REPRODUCTIVE BIOLOGY OF URUGUAYAN THERAPHOSIDS (ARANEAE, MYGALOMORPHAE)

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ABSTRACT.   We describe the reproductive biology of seven theraphosid species from Uruguay. Species under study include the Ischnocolinae *Oligoxystre argentinense* and the Theraphosinae *Acanthoscurria suina*, *Eupalaestrus weijenberghi*, *Grammostola iheringi*, *G. mollicoma*, *Homoeomma uruguayense* and *Plesiopelma longisternale*. Sexual activity periods were estimated from the occurrence of walking adult males. Sperm induction was described from laboratory studies. Courtship and mating were also described from both field and laboratory observations. Oviposition and egg sac care were studied in the field and laboratory. Two complete cycles including female molting and copulation, egg sac construction and emergence of juveniles were reported for the first time in *E. weijenberghi* and *O. argentinense*. The life span of adults was studied and the whole life span was estimated up to 30 years in female *G. mollicoma*, which seems to be a record for spiders. A comprehensive review of literature on theraphosid reproductive biology was undertaken. In the discussion, we consider the lengthy and costly sperm induction, the widespread display by body vibrations of courting males, multiple mating strategies of both sexes and the absence of sexual cannibalism.

Keywords: Uruguayan tarantulas, sexual behavior, sperm induction, life span

Theraphosids are the largest and longest-lived spiders of the world. Despite this, and the early contributions of Petrunkevitch (1911, 1934) and Baerg (1928, 1958), their biology remains poorly known. However, more and more research is currently being carried out. A thorough understanding of theraphosid biology and ecology is necessary from a conservation standpoint because natural populations may be threatened by habitat disturbances and captures for pet commerce. An understanding of theraphosid reproduction is necessary to facilitate captive breeding and to reduce pressures on wild populations. Although the neotropical region is the most speciose in theraphosids, most studies are restricted to a few nearctic species. Phylogenetic systematics of neotropical Theraphosinae was recently analyzed (Pérez-Miles et al. 1996; Bertani 2000; Pérez-Miles 2000) facilitating identification for biological studies and evolutionary interpretation. The reproductive biology of some Uruguayan theraphosids has previously been described by Costa & Pérez-Miles (1992), Pérez-Miles & Costa (1992),

Pérez-Miles et al. (1993), Pérez-Miles et al. (1999) and Costa et al. (2000).

In this paper we report on seven species of theraphosids studied in the field and laboratory during more than 20 years. These species include a wide range of sizes from the small *Homeomma uruguayense* (Mello-Leitão 1946) to the large *Grammostola* spp. During this time, we accumulated a diverse and rich store of information on these different species. This comparative study is discussed through a comprehensive review of the literature on Theraphosidae.

METHODS

Species studied.—The only Ischnocolinae studied was *Oligoxystre argentinense* (Mello-Leitão 1941). It is a small to medium sized theraphosid (Table 1) living in rocky hills throughout Uruguay. The other species studied belong to the Theraphosinae. *Grammostola mollicoma* (Ausserer 1875) is a large-sized species generally living under stones and occasionally in burrows, in hilly zones of Uruguay. Two geographical forms of this species are recognized by color differences and

Table 1.—Carapace length (in mm) of the seven species studied. *G. mollicoma* includes both northern and southern forms.

Species	Females			Males		
	Mean	SD	N	Mean	SD	N
G. inheringi	28.75	1.50	4	26.25	1.77	2
G. mollicoma	20.17	2.47	20	18.14	1.76	20
P. longisternale	10.76	0.87	3	7.57	0.40	3
E. weijenberghi	9.97	1.20	12	10.28	0.88	12
A. suina	9.80	1.70	13	9.23	0.70	12
O. argentinense	7.81	0.97	7	6.42	0.51	5
H. uruguayense	7.13	0.62	4	6.65	0.82	2

also by slight behavioral differences: one form, called "northern", is found above the parallel 33°S and the "southern form" is found below this parallel. Because these forms copulate freely with each other in laboratory conditions, their taxonomic status is uncertain. *Grammostola iheringi* (Keyserling 1891) is also a large-sized species; in Uruguay its distribution is restricted to "Quebrada de los Cuervos", Treinta y Tres. This species does not copulate with either of the *G. mollicoma* forms in laboratory conditions. *Eupalaestrus weijenberghi* (Thorell 1894) is a medium-sized theraphosid living in burrows in meadows throughout the country. *Acanthoscurria suina* Pocock 1903 is medium-sized and lives in both meadows and rocky hills but is distributed only in the southern half of the country. *Plesiopelma longisternale* (Schiapelli & Gerschman 1942) is a medium-sized tarantula that lives throughout the country, and its ecology is similar to that of *A. suina*. Finally, *H.*
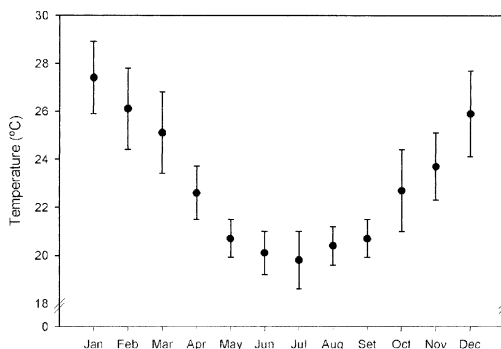

Figure 1.—Room temperature conditions of breeding. Monthly mean and standard deviation were calculated from daily variations during last three years.

uruguayense is a small-sized tarantula, living under buried stones, on hills throughout Uruguay.

Laboratory breeding.—Small specimens were raised in glass jars of 7.5 cm diameter and large specimens were raised in plastic cages with 14 x 20 cm bases. All containers had a substrate of soil or sand, and water provision. They were fed *ad libitum* mainly with cockroaches (*Blaptica* sp.), adult beetles (*Diloboderus* sp.) and *Tenebrio* sp. larvae, according to the size of the spider. Monthly temperature variation in the laboratory is shown in Fig. 1. Behaviors were studied by direct observation and registered by notes and sometimes with photographs. Most observations of sexual behavior were made with the spiders housed in glass containers (base dimensions, 30 x 15 cm).

Field collections and observations.—Field work occurred from 1978–2000. Intensive observations were made between 1987–1990 in hilly zones (Sierra de las Animas, Maldonado, and Quebrada de los Cuervos, Treinta y Tres) and between 1997–2000 in meadows throughout the country. More than 10,000 km were surveyed recording all theraphosids in routes, roads and neighboring fields. Tarantulas were collected mainly by hand but also pit-fall traps (20 cm in diameter) were used several times. About 1000 specimens were recorded, observed or collected, mainly *A. suina* and *E. weijenberghi*. Field observations of sexual behavior were done mainly in the evening and sometimes recorded on video tape and with photographs.

