

# Taking care of the enemy: egg predation by the Darwin wasp *Tromatobia* sp. (Ichneumonidae) on the cobweb spider *Chryso compressa* (Araneae, Theridiidae)

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## Abstract

Some wasp species use spiders as food resources, overcoming several anti-predator barriers that are exerted by spiders. *Tromatobia* ichneumonid wasps are spider egg predators that usually attack Araneidae species, although there are few records of predation on Clubionidae, Philodromidae, Linyphiidae, Tetragnathidae, and Theridiidae spiders. Here, we describe the interaction between *Tromatobia* sp. and *Chryso compressa*, a subsocial theridiid spider that exhibits extended maternal care, in the Atlantic Forest of southeastern Brazil. We observed that the larva of *Tromatobia* sp. develop inside the egg sacs of *C. compressa*, preying on the entire egg mass and building cocoons that change the color and morphology of the egg sacs. Despite these structural modifications, we registered an adult female of *C. compressa* guarding and caring for the cocoons (attacked egg sac) of the predators as if they were offspring (non-attacked egg sac). To the best of our knowledge, this study represents the first record of *Tromatobia* preying on *Chryso* eggs.

**Keywords**

egg sac, maternal care, Pimplinae, Serra do Japi

**Introduction**

Wasps are important natural enemies of spiders and adopt several foraging strategies to subdue their prey (Rayor 1996). For example, some wasp species act exclusively as koinobiont ectoparasitoids (polysphinctine wasps *sensu* Gauld & Dubois, 2006) or predators (spider-hunting wasps – Crabronidae, Pompilidae and Sphecidae; Mayr et al. 2020) of juvenile, sub-adult, or adult spiders. Some other wasp species are specialized in attacking and parasitizing individual eggs (e.g., *Baeus* Austin, 1985) or consuming part of the egg mass of spiders (e.g., *Tromatobia* Gauld et al., 2002). Consequently, spiders have evolved anti-predator mechanisms that prevent wasp attacks.

Spiders can minimize predation risk by avoiding detection, recognition, and access to predators by using several defensive cues and behaviors (Pekár 2013; Gawryszewski 2017). The anti-predator strategies of spiders include crypticity, mimicry, construction of three-dimensional webs (Blackledge et al. 2003) and refuges, presence of thick silk barriers in egg sacs, extended parental care, and, in some extreme cases, group living and sociality (Pekár 2013; Gawryszewski 2017). Understanding how wasps overcome these barriers and succeed in capturing spiders is an interdisciplinary research topic that combines studies on ecology, evolutionary behavior, physiology, and phylogeny.

Darwin wasps of the genus *Tromatobia* Foster, 1869 are specialized in attacking aerial-web building spiders (Fitton et al. 1987, 1988; Finch 2005; Yu et al. 2016; Broad et al. 2018), completing their larval life cycle inside spider egg sacs, and consuming part or the entire egg mass (Austin 1984, 1985; Villanueva-Bonilla et al. 2016). There is high interspecific variation in the number of eggs, from one to 14, that *Tromatobia* females can lay inside spider egg sacs (Nielsen 1923). This variation also occurs within the same species, as *Tromatobia blancoi* Gauld, 1991 can produce six-nine eggs per egg sac of the spider *Araneus thaddeus* (Hentz, 1847) (Jiménez 1987). Although rare, most reports of *Tromatobia*-spider interactions involve Araneidae species of the genera *Araneus*, *Araniella*, *Argiope*, *Cyclosa*, and *Zygiella* (e.g., Nielsen 1923; Jiménez 1987; Fitton et al. 1988; Quicke 1988; Oehlke and Sacher, 1991; Cortés et al. 2000; Sobczak 2012), indicating fine specialization for this family. However, there are a few records of *Tromatobia* attacking Clubionidae, Philodromidae, Linyphiidae, Tetragnathidae, and Theridiidae species (e.g., Austin 1985; Fitton et al. 1988; Oehlke and Sacher 1991; He et al. 1992). In fact, knowledge about the biology, ecology, and behavior of interactions with these minor hosts is scarce and requires further field observations and experimental studies.

