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Natural history of *Phoneutria boliviensis* (Araneae: Ctenidae): habitats, reproductive behavior, postembryonic development and prey-wrapping

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Abstract. *Phoneutria boliviensis* (F.O.P.-Cambridge 1897) is a medically important wandering spider distributed from Central America to northern South America. This study is the first description of the natural history of this species, and presents data on several aspects of its natural history: reproductive and prey wrapping behavior, postembryonic development, and habitats in the departments of Valle del Cauca and Quindio, Colombia. Prior to copulation, the male did not engage in any courtship from a distance, but instead climbed onto the female, adopting the typical copulation position of "modern wandering spiders" (position III). Females laid up to four egg sacs; between 430–1300 hatchlings emerged after 28–34 days. After hatching, spiderlings had a third claw on all their legs and built an irregular web, where they remained until the next molt. Sexual maturity occurred after 14–17 molts, and spiders matured 300–465 days after emerging from the egg sac. The species was found in disturbed habitats associated with both dry and wet tropical forests, usually on the ground with little litter. Spiders wrapped prey in silk, moving in a stereotypically circular pattern around the prey without manipulating threads with their legs. Attachments to the substrate involved rapid movements of the anterior spinnerets, while the others remained immobile.

Keywords: Mating, maternal behavior, Colombia, banana spider

The family Ctenidae is well represented in the Neotropics by medium to large wandering spiders that usually inhabit the forest floor and low vegetation; few are arboreal. In this family, the genus *Phoneutria* currently comprises eight large (17–48 mm) nocturnal wandering spider species that are widely distributed in Central America (Costa Rica) and South America east of the Andes into northern Argentina (Simó & Brescovit 2001; Martins & Bertani 2007). They are generally known as "banana spiders" because they often inhabit this crop. They are considered aggressive, and among the most medically important spiders in the world (Foelix 2010). Their venom has a neurotoxic action (Foelix 2010) and many researchers have analyzed its components and the epidemiology of bites (Bücherl 1953a, b, 1956; Cruz-Höfling et al. 1985; Marangoni et al. 1993; Pineda & Florez 2002; Florez et al. 2003; Garcia et al. 2008; Maguiña et al. 2008).

The natural history of several species in the genus *Phoneutria* has been examined in some studies. Bücherl (1969), Ramos et al. (1998), and Almeida et al. (2000) presented data on the development, activity, reproduction seasonality, and habitat use of *Phoneutria nigriventer* (Keyserling 1891). Simó & Bardier (1989) described the postembryonic development of *P. keyserlingi* (F.O.P.-Cambridge 1897). In the Amazon region, Gasnier et al. (2002) and Torres & Gasnier (2010) offered data on the adult size, sexual dimorphism, habitat use, and temporal changes in body size structure of *P. fera* Perty 1833 and *P. reidyi* (F.O.P.-Cambridge 1897). Dias et al. (2011) modeled the potential geographical distribution of *P. bahiensis* Simó and Brescovit 2001, a threatened species endemic to Brazil.

Phoneutria boliviensis (F.O.P.-Cambridge 1897) is widely distributed in Central America (Costa Rica) to northern South America (Simó & Brescovit 2001). Except for the brief mentions by Valerio (1983) and Hazzi et al. (2013) on geographical distribution expansions, Florez et al. (2003) on the epidemiology of bites and Jäger & Blick (2009) on the introduction into other countries via commerce in banana products, nothing is known regarding its general biology. The following study presents data about the natural history of *Phoneutria boliviensis*: reproductive and prey wrapping behavior, postembryonic development, and habitat. It is based on animals kept in captivity and on complementary field observations.

METHODS

Habitat.—Collections and nocturnal observations were made in localities in the Quindío and Valle del Cauca departments in Colombia (Fig. 1). With the help of a headlamp, I located spiders by the reflection of the light in their eyes. Daylight observations were also performed by turning over rocks and tree trunks and by visual searches of the vegetation.

Reproductive behavior.—Six females and three males collected from Cali, Aguacatal (Table 1, Fig. 1) were kept about 200 m from the collection locality in 30 × 20 cm terraria, with soil as substrate and wet cotton wool moistened daily. The spiders were maintained under ambient conditions of temperature (day/night approximately 27/25°C), humidity, and lighting. The spiders were fed cockroaches, *Periplaneta americana*, two times a week. This methodology allowed observations of egg sacs, time of the emergence of spiderlings, maternal care, and spiderling behavior in the first days. In addition, one female found with an egg sac was left in the field and was monitored daily to compare her maternal and spiderling behavior with those observed in captivity. This female was found in a cleft formed by two rocks at the side of a road.

