Natural history, courtship, feeding behaviour and parasites of *Theridion evexum* (Araneae: Theridiidae)

Gilbert Barrantes and **Ju Lin Weng***

Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, San José, Costa Rica

Summary

Theridion evexum constructs webs in the understory of wet middle-elevation forests in Costa Rica. The spiders construct retreats by curling a leaf and produce a mesh in front of the opening. Long, more or less vertical viscid lines extend from the mesh, and are attached to other leaves. The spiders feed on a large variety of prey (e.g. flies, beetles, earwigs, centipedes), indicating that both flying and walking arthropods are trapped in their webs. The wrapping threads have large viscid globules that rapidly disperse on the prey's surface, forming a thin film. Adult males guard subadult females in their retreats, possibly waiting for them to moult and copulate. As part of courtship, the male places his pedipalps several times on the female's mouthparts, then one pedipalp on her mouthparts and the other on her epigynum before insertion. Eggs were parasitised by *Baeus* (Scelionidae) and juveniles and subadults by *Zatypota petronae* (Ichneumonidae). Eggs were eaten by *Argyrodes* sp. (Theridiidae), and *Solenopsis* ants stole prey accumulated in the retreats and attacked spiderlings and older juveniles.

Introduction

The natural history of several temperate species of *Theridion* is well known (Bristowe, 1958; Nielsen, 1923, 1932a, b). Nearly all descriptions of courtship behaviour in *Theridion* are also restricted to temperate species (Knoflach, 1998, 2004). In contrast, information is fragmentary or absent for most tropical species. There are general descriptions of the distribution and habitat observations for several tropical *Theridion* species (Levi, 1959, 1967) and a more detailed account of the behaviour and biology of the semi-aquatic *T. bergi* Levi, a cave inhabitant (Xavier *et al.*, 1995), and the predatory attack sequence of *T. evexum* Keyserling in captivity (Garcia & Japyassú, 2005). The present study describes the habitat use, web features, courtship behaviour, feeding behaviour, and natural enemies of the Neotropical species *T. evexum*.

Methods

Observations on the occurrence of parasites and predators, prey captured, web structure, and height of webs above the ground were made for two to four hours every two weeks from October 2004 to October 2005 in a 250 m² plot in the Reserva Biológica Leonel Oviedo, Universidad de Costa Rica (9°54′N, 84°03′W; elevation 1200 m). Webs were searched for from ground level to a height of 4 m. Additional observations were made near Río Agres, San Antonio de Escazú (elevation 1400 m). Both sites are located in the western section of

*Current address: Department of Entomology, Kansas State University, Manhattan, Kansas, USA.

the Costa Rican Central Valley where the precipitation averages 2500 mm annually, mainly from May through December, and the mean annual temperature is 18°C.

The descriptions of feeding behaviour, courtship and copulation are based on video recordings of captive spiders made with a digital video camera (Sony DCR – VX1000) which recorded 30 frames/s. Seven mature females maintained in captivity were placed individually on hexagonal truncated-pyramidal wire frames (20 cm high), with a hexagonal cardboard base to which the spiders anchored their web threads, and a paper cone at the apex of the pyramid served as retreat (Fig. 1). The frames were hung 2 m above the floor from a 30 cm long, thin nylon fishing line, which discouraged the spiders from escaping. The web structure of spiders in captivity complemented the field observations. Drawings of mating behaviour were traced from video recordings. Mean values are followed by standard deviations.