RESULTS

Sexual periods.—Sexual activity periods were estimated through the presence of living
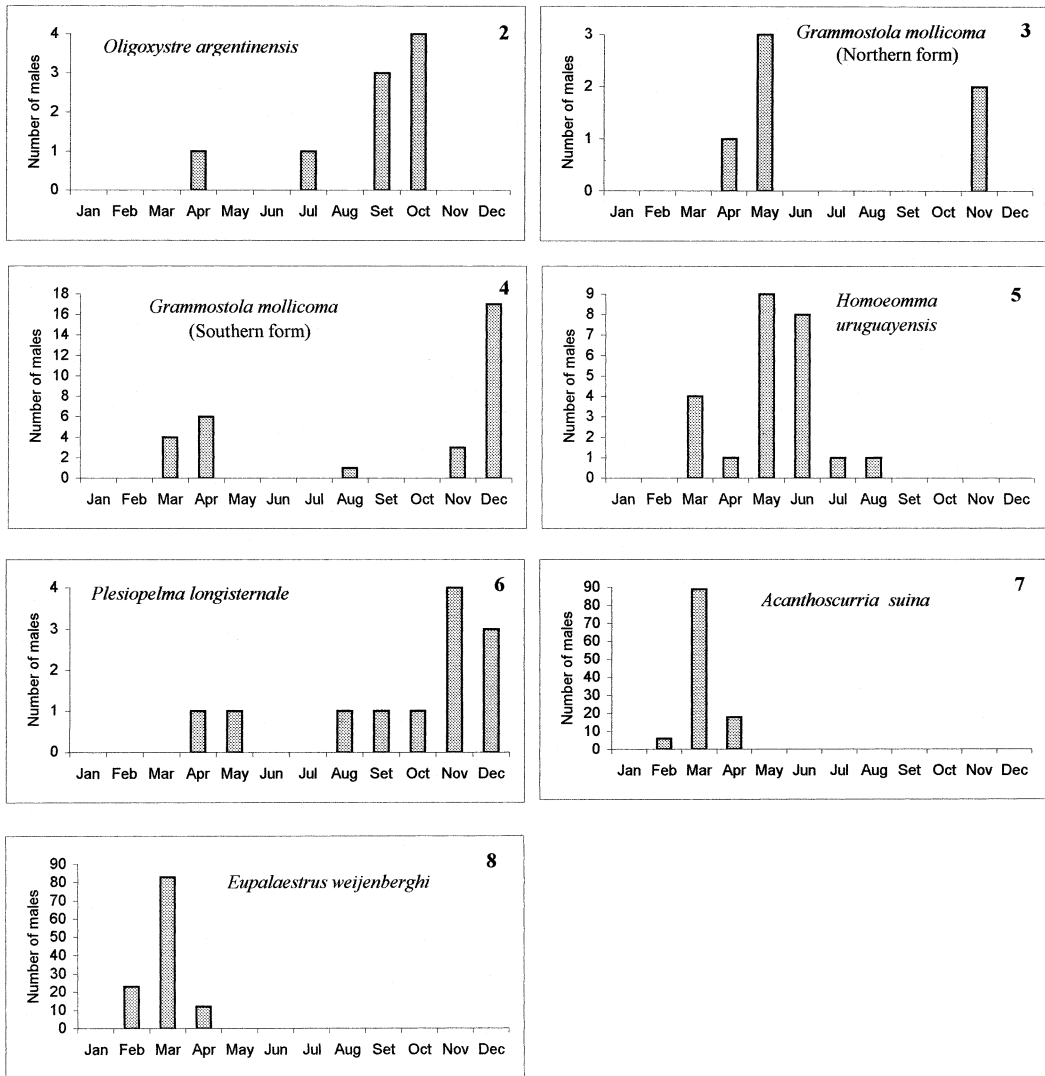
Figures 2–8.—Occurrence of adult theraphosid males in the field along the year. *G. iheringi* was omitted because only two males were found in October.

mature males in the field during the study period (Figs. 2–8). Nine males of *O. argentinense* were collected from April to October. In *G. mollicoma* (southern form), 31 males were collected in autumn and spring with a clear peak in December. In the northern form six males were collected with a similar distribution. Two males of *G. iheringi* were collected in October. Twelve males of *P. longisternale* were collected from April to December. Twenty-four males of *H. uruguayense* were collected in autumn and winter. One hundred eighteen males of *E. weijenberghi*

were collected from the end of February to April. One hundred thirteen males of *A. suina* showed a similar pattern of occurrence.

Sperm induction.—In general terms, sperm induction in Theraphosidae is characterized by the construction of a large and dense sperm web attached to the container walls and usually inclined with respect to the soil. Considering mainly laboratory observations in *G. mollicoma* (southern form) and *E. weijenberghi*, the main behavioral sequence of sperm induction is represented in Fig. 9. Males dig a shallow depression removing soil
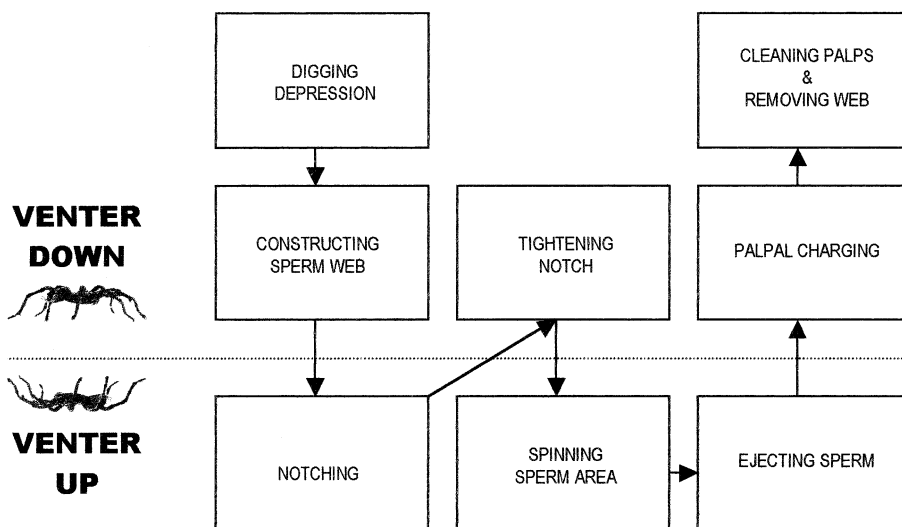
Figure 9.—Diagrammatic representation of a general sequence of behaviors during sperm induction (see text).

