16' | 7 | 3 | — | 0 | 44.5 | 1 | 3h 03' | 3h 12' | 1 | Yes | |
| 5 | 8.8 | 5.5 | 3h 9' | 10.3 | 4 | 13.2 | 2 | 22.4 | 2 | 2h 54' | 3h 03' | 2 | Yes | |
| 6 | 8.1 | 7.7 | — | 5.7 | 2 | 34.7 | 1 | 45 | 1 | 3h 45' (a) | — | 1 | No | |
| 7 | 7.9 | 5.6 | — | 4.5 | 3 | — | 0 | 28.1 | 1 | 2h 37' (b) | — | 1 | — | |
| Mean | 8.3 | 7.1 | 3h 12' | 8.3 | 2.7 | 22.7 | 1.1 | 36.3 | 1.4 | 3h 1' | 3h 7' | 1.4 | Presence: | |
| Values | ±0.4 | ±1.1 | ±49' | ±3.3 | ±1.5 | ±9.2 | ±1.2 | ±1.1 | ±0.8 | ±45' | ±49' | ±0.8 | 80% | |

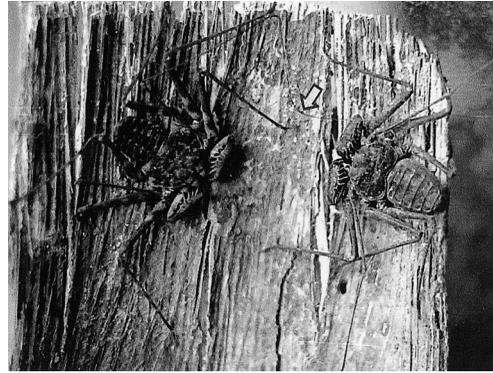


Figure 1.—Courtship in *Phrynus gervaisii*. The male (left) is tapping the females right pedipalp with his left antenniform leg (arrow). This male was able to mate in spite of lacking a part of his right antenniform leg and third leg.

less at the base of a vertical piece of tree bark before the first sexual contact took place. Males and females oriented “face to face” (Fig. 1) and 4.43 ± 1.05 cm apart. In some cases (3 of 10) the female began the contact, approached the male and stayed within one cm of him. As Weygoldt observed, initial “tapping” with the antenniform legs was very light and intermittent. A typical sequence was performed repeatedly (5 ± 2.8 times for courtship, $n = 10$): the male stepped forward, performing tapping and unfolding his pedipalps. Then, the female also did the same sequence (for a more detailed description of each behavior, contact the author).

The male sometimes tried to grasp the female with her unfolded palps (“grasping with unfolded palps”, latency: 8.3 ± 3.3 min) (Table 1). In some sequences (6 of 10) the male performed a behavior that has not been described in either *P. gervaisii* or other whip spiders (“female operculum rubbing”) (Fig. 2). This behavior involves lifting the females caparace and then touching her, from genital operculum to chelicerae, 2–4 times with his palps. The occurrences of “grasping with unfolded palps” and “female operculum rubbing” per mating was higher in the largest males (Table 1).

Contrary to Weygoldt’s observations, in this study the female never performed “shaking” movements with her antenniform legs. After 36.37 ± 10.39 min (from the onset of courtship), staying 8–7 cm from the female, the male emitted an audible sound by rubbing

goldt, the male turned until he faced away from the female: this behavior constitutes the beginning of the second stage, the sperm transfer.

Sperm transfer behavior.—During this stage, the male stayed always below the female on the vertical piece of tree bark. As also observed by Weygoldt, approximately ten minutes after turning (10.60 ± 3.30 min, $n = 7$), the male deposited the spermatophore while his antenniform legs crossed each other backwards and vibrated rhythmically (“vibration”) while touching the female. In general, the latency to the “spermatophore deposition” was shorter in the largest males (Table 1). At the end of this behavior, the male did not cross his antenniform legs; and he executed “shaking” 4 or 6 times together with “vibration” (Fig. 3). Weygoldt (1977) reported that the intense movements of the males antenniform legs during the deposition of the spermatophore were similar to those in courtship. Nevertheless in the present study “shaking” was exclusively performed during the deposition of the spermatophore and also when the female approached it. It could be possible that this difference between the studies reflects the difference in the descriptions or perhaps some variability in the sexual behavior because of the male’s sexual receptivity. After turning until facing the female, the male remained over the spermatophore for 8.31 ± 1.01 min ($n = 5$) (“spermatophore protection”), perhaps providing protection for the spermatophore until it hardened. In this study I did not observe the male grabbing the deposited spermatophore as was reported by Weygoldt (1977).