Results

Distribution and web features

Both patches of forest where we found *T. evexum* had permanent streams. The abundance of the spider seemed to decrease in drier areas of these patches, suggesting that this species prefers humid environments. Their webs occurred in the understory, from *c.* 10 cm up to 1.7 m above the forest floor, in places where the forest canopy was relatively dense. Most of the more than 2000 webs observed were constructed on herbaceous plants, at
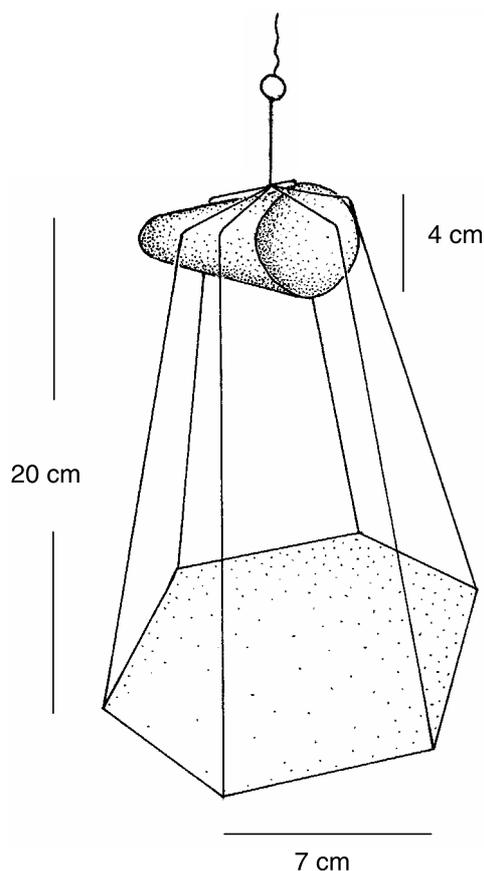

Fig. 1: Wire frame used to maintain spiders in captivity.

Fig. 2: Web of *Theridion evexum*. Note the mesh in front of the retreat mouth and the nearly vertical sticky lines (photo by G. Saborío).

heights between 30 cm and 1 m. Webs were seen on at least 27 species in 18 families of plants.

The web has a retreat that the spider builds by curling a leaf, forming a conical structure (Fig. 2). Leaf rigidity did not preclude *T. evexum* from constructing their retreats, since the leaves used varied from thick, rigid leaves (e.g. *Ficus* sp.; Moraceae) to very soft leaves (e.g. *Impatiens* sp.; Balsaminaceae). The spider weaves a loose mesh just beyond the open end of the retreat. From this mesh extend long sticky threads (up to 30 cm), most of them directed downward, but long threads in a few webs were directed laterally or upward. These capture threads were attached to other leaves and had relatively large viscid globules (mean length 0.049 ± 0.011 mm; mean width 0.026 ± 0.006 mm; $n=10$) along nearly their entire length (mean number of viscid globules per cm$=41.0 \pm 13.0$; $n=7$ threads from three webs). In a sample of 17 webs, there were between 5 and 25 threads directed downward and only one web had eight sticky threads directed upward. In captivity the seven mature females constructed webs with sticky threads in both directions. The number of long sticky lines reached much higher values than in natural conditions; one spider built a web with 63 sticky threads, 21 of them directed upward. The first web that these spiders constructed in captivity had between two to ten downward threads. The spiders then continued adding more lines and after 8–10 days the first upward sticky thread appeared. This indicates that the spiders do not remove the sticky lines and that the lines in nature are probably destroyed by environmental factors (e.g. rain, wind, falling objects, prey).

Attack and feeding behaviour

Theridion evexum in nature fed on a large variety of prey, including flies (e.g. Micropezidae, Syrphidae,

Muscidae, Sarcophagidae, Drosophilidae), treehoppers (Membracidae), grasshoppers (Tettigoniidae), caterpillars (e.g. Geometridae), butterflies (e.g. Ithomiidae), beetles (e.g. Scarabaeidae, Chrysomelidae), damselflies (Calopterygidae), earwigs, and centipedes. It is evident that the relatively small size of this spider did not prevent it attacking large arthropods (spider mean total body length 5.56 ± 0.40 mm, $n=6$ adult females). The attack and feeding behaviour of *T. evexum* (described previously by Garcia & Japyassú, 2005) does not differ from the relatively stereotyped behaviour described for other theridiids (Nielsen, 1932a; Whitehouse, 1987). When a prey was trapped on a sticky thread, the spider descended, walking slowly face-down along the thread to which the prey adhered, continually waving legs I slowly in front ($n=47$ attacks by seven spiders). The first contact with the prey was a gentle touch with one leg I. If the prey was large (e.g. a tipulid fly, damselfly), the spider slowly moved one leg I along the prey's body. The spider then turned 180°, and hanging by legs I, began to fling sticky wrapping threads onto the prey with legs IV. With large prey, wrapping threads were flung upwards from below the lower part of the prey's body. This orientation of wrapping possibly reduces the prey's probability of escaping.