adhered to silk threads. The sperm web is constructed over the course of a few hours. With its ventral surface towards the web, the male moves under the sperm web producing a notch in an edge and separating the sperm web from the substrate. Then this web remains hanging up, loose and fixed by the other edges. Later the male moves from under the web and climbs on it to pull the web on a side tightening the notch. This notch is semicircular and clearly delimited (Fig. 10). The male moves beneath the sperm web again, with the venter upward, spinning, especially in an area close to the notch. Apparently the male orients himself placing coxae IV hairs against the notch edge and consequently the genital opening is placed under the reinforced area of the web where he deposits a sperm droplet. During this deposition the prosoma remains out of the web. Then the male gets out and stands on the web with the venter oriented downward, searches for the web edge and seeks the droplet with the palps. Once found, the male starts alternate rapid palpal movements contacting the tip of the palpal bulb with the droplet (palpal charging). The embolus has an angle of approximately 90° with the palpal tibia during sperm charge. Afterwards, the male cleans his palps with the mouth parts and usually pulls out the web and eats it.

The main characteristics of sperm induction are given in Table 2. In one case of *G. mol-*

licoma (southern form) we observed a sperm induction in detail. During sperm web construction, the spinnerets contacts had a frequency of 54 per minute. Web size was 12 cm in length by 8 cm in width and one edge was fixed to the cage wall 4.5 cm above the soil. The male spent 13.5 min spinning the sperm area. Then he took the sperm deposition position and rubbed the genital area against the web alternating with palpal grooming movements, this maneuver took 30.2 min. The sperm droplet deposition was performed in less than 2 min. The male spent 4.3 min to locate the sperm droplet. Palpal charging was done mainly by movement of the patella-tibia joint; distal segments of palps oscillated alternately forward-and-backward. Each palp initially oscillated at 190 times per minute, this increased to 220 and then decreased slowly to 170 (at 24 °C). The whole charging period took around 2 h (end not observed). Finally the male removed and ate the web.

In northern populations of *G. mollicoma*, only one sperm induction was observed in July. One male *G. iheringi* molted to adult on 6 March and made his first sperm induction 10 d later. Two males of this species were observed building sperm webs: 5 h and 2 d before sperm deposition, respectively. In the small-sized *H. uruguayense*, one male made a sperm web 15.6 mm wide. He remained under the web for more than an hour and deposited
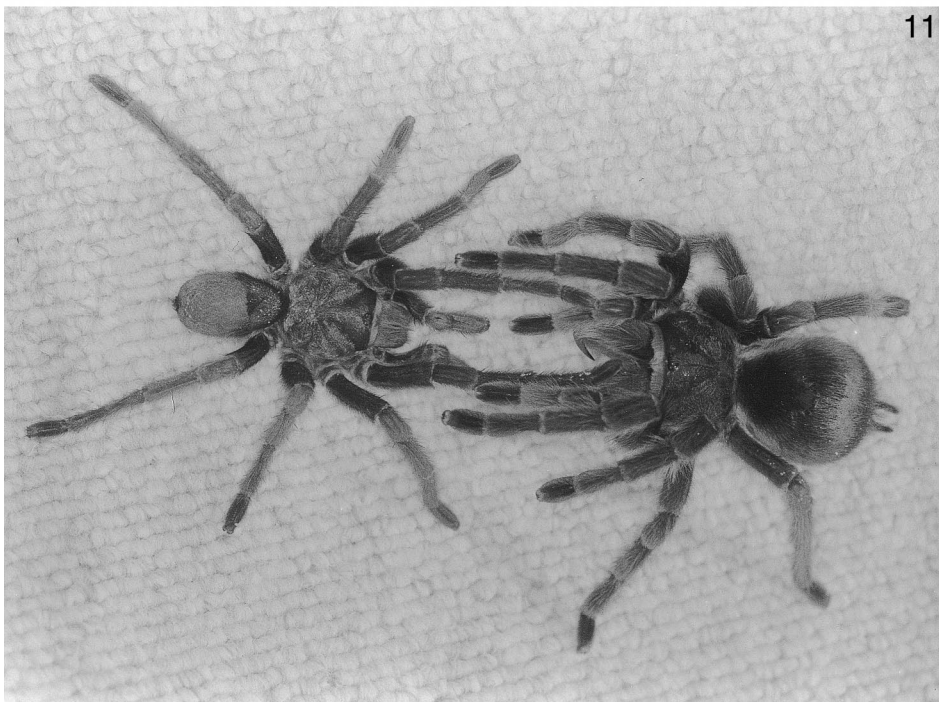
Figure 10.—Male of *E. weijenberghi* before sperm deposition. See the notched edge of sperm web.
Figure 11.—Male (at left) of *G. mollicoma* (Southern form) extending his forelegs and taps the female.
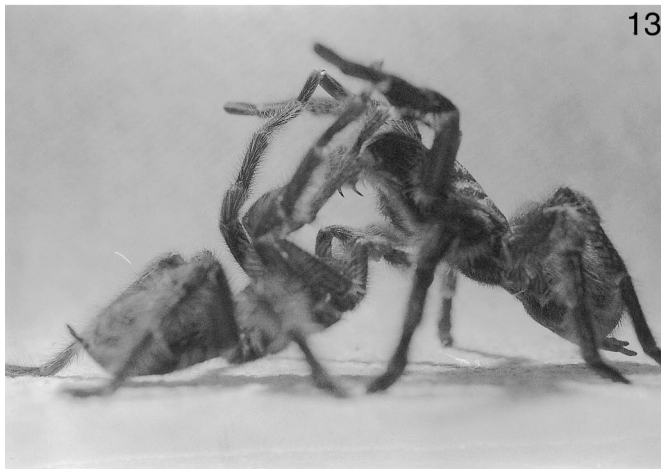
Figure 12.—Male (at left) of *G. mollicoma* (Northern form) trying to clasp open fangs of female. Male left leg II is raised to beat female.

Figures 13–14.—Male of *G. iheringi* clasping female fangs and advances downward with palps alternate movements which contact female venter; 12. Lateral view (male at left); 13. View from the back of the male.

Table 2.—Characteristics of sperm inductions observed in laboratory conditions. (– = No data).