When “vibration” and “shaking” became more vigorous the female moved her antenniform legs forward so that they were touched intermittently by the male’s. The combination vibration-shaking was performed 10–15 times from the beginning of spermatophore protection until the end of the female approach to the spermatophore. Although my description of the female approach to the spermatophore is similar to that of Weygoldt (1977), many details can be added. The female performed gentle movements up and down before picking up the sperm packages. Then, the male increased the intensity and duration of vibration-shaking. Immediately afterwards, she moved over the spermatophore and picked up

the sperm masses (Fig. 3). The dorsal appendages of the spermatophore sloped a little down when the female placed her body over them (Fig. 4). Finally, the female rose and let her body down twice more on the spermatophore before moving away.

Copulatory courtship: The male usually continued vibrating his antenniform legs just as the female took up the sperm packages (Figs. 3–4). During this behavior the males antenniform legs intermittently touched those of the female. In contrast, she neither moved her antenniform legs nor touched the male during this phase (however, before this phase, she did it while the male touched her during the deposition of the spermatophore). Weygoldt (1977) did not mention in his general description that those male vibrating movements occurred again when female picked up the sperm packages. Copulatory courtship was executed in five analyzed sequences, and in all of these the sperm transfer was successful. The female did not pick up the sperm packages in another sequence where no copulatory courtship was performed by the male. Although the copulatory courtship sometimes could include typical movements of “tapping” and “shaking”, these behaviors were more common during the precopulatory courtship.

Post-sperm transfer stage.—After picking up the sperm packages, the female raised her body and ended any contact with the spermatophore (Fig. 3). Weygoldt (1977) did not offer details of this stage. Agonistic behavior did not occur either before or after the separation. In two cases the female moved away first, while the male remained still and then he ate the emptied spermatophore almost completely (the basal part of the stalk remained attached to the soil). In contrast, the female never ate the spermatophore. The ingestion of the post-insemination spermatophore by the male has not been mentioned before for *P. gervaisii*. In species of *Charinus* Simon 1892 the male performed the same behavior whereas in another Phynidae, *P. marginemaculatus* C. L. Koch 1841, it was the female that ate the empty spermatophore (Weygoldt 1969, 1977, 1990). A male was able to mate again and deposit another spermatophore six days after mating. The females mated again one or two days after mating with the same or a different male.