Matings were observed at night involving three males and four females (two females were immatures that were raised to maturity, and thus virgins) in the same terraria and conditions describe above. For each encounter, I carefully introduced the male into the larger container housing the female's terrarium

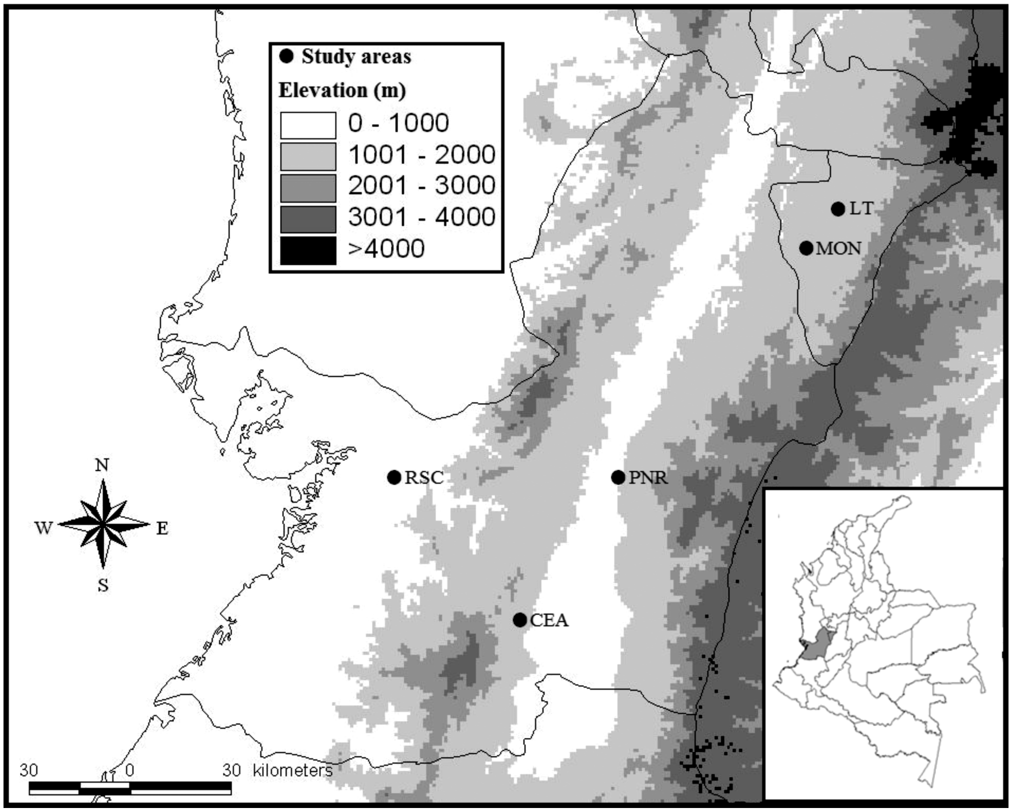

Figure 1.—Study areas in the Valle del Cauca and Quindio departments in Colombia. RSC = Reserva Natural San Cipriano; PNR = Parque Natural Regional "El Vinculo"; CEA = Cali "El Aguacatal"; LT = La Tebaida; MON = Montenegro.

about 20–25 cm from the female. I performed 12 male-female pairings in all combinations, and both males and females were given four possible mating opportunities. Male pre-copulatory and copulatory courtship behavior and copulation are defined as in Eberhard & Huber (1998). Male courtship refers to those behaviors that induce the female to respond in a way that favors the male's reproduction (Eberhard 1996). Copulation consists of all genitalic contact between a particular male-female pair, including the insertion of the embolus into the epigynal opening (Eberhard & Huber 1998).