Species	Months (and number) of observation	Duration of sperm web construction (h)	Duration of spinning + sperm depositions (min)	Duration of palpal charging (min)	Frequency of palpal charging (one palp) (per min)	Occurrence of sperm web removal
G. iheringi	Mar (1), Apr (1), Jun (1), Sep (1), Oct (2)	5 2	30 19	102 36	146 132	Yes
G. mollicoma Southern form	Mar (2), May (2), Jul (2), Sep (1), Dec (1)	3.3	45.7	120	170 to 220	Yes
P. longisternale	Aug (1), Nov (1)	—	19.4	108	141	Yes
E. weijenberghi	Mar (10), Apr (2), May (4)	—	—	30 55	52 94	Yes
A. suina	Mar (7), Apr (4), May (1), Jun (1)	—	—	98	135 121	Yes
H. uruguayense	Apr (1), May (1)	—	20	100 124	138 94	Yes
O. argentinense	Feb (1), Mar (1), Apr (4), May (2), Jun (1), Jul (1), Ago (6), Oct (2), Nov (1)	2.1	1.3 to 20	52.3 ± 15.7 $n = 7$	127.4 ± 24.0 $n = 7$	Yes

a sperm droplet of 3 x 1 mm. Palpal movements had an amplitude of 1 mm; when the embolous contacted the droplet, palpal organ tips were separated by approximately 1.5 mm.

Two sperm webs of *E. weijenberghi* were found in abandoned burrows in the field together with tarantula exuviae; one sperm web was found on 29 February and the other on 14 March. Two males of *E. weijenberghi* and two of *A. suina* performed 4 sperm inductions each during two months, in the laboratory. During sperm deposition in males of *O. argentinense* we observed lateral abdominal movements similar to those performed when spinning; in one case a frequency of 26 movements per minute was observed. The sperm droplet was oval (2.5 x 1 mm).

Courtship and Mating.—With the exception of *H. uruguayense*, we observed male courtship behavior in all species after contact with female silk but before direct contact with her in both the field and the laboratory. Courtship generally included: body vibration caused by leg III movements, palpal drumming, tapping the female with extended forelegs (Fig.11), male body movement downward and male pushing female (Fig. 12), female threat-like behavior (raising the carapace and open-

ing fangs), and clasping female's open fangs with male tibial apophysis (Figs. 13, 14). Then the male pushed the female, raising her and extending his palps (Fig. 15). At this moment we generally observed alternate palpal movements which contacted the female on her venter. Females arched backwards (dorsal flexion) up to an angle of 90° between carapace and abdomen. The usual sequence of events was: male body vibrations, tapping with extended forelegs, male pushing and clasping female fangs. Palpal insertions were few, brief and alternate; also copulation duration was brief (see below). At the end of the copulation, the males vibrated, tapped the females with forelegs, and unclasped. Males usually then walked away or, more rarely, re-initiated courtship and mating.

Species-typical behaviors, as they differ among the species, are shown in Table 3. In the field, courted females of *E. weijenberghi* displayed foreleg dorsal-ventral rapid movements at the entrance of their burrows. Males of *E. weijenberghi* and *A. suina* courted at the burrow entrance and partially penetrated the burrow, keeping the hind legs out. Then body vibration, palpal drumming, and leg tapping behaviors attracted the females, and mating
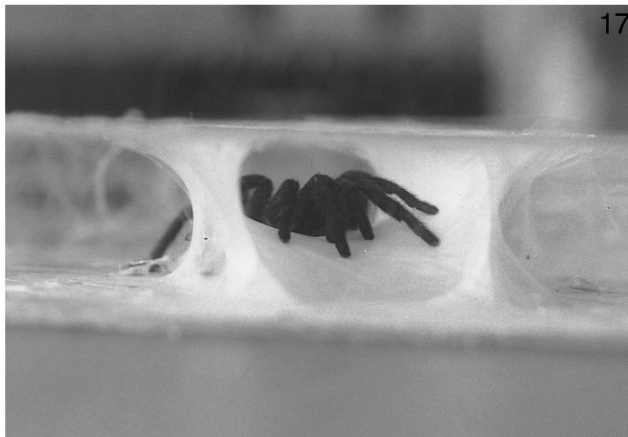
Figure 15.—Copulatory position in *G. mollicoma* (Northern form): male (at left) extending his palps.

Figure 16.—*G. iheringi* couple showing an aggressive postcopulatory behavior (male at left). This display seems to be rare in theraphosids.

Figure 17.—*O. argentinense* female in her nest with the fixed egg sac below her. Petri dish was cut to facilitate vision.

Table 3.—Courtship and mating behaviors which showed qualitative interspecific differences (see text).

Species	Phero-mone recogni-tion	Female leg display	Leg II beating	Female threat-like behavior	Palpal touching female venter	Female dorsal flexion	Posmat-ing threaten-ing display
G. iheringi	Yes	No	Yes	Yes	Intense	Yes	Yes
G. mollicoma							
Southern form	Yes	No	Yes	Yes	Yes	Yes	No
Northern form	Yes	No	Yes	Yes	Yes	Yes	No
P. longisternale	Yes	No	No	Yes	Yes	Yes	No
E. weijenberghi	Yes	Yes	No	Yes, but inconspicuous	Yes	Pronounced	No
A. suina	Yes	No	No	Yes	Yes	Pronounced	No
H. uruguayense	?	No	No	Yes	Yes	Pronounced	No
O. argentinense	Yes	No	No	Yes	Yes	Yes	No

took place at the burrow entrance. In the laboratory, *Grammostola* spp. and *P. longisternale* copulated in an open arena (without a burrow) but in the other species, couples frequently lost their equilibrium when mating in this condition. In *Grammostola* spp. courtship, a singular behavior was observed: the male beat spasmodically with legs II on the female's legs; these movements could be alternate or synchronous with both legs. In this genus the most frequent sequence was body vibration, legs II beating, and pushing female. Beating was also observed during unclasping. The number of insertions, insertion duration and copulation duration of the species studied are given in Table 4.

No sexual cannibalism was observed. In *G. iheringi* a ritualized display was usual when unclasping which involved both partners face to face, with open fangs contacting each other (Fig. 16). After that the males moved away,

and no injuries were produced in these interactions.

Egg sacs.—Egg sacs of *P. longisternale* were observed in the field in December and January (two egg sacs examined in the laboratory cointained 103 and 111 eggs). In *G. mollicoma* (southern form) five egg sacs were observed: one on 14 December (288 eggs), two in January (one of 4.8 x 3.9 x 2.0 cm, 199 spiderlings in fourth and fifth stages according to Galiano 1969), two in February and one in early March (137 spiderlings in fourth stage according to Galiano 1969) in the field. Two other females were observed in their retreats in the field with emerged spiderlings in February and March. In the laboratory, the egg sac construction in *G. iheringi* (23 April, 28 November, 8 and 30 December) was characterized by the complete covering of the inner walls of the plastic cage (23 x 14 x 10 cm) by dense web, as described by Mel-

Table 4.—Copulation duration, number of insertions and insertion duration in the species studied. *Copulation interrupted by loss of equilibrium; **one copulation interrupted by female rejection; —no data.

