

Web architecture alteration of the orb web weaving spider *Metellina merianae* (Araneae, Tetragnathidae) induced by the parasitoid *Megaetaira madida* (Ichneumonidae, *Polysphincta* group)

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Abstract. The polysphinctine wasp *Megaetaira madida* (Haliday, 1838) is a koinobiont ecto-parasitoid of spiders of the genus *Metellina*. Under the influence of the parasitoid's final instar larva, the spider host *M. merianae* (Scopoli, 1763) built a three-dimensional web architecture, which differed considerably from the capturing orb web. The alteration of spider web behaviour induced by a parasitoid larva in this host-parasitoid pair is described for the first time.

Keywords: behavioural manipulation, host-parasitoid interaction, spider web, wasp

Zusammenfassung. Durch den Parasitoid *Megaetaira madida* (Ichneumonidae, *Polysphincta*-Gruppe) induzierte Veränderungen im Netzbau von *Metellina merianae* (Araneae, Tetragnathidae). Die Schlupfwespe *Megaetaira madida* (Haliday, 1838) aus der *Polysphincta*-Gattungsgruppe ist ein koinobiontischer Ektoparasitoid von Spinnen der Gattung *Metellina*. Unter Einfluss des letzten Larvenstadiums des Parasitoiden baute die Wirtsspinne *M. merianae* (Scopoli, 1763) dreidimensionale Netze, deren Architektur erheblich von der normalen Fangnetze abweicht. Die Veränderung des Netzbauverhaltens einer Spinne durch die Larve eines Parasitoiden wird erstmals beschrieben.

Koinobiont parasitoid wasps from the *Polysphincta* genus-group sensu Gauld & Dubois (2006) are all exclusively associated with spider hosts and their host range is taxonomically restricted (mostly to genus level) (Fitton et al. 1987). The female wasp temporally paralyzes the spider and oviposits on the dorsal side of the spider's opisthosoma/prosoma, where the larva develops while the spider continues foraging. Shortly before pupation, the final stage larva can manipulate the web-spinning activity of the host in order to establish effective protection against enemies and an environment for parasitoid pupation (e.g. Eberhard 2000a, Korenko et al. 2014). This modified web which protects the parasitoid pupa after the spider's death is called the 'cocoon web', a term first introduced by Eberhard (2000a), in which some components of the normal web are reduced (e.g. the web spiral, radii) and others are reinforced (e.g. radii, the central hub, the frame) or multiplied (e.g. threads). These effects of the larva are apparently due to chemical products that are introduced into the spider, but the active compounds involved have not yet been identified (Eberhard 2010).

The polysphinctine parasitoid *Megaetaira madida* (Haliday, 1838) is distributed in several parts of the Palaearctic associated with spiders of the family Tetragnathidae (Yu et al. 2012). Its host range exclusively includes spiders of the genus *Metellina*, which build a typical orb web with a small hole in the hub (e.g. Roberts 1995). The spiders *Metellina menzei* (Blackwall, 1869), *Metellina merianae* (Scopoli, 1863) and *Metellina segmentata* (Clerck, 1757) have already been reported as hosts of *M. madida*, but host utilisation including web architecture modification induced by parasitoid final stage larvae has never been documented (Fitton et al. 1987, 1988). Several specimens of *M. madida* were reared by Nielsen (1923) in small tubes. Unfortunately, the small space in the tubes did not allow the observation of innate web building behaviour or its modification

induced by the parasitoid larva. Nielsen observed that wasp cocoons were surrounded by a tangle of threads which were present in all parts of the tubes. Further, Nielsen collected one cocoon attached to a spruce twig in the field with no silk structure surrounding the cocoon. This resembles the situation in which the parasitized spider falls off the web in the period when the parasitoid larva reaches its final stage and is diverted from building any silk structure. Here, I present new host records and the first note on behavioural manipulation of a spider host by *M. madida* from Italy.

Material and methods

I collected parasitized spiders of the genus *Metellina* from the edge of a deciduous forest in Monterosso Grana (Province of Cuneo, Italy, 44°24'20"N, 7°19'17"E) over a two-day period at the end of October 2014. Spiders were collected by beating tree canopies and undergrowth (30 to 200 cm above the ground) with a square-shaped beating net (1-m² area) placed underneath. Each spider was visually inspected for the presence of a parasitoid larva.

The spider hosts were reared in plexiglass experimental arenas (frame 220 × 220 mm, depth 20 mm) with paper tape on four sides of the frame so that the spiders could build webs. The spiders were fed with a surplus of prey (small crickets and *Drosophila* flies). The web building activity of parasitized spiders was observed until the larva killed and consumed the spider and pupated. I used a Canon EOS 500D digital camera with an EF-S 18–55 mm lens to record the architecture of the cocoon web.

Results

Two parasitized *Metellina* spiders, one *M. segmentata* and one *M. merianae*, were collected on 29th October. The parasitoid larva on *M. segmentata* died after ten days in the laboratory and when the spider host moulted the shrivelled dead larva fell out with its exuvia. The parasitoid larva on *M. merianae* pupated on 28th December 2014 and the male wasp emerged on 12th January 2015. In the latter spider host, the architecture of the normal web and the modified cocoon web induced by the final stage larva of *M. madida* were observed.