Herein, we report the interaction between the egg predator wasp *Tromatobia* sp. (Ichneumonidae) and the cobweb spider *Chrysso compressa* (Keyserling, 1884) (Theridiidae) in the Brazilian Atlantic Forest, with notes on the behavior of the *C. compressa* guarding the predator's cocoon.

## Materials and methods

### Study species

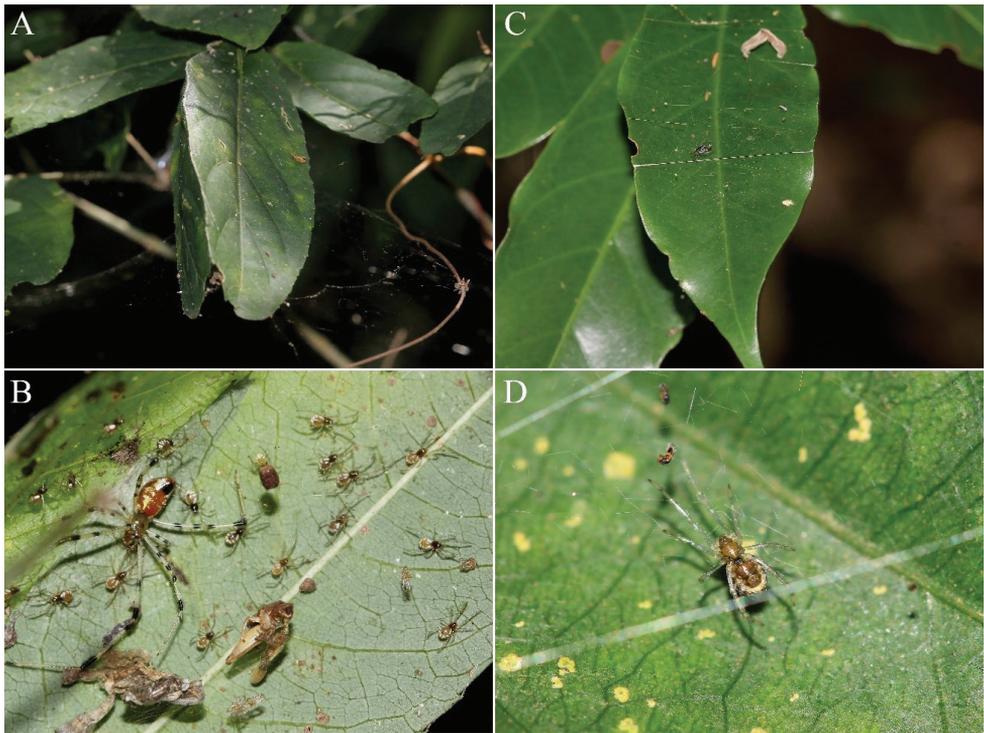
*Chrysso compressa* belongs to a genus with 64 valid species distributed mainly in America and Asia (Levi 1957; World Spider Catalog 2022). Some of these species are known to exhibit subsocial behavior with extended maternal care (Miller and Agnarsson 2005; Yip and Rayor 2014). Such behavior involves a temporary period of coexistence of offspring in the maternal nest, when spiderlings cooperate in prey capture, feeding, and web maintenance before they disperse and live solitarily (Lubin and Bilde 2007). *Chrysso compressa* occurs in the Brazilian Atlantic Forest, where it constructs irregular webs on shrubby vegetation, and females care for their offspring until the juvenile stage (Santiago 2022). Adult spiders build refuges using two green leaves that are connected by silk, thereby forming a roof-like structure, which shelters the female and its offspring under the abaxial surface of the leaves (Fig. 1A, B). After dispersion from the nest, the juvenile spider moves to the adaxial surface of another leaf and takes refuge by connecting the side of edges of the leaf using silk threads (Fig. 1C, D).