Species	Copulation duration (minutes)			Number of Insertions			Insertion duration (seconds)		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
G. mollicoma S	16.7	15.8	4	16.3	4.3	4	19.6	2.3	2
G. mollicoma N	3.8	1.1	7	6.6	5.0	7	16.6	3.1	3
G. iheringi	6.1	5.1	3	5.3	2.3	3	18.8	6.7	2
A. suina	—	—	—	2.0	—	1*	—	—	—
E. weijenberghi	0.5	0.1	2**	2.0	0	2	—	—	—
P. longisternale	5.3	2.1	6	4.2	0.8	6	—	—	—
H. uruguayense	>0.7	—	6*	1.3	0.5	4*	—	—	—
O. argentinense	0.4	0.1	2	3.0	1.4	2	—	—	—

Table 5.—Mature lifespan of males.

Species	Captured as adults (in months)			Complete (in months)	
	Mean	SD	*n*	X	*n*
G. mollicoma S	33.3	7.4	4	48	1
G. mollicoma N	29.1	17.3	4	36	1
G. iheringi	—	—	—	45.6	1
A. suina	3.9	1.2	21	6.8	1
E. weijenberghi	6.1	1.1	19	8.7	1
P. longisternale	—	—	—	19	1
H. uruguayense	3	—	1	4.1	1
O. argentinense	4.5	0.3	2	13.5; 11.1	2

chers (1964) in *Pamphobeteus nigricolor* (Ausserer 1875). Three *A. suina* made egg sacs in the laboratory on 6 & 8 December and 29 September; they were eaten on 5 January, 29 December and 30 September, respectively.

A complete cycle: female molting—copulation—egg sac construction and spiderling emergence in *E. weijenberghi* was observed in a laboratory container with soil and a burrow. Molting took place on 8 December, copulation on 20 July, egg sac construction on 14 November and spiderling emergence on 27 January. We estimated there were more than 100 spiderlings. Egg sac care by the female involved the positioning of the egg sac in the entrance of the burrow, maintaining it under her body. When spiderlings emerged she partially plugged the burrow entrance with silk, soil and egg sac remains. The spiderlings moved away from the container on 14 February. The female molted again on 4 March. In the field we found empty egg sacs near burrow entrances on 15 & 27 February, and two cases on 7 March. The last of these egg sacs contained 541 chorions and two sizes of exuviae. A female with an egg sac containing spiderlings was observed on 27 February. Two other *E. weijenberghi* made egg sacs in the laboratory in November and on 8 December, and were eaten on 17 & 29 December, respectively.

O. argentinense (three observations in the laboratory, in petri dishes) made egg sacs during November. Females constructed silk tubes with dense walls of 3.5–4 cm in length and 3 cm in diameter. The egg sacs were flattened, discoid (1.2 cm in diameter) and remained fixed inside the tube wall (Fig. 17). Two egg sacs were fixed vertically and one was fixed horizontally. Females remained close to the egg sacs. One of the females reached maturity in the laboratory, mated and made a viable egg sac: spiderlings emerged 37–41 d after oviposition. Neonates were pale yellow, but molted immediately becoming light brown. Seventy-one spiderlings were counted from this egg sac. The other female ate the egg sac on 4 December.

Egg sacs made in the laboratory were generally eaten or abandoned with the exception of one case in *P. longisternale* reported by Costa & Pérez-Miles (1992), one case in *E. weijenberghi* and another in *O. argentinense* (this paper).

Lifespan.—Theraphosid males have a shorter lifespan than females and do not molt when adults. Most males were captured as adults and only part of their adult life was recorded; some males molted to maturity in the laboratory and the whole adult lifespan was recorded (Table 5).

Considering the extremely long lifespan of theraphosid females, very few data were recorded in the laboratory and most were taken from individuals captured as adults. In the smallest sized *H. uruguayense* a female lived more than 11 y and molted 5 times in this period while a female of *P. longisternale* lived more than 4 y. In *G. mollicoma* (southern form) three females lived more than 12, 16 & 20 y as adults. Two females reared since neonate stage, reach adulthood at 9 & 13 y. Consequently, based on laboratory results, we estimate the maximum lifespan of *G. mollicoma* to be about 30 y. Molting frequency of adult females was measured in the laboratory: two females of *H. uruguayense* molted every 2 y; one *P. longisternale* molted every 1.5 y; one *G. iheringii* molted every 2 y; five *G. mollicoma* (northern form) molted every 2 y, and
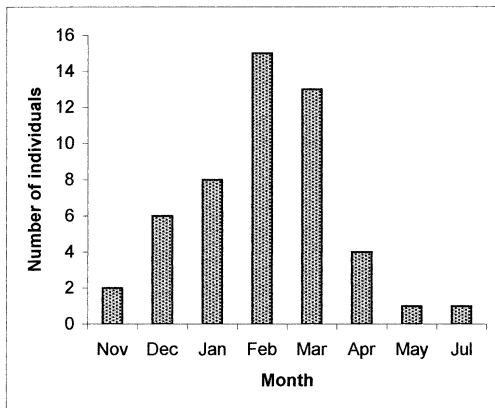
Figure 18.—Annual distribution of molts in adult females of *G. mollicoma* (southern form).

16 of the southern form molted every 2.3 ± 0.9 (range 1–5) y. In *G. iheringi*, *G. mollicoma*, *P. longisternale*, *H. uruguayense* and *E. weijenberghi* adult molts took place mostly in February and March. One adult female of *E. weijenberghi* molted five times during 7 y. Females of *A. suina* molted annually, during the summer. In *G. mollicoma* (southern form) annual molting distribution is shown in Fig. 18. One adult female of *O. argentinense* molted yearly during the summer, during 3 y.