Post-embryonic development.—In order to determine intermolt period in each instar and number of molts and necessary time to reach to sexually maturity, I raised 43 spiderlings taken at random from two egg sacs obtained from two of the six females. The spiderlings were housed individually in plastic cylinders (4 cm diameter × 6 cm high) until the fifth instar, when they were transferred to larger plastic cylinders (10 cm diameter × 15 cm high). A moistened cotton ball was supplied weekly. Juveniles up to the fifth instar were fed with *Drosophila melanogaster* larvae and adults raised in the

Table 1.—General characteristics of the areas studied and ctenids living sympatrically with *P. boliviensis*. Forest types were classified follow Holdridge's life zone. A.M.T. = annual mean temperature; A.M.P. = annual mean precipitation.

Locality	Forest type	Coordinates (Lat. N; Lon. O)	Elevation range (m)	A.M.T. (°C)	A.M.P. (mm)	Sympatric ctenids
Reserva Natural San Cipriano	Tropical rainforest (bp-T)	3° 50′ 20″; 76° 53′ 52″	0–80	26	5200	*Acanthoctenus* sp, *Ancylometes bogotensis*, and *Cupiennius granadensis*
Parque Natural regional "El Vinculo"	Tropical dry forest (bs-T)	3° 50′ 23″; 76° 18′ 07″	950–1100	25	1400	*Cupiennius bimaculatus*
Cali "El Aguacatal"	Tropical dry forest (bs-T)	3° 27′ 31″; 76° 33′ 45″	1000–1100	25	1300	*C. bimaculatus*
La Tebaida	Premontane wet forest (bh-PM)	4° 26′ 59″; 75° 48′ 01″	1200–1300	22	1700	*Cupiennius bimaculatus* and *C. coccineus*
Montenegro	Premontanewet forest (bh-PM)	4° 33′ 13″; 75° 43′ 03″	1300–1400	21	2100	*Cupiennius bimaculatus* and *C. coccineus*

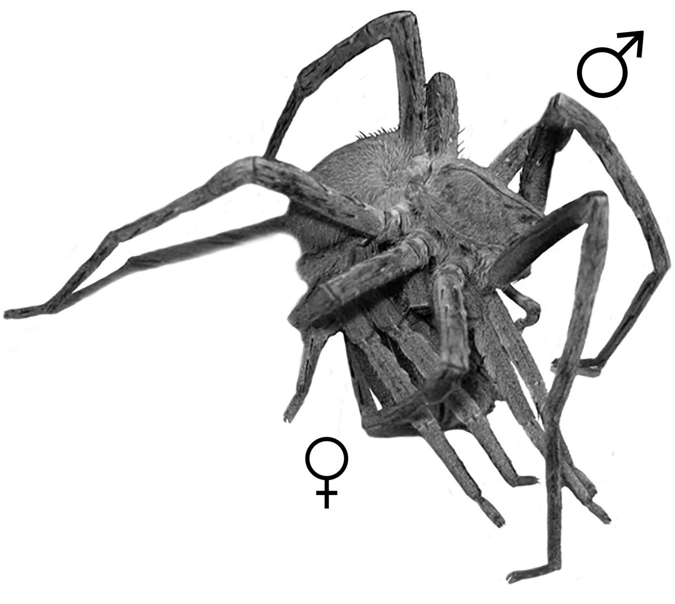

Figure 2.—Mating position of *P. boliviensis*.

laboratory. Older spiderlings were fed field-collected crickets and juvenile *Periplaneta americana* raised in the laboratory. Spiderlings were fed and checked for molting three times a week. I consider spiderlings that recently emerged from the egg sac as second instar individuals (Foelix 1996).

Vouchers specimens are deposited in the arachnological collection of Museo de Entomología de la Universidad del Valle (MUSENUV), Cali, Colombia.

Prey-wrapping behavior.—Previous studies have shown that wrapping behavior varies both qualitatively and quantitatively depending on prey size and species (see references in Barrantes & Eberhard 2007). In this study, I focused on determining whether or not *Phoneutria boliviensis* exhibited a given general behavior pattern, rather than whether or not this behavior was omitted under certain conditions. I always used adults of *Periplaneta americana*, a difficult prey for the spiders. In four of the six females collected, I observed eight prey-wrapping episodes (two for each female). Video recordings were made with a digital Canon PowerShot ELPH 100 HS camera.

Behavioral and postembryonic developmental data are presented as mean ± SD (range: min-max). Because of the small samples, they are meant only to provide general descriptions of magnitudes, rather than to characterize the behavior of this species.