### *Tromatobia* sp.

The undetermined *Tromatobia* differs from the Costa Rican species (see Gauld et al. 1998), the South American *T. lineiger* Morley, 1914 (digital images analysed), and *T. huebrichi* (Brèthes, 1913) (see Porter 1979) by the combination of the following character states: pronotum without a small shelf-like projection; small ovipositor, 1.0–1.1 times as long as hind tibia; mesosoma reddish and metasoma blackish with thin white strips on the posterior margin of tergites. It was not possible to make a detailed comparison of most South American species (except *T. lineiger* and *T. huebrichi*) because the descriptions are old and succinct, based mainly on coloration. So we prefer to proceed with caution and leave it as an indeterminate species.

### Study area

We conducted our study near the Base de Estudos de Ecologia e Educação Ambiental da Serra do Japi, Jundiáí, São Paulo, Brazil (1000 m above sea level; 23°13'53"S, 46°56'09"W), where there is a well-established and easily accessible population of *C. compressa* (Santiago 2022). The site is an environmentally protected area that constitutes one of the few remnants of the Atlantic Forest in southeastern Brazil. The reserve has a predominantly semi-deciduous mesophyll forest with distinct phytophysiognomies along an altitudinal gradient from 700 to 1300 m above sea level (Leitão-Filho 1992). The climate is CWA in Köppen's classification (Alvares et al. 2013), which is characterized by hot/rainy summers and cold/dry winters with average monthly temperatures ranging from 13.5 °C in July to 20.3 °C in January (Pinto 1992). Serra do Japi is a hotspot for spider-wasp interactions and is one of the most studied areas with respect to these interactions in the Neotropical region (Gonzaga et al. 2017).



**Figure 1.** **A** upper view of the refuge of leaves constructed by subadult and adult individuals of *C. compressa* **B** adult female of *C. compressa* and the offspring (3<sup>o</sup> and 4<sup>o</sup> instar spiders) within the refuge under the abaxial surface of the leaves **C** refuge of juvenile spiders on the adaxial leaf surface **D** post-dispersion juvenile of *C. compressa* on its refuge. Photos: Brenda Santiago.

## Field observations and data collection

One of us (first author BKSS) conducted monthly inspections from April 2021 to March 2022 to collect adult females and egg sacs of *C. compressa* on shrubby vegetation along forest edges and ecological trails in the study area. Each inspection consisted of visual searches with a sampling effort of four to five hours during the daytime (09:00 to 13:00). We maintained the female spiders we found and their respective egg sacs in the laboratory inside individual plastic pots containing pieces of cotton soaked in a liquid nutrient solution. We then recorded traits of non-attacked and attacked egg sacs (e.g., color, shape, number of eggs, and number of wasp cocoons), in addition to biological and behavioral data on maternal care performed by *C. compressa*. We also recorded under laboratory conditions the behaviors of one adult female spider guarding its own egg sac (hereafter “native”) attacked by *Tromatobia* sp., and after we offered an attacked egg sac acquired from another spider in the field (hereafter “alien”). We fixed the adult wasps that emerged from the cocoons in 70% alcohol for subsequent identification. To obtain digital images of adult wasps and pupa, we used a Leica DMC4500 digital

camera attached to a Leica M205A stereomicroscope and stacked multiple layers using the software Leica Application Suite V4.10.0.

We deposited wasp voucher specimens in the Invertebrate Collection of Instituto Nacional de Pesquisas da Amazônia (curator J. A. Rafael) and spiders in the arachnid collection of the Taxonomic Collections of Universidade Federal de Minas Gerais (curator A. J. Santos).