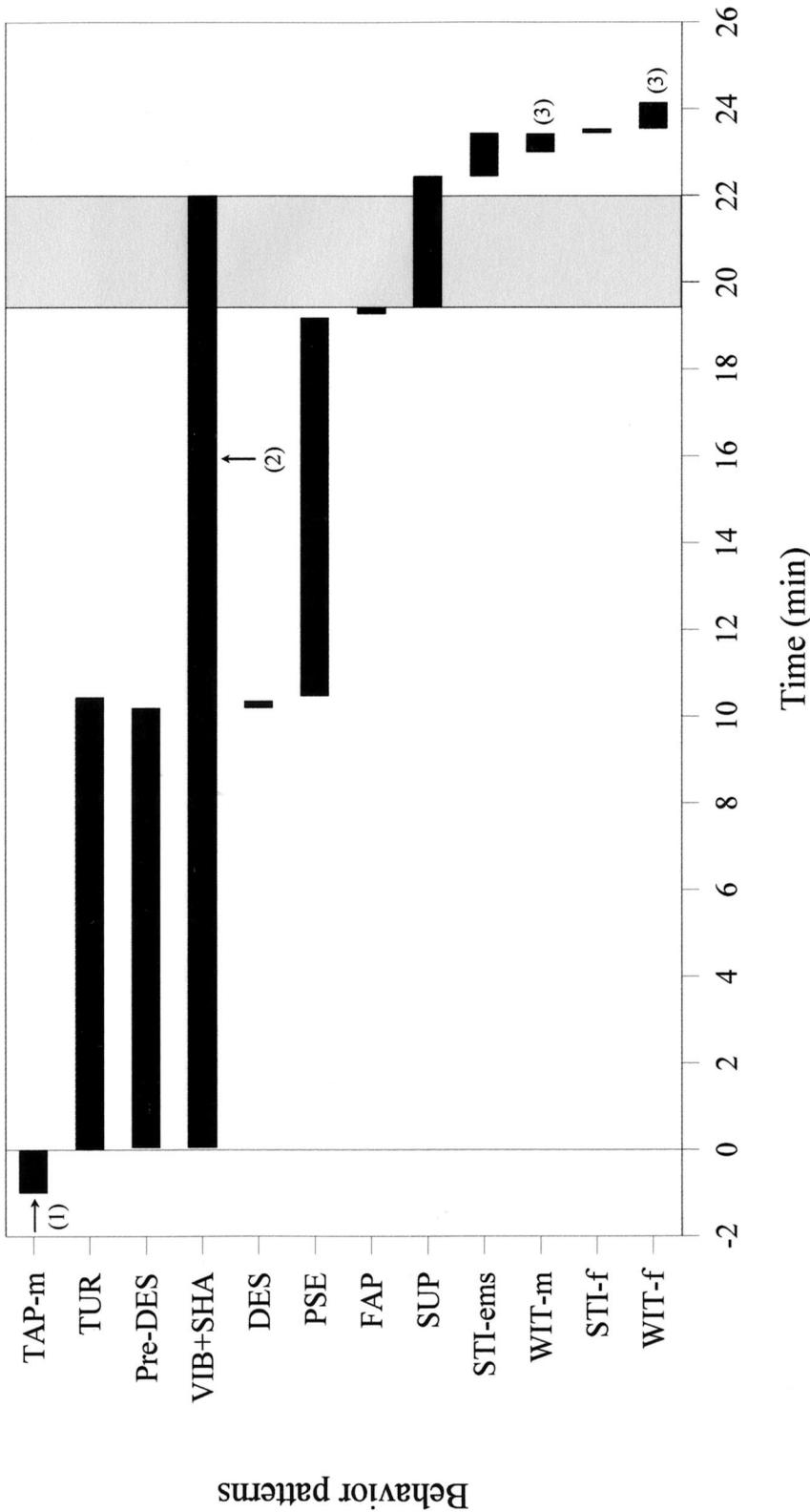


Figure 3.—Diagrammatic chronology of the sperm transfer stage in *P. gervaisii*, beginning with the male “turning” (TUR) (Time = 0), showing the time course of a typical mating sequence. The vertical gray area shows the copulatory courtship stage. Abbreviations: DES = spermatophore deposition; FAP = female approaching to the spermatophore; PSE = spermatophore protection; Pre-DES = preparatory stage for spermatophore deposition; STI-f = female stillness; STI-ems = STI-f over used spermatophore; SUP = sperm packages uptaking; TAP-m = male tapping with antenniform legs; TUR = male turning; VIB + SHA = combination of the male behavior patterns “antenniform legs vibration and shaking”; WIT = individual withdrawal (male: m; female: f). Other references: (1) the male was performing TAP before turning; (2) the intensity of the vibrating movements increased. Each ends (3) when either partner is more than 10 cm away from the transfer site.