RESULTS

Habitat observations.—Sixty-nine individuals were found in remnants of dry forests, premontane wet forests transformed into banana plantations and rain forests (Table 1). In the dry and wet premontane forest, spiders were always associated with synanthropic environments. I also observed the spiders in forest edges or adjacent habitats (roadsides). During the day, I found spiders ($n = 20$) under rocks, piles of banana leaf litter, and building rubble (tiles and bricks) near the forests or banana plantations. At night, I observed spiders ($n = 49$) on the ground with scattered litter ($n = 40$) and a few in low vegetation, usually below 40 cm above the ground ($n = 9$).

Mating behavior.—Mating occurred in four of 12 couples that were placed together. In no case did the male court the female from a distance. The males reacted to contact with female silk using palpal movements and began to search for the female by keeping their palps near the substrate, maintaining contact with female silk and slowly tapping in different directions with their first legs. When the male contacted the female, he turned until they were head-to-head, and touched her very quickly (less than 2 s) with his forelegs. If the female was not receptive ($n = 8$), she rapidly ran away. However, if she was receptive ($n = 4$), the male climbed over her so that they faced opposite directions and she drew in her legs close to her body so that the patellae of all her legs almost touched each other above her carapace. The male moved laterally to the sides of the female's body and contacted her epigynum with one palp. The mating position was type III, as in Foelix (2010) (Fig. 2). Copulation lasted less than 15 s and the male's extended palp moved rapidly to touch the epigynum briefly. In three pairs, it was possible to record palpal insertions; in two, there was only one insertion and in the other there were two, one on each side of the epigynum. In the video recording, I observed that the spines on the male's legs became erect momentarily at the beginning of each palpal insertion. After mating completion, the male ran away.

Post-embryonic development.—Five of the six females attached egg sacs ($n = 10$) to the terrarium wall, always above the ground. Egg sacs were white, with a flat face of an average diameter of 28 mm ± 4 (range 22–33, $n = 10$) against the wall and a convex face (Fig. 3). Spiderlings emerged on average 30 ± 2 days (range 28–34, $n = 5$) after the egg sacs were produced. The average number of offspring per egg sac was 836 ± 436 (range 430–1300, $n = 5$). Before hatching, females only left the egg sacs for short periods, moving down in the terrarium to drink. However, they still preyed on food that was placed in the terrarium away from the egg sacs. They were more aggressive while guarding, lifting their first pair of legs, opening their fangs, and making lateral movements of the body as is characteristic of the genus (Simó & Brescovit 2001) (Fig 4.).

Twice I observed the emergence of spiderlings, one hour after the females began to bite the egg sac with her chelicerae repeatedly in different parts about once per minute. After hatching, spiderlings emerged and built an irregular web where they remained until their second molt (Figs. 5, 6). Spiderlings began to leave the communal web 15 days after emerging from the egg sac when all had molted, and they then began to feed.

Spiderlings in the second instars had a third claw on all their legs that in the following instars was lost and replaced by a dense claw tuft.

The mother and offspring behaviors just described were also observed in the field. The female stayed near the egg sac, while the spiderlings built the irregular web; when they dispersed a day after their second molt, she was still nearby. After the spiderlings had dispersed, the female also vanished.

When the communal web made by the spiderlings was disturbed by strong vibrations applied with a brush, most of them moved away a short distance, but returned to the web after 10 min. When some spiderlings were removed from the communal web and placed in another terrarium, they soon formed a group. This behavior ceased within a few days after the second molt.