## Results

We collected 22 egg sacs of *C. compressa* (N = 6 in January, N = 10 in February, N = 4 in March, N = 1 in April, and N = 1 in May), of which five (22.7%) were attacked by *Tromatobia* sp. Healthy egg sacs harboured an average of  $46 \pm 21$  eggs (N = 17), were light in color, round-shaped (diameter =  $10.1 \pm 3.7$  mm, N = 17), and were usually located under the bodyguard of the adult female (Fig. 2A). The morphology of egg sacs that were attacked by *Tromatobia* sp. was found to be altered after the development of wasp larva; they were elongated and oval (average total length =  $9.1 \pm 1.2$  mm and average total width =  $2.5 \pm 0.9$  mm, N = 3), with the shape of cocoons adhered to each other longitudinally, on their longer sides. At this stage, the wasp cocoons, grey or brownish in color (Fig. 2B) became exposed and interspersed with a few silk remnants of the original egg sac (Fig. 2C). The attacked egg sacs that were collected in the present study contained two (N = 3) or three (N = 1) cocoons of *Tromatobia* sp. Adult wasps emerged through holes with approximately 2 mm in diameter located in the apical portion of the cocoon (Fig. 2D). In total, we obtained nine adult individuals of *Tromatobia* sp. (Fig. 2E), five females (average body length =  $7.3 \pm 0.9$  mm) and four males (body length =  $6.6 \pm 0.8$  mm).

We observed that the maternal care provided by *C. compressa* included the protection of egg sacs under the female body, between the forelegs and held by the pedipalps. We also registered the same behavior of females protecting the cocoons of *Tromatobia*, even in the case when predators had already fed on the entire egg mass (Fig. 2B). In addition, we observed that the spider we offered an alien egg sac adopted and attached it to the native egg sac. The spider bodyguarded both egg sacs containing wasp cocoons until an adult wasp emerged from the native egg sac. At this time, we removed the female spider and left the alien egg sac alone and undisturbed for 68 days; however, adult wasps did not emerge from this egg sac. Then we opened it carefully and found a cocoon with a dead male adult wasp almost fully-developed inside (Fig. 2F).

## Discussion

To the best of our knowledge, this is the first report on an interaction between *Tromatobia* and *Chryso*. Previous studies have indicated a strong affinity of *Tromatobia* for araneid orb-web spiders, with a few unusual records of attacks on other families



**Figure 2.** **A** adult female of *C. compressa* taking care of the egg sac **B** adult female of *C. compressa* taking care of cocoons of the egg predator wasp *Tromatobia* sp. **C** cocoon of the egg predator wasp *Tromatobia* sp. **D** cocoon hole through which adult wasps of *Tromatobia* sp emerge. **E** lateral view of an adult female of *Tromatobia* sp., and **F** lateral view of an adult wasp that did not emerge from the cocoon. Photos: Brenda Santiago and Diego Pádua.

including Theridiidae that construct three-dimensional webs. However, some records are rather poorly documented and potentially unreliable. Thus, our report is probably the best-documented record of *Tromatobia* parasitising non-araneid spiders. We showed that *Tromatobia* wasps could overcome anti-predator barriers and affect more than 20% of *C. compressa* egg sacs. Unlike the case of egg parasitoid species, in which

each wasp attacks an individual spider egg, *Tromatobia* sp. consumes the entire egg mass and affects the spiderling population to a greater extent. We recorded two to three cocoons per egg sac, similar to the observation made by Sobczak et al. (2012) for the sympatric orb-web spider *Araneus omnicolor* Keyserling 1893. However, other studies have reported instances where up to 14 individuals were observed per egg sac in *Tromatobia* species (e.g., Nielsen 1923; Jiménez 1987). Hence, is still unknown whether there is an optimal number of eggs and whether and how larvae compete for food resources.