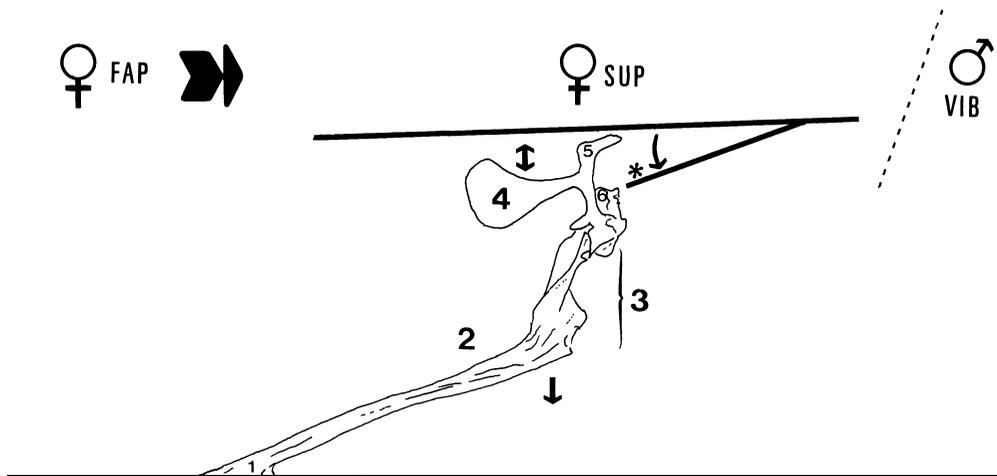


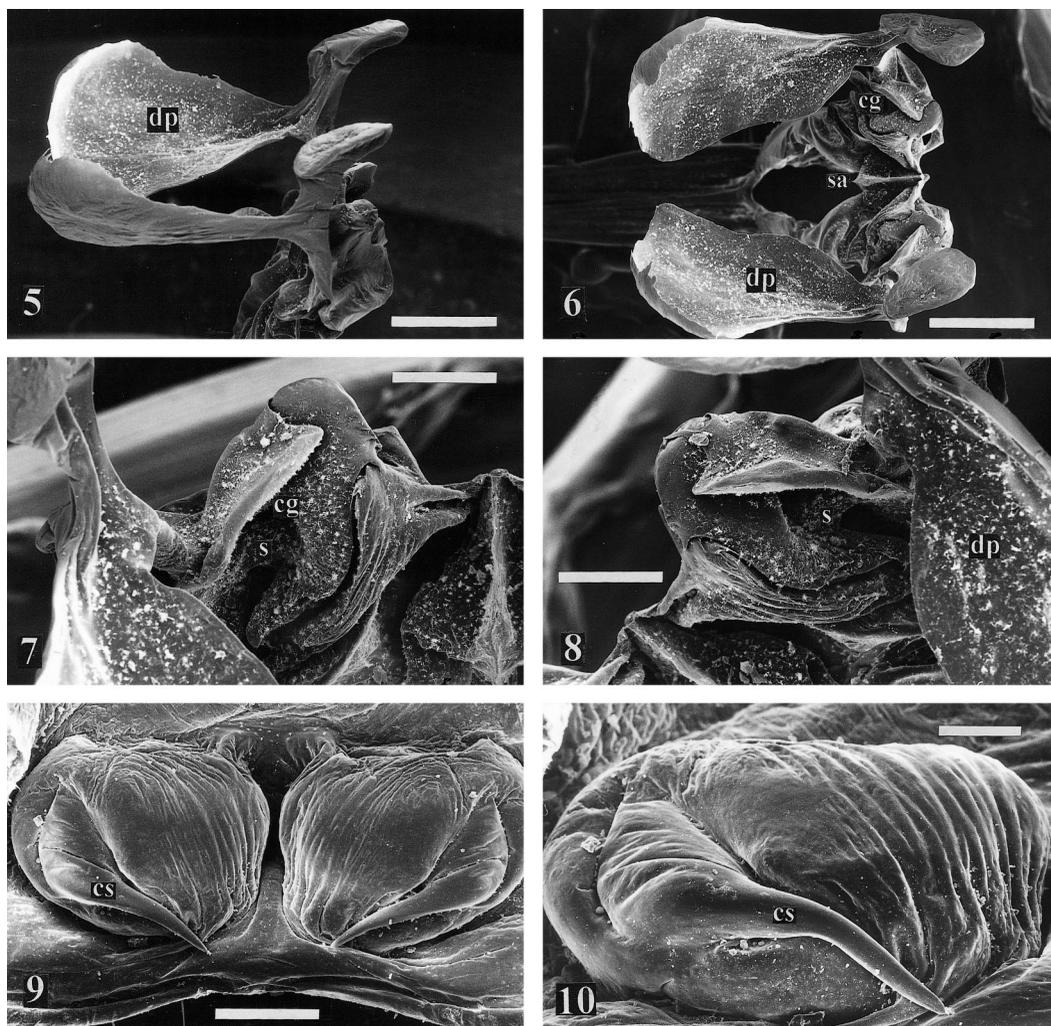
Figure 4.—Schematic lateral view of the position and movements of the female over a spermatophore during the sperm transfer stage. *: location of the gonopods in the internal face of genital operculum. The male continues performing VIB. Other abbreviations: FAP = female approaching; SUP = sperm package uptaking. Parts of spermatophore: 1 = foot, 2 = basal region of stalk, 3 = medial-distal region of stalk which withstands pressure from the females body, 4 = large region of the horn, 5 = distal region of the horn, 6 = copulatory grooves.

