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Pompilid Wasp Interactions with Burrowing Tarantulas: *Pepsis cupripennis* versus *Eupalaestrus weijenberghi* and *Acanthoscurria suina* (Araneae, Theraphosidae)

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Abstract

A female *Pepsis cupripennis* attacked females and large juveniles of *Acanthoscurria suina* and *Eupalaestrus weijenberghi* in their own burrows, under laboratory conditions. Males of both spider species were also attacked in open arenas but with minor success. The wasp buried the immobilized tarantulas in special chambers excavated from the spider's burrows. An egg was deposited by the wasp on the spider's abdomen and its development into an adult wasp was studied. On two spiders the eggs were spoilt and the hosts completely recovered. In the other six spiders development proceeded, reaching the adult stage in five cases. Two female wasps were obtained from large spiders and three males were obtained from small hosts. The wasp apparently needed a spider six times heavier than herself to obtain a daughter. Spider size estimation by the wasp and ecological defensive mechanisms of the spiders are discussed.

Keywords: Burrowing tarantulas, pompilid predation, *Pepsis cupripennis*, *Acanthoscurria suina*, *Eupalaestrus weijenberghi*, Uruguay.

Introduction

Pompilid wasps are predator-parasitoids of large spiders. Species of the genus *Pepsis* are characterized by their large size and ability to capture the largest spiders, the theraphosids or tarantulas (Williams, 1956; Gertsch, 1979). Petrunkevitch (1926) reported the predation of *Pepsis marginata* on *Cyrtopholis portoricae* in Puerto Rico. He described interactions in open laboratory arenas, including attacks, immobilization of the spider and sucking of its fluids, burying of the spider, and placing an egg on the spider's abdomen. In the United States, Williams (1956) studied the predation of some pomplilids on theraphosids under laboratory conditions, mainly *Pepsis thisbe* on *Aphonopelma* sp., describing interactions, burying of prey and development of the wasp larvae until adult stage. Cazier and Mortenson (1964) also reported a field observation on *Pepsis formosa formosa* dragging and burying a male of *Aphonopelma chalcodes*. Punzo (1994a, b) reported hunting and burying behaviors of *Pepsis thisbe* on *Aphonopelma echina* in both field and laboratory conditions, as well as the larval development of the wasp.

Theraphosids show a high species richness in the Neotropics, but paradoxically reports of pompilid predation are limited to Puerto Rico. In Uruguay, *Acanthoscurria suina* Pocock and *Eupalaestrus weijenberghi* (Thorell) are the most common theraphosids and they are frequently sympatric, living in burrows in the meadows (Pérez-Miles et al., in press). *Pepsis cupripennis* Taschenberg is a large pompilid (approximately 40 mm of body length) found in sympatry with these theraphosids. In this paper, we report the predation of a single female of *P. cupripennis* on adult and large juveniles of these tarantulas under laboratory conditions. Burying behavior, larval development, and characteristics of the wasp offspring are described.

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Material and methods

One female *Pepsis cupripennis* was collected in a meadow on March 24, 2000 in Solymar Norte, Canelones, Uruguay (Fig. 1). She was maintained in the laboratory in a cylindrical container of 40 cm diameter and 21 cm height with soil and leaf litter and fed with sugar solution and water. Wasp – spider encounters involved seven individuals of *E. weijenberghi* and six individuals of *A. suina*, mostly collected in Canelones, Uruguay, with the exception of two females of *E. weijenberghi* collected in Durazno and Flores, Uruguay. Male spiders were housed in glass jars of 7.5 cm diameter with soil. Female spiders and large juveniles were housed in glass containers of 30 × 15 cm base and 30 cm height with soil (10 cm deep) where the spiders lived in burrows artificially constructed against a glass wall and later adapted by the spider. All spiders were fed mainly with cockroaches (*Blaptica dubia*) and provided with water.