Behavioral manipulations of hosts induced by parasitoid species have been well-studied in the last few years (Weinersmith 2019). In cases involving spiders and wasps, parasitoid species can alter host behavior by inducing the construction of modified webs that are used to protect the cocoon, thereby maximizing survival (Eberhard 2000, 2010; Gonzaga et al. 2017). However, *Tromatobia* sp. does not change the behavior of *C. compressa* but takes advantage of bodyguarding, a pre-existing behavior of maternal care. Although there is an evident morphological change in the egg sac, the wasp may use concealment mechanisms, such as chemical or tactile camouflage (Kaminski et al. 2020), to deceive adult spiders. We observed that the wasp of the alien egg sac that was adopted by *C. compressa* in the laboratory did not emerge from the cocoon after we removed the female spider. This anecdotal report suggests that the presence of adult females may be important for wasps. Hence, the effect of bodyguarding behavior on wasp survival should be further investigated in future studies.

Egg protection is crucial for the survival of spider progenies given the high diversity of selective pressures exerted by multiple predators and parasitoids (Bristowe 1971; Li et al. 1999; Yip and Rayor 2014). The behavior of many spider species that keep their egg sacs suspended, for example, is a strategy to avoid attack by wandering generalist predators, such as ants (Turnbull, 1973), but using this strategy can increase the conspicuousness of egg sacs to visually oriented predators (e.g., birds and wasps, Hieber 1992). Instead, egg sacs of *C. compressa* are usually under female guard within the refuge, and attacks may occur during foraging when females move to the web to catch prey. However, it is still unknown how *Tromatobia* sp. adults overcome the barriers of *C. compressa* in detecting, reaching, and successfully attacking egg sacs. In this way, further investigation should focus on identifying specific behaviors performed by the wasps and cues provided by spiders that facilitate egg predation.

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## References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLDM, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorological Journal* 22: 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Austin AD (1984) The fecundity, development and host relationships of *Ceratobaeus* spp. (Hymenoptera: Scelionidae) parasites of spider eggs. *Ecological Entomology* 9: 125–138. <https://doi.org/10.1111/j.1365-2311.1984.tb00707.x>
- Austin AD (1985) The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. *Journal of Natural History* 19: 359–376. <https://doi.org/10.1080/00222938500770261>
- Bristowe WS (1971) *The World of Spiders*. Collins, London.
- Broad GR, Shaw MR, Fitton MG (2018) The ichneumonid wasps of Britain and Ireland (Hymenoptera: Ichneumonidae): their classification and biology. *Handbooks for the Identification of British Insects* 7: 1–418.
- Blackledge TA, Coddington JA, Gillespie RG (2003) Are three-dimensional spider webs defensive adaptations? *Ecology Letters* 6: 13–18. <https://doi.org/10.1046/j.1461-0248.2003.00384.x>
- Cortés JP, Daza EF, Palacio E (2000) Registro de *Tromatobia* sp. (Hymenoptera: Ichneumonidae) como parasitoide de huevos de la araña *Araneus granadensis* (Araneae: Araneidae). *Folia Entomologica Mexicana* 28: 2–4.
- Eberhard WG (2000) Spider manipulation by a wasp larva. *Nature* 406: 255–256. <https://doi.org/10.1038/35018636>
- Eberhard WG (2010) Recovery of spiders from the effects of parasitic wasps: implications for fine-tuned mechanisms of manipulation. *Animal Behaviour* 79: 375–383. <https://doi.org/10.1016/j.anbehav.2009.10.033>
- Finch OD (2005) The parasitoid complex and parasitoid-induced mortality of spiders (Araneae) in a Central European Woodland. *Journal of Natural History* 39: 2339–2354. <https://doi.org/10.1080/00222930502005720>
- Fitton MG, Shaw MR, Austin AD (1987) The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* 90: 65–93. <https://doi.org/10.1111/j.1096-3642.1987.tb01348.x>
- Fitton MG, Shaw MR, Gauld ID (1988) Pimpline ichneumon-flies Hymenoptera, Ichneumonidae (Pimplinae). *Handbook for the Identification of British Insects*, Royal Entomological Society of London, London, U.K., 110 pp.
- Gauld ID, Ugalde J, Hanson PE (1998) Guía de los pimpline (Hymenoptera: Ichneumonidae) de Costa Rica. *Revista de Biología Tropical* 46: 1–189.