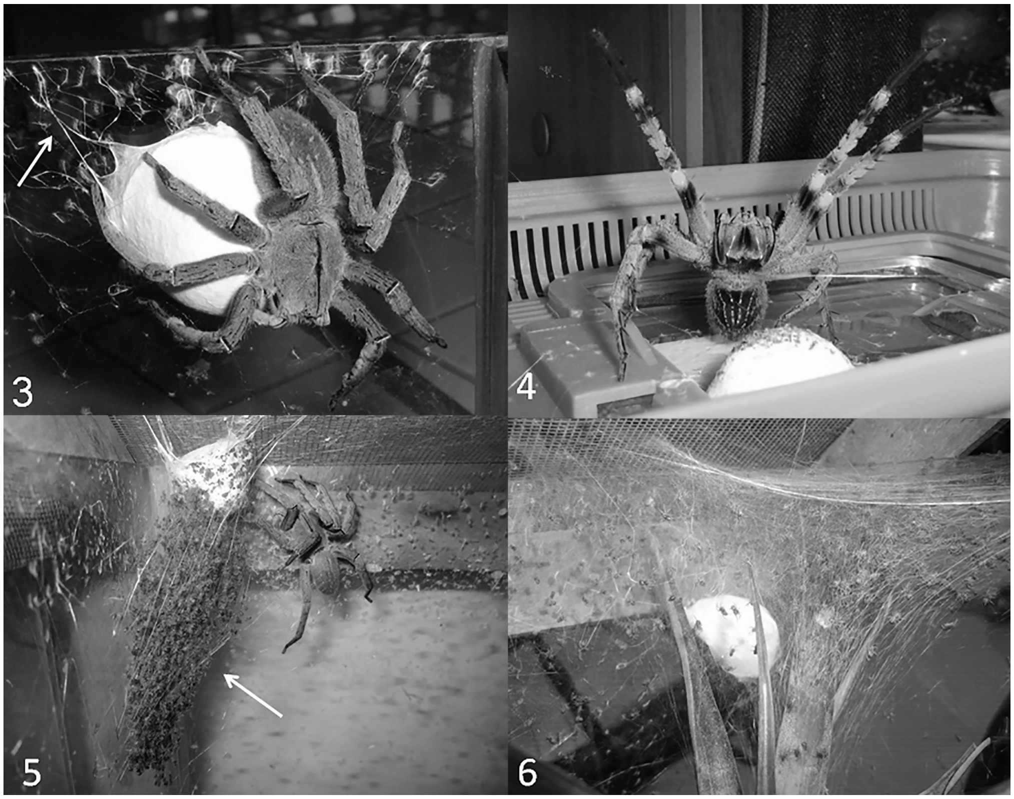

Figure 3–6.—Maternal behavior and communal web of the spiderlings. 3, Female above the egg sac protecting it, white arrow indicates attachment threads; 4, female defending the egg sac; 5, Communal web of the spiderlings, white arrow indicates the group of spiderlings; 6, Detail of the communal web.

Number and duration of the molts.—Four females reached maturity after 14, 15, 16 and 17 molts respectively. There was no pattern of increase or decrease in the instar duration (Table 2). However the duration of the first instar was always the shortest and presented less variation than the others. The mean time from emergence of the spiderlings until maturity was 396.7 ± 72 days (range 300–465).

Table 2.—Duration (days) of *Phoneutria boliviensis* nymphal instars.

Instar	n	Mean ± SD	Range
II	43	11 ± 3.0	7–16
III	35	20 ± 2.7	16–26
IV	26	21.1 ± 9.5	9–47
V	19	26 ± 8.3	14–39
VI	16	30 ± 11.7	17–53
VII	6	31 ± 13.8	16–52
VIII	6	25 ± 2.4	22–28
IV	6	23 ± 3.7	20–29
X	5	24.2 ± 2.6	21–28
XI	4	23.7 ± 4.2	18–28
XII	4	27.5 ± 3.3	23–30
XIII	4	41.2 ± 13.2	29–60
XIV	4	28.2 ± 5.6	23–34
XV	3	39.3 ± 10.8	27–47
XVI	2	39 ± 15.5	28–50
XVII	1	29 ± 0	29

Prey-wrapping behavior.—When a spider captured and bit a cockroach, it waited a few minutes until the insect finished moving. If the spider was on the floor, she climbed the terrarium wall (no more than 15 cm) and turned to face down (Fig. 7A) after the cockroach stopped moving (the antennae sometimes still moved). The spider inclined her abdomen toward the wall to attach silk, and then turned in a semicircular path around the prey keeping the cockroach in her chelicerae (Fig. 7B), while she made a third attachment to the surface. The silk from the first attachment still remained on the spinnerets so that a sheet of silk covered the prey (Fig. 7C). Holding the cockroach in her chelicerae, the spider continued this stereotyped circular motion, adding more silk to the prey. As the cockroach became more tightly attached to the substrate, the spider sometimes released its hold with the chelicerae while continuing to wrap it. The attachments disks were never on the prey, but on the surface around on it. Throughout this process, the palps repeatedly contacted the prey. The average number of attachments per turn was 2.4 ± 0.7 SD (range 1–3) and the average total number of attachments was 9.6 ± 2.1 SD (range 7–13). At the conclusion of prey wrapping, the spider lifted the cockroach with its chelicerae and moved slightly forward, causing the threads to the substrate to tighten. The mean duration of the prey wrapping was 81 s ± 13 SD (range 65–100).