For encounters with females and large juveniles, the wasp was introduced into their containers. For encounters with males, each male was introduced into the wasp's container. All behaviors of the wasp and the spiders were directly observed, and two wasp attacks were also video-taped. If the wasp attack did not occur within a period of 30 min the experiment was ended. Otherwise, the observation was continued until the spider was buried, and thereafter the wasp was returned to her container. Once the spider was buried, we carefully excavated the chamber with the immobilized spider, removed it and measured the chamber and funnel. The immobilized spider was placed into an artificial observation chamber made with soil and covered with glass to facilitate observation. This chamber was moistened and observed daily, and photographed twice a week. Wasp pupal cocoons were periodically weighed. After the emergence of imagines, sexual encounters were staged.

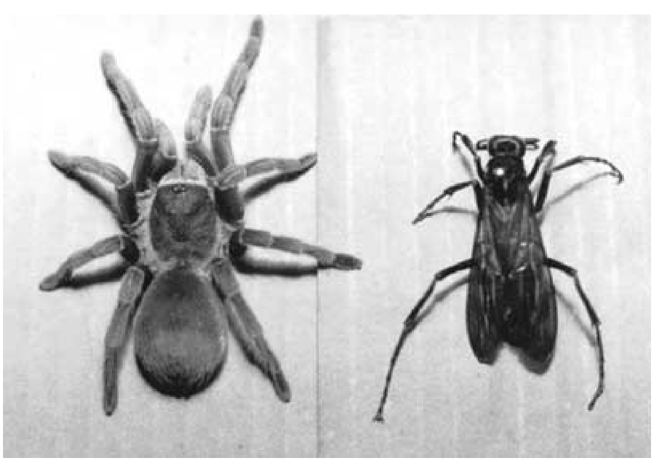


Fig. 1. Penultimate male (no. 2) of *Acanthoscurria suina* (left) in recuperation from the wasp's sting after the failure of the larva's development, and fixed female *Pepsis cupripennis* (right, head–apex = 40 mm length).

For the study of the sexual behavior of wasps, pairs were placed in a glass container (47 × 24 cm at base, 35 cm high) with soil and living plants (*Tradescantia* sp., Commelinaceae). In the experiments, each male was placed consecutively with the same female during 30 min in order of male weight, to elucidate female choice related to male size or priority. In the first experiment (December 7, 2000), males were introduced in an increasing order and in the second (December 11, 2000) in decreasing order. Adult wasps were deposited in the Entomological Collection of Facultad de Ciencias (EFC), Montevideo and in the Museo Argentino de Ciencias Naturales, Buenos Aires. Rests of eaten spiders were deposited in EFC.

Results

Wasp attacks on female spiders

In six of the seven wasp encounters with spiders in burrows, the wasp entered the burrow attacking the spiders. One female of *A. suina* was not attacked by the wasp. In this case, the wasp had attacked and buried another spider only 24 hours before (Table 1). The other three attacks on *A. suina* were successful. Of three attacks on *E. weijenberghi*, two were successful and one failed to immobilize the spider which was entrenched in the long and narrow end of her burrow (terminal tube).

Usually the wasp found the burrow entrance and immediately entered while vibrating its wings. In a case where the burrow entrance was sealed by the spider with soil and silk, the wasp removed the plug. The wasp walked slowly into the burrow, waving her extended antennae. Frequently, the spider advanced on the wasp and sometimes tried to attack her (*A. suina*). When contacted with the spider, the wasp curved her abdomen between her legs while intensively touching the spider with her antennae. When the spider tried to escape (frequently *E. weijenberghi*) the wasp pursued her. *Eupalaestrus weijenberghi* presented her abdomen towards the wasp while *A. suina* tried to bite and/or to exit from the burrow. The wasp tried to bite the spider's legs to obtain a point of support for stinging the spider repeatedly. Stings were frequent around the sternum, and/or the coxal joints. When the spider tried to escape from the burrow, the wasp retained her by biting and hanging onto the spider with her hind legs. One *A. suina* escaped but was recaptured by the wasp near the burrow entrance. The spiders were immobilized approximately 1 min after the start of the attacks.

In one case when the terminal tube was short, the spider (*E. weijenberghi*) penetrated into the tube with the abdomen pointing towards the wasp. The wasp tried to reach to the spider's cephalothorax extending her abdomen between the spider's body and the tube wall. Finally the wasp stung the spider several times and later took the spider out of the tube and immobilized her. In this case 22 min elapsed from the beginning of the attack until the wasp moved away after

Table 1. Predation experiments carried out with one female Pepsis cupripennis versus Acanthoscurria suina (As) and Eupalaestrus weijenberghi (Ew) under laboratory conditions. Spiders no. 4 and 7 were repeatedly presented to the wasp.