- Gauld ID, Wahl DB, Broad GR (2002) The suprageneric groups of the Pimplinae (Hymenoptera: Ichneumonidae): a cladistic re-evaluation and evolutionary biological study. *Zoological Journal of the Linnean Society* 136: 421–485. <https://doi.org/10.1046/j.1096-3642.2002.00031.x>
- Gauld ID, Dubois J (2006) Phylogeny of the *Polysphincta* group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids. *Systematic Entomology* 31: 529–564. <https://doi.org/10.1111/j.1365-3113.2006.00334.x>
- Gawryszewski FM (2017) Anti-predator strategies. In: Viera C, Gonzaga MO (Eds) *Behaviour and Ecology of Spiders: contributions from the neotropical region*. Springer: New York (US), 397–415. [https://doi.org/10.1007/978-3-319-65717-2\\_15](https://doi.org/10.1007/978-3-319-65717-2_15)
- Gonzaga MO, Kloss TG, Sobczak, JF (2017) Host behavioural manipulation of spiders by ichneumonid wasps. In: Viera C, Gonzaga MO (Eds) *Behaviour and Ecology of Spiders: contributions from the neotropical region*. Springer: New York (US), 417–434. [https://doi.org/10.1007/978-3-319-65717-2\\_16](https://doi.org/10.1007/978-3-319-65717-2_16)
- He JH, Tang YQ, Chen XX, Ma Y, Tong XW (1992) Ichneumonidae. In: Peng JW, Liu YQ (Eds) *Iconography of forest insects in Hunan China*. Hunan Science Publisher, 1211–1249. [in Chinese with English summary]
- Hieber CS (1992) Spider cocoons and their suspension systems as barriers to generalist and specialist predators. *Oecologia* 91: 530–535. <https://doi.org/10.1007/BF00650327>
- Jiménez ML (1987) Relaciones biológicas entre arañas y avispas. *Folia Entomologica Mexicana* 73: 173–183.
- Leitão-Filho HF (1992) A flora arbórea da Serra do Japi. In: Morellato LPC (Ed.) *História natural da Serra do Japi: ecologia e preservação de uma área florestal no Sudeste do Brasil*. Editora da Unicamp/Fapesp, Campinas, 40–42.
- Levi HW (1957) The spider genera *Chryso* and *Tidarren* in America. *Journal of the New York Entomological Society* 63: 59–81.
- Li D, Jackson RR, Barrion AT (1999) Parental and predatory behaviour of *Scytodes* sp., an aneophagic spitting spider (Araneae: Scytodidae) from the Philippines. *Journal of Zoology London* 247: 292–310. <https://doi.org/10.1111/j.1469-7998.1999.tb00993.x>
- Lima LD, Trigo JR, Kaminski LA (2020) Chemical convergence between a guild of facultative myrmecophilous caterpillars and host plants. *Ecological Entomology* 46: 66–75. <https://doi.org/10.1101/2020.06.29.178319>
- Lubin Y, Bilde T (2007) The evolution of sociality in spiders. *Advances in the Study of Behavior* 37: 83–145. [https://doi.org/10.1016/S0065-3454\(07\)37003-4](https://doi.org/10.1016/S0065-3454(07)37003-4)
- Mayr AV, Peters MK, Eardley CD, Renner ME, Röder J, Steffan-Dewenter I (2020) Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. *Journal of Biogeography* 47: 854–865. <https://doi.org/10.1111/jbi.13753>
- Matsumoto R (2016) Molecular phylogeny and systematics of the *Polysphincta* group of genera (Hymenoptera, Ichneumonidae, Pimplinae). *Systematic Entomology* 41: 854–864. <https://doi.org/10.1111/syen.12196>
- Miller J, Agnarsson I (2005) A redescription of *Chryso nigriceps* (Araneae, Theridiidae) with evidence for maternal care. *Journal of Arachnology* 33: 711–714. <https://doi.org/10.1636/H04-10.1>
- Nilsen E (1923) Contributions to the life history of the Pimpline spider parasites *Polysphincta*, *Zaglyptus*, *Tromatobia* (Hymenoptera: Ichneumonidae). *Entomologiske Meddelelser* 14: 137–205.