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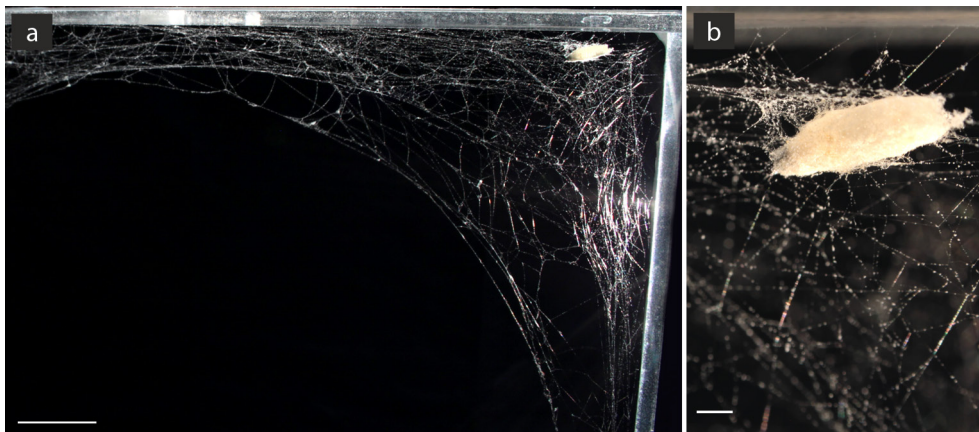


Fig. 1: **a.** Cocoon web built by a *Metellina merianae* spider host induced by the final stage larva of the parasitoid *Megaetaira madida*; **b.** detail of cocoon. Scale = 20 mm (a) and 2 mm (b)

The parasitized host *M. merianae* rebuilt its orb web several times until the larva reached its final stage, when the spider, under the influence of the parasitoid, built a unique three-dimensional (3D) structure in the upper part of the arena (Fig. 1a). This 3D cocoon web had no clear counterpart in the webs of unparasitized spiders. The wasp cocoon was placed in an upper corner of the experimental arena with a high density of threads (Figs 1a, b).

Discussion

Several studies have been devoted to the behavioural manipulation of orb web building spiders from the family Tetragnathidae by polysphinctine wasps. Wasps of the Neotropical genus *Hymenoepimecis* associated with spiders of the genus *Leucauge* were observed to induce the construction of a two-dimensional (2D) cocoon web which consisted of a reduced number of radial threads radiating in a plane from a central hub; the cocoon was suspended from this central hub. This type of cocoon web is documented in *Hymenoepimecis argyraphaga* Gauld, 2000 associated with *Leucauge argyra* (Walckenaer, 1841) (Eberhard 2000a, 2000b, 2001) and *Hymenoepimecis japi* Sobczak, Loffredo, Pentead-Dias & Gonzaga, 2009 associated with *Leucauge roseosignata* Mello-Leitão, 1943 (Sobczak et al. 2009). A cocoon web with a similar 2D architecture, but protected by the 3D structure of a tangle positioned below the hub, was documented in the interaction between *Hymenoepimecis tedfordi* Gauld, 1991 and *Leucauge mariana* (Keyserling, 1881), and *Hymenoepimecis jordanensis* Loffredo & Pentead-Dias, 2009 and *Leucauge volupis* (Keyserling, 1893) (Gonzaga et al. 2015). It is interesting that the larva of the taxonomically distant Costa Rican wasp *Eruga gutfreundi* Gauld, 1991 induced its *Leucauge* host (*L. mariana*) to build a 3D cocoon web (Eberhard 2013). The cocoon web of the orb web weaving spider *Tetragnatha montana* Simon, 1874 induced by the final stage larva of the Palearctic wasp *Acrodactyla carinator* (Aubert, 1965) consisted of one highly reinforced main thread, tensioned mostly by a reinforced side thread (Korenko et al. 2015). *Acrodactyla carinator* was misidentified as Holarctic *Acrodactyla quadrisculpta* (Gravenhorst, 1820) in studies by Korenko et al. (2015) and Belgers et al. (2013) (material revised by K. Holy and K. Zwakhals). Additional investigation revealed that the cocoon web of *T. montana* induced by the larva of *A. quadrisculpta* has the same architecture as that induced by *A. carinator* (Korenko unpubl. data).

The cocoon web induced by *M. madida* resembled the cocoon web of *E. gutfreundi* from Costa Rica in the sense that both were 3D structures and the cocoons were oriented horizontally; however, the morphologies of the cocoons were considerably different (cocoon circular in cross-section covered by curled structure of *M. madida* vs. square in cross section with paper smooth surface in *E. gutfreundi*). The cocoon of *M. madida* had a densely-woven cocoon wall covered by curled fibres of various lengths and was circular in cross section (Fig. 1b), whereas the cocoon of *E. gutfreundi* had a paper-like smooth surface and was square in cross section (Eberhard 2013).

The wasp *M. madida* was formerly included in the genus *Acrodactyla*, also known as the *madida* species-complex, but Gauld & Dubois (2006) excluded it because it lacked several features characteristic of the remaining *Acrodactyla* species. *Megaetaira madida* was the only valid species within the genus *Megaetaira*, but two other *Acrodactyla* species have recently been transferred to this genus (Matsumoto in press). Their relatedness to *M. madida* is also supported by the host range of *M. varicarinata* (Uchida & Momoi, 1958) associated with *Meta reticuloides* Yaginuma, 1958, which is related to the genus *Metellina*, the exclusive host of *M. madida* (Takasuka pers. comm.). Although wasps of both *Acrodactyla* and *Megaetaira* are associated with orb web building spiders from the family Tetragnathidae, their manipulation of the spider web architecture differs considerably. *Acrodactyla* wasps induce the production of a strong 2D cocoon web where the wasp cocoon is attached to the strongest main silk line (Korenko et al. 2015). In contrast, the cocoon web induced by *M. madida* is a densely woven 3D structure. However, both strategies are effective for protecting the parasitoid during the pupal stage and both are also used by other polysphinctine parasitoids. More observations of host parasitoid interactions are necessary to reveal further details of the host utilisation of this sparsely occurring spider parasitoid.

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