Spider number	Species	Sex	Date	Attack	Arena	Spider: Immobilized	Buried	Fate	Wasp Larval development
1	Ew	female	24 March	yes	burrow without tube	yes	yes	eaten	complete
2	As	juvenile male	27 March	yes	burrow	yes	yes	recuperation	small larva dead
3	Ew	female	29 March	yes	burrow, short tube	yes	yes	eaten	complete
4	As	female	30 March	no	burrow	–	–	–	–
4	As	female	31 March	yes	burrow	yes	yes	eaten	complete
5	Ew	female	05 April	yes	burrow, long tube	no	–	–	–
6	As	juvenile male	05 April	yes	burrow	yes	yes	eaten	complete
7	Ew	male	07 April	no	open field	no	–	–	–
8	As	male	07 April	yes	open field	yes	yes	recuperation	small larva dead
7	Ew	male	14 April	no	open field	–	–	–	–
9	As	male	14 April	yes	open field	yes	yes	eaten	pupa dead
7	Ew	male	24 April	no	open field	–	–	–	–
10	Ew	male	25 April	no	open field	–	–	–	–
11	Ew	male	25 April	no	open field	–	–	–	–
12	Ew	male	25 April	yes	open field	yes	no	–	–
13	As	male	28 April	yes	open field	yes	yes	eaten	complete

drinking fluids. In another case a female *E. weijenberghi* moved deeply into a long and narrow tube where the wasp could not reach her. The wasp spent 27 min trying to sting the spider but then abandoned the burrow, leaving the spider unharmed.

Wasp attacks on male spiders

Of nine wasp encounters with male spiders in the open arena, only four resulted in successful attacks: all of three encounters with *A. suina* and one (of six) with *E. weijenberghi*. Both spider species showed different defensive behaviors in the presence of the wasp. *Eupalaestrus weijenberghi* elevated the body and raised the abdomen somewhat, constantly orienting it towards the wasp. Usually *E. weijenberghi* males did not try to escape from the wasp. The wasp investigated the spider with the extended antennae, performed few wing vibrations and curved her body moderately but she did not attack except in one case when she stung the male that died and was abandoned. In the other cases, the spider and the wasp ignored one another after the encounter.

Males of *A. suina* usually threatened the wasp by raising of the forelegs and opening of the chelicerae. Wasp attacks were similar as described above and spiders tried to bite the wasp and/or escape. Male defensive actions in the open arena led the wasp to spend more time and effort than females in burrows. The wasp spent 11.6 min (±0.8, four cases) from start to final of attacks on males whereas attacks on females lasted only 5.3 min (±2.3, three cases, with the female in the short terminal tube eliminated). Males frequently escaped and were pursued by the wasp which performed short flights. Males also used their long legs to maintain distance from the wasp. Of four successful attacks on males only one 'final sting' was observed.

Spider immobilization

Once a spider was immobilized, the wasp inserted her sting deeply into the spider's mouthparts while biting the coxae of the anterior legs or the palps. After this final sting, the wasp cleaned her antennae, wings, and legs, and rubbed her body against the soil. The wasp alternated these grooming behaviors with drinking fluids from the sting sites and from the spider's mouthparts. If the spider was immobilized outside the burrow, the wasp transported her back inside the burrow. In other cases, the wasp removed the spider from the burrow to facilitate the excavation of a nest chamber, returning the spider after that. In these cases, the wasp periodically alternated excavation with contacts with the spider. Males of *A. suina* were buried by the wasp, while the male of *E. weijenberghi* was abandoned.

Burying and oviposition

Those spiders that were captured and immobilized in their burrows (five cases) were also buried in them. The wasp constructed a horizontal funnel which started in the bowl of the spider burrow and ended in a chamber. The chamber was shaped like a prism, with rounded corners, and its walls were thoroughly compacted as a result of pressure applied by the apex of the wasp's abdomen. Dimensions of funnel and chamber are given in Table 2. A significantly positive

Table 2. Dimensions of brood chamber, funnel and egg size of Pepsis cupripennis.