Sexual behavior in injured males.—Males of *P. gervaisii* were able to mate even if one of their antenniform legs was injured. The three males captured in this condition (prosome length: 8.04 ± 0.72 mm) were able to mate normally with non-injured females (prosome length: 7.46 ± 0.26 mm). One of those males also lacked the tarsus of the third pair of legs (Fig. 1). In addition, one of them mated again and deposited a new spermatophore after a week. In an injured male, the typical light touches of “tapping” became more similar to “vibration”. Such a male always touched the females antenniform legs with only his non-injured leg. When an antenniform leg was partially amputated, its healthy part moved simultaneously with the other leg during the deposition of the spermatophore, vibration and shaking. A female captured in similar condition did not approach the spermatophore.

Pre-insemination spermatophore and female genitalia.—The basal region of the stalk of the intact, pre-insemination spermatophore is inclined at approximately 30° in relation to the soil (Fig. 4). The two parts of the medial region of the stalk are slightly separated from each other. The medial-distal region forms an angle of $50\text{--}55^\circ$ with the basal region. The distal region is wrinkled and has one “copu-

latory groove” in each of the two sides (Fig. 6). These grooves contain in their basal-medial parts the two small sperm packages (Figs. 7–8). The apical part of the spermatophore head has two well developed dorsal horn-like appendages (see Figs. 5–6). The wider region of these horns has irregular edges, unlike the drawing by Weygoldt (1977) in which they appear very uniform. Further, the distal region of each horn is like a “finger” with its dorsal part slightly flattened, but not oriented toward the internal side of the spermatophore as in Weygoldt’s figures. Inside the horns and the distal part of the stalk is a whitish substance that contains abundant spherical cells with many granular bodies. The quantity of the whitish substance is variable among different spermatophores. As with other phrynids, in *P. gervaisii* each of the females gonopods is equipped with a distal, claw-like, hard and dark sclerite (Figs. 9–10). At the base of each is a seminal receptacle (for other details see Weygoldt, 1990, 1998). In this study it has been verified that the female could move the gonopods in all directions, mainly towards both sides. These movements are possible because the females are able to selectively inflate parts of the soft bases of their gonopods, probably by contracting the adductor muscles.

Sperm transfer mechanism.—During



Figures 5–10.—Scanning electron micrographs of spermatophore (5–8) and female genitalia (9–10) of *P. gervaisii*. 5. Lateral view of the spermatophore head. 6. Dorsal view of spermatophore head; showing the well developed dorsal appendages resembling horns. 7. Dorsal-anterior view of the left copulatory groove. 8. View of the right copulatory groove. 9. Internal view of the posterior end of the genital operculum, showing the gonopods with their soft bases and distal claw-like sclerites. 10. Posterior-lateral view of the left gonopod, showing the slight curvature presented in the medial part of claw-like sclerite. Abbreviations: cg = copulatory groove, cs = claw-like sclerite of gonopod, dp = horns of spermatophore, s = place of the sperm package, sa = spine-like apophysis of spermatophore. Scale bars: Figs. 5, 6 = 0.75 mm; 7–9 = 0.25 mm; Fig. 10 = 100 μ m.

sperm transfer, the female moved the genital operculum slightly forwards (Fig. 4) so the two finger-like regions of the spermatophore's horns entered her genital atrium. Meanwhile the ventral side of the opisthosoma, just behind the operculum, rested on the large expansions of the horns. Then the female moved her body up and down slightly and rhythmically (Fig. 4), inserting a claw-like sclerite in

each copulatory groove of the spermatophore. Wrinkles appeared in the medial-distal region of the stalk as the stalk buckled under the pressure of the females body during the copulatory movements. When the female's body was completely over the spermatophore, the spine-like apophysis of the spermatophore (Fig. 6) touched the ventral side of her opisthosoma. Each claw-like sclerite pulled one

sperm package into the apical part of the copulatory groove. Finally, she lifted her body and the sperm packages remained under her claw-like sclerites in the genital atrium. In one case a sperm package, containing both encapsulated and dried spermatozoa, remained attached under the claw-like sclerites for one week. The gonopods of one captured female contained completely dried sperm packages.