The sticky globules of the wrapping threads of this species (Fig. 3A) were quite large and variable in size (length range 0.084–0.67 mm, width range 0.059–0.42; $n=4$). The sticky globules dispersed extensively and rapidly on the prey, creating a film that dried quickly (Fig. 3B), making it an effective method of subduing large prey. Spiders began attacks on relatively large prey by throwing viscid threads on the prey's body, interrupting wrapping several times to bite the prey. When a prey was completely subdued, it was carried to the retreat hanging from one leg IV. Drosophilids attacked by spiders in captivity were scarcely wrapped, and then bitten once and carried to the retreat. Viscid globules were not observed on the threads used to wrap drosophilids, but they were easily seen in video records early in attacks on large prey.

Male behaviour

Males were recognised in the field when they reached the penultimate stage (subadults), when the pedipalps form a thick yellowish-green mass. In the population studied, subadult and adult males were relatively abundant from June to August, and most of them inhabited their own web (Barrantes & Weng, in prep.). Subadult males produced sticky web and wrapping threads, and captured their own prey. On the contrary, adult males were not inclined to repair or construct their own webs. Adult males ($n=3$) maintained in enclosures with plants did not construct webs. In nature they were able to produce sticky wrapping threads to capture prey, but the viscid globules on these threads were only about one quarter the length and width of the globules produced by females (globules produced by males were observed under the microscope but not measured).

Adult males may displace juvenile spiders to use their webs. On one occasion we observed an adult male in the web of a juvenile, which was sitting outside the retreat. In another case, an adult male was inside the retreat and a juvenile was hanging beneath the retreat's entrance, barely alive and with only three legs; two of the juvenile's legs were still inside the retreat.

Adult males apparently recognised and stayed with subadult females. Seven retreats had an adult male and a female inside. Five of these females were subadults, one was a recently moulted adult female with the moulted skin still inside the retreat, and the last was also a pale, recently moulted female, whose colours became darker during the subsequent two hours.

Courtship behaviour and copulation

We videotaped courtship behaviour and copulation, involving a non-virgin female, once in captivity. As soon as the male was placed on the web, he entered the retreat, approaching the female without any visible long-range precopulatory courtship (e.g. plucking threads) or sperm-web construction. The female began to move slowly towards the male and both slowly waved their first legs. For a period of 31.3 s, both spiders palpated each other's first legs; the female occasionally also palpated the male's legs with her third legs. The male and female then changed from their horizontal upside-down position to a typical copulatory posture (Knoflach, 2004). The male turned face down and the female raised her abdomen slightly so that their faces were near each other and the longest axes of their bodies formed an angle of about 70°. Then the female began to pull her body upwards by flexing her legs, without changing her orientation, until her mouthparts contacted the male's pedipalps which were bent about 60° in front of him. The male then moved away a few mm and both continued the leg tapping behaviour for about 3 s, and then the male redirected his pedipalps to the female's mouth and repeatedly contacted her mouthparts, and then rapidly withdrew them (flapping movement).