Spider Number	Species	Sex	Chamber length (cm)	Chamber width (cm)	Chamber height (cm)	Funnel length (cm)	Egg size (cm)
1	Ew	female	6.0	4.0	2.5	–	0.6 × 0.2
2	As	juvenile male	6.2	3.5	3.0	1.5	0.6 × 0.2
3	Ew	female	6.1	3.0	2.9	5.8	0.6 × 0.2
4	As	female	5.5	2.7	2.2	7.5	–
6	As	juvenile male	7.5	3.0	2.2	6.5	–
8	As	male	7.0	3.0	2.5	12.0	–
9	As	male	6.0	4.0	2.5	10.0	–
13	As	male	7.0	3.5	2.8	–	0.5 × 0.2

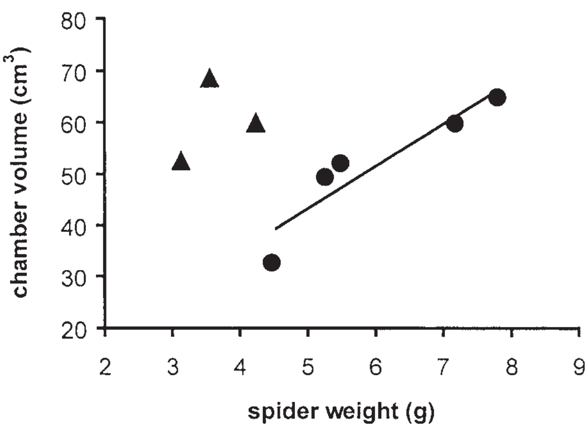


Fig. 2. Spider weight in relation to the volume of the brood chamber. A significant correlation ($r = 0.93$, $p < 0.05$) was found between females' and large juveniles' weights (circles) and chamber volume. Adult males (triangles) do not seem to follow this trend.

correlation was found between female or juvenile spider weight and estimated chamber volume (Fig. 2). The three male spiders captured at open arenas were transported to and buried in burrows excavated by the wasp. The funnel started at the soil surface followed by an inclined portion, turned horizontally next to the container floor and ended in an ovoid chamber. Male chamber dimensions seem to be a different data population of major values with respect to previous five cases (Fig. 2).

All spiders were found in the chamber with their legs pointing towards the funnel; probably the spiders were pulled by the wasp by their spinnerets. In all buried spiders, the funnel was completely filled with compacted soil making the entrance indistinguishable from the surrounding soil or bowl wall. The spiders were lying on their dorsum or side. A single egg was always deposited on the most elevated part of the abdomen. The egg was usually placed near the posterior book lungs, under the epigastric furrow or near the caudal extreme of the abdomen. The female wasp died on 4 May, 2000, 41 days after capture.