While the spiders fed, they sometimes repeated prey wrapping several times, but with shorter durations and fewer attachments than the initial wrap. In seven of the eight observations, the wrapping lines formed from the first two

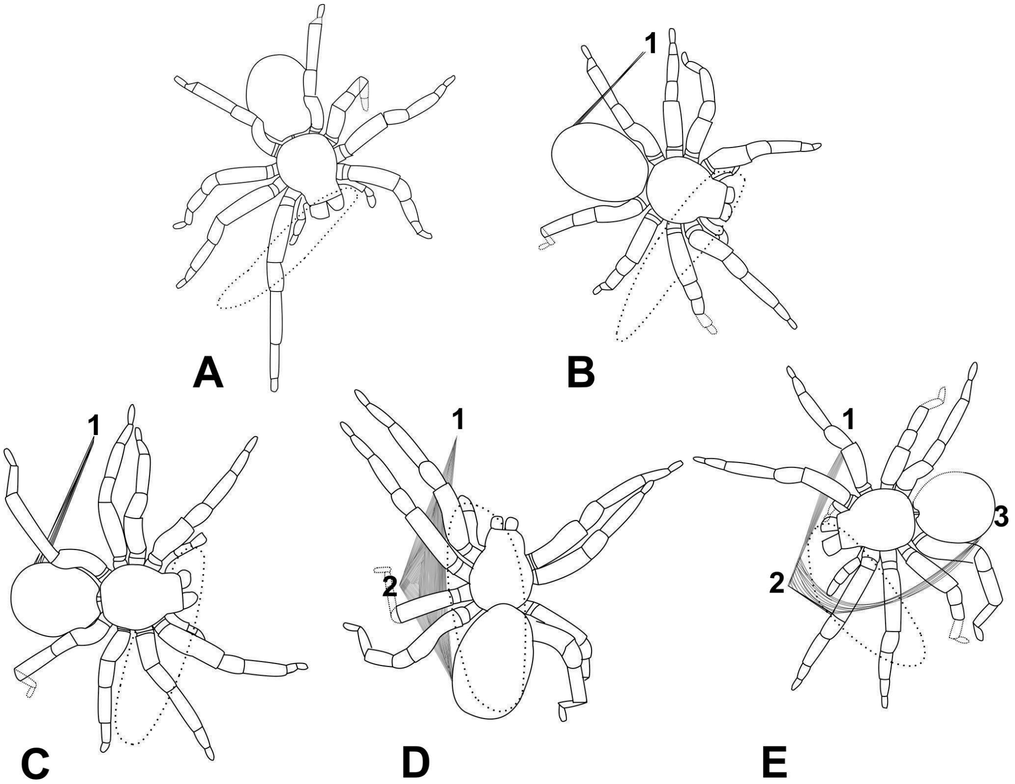

Figure 7.—Prey wrapping behavior sequence of *Phoneutria boliviensis* (the numbers indicate the order of the attachments). After the third attachment, the cockroach is fixed to the substrate.

attachment disks that the spider made did not contact the cockroach. The general pattern of attaching wrapping lines on prey was in one direction (Fig. 9). When the spider began to make this circular motion, it was always performed in a clockwise direction without changing course. I observed that the silk was slack and consisted of numerous threads. In no case did any leg hold any line which was being produced or to which the spider was attaching.

Because the spiders wrapped the prey while on the vertical glass wall of the terrarium, it was possible to observe the movement of the spinnerets as they produced silk. Silk emerged from all three pairs of spinnerets. Only the anterior