During each flap the male extended his pedipalps, contacted the female's mouthparts with the tip or lateral part of both bulbs (Fig. 4A), and rapidly withdrew them. This cycle was repeated 13 times; each mouth contact lasted on average 0.06 s (± 0.03 s), and the period between touches averaged 0.34 s (± 0.13 s, $n=12$). Each time the male's pedipalps approached the female's mouthparts, her palps tapped them rapidly, but the rest of her body remained motionless. After this first bout of flapping, the male continued with a similar movement, but this time only his right pedipalp contacted the female's mouth while the tip of his left bulb contacted her epigynum (Fig. 4B). He repeated this movement 26 times (mean contact time$=0.08 \pm 0.05$ s, $n=15$; mean time between flaps$=0.33 \pm 0.13$ s, $n=14$), but after the second and fifteenth flaps to the mouth and epigynum, the male flapped both pedipalps once to the female's mouth. After this second bout of movements the male inserted his left pedipalp in the female's epigynum for 12
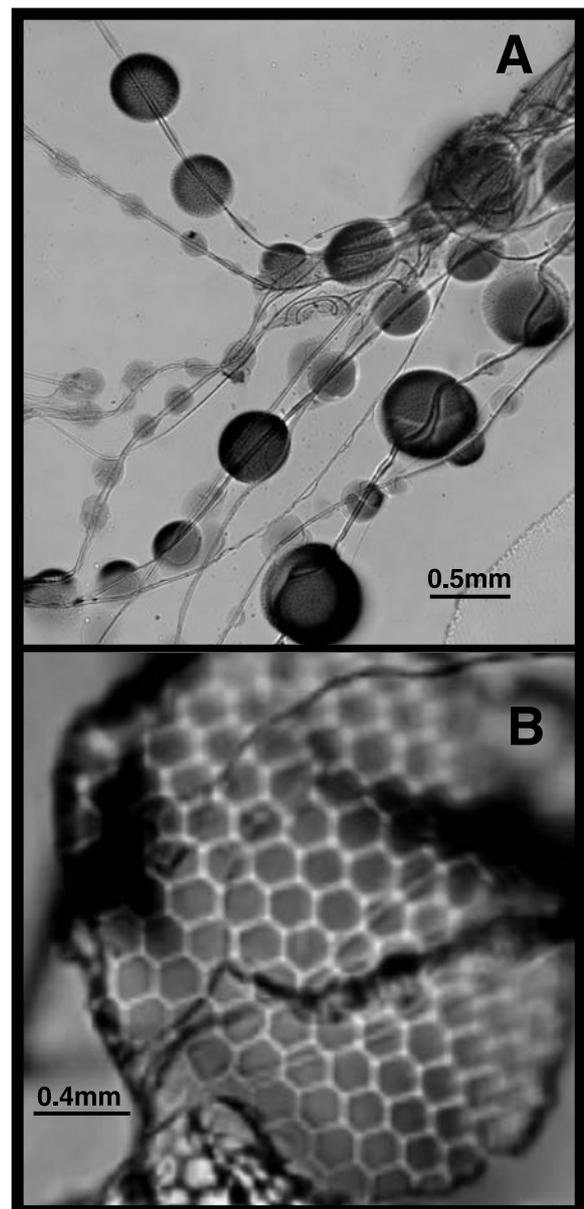

Fig. 3: **A** Sticky globules present on the wrapping threads of *T. evexum*; **B** A thin coat formed after the viscid globules of wrapping threads spread and dried on the surface of a damselfly eye.

seconds. The angle did not allow us to observe in which side of the epigynum the palp was inserted.

After the first insertion the male moved about 1 cm away from the female and during 14 s his abdomen jerked 13 times as it bent ventrally, possibly producing stridulations (Knoflach, 2004). As the male jerked his abdomen, the female approached slowly, tapping him with her palps and first and third legs, while the male palpated her legs with his first legs for 41 s. The male then began to rock back and forth in front of the female, extending his pedipalps towards her epigynum with each forward movement. The male did not contact her mouth or epigynum with his pedipalps, but instead he rapidly flipped the bulbs of his pedipalps alternately up and down while oscillating. The flips were short, with the bulbs barely passing over each other as they moved. After 28 rocking movements, both male and female again assumed copulatory positions: the female turned

to a face-down position, while the male was upside-down in an almost horizontal position, facing her epigynum. From this position the male inserted his right pedipalp in the right aperture of the epigynum (ipsilateral insertion) as he retracted his left pedipalp in front of his face (Fig. 4C). The right pedipalp was stretched during insertion.

Soon after insertion, the haematodochae inflated and remained so for the rest of the 26 s of copulation. The female remained basically immobile, except for slight movements of her palps which did not contact the male. However, during the last 19 s the tip of the tarsus of her right third leg contacted the bulb of the male's pedipalp, and movements during the last 10 s suggested that this leg was pushing the bulb; the tarsus twice slipped over the bulb. Additionally, within the last 6 s she moved her right first leg 11 times towards the epigynum and contacted the bulb of the male's pedipalp with the tip of the tarsus. After finishing this second insertion the male approached the female three more times, jerking his abdomen and tapping her with his first legs. However, each time the female lunged at him and chased him away, and he then left the web. The mating, including both insertions and the associated behaviour, lasted 4.7 min. The male did not charge his pedipalps with sperm during the courtship or copulation, indicating that males charge their pedipalps before encountering a female.

Natural enemies

The egg sac of *T. evexum* was globular with white outer fibres. The spiderlings emerged from the egg sac after 23–25 days ($n=2$, in the field) and during this time the female spider protected the sac against parasites and predators. Particularly, during approximately the first ten days her legs I–III and her palps were frequently in contact with the outer wall of the egg sac. However, the guarding behaviour did not prevent the wasp *Baeus* sp. (Scelionidae) from parasitising the eggs. We opened up two egg sacs when the first *Baeus* were observed emerging and found that 42 of the 140 eggs in one sac, and five of the 142 eggs in the second were parasitised. These egg sacs were collected in the field when spiderlings were about to emerge from the egg sac.