Wasp development

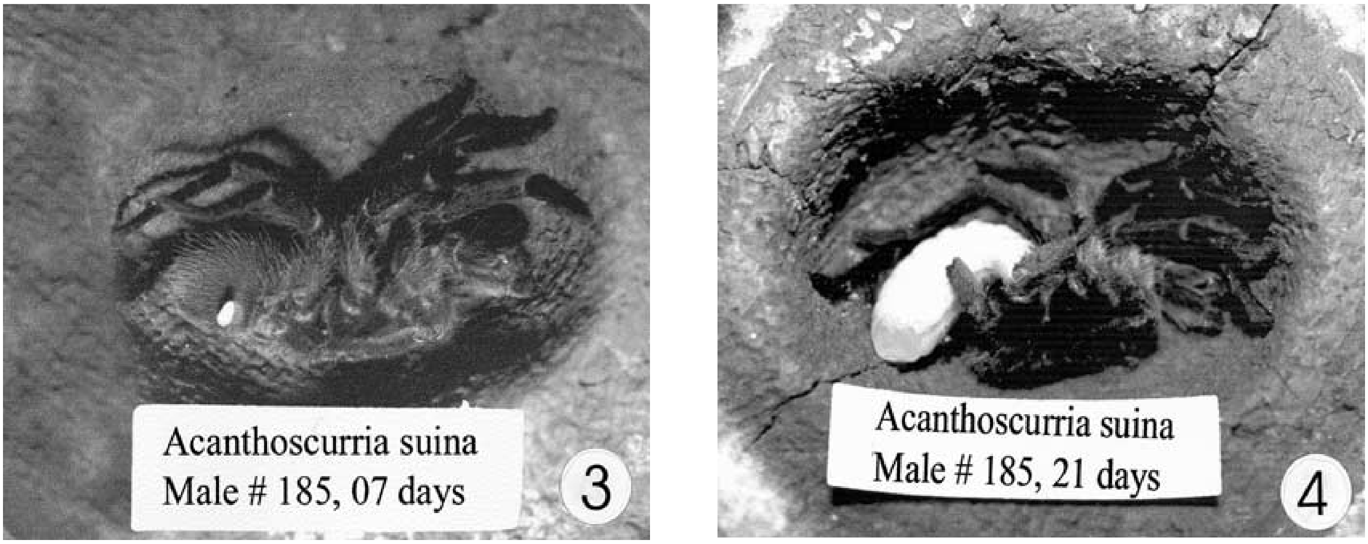
The development of the wasps from egg to adult emergence took a mean of 237.40 days (±15.63 SD), with an egg-larval period of 18.67 ± 2.25, and a pupal phase of 218.60 ± 17.78 days. The egg–larval growth sequence is given in Figs. 3, 4. Except the cuticle, the entire spider including legs and palps was eaten by the wasp larva. The larva reached narrow parts of the spider body due to its small head. Once the spider was eaten, the larva spun an opaque pale brown cocoon with mouth silk and moulted to a pupa, remaining in this state until the warm season. Immediately after cocooning, a wet zone appeared at the narrow pole of the cocoon, probably due to the first defecation ('meconium'). Cocoon size averaged 4.29 ± 0.41 cm in length and 1.63 ± 0.19 cm in diameter. The changes of pupal weight are given in Fig. 5, with the initial pronounced loss of weight coinciding with defecation. After that and until wasp emergence, cocoon weight changed only slightly.

Wasp emergence

Of the six cocoons obtained, five wasps emerged successfully while the sixth (a male) died due to fungal infestation during the pupal stage. Wasps emerged by cutting a cap into the widest pole of the cocoon (Fig. 6). Three males emerged simultaneously on November 26, one female emerged on November 30, and another female emerged on December 3. Female wasps were obtained from heavy spiders (*E. weijenberghi* females) while males were obtained from lighter ones (Table 3). The entire yield of the spider by the wasp was very low, averaging 15.96 ± 5.55%.

Sexual encounters of wasps

Experimental copulations among adult wasps were tried on December 7 and 11. Each male was introduced into the female's container for 30 minutes. In the first trial, males were introduced one at a time, in an order of decreasing weight. The first (=largest) male copulated 9.2 min. He mounted on the female's back, and then remained hanging



Figs. 3, 4. Development of the wasp *Pepsis cupripennis* on a male of *Acanthoscurria suina* under laboratory conditions. (3) Egg. (4) Almost mature larva (four days before pupation).

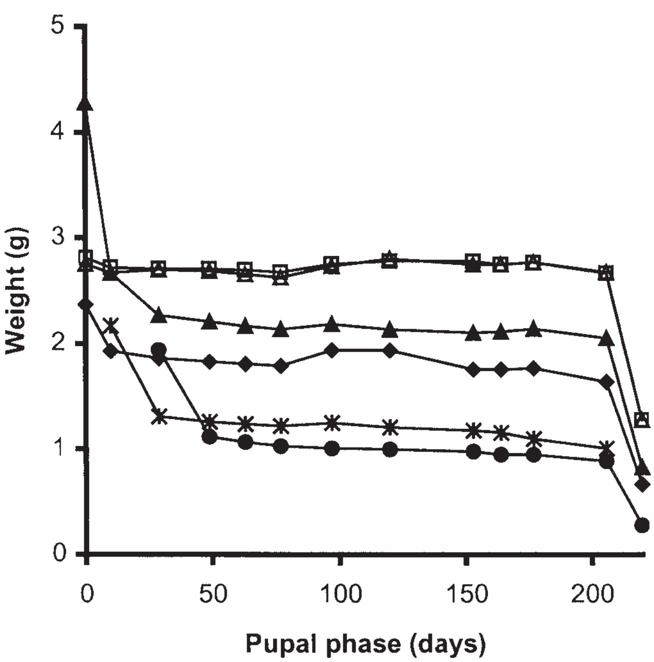


Fig. 5. Progressive loss of weight from pupation to adult wasp emergence, through time. Initial abrupt decrease corresponds to first defecation. Terminal right points correspond to emerged adult wasps: empty triangles and empty squares are females, the asterisks correspond to a male that did not emerge due to fungal infestation, and the other are adult males.