Post-insemination spermatophore.—Differences between pre-insemination and post-insemination spermatophores are small but well defined. For instance, the wide regions of the horns of the post-insemination spermatophore are partially oriented downwards (i.e., they are not horizontal in relation to the surface) because of the pressure exerted by the female during her movements over the spermatophore. The finger-like region of each horn is more flattened and the stalk is also more inclined toward the surface. In addition, the apical part of the stalk usually became more folded on itself when the females movements were very intense.

DISCUSSION

Sexual behavior.—Although some of the differences reported here with respect to Weygoldt's work are only due to the fact that the previous descriptions were more general, a number of the observations in the current study are truly novel, such as "pedipalp rubbing" and "female operculum rubbing" and could indicate the existence of geographical variation between the two populations. Further analysis in different populations of other whip spider species may elucidate the degree of geographical variability in the sexual behavior of this group.

The courtship is usually begun by the male in arachnids (e.g., spiders: Foelix 1996; scorpions: Polis & Sissom 1990), although the female can perform some mechanical signals to attract a vagrant male (Polis & Farley 1979). However, like other whip spiders, females of *P. gervaisii* began the courtship (e.g., in a sequence she approached the male and tapped to him as if alerting him to her presence). Probably, the "female initiative" is more favored in whip spiders because of the lack of strong intersexual aggressiveness which is very common in other groups such as camel spiders and scorpions (Punzo 1998; Peretti & Acosta 1999; Peretti et al. 1999). This last

characteristic differs, at least in the studied population, from interspecific aggression. Only individuals of *Phrynus gervaisii* inhabited the nests of the ant *Paraponera clavata* whereas in a near fallen trunk a male of *Paraphrynus laevifrons* (Pocock) was captured (Peretti pers. obs.). A female of *P. gervaisii* killed and ate that *P. laevifrons* male after they were placed together in a terrarium. Agonistic behavior among *P. gervaisii* females included strong touches with their pedipalps and chelicerae.

The various parts of courtship probably serve specific functions. For example, the initial stage may be used to assess sexual receptivity. During this stage, "tapping" and "grasping with unfolded palps" could signal each individual's inclination to continue the courtship. And the male may use additional behaviors to elicit female cooperation. For example, "female operculum rubbing" may have a stimulatory function since the female always became more receptive after the male performed it. Because this behavior has not been observed in other amblypygid species, comparison cannot be made for the Order. However, comparing this behavior with those of other arachnids, such as scorpions, "female operculum rubbing" resembles "tickling" of some buthids (Polis & Sissom 1990). Indeed, males of *Zabius fuscus* (Thorell) often perform "tickling" with the first pair of legs on the females genital operculum. In relation to other behaviors of *P. gervaisii*, further studies are needed to determine whether the audible sound emitted during "pedipalp rubbing" can be detected by the female (directly or via the substratum).

When the courtships of phrynid Amblypygi are compared, all contain "vibrations" or the equivalent (e.g., with more or less shaking movements). This similarity demonstrates the uniformity existing in the courtship of the whip spiders (Weygoldt 1990, 1998, etc.). Like in other arachnids (Eberhard 1994; Peretti 1997, pers. obs.) the copulatory courtship of *P. gervaisii* could function to stop the female from leaving before picking up the sperm packages. However, the ultimate function of the copulatory courtship in a context of cryptic female choice (Eberhard 1991, 1996) has not yet been studied.