Subadult females, subadult males, and immatures were found to be parasitised by the wasp *Zatypota petronae* Gauld (Ichneumonidae). This wasp glues its eggs on the anterior part of the dorsum of the spider's abdomen (konobiont ectoparasitoid), and after emerging the larva feeds on the spider's haemolymph (Gauld *et al.*, 1998), killing the host spider after the larva reaches its last instar (details in Weng & Barrantes, in prep.).

Argyrodes sp. is another threat to the eggs. This spider predated the eggs through the wall of the egg sac; we observed egg predation only twice but *Argyrodes* is a frequent dweller in webs of *T. evexum*. Thus, it is possible that predation of eggs by *Argyrodes* occurred more frequently. The ant *Solenopsis* sp. (Formicidae)

was capable of entering the spider's retreat and stealing the spider's prey and killing some spiderlings. The egg sac was normally deep inside the retreat, nearly touching the leaf surface. However, when the retreat was invaded by ants, the spider moved the egg sac and hung it in the centre of the retreat from a mesh that the spider
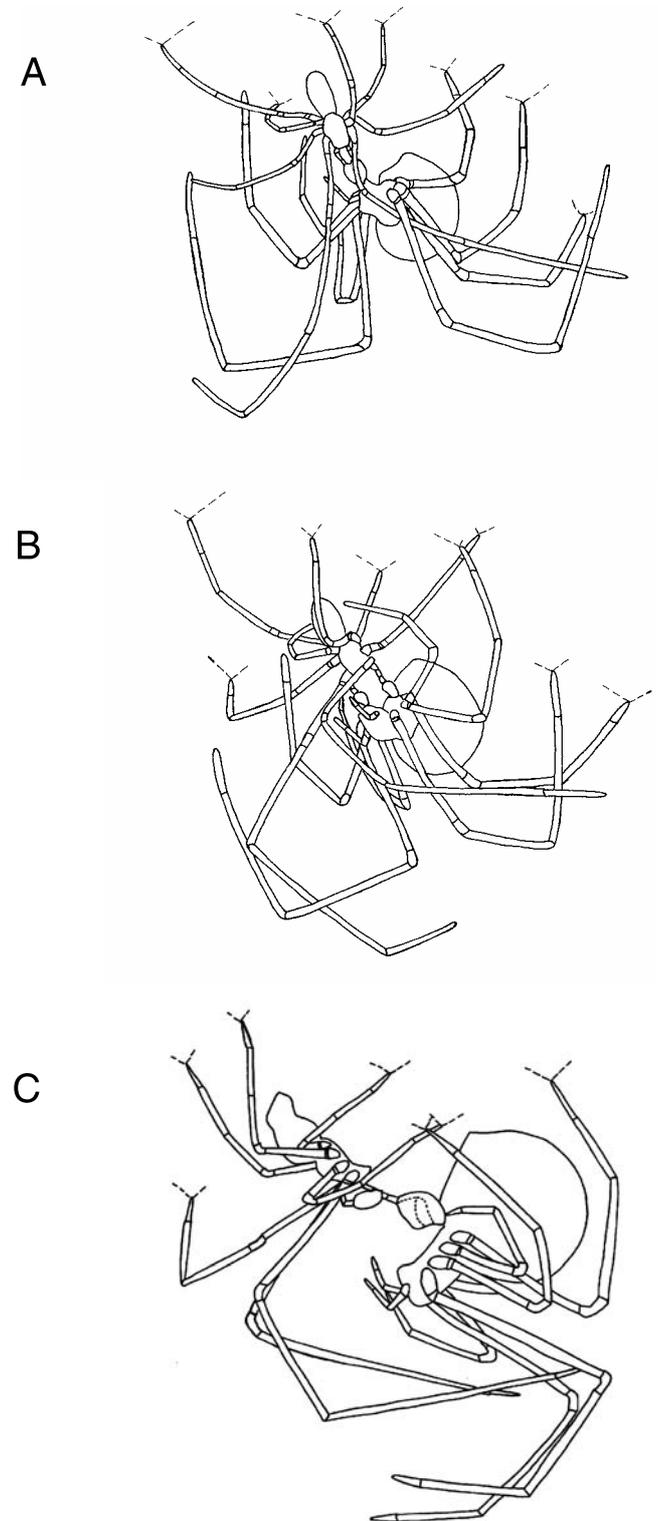