from their copulatory organs. The second male copulated for 20 s in the mounting position while the third male did not copulate. In the second trial, males were introduced in an order of increasing weight. The first (=smallest) male copulated 5.5 min in both the mounting and hanging position. The second male mated twice, during 9 and 13 s respectively, in the mounted position. The third male copulated for 60 s in the mounted position.

Fig. 6. Open pupal cocoon of the same wasp as in Figs. 3 and 4 after emergence of an adult male.

Recuperation of two spiders

In two cases, the eggs fell off the spider's abdomen and died due to the manipulation. Both spiders gradually recovered their motility and coordination. After eight months they fed and showed threat displays. One of the spiders, collected as an adult male, showed a longer life span (10 months since the death of the egg) than the other males reared in the laboratory (4.14 ± 1.92 months, n = 20). The other spider moulted to an adult male (ten months after sting) and had a normal life-span (five months as an adult).

Table 3. Weight of captured spiders and characteristics of the larval development of Pepsis cupripennis.

	Spider			Wasp		
Species	Sex	Weight (g)	Feeding phase (days)	Pupal phase (days)	Weight at emergence (g)	Sex
Ew	female	7.18	17	234	1.28	female
Ew	female	5.49	19	230	1.28	female
As	female	4.47	17	223	0.67	male
As	juvenile male	5.26	18	217	0.83	male
As	male	3.50	23	189	0.28	male

Discussion

Wasp predation and spider antipredatory tactics

The few articles on wasp predation on tarantulas usually report wasp transportation of the spider across open fields (Brazil & Vellard, 1926; Cazier & Mortenson, 1964; Sanjurjo-Gómez, 1967). Laboratory observations by Petrunkevitch (1926) and Williams (1956) were made in open arenas which made it impossible to observe capture of spiders in their burrows. However, Punzo (1994b) observed predation of *P. thisbe* on tarantulas inhabiting burrows in both field and laboratory conditions. He reported that *A. echina* is forced to emerge from the burrow to be captured. This author assumed that the wasp is unable to hunt into the burrow and forces the spider to be attacked in open field (desert) in favorable diurnal conditions for the wasp. On the contrary, we confirmed the ability of the wasp *P. cupripennis* to successfully attack the spiders in their burrows, under laboratory conditions. Furthermore, the wasp used the spider burrow to start the construction of the brood chamber. Williams (1956) and Punzo (1994b) reported that *P. thisbe* entices or drives *Aphonopelma* spp. out of the burrow, whereas we interpret the leaving of *A. suina* from the burrow as an attempt to escape and thus an adaptive behavior. In our study, the wasp was also able to immobilize males and large juveniles of *A. suina.* The shape and size of the burrow bowl of the spider were adequate for the wasp to maintain a safe distance from the spider while stinging it. The hard cuticle and the spinose legs make the wasp invulnerable. Thus, escape is the best defense tactic for *A. suina*, which inhabit meadows where potential refuges are available for avoiding its hunter. This is not the case for *A. echina* at desert conditions.

In contrast, the terminal long tube of *E. weijenberghi* seems to be a defensive mechanism against the wasp (Fig. 7). In the field, we have always found *E. weijenberghi* living in burrows with a long and narrow terminal tube (Pérez-Miles et al., in press). Petrunkevitch (1926) reported an unsuccessful attack of *Pepsis marginata* on a *Cyrtopholis portoricae* retreating facing downwards in the terminal narrow space of the end of the burrow. In the field, *A. suina* burrows always lacked the terminal tube (Toscano-Gadea et al., 1999, Pérez-Miles et al., 2000), making this species more vulnerable to the wasp. We hypothesize that *A. suina* is always sympatric with *E. weijenberghi* to minimize wasp attacks by a dilution effect.