It was surprising that the males that had only one antenniform leg were still able to

perform pre- and post-copulatory courtship. Healthy females even cooperated with them (e.g., by moving an antenniform leg close to the males broken one). Weygoldt & Hoffmann (1995) has photographs (figs. 5–10) that show an injured male of *Phrynichus cf. ceylonicus* (C.L. Koch 1843) (Phrynichidae) mating with a healthy female. The same has been observed in another phrynichid, *Damon gracilis* Weygoldt 1997 (Weygoldt 1998: figs. 9–13). It would be very interesting to study experimentally the courtship of these accidentally asymmetrical males. The position that a *P. gervaisii* male occupies on the tree bark (always below the female during sperm transfer) agrees with that observed by Weygoldt & Hoffmann (1995) in *Damon diadema* (Simon 1876) (Damonidae). That position could facilitate a better penetration of the claw-like sclerites in the copulatory grooves. In fact, the opened parts of the latter stay facing upwards so that the claw-like sclerites can pull out the sperm packages without losing them.

Sperm transfer mechanism and genitalia.—Copulatory grooves of the spermatophore could act as conductors leading the claw-like sclerites of the females gonopore towards the sperm packages. The two horn-like dorsal appendages of the spermatophore could have a double function: their finger-like anterior region fits tightly in the female genital atrium; meanwhile their wide posterior region offers an effective base in which the female can rest to coordinate her movements. In addition, the distal part of the stalk provides a suspension area when the female rests on the horns. The whitish substance observed inside the horns and part of the stalk could help in the copulatory process by absorbing the pressure exerted by the females body. The spine-like apophysis of the spermatophore might function as a communicatory device since it contacts the ventral face of the female just as her gonopods reach the sperm packages. It would be interesting to determine whether the size of the spermatophore including the copulatory grooves varies among the males, since the size of the claw-like sclerites varies among females from different post-adult stages. In a scorpion, *Bothriurus bonariensis* (C.L. Koch 1842) the spermatophore tends towards an average size that allows all females -independent of their body sizes- to use them without difficulty (Peretti et al. 2001).

The female genitalia of *P. gervaisii* as well as those of other Phrynichidae show mechanical properties (e.g., genital appendages that can pick up the sperm packages) which may permit female control of immediate post-copulatory processes by exercising some type of “cryptic female choice” (Thornhill 1983; Eberhard 1996). For example, the sperm packages can be transferred immediately from the gonopods to the seminal receptacles or they can be stored in place which results in dehydration. Although the movements of the gonopods are limited, they would be enough to manipulate and squeeze the sperm packages in order to facilitate the expulsion of the semen (Weygoldt 1977). In addition, the movement of the adductor muscles could induce the movement of the spermatozoa towards the seminal receptacles (Weygoldt 1990, 1999). Weygoldt (1999) mentioned that clear interspecific differences in spermatophores exist among the Phrynichidae. The “species mate recognition system” hypothesis (Paterson 1985) is hardly acceptable to explain spermatophore diversity since different types of sexual signals (e.g., tapping, shaking, vibrations, etc.) are typically produced by both sexes during courtship. Although the sculpting of the spermatophore creates a large, hard and elastic head with a minimum of material (Weygoldt 1999), the need for structural integrity does not explain the great diversity in shapes since structural integrity could also be achieved by a more or less uniform morphology. Might the differently sculpted structures have evolved to aid the female in detecting the different parts of the spermatophore and finding the sperm packages? From a sexual selection perspective, the “internal courtship” hypothesis clearly predicts a conspicuous interspecific diversity in male genitalia and a relative uniformity in the females (Eberhard 1985, 1990, 1996). However, future studies are necessary to support this idea for whip spiders since their spermatophores do not seem to have structures to stimulate females. The other sexual selection hypothesis, “the mechanical fit” (Eberhard 1985; Huber 1993, 1995), might not be directly applied to amblypygids because of the apparent lack of close morphological correlation between the male and females genitalia. An evaluation of this hypothesis requires an analysis of all intraspecific differences since, at least in the studied

population of *P. gervaisii*, slight differences were detected among spermatophores of different males (e.g., in the horn-like distal extensions and in the copulatory grooves). Perhaps these differences affect the uptake of the sperm package by the female just as variations in lamella structures of scorpion spermatophores affect sperm transfer (Peretti 1993, 2000; Peretti et al. 2001).

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