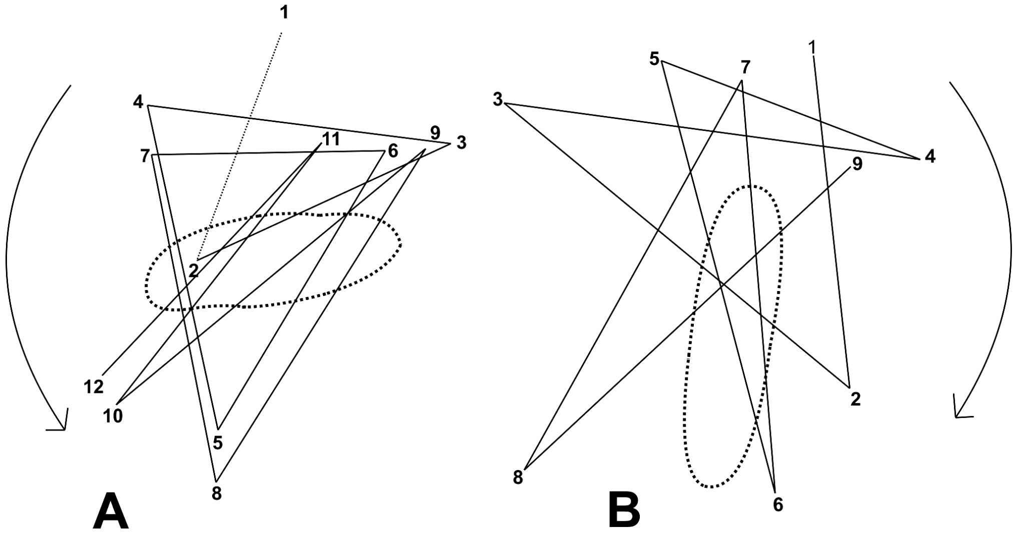

Figure 8.—Patterns of attachments of wrapping lines by two individuals of *Phoneutria boliviensis* (the numbers indicate the order of the attachments and arrows the direction taken by the spider). The silk is slack and due to the circular movement of her body, the threads do not pass straight over the prey as schematized, but instead are curved around it.

spinnerets moved when an attachment was made in alternated fashion. The immobile posterior lateral spinnerets (PLS) were usually in an asymmetric position, depending on the direction taken by the spider in the circular motion pattern; for instance, if the spider was moving to the left, the right PLS was always raised and the left PLS was lowered touching the substrate. These asymmetric positions of the spinnerets created the silk sheet shown in Fig. 7D.

DISCUSSION

Phoneutria boliviensis has been associated with wet and very wet forest ecosystems with annual precipitation > 2500 mm. Valerio (1989) indicates that in Costa Rica this species is restricted to wet and very wet forests in tropical life zones system (Holdridge system) and altitudes not exceeding 600 m; Florez et al. (2003) recorded this species in the Urabá region, Colombia, an area known for its high precipitation; Martins & Bertani (2007) consider it to be a typical species of the Amazon region. In this study, I also found *P. boliviensis* in rainforests, and also in remnants of dry forests with annual precipitation of 1300–1400 mm and at elevations of up to 1400 m. Thus this species is not restricted to lowland rainforests.

In the mating process, male *P. boliviensis* made palpal movements when contacting female silk. These movements apparently are similar to those described in some species of lycosids (Tietjen & Rovner 1980), and allow the male to locate the female by following her silk (Tietjen 1977; Tietjen & Rovner 1980). Male *P. boliviensis* did not court from a distance prior to mating. Folly-Ramos et al. (2002) found that *P. nigriventer* also lacks courtship. It appears that the female recognizes the male when he contacts her because if the female is receptive, she adopts a passive posture when touched. In contrast, *Cupiennius* spp. Simon 1891 and *Ancylometes bogotensis* (Keyserling 1877) have elaborate courtship before mating, involving rhythmic movements of the first pairs of legs and palpal drumming which sends vibrations through the substrate (Merrett 1988; Barth 2002). In addition, *A. bogotensis* and *C. coccineus* F.O. Pickard-Cambridge 1901 are unique among ctenids in wrapping the legs of the female with silk during mating (Merrett 1988; Schmitt 1992). Other ctenid species like *Ctenus medius* Keyserling 1891 and *Isoctenus* sp. Bertkau 1880 have less elaborate courtship involving only vibrational motions of the first pair of legs (Folly-Ramos et al. 2002; Pellegati-Franco 2004). The erection of the leg spines at the beginning of each palpal insertion by the male is due to increased body pressure during insertion and expansion of the hematodocha (Foelix 2010).

The mating position of *P. boliviensis* was type III (Foelix 2010), typical of the "modern wandering spiders" such as Anyphaenidae, Clubionidae, Lycosidae, Pisauridae, Salticidae, Tengellidae, Trechaleidae and Thomisidae (Sierwald & Coddington 1988; Costa 1993; Huber 1995; Barrantes 2008; Foelix 2010). The ctenids species mentioned above, except *C. medius*, use this same mating position. Thus this behavior could be a tentative synapomorphy as families sharing this trait belong to the monophyletic RTA (retrolateral tibial apophysis) clade.