Fig. 4: Partial sequence of the courtship and copulation in *T. evexum*. **A** Male with both pedipalps on the female's mouthparts; **B** Male with his right pedipalp on the female's mouthparts and the left pedipalp contacting her epigynum; **C** Insertion of the right pedipalp on the right side of the epigynum (ipsilateral insertion); note the tarsus of the female's right third leg touching the bulb of the male's pedipalp.

constructed with some sticky threads ($n=2$). Attacks by ants were relatively infrequent (3 out of 19 visits) and restricted to a small area of the study population.

Discussion

The web of *T. evexum* seems to be designed to capture walking prey. However, unlike the more or less vertical lines present in webs of other theridiid species, such as *Nesticodes rufipes* (Lucas), *Steatoda bipunctata* (Linnaeus), or *Latrodectus geometricus* C. L. Koch (Nielsen, 1923, 1932a, b; Benjamin & Zschokke, 2002; Agnarsson, 2004), where the viscid globules are restricted to the farthest end of the capture threads and the anchor point of these threads is easily broken, in *T. evexum* the viscid globules are distributed along most of the length of the capture lines (Garcia & Japyassú, 2005), which are strongly attached to the substrate. The characteristics of the webs of this spider are apparently designed to capture both flying and walking arthropods, as indicated by the large variety of prey items found in them.

Males of *T. evexum* guarded the subadult females in their retreats until they became adults. This guarding behaviour is widespread in Theridiidae, Araneidae, Tetragnathidae and Linyphiidae (Foelix, 1996; Knoflach, 2004) and assures the male's access to virgin receptive females.

The copulatory behaviour of *T. evexum* (only one non-virgin female observed) shares features with the two types of copulatory behaviour defined by Knoflach (2004) for theridiids, the *Steatoda* type and the *Theridion* type. Sperm induction independent of copulation is typical for the *Steatoda* type, whereas both the absence of a mating web and the presence of copulation by male approach are typical for the *Theridion* type. A unique feature is the role of the male pedipalps in contacting the female's mouthparts in *T. evexum*. This behaviour may induce the female to allow the male to copulate, and/or to receive and use his sperm. However, further information is needed, particularly on virgin females, for comparison with these preliminary observations.

In general, the prey attack behaviour of this species (Garcia & Japyassú, 2005; and our results) is similar to that described for other theridiids (Bristowe, 1958). However, *T. evexum* produced much larger viscid globules on the wrapping threads than at least six other theridiid species: *Achaearanea tesselata* (Keyserling), *A. tepidariorum* (C. L. Koch), *Helvibis longicauda* Keyserling, *Nesticodes rufipes*, *Tidarren sisyphoides* (Walckenaer) and *Latrodectus geometricus* (pers. obs.). The large globules of viscid material disperse easily on the prey's surface, probably reducing the prey's chances of escaping.

Retreats are widespread among the Theridiidae, but they vary greatly between species. Several species use little bits of vegetation [e.g. *Achaearanea lunata* (Clerck)], sand and other soil particles [e.g. *A. riparia* (Blackwall)], a dead rolled leaf (Nielsen, 1932a), or the undersurface of an unmodified leaf [e.g. *Paidiscura*

pallens (Blackwall)] (Bristowe, 1958). The retreat constructed by *T. evexum*, a folded leaf, has been described for *Enoplognatha ovata* (Clerck) (Nielsen, 1932a), and is also present in *Chrysso cambridgei* (Petrunkevitch), a species that constructs a web very similar to that of *T. evexum* (pers. obs.). Convergence in web features is widespread between genera of Theridiidae (Benjamin & Zschokke, 2003; Eberhard & Agnarsson, in prep.).

The natural enemies of *T. evexum* include egg predators (e.g. *Argyrodes*), egg parasitoids (e.g. *Baeus*), and parasitoids (e.g. *Zatypota petronae*) that kill immature spiders. *Zatypota* wasps are apparently specialist ectoparasites of theridiid spiders (Gauld *et al.*, 1998), whereas *Baeus* species apparently attack exclusively eggs of spiders in different families. The presence of *Baeus* may explain the egg-guarding behaviour that we frequently observed in *T. evexum*.

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