DISCUSSION

Reproductive activities in these theraphosids of the temperate region coincide with seasonal changes. *Eupalaestrus weijenberghi* and *A. suina* showed a restricted sexual period of only 2 mon in late summer and early autumn. In Arkansas (in a similar latitude to Uruguay, but in the Northern Hemisphere) Baerg (1958) reported the sexual period for northern tarantulas (*Aphonopelma* spp.) in the summer. In desert conditions, Prentice (1997) found two clear breeding seasons for *Aphonopelma* spp.: fall and summer; Punzo & Henderson (1999) reported a summer sexual period for *A. hentzi* (Girard 1852). In an arid area of Australia, males of *Selenocosmia stirlingi* Hogg 1901 probably reach maturity in summer (Kotzman 1990). In Uruguay, most species showed a wider period of sexual activity, which was reduced in colder and warmer months. The exceptional sexual activity period of *H. uruguayense* in cool-cold season (autumn and winter) could be interpreted as an ecological strategy to avoid predation due to its small

size, as suggested by Pérez-Miles et al. (1993). Coincidently, another very small, sometimes sympatric mygalomorph spider, the mecicobothriid *Mecicobothrium thorelli* Holmberg 1882, also has a similar sexual period (Pérez-Miles et al. 1993; Costa & Pérez-Miles 1998).

Seasonal mass movements of males is a widespread phenomenon in tarantulas usually related to weather conditions and sexual activity. It also has been interpreted as a form of migration by some authors (Baerg 1958; Magnusson 1985) due to the coordinated movements of the spiders. We did not observe coordination in male mass movements in Uruguayan tarantulas which was in agreement with observations of Janowsky-Bell & Horner (1999) in *A. hentzi*.

The restricted sexual period of *A. suina* and *E. weijenberghi*, together with the high frequency of "walking males" could be related to the ecological pattern of these species. They live in open fields (meadows) and no refuges are known for adult males, while females live permanently in burrows. The "walking males", concentrated in time and space, may reflect a strategy for saturation of predators occurring in this season. Also the co-occurrence of these species could reinforce the saturation of predators. The brief life-span of adult males (only 2 mon in nature) is artificially increased in laboratory conditions, but is also lower in comparison with the other Uruguayan tarantulas. Consequently, the sperm storage period in the field is always extended (at least 8 mon), considering that egg sac production takes place in December. Baerg (1958) reported that in *Aphonopelma* spp. the sperm remains stored for 10 mon (August–June in the northern hemisphere).

It is usually expected that males of large-sized species have a longer life-span than that of small-sized species. For example the small *H. uruguayense* lives 3–4 mon while large *Grammostola spp.* live around 30–45 mon. *E. weijenberghi* and *A. suina* males are exceptions to this, because they are relatively large-sized and have a very reduced life-span. This fact is probably related to their habitat: the other long-lived species occupy hilly zones with major availability of cryptozoic refuges. These ecological characteristics could also explain the prolonged sexual periods in *Gram-*

mostola spp., *P. longisternale*, and *O. argentinense*.

Sperm induction.—The large size of the sperm mat of theraphosids compared to Araneomorphae, involves a substantial cost in time and effort by these spiders. The behavioral sequence observed in sperm induction agrees in general terms with the accurate description of Petrunkevitch (1911) in *A. hentzi*. This author reported that the sperm droplet is placed "on top of the web" and palps were charged through the sperm web but Petrunkevitch (1934) observed that the sperm droplet is placed hanging from the underside of the sperm web in *Cyrtopholis jamaicola* Strand 1908. This last observation agrees with Gerhardt (1929, 1933), Baerg (1958), and with our observations. Male behavior involving coxae IV to "select" the exact site to place the sperm droplet agrees with the observation of Petrunkevitch (1934) in *C. jamaicola*.

The construction of a reinforced area in the sperm web (where the droplet is deposited) was also reported for theraphosids by Petrunkevitch (1911), Baerg (1928), Gerhardt (1929) and Melchers (1964). Probably this area has specialized silk that prevents the droplet from diffusing into the rest of the web. Gerhardt (1929) in *Avicularia avicularia* (Linnaeus 1758), Petrunkevitch (1934) in *Cyrtopholis jamaicola*, and Melchers (1964) in three theraphosid species, reported the presence of an adhesive substance deposited from the genital pore on the web before the sperm droplet deposition. Melchers (1964) also described glandular organs probably responsible for this secretion (epigastric glands: Lopez, 1987). We did not observe any similar substance in the species studied but our observations were made without magnification.

The sperm droplet was oval in all species studied and the spiders were oriented perpendicular to the major axis of the droplet during charge. This could facilitate the lateral contact of the palpal organs.

Theraphosid males spend a long time in sperm induction in comparison to other spiders (Gerhardt 1929). Males of species that live in rocky environments showed higher sperm charge durations in comparison with *E. weijenberghi* that live strictly in open fields. In the latter species the short duration of sperm charge could be related to the scarcity of protected sites for this conspicuous event.

Petrunkevitch (1911) indicated that papal charging duration was more than an hour in *A. hentzi* and in 1934 indicated 90 minutes for *C. jamaicola*; Gerhardt (1929) reported 40–128 min in *A. avicularia* and Melchers (1964) 90 min in *P. nigricolor*. Minch (1979) reported a sperm induction duration of 23–85 min in *Aphonopelma chalcodes* Chamberlin 1940. In *E. weijenberghi*, a higher frequency of palpal movements during sperm charge could be expected to compensate for the short duration, but that was not the case. The total number of palpal organ contacts with the droplet was 3,000–10,000, similar to *O. argentinense* (10,000) but fewer than *G. mollicoma* southern form (45,000). The number of contacts estimated from Petrunkevitch (1911) in *D. hentzi*, by Gerhardt (1929) in *A. avicularia*, by Petrunkevitch (1934) in *C. jamaicola*, by Baerg (1928, 1958) in *Aphonopelma* spp., by Melchers (1964) in *P. nigricolor* and by Minch (1979) in *A. chalcodes* are within the range of Uruguayan species assuming these authors counted movements of only one palp.

Sperm induction was very frequent in the laboratory, with the same male recharging his palpal organs several times (a record of more than 17 sperm inductions in six weeks was reported by Baerg 1958). This could be interpreted in two ways: (1) the sperm charged during one sperm induction is not enough to inseminate several females (sex ratio is biased toward females in adults) or, (2) there is some selective pressure to avoid old sperm in the palps. The first sperm induction is performed early by males after maturation: Minch (1979) observed one male of *A. chalcodes* that made his first sperm induction 10 d after maturity as we observed in *G. iheringi*. Baerg (1958) also indicated that males of *A. hentzi* performed their first inductions 3–15 d after maturation, in the field. Prentice (1997) reported the first sperm inductions of males of *Aphonopelma* spp. 3–21 d after maturity. This author also observed first sperm induction in *A. joshua* inside the burrow if it is sufficiently wide in any region, as we observed in *E. weijenberghi*. Gerhardt (1929) reported the first sperm induction in *A. avicularia* 28 d after maturity.