- Oehlke J, Sacher P (1991) Speziation bei Parasitoiden am Beispiel von Schlupfwespen (Ichneumonidae: Pimplinae). Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologisches Museum und Institut für Spezielle Zoologie (Berlin) 67: 169–176. <https://doi.org/10.1002/mmnz.19910670122>
- Pekár S (2014) Comparative analysis of passive defences in spiders (Araneae). Journal of Animal Ecology 83: 779–790. <https://doi.org/10.1111/1365-2656.12177>
- Pinto HS (1992) Clima na Serra do Japi. In: Morellato LPC (Ed.) História Natural da Serra do Japi: ecologia e preservação de uma área florestal no Sudeste do Brasil. Editora da Unicamp/Fapesp, Campinas, 30–38.
- Porter CC (1979) Ichneumonidae de Tarapaca. 1. Subfamily Ephialtinae (Hymenoptera). Idesia 5: 157–187.
- Quicke DLJ (1988) A new host record for *Tromatobia notator* (Hym., Ichneumonidae). Entomologist's Monthly Magazine 124: 164.
- Rayor LS (1996) Attack strategies of predatory wasps (Hymenoptera: Pompilidae; Sphecidae) on colonial orb web-building spiders (Araneidae: *Metepeira incrassata*). Journal of the Kansas Entomological Society 69: 67–75. <http://www.jstor.org/stable/25085706>
- Santiago BKS (2022) Interações entre vespas parasitoides/predadores e aranhas construtoras de teias tridimensionais (Theridiidae) na Serra do Japi, Jundiá, São Paulo. Dissertação de Mestrado. Universidade Estadual de Campinas.
- Sobczak JF (2012) Description of the male *Hymenoepimecis japi* Sobczak et al., 2009 (Hymenoptera, Ichneumonidae) parasitoid of *Leucauge roseosignata* Mello-Leitão, 1943 (Araneae: Tetragnathidae). Brazilian Journal of Biology 72: 945–947. <https://doi.org/10.1590/S1519-69842012000500023>
- Sobczak JF, Loffredo APS, Sobczak JCMSM (2012) First record of egg sac predation of the wasp *Tromatobia* sp. Foster, 1869 (Hymenoptera: Ichneumonidae) upon *Araneus omnicolor* (Keyserling, 1893) (Araneae: Araneidae). Revista Ibérica de Aracnología 20: 113–115.
- Turnbull AL (1973) The ecology of the true spiders (Araneomorphae). Annual Review of Entomology 18: 305–34. <https://doi.org/10.1146/annurev.en.18.010173.001513>
- Villanueva-Bonilla GA, Onody HC, Santos BF, Vasconcellos-Neto J (2016) First record of egg sac predation on a wall crab spider Selenopidae (Araneae) by the wasp *Camera lunavenatrix* sp. n. (Ichneumonidae, Cryptinae). Journal of Hymenoptera Research 49: 65–79. <https://doi.org/10.3897/JHR.49.7862>
- Weinersmith KL (2019) What's gotten into you?: a review of recent research on parasitoid manipulation of host behavior. Current Opinion in Insect Science 33: 37–42. <https://doi.org/10.1016/j.cois.2018.11.011>
- World Spider Catalog (2022) World Spider Catalog. Natural History Museum Bern. <https://doi.org/10.24436/2> [accessed on 09 August 2022]
- Yip EC, Rayor LS (2014) Maternal care and subsocial behaviour in spiders. Biological Reviews 89: 427–449. <https://doi.org/10.1111/brv.12060>
- Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015. Nepean, Ontario, Canada, database on flash-drive. <https://www.taxapad.com> [accessed on 19 December 2022]