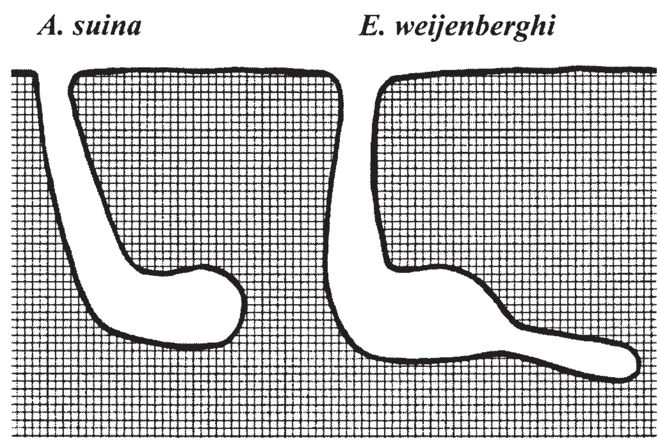


Fig. 7. Schematic drawings of the two types of spiders' burrows. Note the narrow terminal tube of *E. weijenberghi*.

Costs and benefits of predation

The wasp (weight: 1.88 g) must capture a spider six times heavier than herself (11 g) to produce a daughter of her weight while lighter spiders are used to generate sons. These requirements would reduce optimal prey selection to large and thus old adult females of *A. suina*. Punzo also (1994a) found that the size of the wasps emerging was strongly correlated to the size of the parasitized tarantula. Our results clearly suggest that wasps can estimate prey weight, because larger spiders generated female wasps while smaller ones generated males. Weight estimation is also supported by the relation found between spider size/weight and the volume of brood chamber. An intrinsic limit for the wasp in capturing could be the immediate previous captures (less than 48 hours before). The only observed case without attack of a spider in its burrow could be explained by the delay in wasp venom replenishment. Petrunkevitch (1926) interpreted in the same way the longer duration of second sting. Williams (1956) observed ten captures by *P. thisbe* in 32 days, in the laboratory. Punzo (1994b) studied series of ten consecutive captures on *A. echina*, and found that the wasp improved her performance in prey capture as a function of encounter experience.

As did *P. cupripennis*, *P. thisbe* also pulled the spider by its spinnerets when placing it in the brood chamber (Williams, 1956). This behavior probably prevents displacement of the egg glued to the spider abdomen.

Our results on male spiders in open arenas suggest that the wasp preferred *A. suina* over *E. weijenberghi*. However, in the field the capture of males seems to be infrequent because: (1) the defensive abilities of males; (2) the lower benefit provided by small spiders, which can be used only to generate sons; (3) high energy and time costs required the construction of a brood chamber and burrow entrance. Coincidently, we did not find wasps carrying male spiders in the field.

Cazier and Mortenson (1964) indicated that the wall of the brood chamber was elaborated with the mandibles in *P. formosa* while we observed that *P. cupripennis* used the abdomen to form the chamber walls. These abdominal maneuvers are probably dependent of the consistency of the soil and consequently of the humidity of the substrate. Punzo (1994b) observed that *P. thisbe* enclosed the immobilized spider *A. echina* directly in its non-modified burrow.

Wasp lifespan and mating

We found adult wasps mainly in late summer (13 of 17 occasional observations were done in March), expecting an annual period of development. However, in captivity, adult wasps emerged in less than a year probably due to laboratory conditions. Williams (1956) found adult *P. thisbe* during the entire summer in the Northern Hemisphere (California, USA). He reported that when the wasp captured a spider in early summer her adult sons emerged in late summer (after 2–3 months); but when the wasp captured prey in late summer her adult sons emerged the next summer (life cycles of 249 and 350 days). Similar findings were reported by Punzo (1994a) from this species in a Texas desert.

Female wasps copulated longer on the first mating than in the second and third, suggesting that main sperm transfer takes place in first copulations. Second and third copulations were dramatically short to assure sperm transfer. Sexual selection for first male can occur in this species but also size could be an important selective factor as pointed by Punzo (1994a) in *P. thisbe*.

Acknowledgments

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