The sperm web destruction observed in Uruguayan species was also reported by Gerhardt (1929) in *A. avicularia*, by Petrunkevitch (1934) in *C. jamaicola*, by Baerg (1958)

in *Aphonopelma* spp., by Melchers (1964) in *P. nigricolor* and by Minch (1979) in *A. chalcodes*.

Courtship and mating.—Chemical sexual communication in theraphosids was suspected by Baerg (1958) and observed by Minch (1979), Prentice (1997), Shillington & Verrell (1997), Yañez et al. (1999), thereby discrediting previous hypotheses about the absence of chemical cues in these spiders (Petrunkevitch 1911; Baerg 1928; Platnick 1971). Our results agree with the existence of female contact sex pheromone. The exception in *H. uruguayense* could be attributed to the low number of observations or to the absence of female silk in the laboratory recipients. Obviously, pheromones on female silk facilitates the sexual encounter and species recognition.

Body vibrations caused by leg III movements were observed in all Uruguayan theraphosids and were also described for *A. chalcodes* (Minch 1979) and in Mecicobothriidae (Costa & Pérez-Miles 1998). Prentice (1997) described body vibrations in *Aphonopelma* spp. including audible stridulation in *A. joshua*. Similar behavior (quiver/shaking) has also been described in *A. avicularia* (Gerhardt 1929) and *Aphonpelma* spp. (Shillington & Verrell 1997; Punzo & Henderson 1999). Considering that mecicobothriids + microstigmatids are the sister group of the rest of Tuberculotae (a clade that includes theraphosids) (Raven 1985), an early acquisition of this behavior is suggested. Body vibrations (shaking) were also described for *Brachypelma klaasi* (Schmidt & Krause 1994) by Yañez et al. (1999). The possible function of this behavior is distant seismic communication. Also body vibrations in the entrance of the burrow could generate air waves of low frequency. This behavior causes females of *A. suina* and *E. weijenberghi* to emerge from the retreat, whereas in *A. chalcodes* females emerge due to male tapping with front legs (Minch 1979).

Palpal drumming is a widespread behavior in the Theraphosidae (Costa & Pérez-Miles 1992; Minch 1979; Stradling 1994; Shillington & Verrell 1997; Punzo & Henderson 1999; Yañez et al. 1999) and could involve acoustic/vibratory signals just as body vibrations could. Tapping movements with the forelegs on the substrate are frequent in *Aphonopelma* spp. (Baerg 1958; Prentice 1997; Shillington & Verrell 1997), but we only observed this behavior in *A. suina* and *E. weijenberghi*, suggesting its function as a communication mechanism is mainly useful for burrowing spiders.

Tapping movements (leg fencing) with male forelegs on the female cause the female to assume a threat posture with open fangs as was observed by Petrunkevitch (1911) in *D. hentzi*, Gerhardt (1929) in *A. avicularia*, Baerg (1958), Minch (1979), Shillington & Verrell (1997) and Punzo & Henderson (1999) in *Aphonopelma* spp. This female ''aggressive'' display is a necessary condition for the male to clasp (Gerhardt 1929 in *Phormictopus cancerides* (Latreille 1806)). As is well known for theraphosids, all the species studied here have specialized tibial apophyses to clasp female chelicerae and improve male security during copulation. This clasping also supports the female so the male can reach the genital area. In *E. weijenberghi* we observed an active female display with foreleg and palpal movements, which possibly orients the male in the open field at a relatively short distance. This female ''courtship'' behavior is unusual in theraphosids and could involve the generation of airborne vibrations.

The male spasmodic beating with legs II was unique to *Grammostola* and could be a synapomorphy for this genus. Its function could be the relaxation of female fangs, taking into account that it is mainly displayed during clasping and unclasping.

In *A. avicularia*, females live in arboreal silken retreats and copulation takes place outside the retreat (Stradling 1994). In the species living in burrows, copulation always takes place at the entrance (Costa & Pérez-Miles 1992; Shillington & Verrell 1997; Yañez et al. 1999). This location for mating is probably due to space limitations in the female's burrow; it also avoids the risk to the male of being closed into the burrow. The predation risk of the couple in an exposed mating site is minimized by the brief copulation duration (lasting only a few minutes), which was also reported for other theraphosids (Gerhardt 1929; Baerg 1958; Minch 1979; Stradling 1994; Huber 1998; Punzo & Henderson 1999). In summary, in all species studied a low number of brief insertions was recorded. Differences in the number of insertions and copulation duration between the southern and northern form

of *G. mollicoma* may help clarify the taxonomic status of these forms.

In theraphosid spiders it is difficult to establish which palpal organ (left or right) penetrates in which female spermathecal gonopore (left or right), because female gonopores are placed in a common atrium which opens into the epigastric furrow. Additionally, observation is made difficult by the brief copulation, the position, and the very hairy features. Despite the description of ipsilateral insertion (right in right, left in left; Minch 1979), an indiscriminate insertion pattern was found in *O. argentinense* using monopalpectomized males (Costa et al. 2000).

The passivity and relaxed condition of the female is probably maintained by male palpal touches on the female venter during copulation, a similar behavior (palpal boxing) was described by Petrunkevitch (1911) in *D. hentzi*, by Brazil & Vellard (1926) for *Grammostola* spp., by Gerhardt (1929) for *A. avicularia* and by Yañez et al. (1999) for *B. klaasi*.

The frequent loss of equilibrium during copulation in most species studied (with the exception of *Grammostola* spp. and *P. longisternale*) could be related to their adaptation to mate strictly in the entrance of burrows; females maintain part of the body inside the burrow. The male pushes the female backward and she leans part of her body on the soil and burrow wall. The extreme case of female dorsal flexion was observed in *E. weijenberghi* where copulation probably cannot occur in the open field; a similar flexion was reported in other species living in burrows (Petrunkevitch 1911; Baerg 1958). Female dorsal flexion was also reported in *A. avicularia* and *P. cancerides* by Gerhardt (1929).