According to my observations made of this species both in captivity and in the field, *P. boliviensis* demonstrated effective maternal care, consisting mainly of her remaining with the egg sac and defending it until the spiderlings emerged and dispersed within a few days after molting. This behavior by mothers could prevent predation on spiderlings because females were more aggressive during this period. Toyama (1999) reported a similar maternal behavior in *Cheiracanthium japonicum*, which greatly improved survival and development of eggs as well as spiderlings in the field.

The shape of the egg sac, maternal behavior, the construction of a communal web by the spiderlings, and dispersal following the second molt are all traits shared with some other ctenids such as *Phoneutria keyserlingi* (Simó 1989); *Parabatinga brevipes* (Keyserling 1891); *Asthenoctenus borellii* Simon 1897 (Simó et al. 2000); *Ctenus medius* (Folly-Ramos et al. 2002); *Ctenus fasciatus* Mello-Leitão 1943 and *Enoploctenus cyclothorax* (Bertkau 1880), however *C. fasciatus* usually put grains of dirt on the egg sac, apparently for camouflage (Pellegatti-Franco 2004). Other ctenids, such as *Cupiennius* spp., differ by carrying the egg sac on spinnerets (Barth 2002) or with the chelicerae, as in *Ancylometes bogotensis*, *Ctenus amphora* Mello-Leitão 1930 and *C. crulsi* Mello-Leitão 1930 (Merrett 1988; Höfer et al. 1994).

It is well known that the middle claw is important for web spiders because they use it to catch hold of the silk threads of their webs (Foelix 2010). In *Phoneutria boliviensis* and maybe other ctenids mentioned above, the presence of this claw in early instars is necessary because the spiderlings build a communal web after emergence. Homann (1971) also mentioned the presence of a middle claw in early instars of *Ctenus medius*, *Cupiennius salei* (Keyserling 1877), and *Phoneutria keyserlingi*. Others ctenids species of *Ancylometes* and *Cupiennius*, also have a third claw. The *Cupiennius* adults have a much reduced middle claw (Barth 2002; Höfer & Brescovit 2000). According to Silva (2004), the occurrence of a middle claw could be an ancestral condition for the ctenoid spiders.

There are two general contexts in which the spiders wrap their prey: to restrain active prey and prevent their escape ("immobilization wrapping") and to form more compact and manageable packages ("post-immobilization wrapping") (Eberhard 1967; Robinson et al. 1969; Rovner & Knost 1974; Barrantes & Eberhard 2007). *Phoneutria boliviensis* performed only "post-immobilization wrapping." The cockroach became more compact during the wrapping process, and became more securely fastened to the vertical substrate. This allowed the spider to occasionally release the prey with her chelicerae and chew on another part without falling. The circular pattern of wrapping and the movement of the anterior spinnerets of *P. boliviensis* was similar to observations of *Rabidosa* (=*Lycosa*) *rabida* (Walckenaer 1837) and *R. punctulata* (Hentz 1844) (Rovner & Knost 1974), which also perform this behavior while above the ground (in vegetation).

While wrapping, *P. boliviensis* does not manipulate threads with any legs, but rather attaches threads to the substrate through body movements. Pulling wrapping silk using movements of the body is ancestral in araneomorph spiders and its homology is supported by the similarity in their asymmetrical use of PLS described in several families (Barrantes & Eberhard 2007). Such asymmetry alters the distribution of lines on the prey package from that expected if the spinnerets were used symmetrically. In the case of the prey-wrapping behavior of *P. boliviensis*, the asymmetric position of the PLS create a silk sheet that encases the prey more efficient than if the PLS were in a symmetric position, creating only a swath of lines.

In *Rabidosa rabida*, Rovner & Knost (1974) sealed each pair of spinnerets separately with paraffin to identify the functions of the types of silk they produced during prey wrapping. The anterior spinnerets produced attachment discs with lines from the pyriform glands. In addition, the anterior spinnerets produced drag lines from the ampullate glands. The median and posterior spinnerets produced wrapping silk from the aciniform glands. The movements of the anterior spinnerets of *P. boliviensis* while attaching lines to the wall presumably resulted in the zigzag pyriform lines typically seen in attachment discs.

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