Brazil & Vellard (1926) reported sexual cannibalism in some Neotropical theraphosids with the exception of *G. longimana*. Bücherl (1952) reported the "massacre" of males caused by females in 14 of 15 species of theraphosids studied. He explained it as a first maternal (nutritional) action. Based on this, Lourenço (1978) expected a sex ratio biased in favor of males in *A. atrox*. Punzo & Henderson (1999) found 20% sexual cannibalism during courtship of *A. hentzi* in staged encounters. Despite this, we observed no sexual cannibalism in the field or laboratory. From our results, and according to Petrunkevitch (1911), Gerhardt (1929), Baerg (1958), Minch

(1979), Stradling (1994), Shillington & Verrell (1997) and Prentice (1997) the absence of sexual cannibalism seems to be the rule for theraphosids. However, occasionally we observed a female of *A. suina* eating a conspecific male in the burrow entrance. Celerier (1981) studying the Eumenophorinae *Scodra griseipes* Pocock 1897 (now *Stromatopelma*) reported that in 83 attempts 13 males were eaten. However, rare postcopulatory female attacks were reported in *A. iodium* by Prentice (1997), Shillington & Verrell (1997) in *Aphonopelma* sp., and in *B. klaasi* by Yañez et al. (1999). Males and females probably reach adulthood with a 1:1 sex ratio but in nature the sex ratio is strongly biased in favor of females because of their longer lifespan. For this reason males are expected to have evolved efficient defenses against sexual cannibalism, mainly because males probably copulate several times in their lives (Buskirk et al. 1984). Baerg (1958) reported one male *Aphonopelma* spp. copulated 12 times in captivity and estimated a sex ratio of 1 male to 6 or 7 females, in the summer. Shillington & Verrell (1997) observed that females of *Aphonopelma* sp. copulated 5–7 times. Stradling (1994) reported a male of *A. avicularia* that mated with 5 females. Celerier (1981) stated that one male of *S. griseipes* can copulate with several females. Taking into account the abundance of females, a strong intrasexual competition among males is not expected and we did not observed male–male fighting nor female mate guarding. Male competition could be restricted to finding females as discussed by Shillington & Verrell (1997). A post-copulatory aggressive display observed in males of *G. iheringi* resembles the female-female interactions reported by Pérez-Miles & Costa (1992) and its interpretation remains obscure.

Egg sacs.—*A. avicularia* makes only one egg sac per year in the tropics (Stradling 1994). All species studied apparently produced only one egg sac per year, mainly during the warm period. Baerg (1958) observed egg sac care in the summer in *Aphonopelma* spp. and Prentice (1997) observed it in *A. joshua*. Brazil & Vellard (1926) reported that *G. actaeon* and *G. longimana* molt 2 mon after egg sac production. Coincidentally, Bücherl (1952) reported that females molt after spiderling dispersion. Lourenço (1978) found the

occurrence of egg sacs during a prolonged period in *A. atrox* (spring–summer) in the tropical region. In our study egg sacs were observed in the field mostly in the summer (temperate region).

The period from oviposition to emergence of spiderlings was reported by Stradling (1994) in *A. avicularia* as 51 d, by Celerier (1981) in *S. griseipes* as 52.5 d, by Baerg (1958) in *Aphonopelma* spp as 56 d, by Ibarra-Grasso (1961) in *G. burzaquensis* as more than 50 d, and by Costa & Pérez-Miles (1992) in *P. longisternale* as 49 d. Except for the Ischnocolinae *O. argentinense* with attached egg sac (also reported by Goloboff 1987) all other Uruguayan tarantulas are Theraphosinae and have free cocoons. Attached egg sacs were reported also for a few Old World Harpactirinae and Eumenophorinae (Marshall et al. 1999). More knowledge about the egg sac condition in Theraphosidae may clarify phylogenetic trends. We did not observe the incorporation of urticating hairs into the egg sacs in the studied species as was reported by Melchers (1964) and Marshall & Uetz (1990).

Two complete successful reproductive cycles were reported here in *E. weijenberghi* and *O. argentinense*, both from females that molted in the laboratory. Reproductive success in captivity in theraphosids is unusual and was indicated for the first time by Celerier (1981) in *S. griseipes* and then by Costa & Pérez-Miles (1992) for *P. longisternale*. Usually in theraphosids egg sacs made in the laboratory are eaten or abandoned.

Life span.—The adult life span of male tarantulas under laboratory conditions seems to be an overestimation of what occurs under field conditions. This was clear in *E. weijenberghi* and *A. suina* in which adult life was estimated in the field using pit-fall traps and periodic collection. In these species adult males were recorded in the field mostly in March and April while in the laboratory they live 6 and 4 mon, respectively. As in other spiders, male life-style is very different from juveniles and females; males wander seeking females, incurring a high cost of energy and risks, and they rarely feed. At the end of the breeding season they have lost body mass and their abdomens are very reduced (Janowsky-Bell & Horner 1999).

In the laboratory conditions are the opposite, which could explain their long life. The long life-span of theraphosids is well known. In the Aviculariinae *A. avicularia* males reach adulthood at 2.5 y living 2–4 mon as adults; females mature in 3 y and can live as long as 7 y, under tropical conditions (Stradling 1978, 1994). Celerier (1981) reported that males of *S. griseipes* live 0.4–0.7 y as adults while females live up to 6 y. Males of this species reach maturity between 1.1 and 1.2 y while females mature between 1.3 and 1.7 y. Baerg (1928, 1958) reported that males of *Aphonopelma* spp. live up to 1 y as adults, reaching maturity in about 10–13 y while females reach maturity in 10–12 y. Also Gerhardt (1929) found that a male of *P. cancerides* lived 1 y in the laboratory. Ibarra-Grasso (1961) reported that *G. burzaquensis* reach adulthood in 6 y and males live 2–4 y as adults while a female lived more than 15 y as an adult. Galiano (1984, 1992) found that males of *Acanthoscurria sternalis* Pocock 1903 reach maturity in 4–6 y and females in 6 y; males live 9 mon–2.5 y as adults while a female lived 9.5 y as adult. Marshall & Uetz (1993) found that in *Theraphosa blondi* (Latreille 1804) both sexes mature in 2.7 y. In *Brachypelma* spp., males live 7 or 8 y to maturity, living less than 1 y as adults, while females live 9–10 y as juveniles and 10 y as adults (Locht et al. 1999). Brazil & Vellard (1926) indicated that males of *G. actaeon* can live up to 18 mon as adults. Millot (1943) recorded a female of *Grammostola* sp. from Uruguay living 12 y as an adult.

Our study confirmed that females of large sized theraphosids can live 30 y in captivity (*G. mollicoma* southern form lived 10 y to maturity and 20 y as an adult). As far as we know, this is a record for life-span in spiders. Stradling (1978) found in *A. avicularia* that adult females molt annually as also indicated by Celerier (1981) for *S. griseipes*. Baerg (1958) found that adult females molt each year or each two years. In agreement with Gerschman & Schiapelli (1950), Ibarra-Grasso (1961) and Prentice (1997), we found that large theraphosids molted about every 2 y, as adults.

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