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SHORT COMMUNICATION

Who wins? Ray spiders (*Theridiosoma gemmosum*) (Araneae: Theridiosomatidae) versus egg sac parasitoids

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Abstract. This is the first report on the parasitoids of egg sacs of *Theridiosoma gemmosum* (L. Koch, 1877) (Theridiosomatidae). The parasitic wasps *Gelis melanocephalus* (Schrank, 1781), *Gelis mangeri* (Gravenhorst, 1815) (Ichneumonidae) and *Pachyneuron solitarium* (Hartig, 1838) (Pteromalidae) were recorded as solitary parasitoids of egg sacs of *T. gemmosum* in Poland. The degree of parasitism of *T. gemmosum* egg sacs in three different years was 21.4–42.9%, and the reproductive fitness of female spiders in all cases of parasitized cocoons was zero. It seems that the suspension system of the egg sacs of ray spiders is not a barrier against egg sac parasitoids, including apterous species. We hypothesize that, at least in the case of *G. melanocephalus*, the size of the spider's egg sac is implicated in the ovipositional decision of the female parasitoid.

Keywords: Ectoparasitoids, ichneumonid, pteromalid

The mortality of eggs is considered the major limiting factor in the spider life cycle (Austin 1985; Foelix 2011). Mortality is caused by fungi, and by various predators and parasitoids. The latter may have the most significant impact (Polis et al. 1998), although in the case of range expansion of the wasp spider, *Argiope bruennichi* (Scopoli, 1772), there is no indication that egg sac parasitoids are a limiting factor (Wawer & Kostro-Ambroziak 2016). Parasitoids feeding on spider eggs either develop individually within eggs (e.g., Scelionidae), or feed on spider egg masses (e.g., Eulophidae, Mantispidae, Ichneumonidae, Phoridae) (Fitton et al. 1987; Finch 2005). Some parasitoids (e.g., *Baeus achaearaneus* Loiácono, 1973) (Scelionidae) locate a large number of egg sacs and parasitize only a portion of each egg mass, while others (e.g., *Tetrastichus* sp.) (Eulophidae) locate a small portion of available cocoons but maximize the utilization of eggs in the sac and destroy up to 100% of egg masses (Valerio 1983). Hence, the reproductive fitness of spider females differs depending on the parasitoid's strategy. In order to reduce the attack of parasitoids on broods, spiders have developed several strategies, including modifying the architecture and coloration of egg sacs or camouflaging the outer layer, and many spiders engage in active parental care of their offspring (e.g., Hieber 1992; Foelix 2011; Barrantes et al. 2014).

Theridiosoma gemmosum (L. Koch, 1877) – a 'ray spider' in the family Theridiosomatidae – is found in Europe, Central Asia and North America (Platnick 2011). Due to its minute size, the presence of this spider is usually recorded by the discovery of its web (Bristowe 1958) or characteristic cocoons which consist of a long stalk attaching each egg sac to the suspension area made by the female spider prior to oviposition (Hajer et al. 2009). This suspension system has evolved multiple times among spiders, and is present in the families Agelenidae, Deinopidae, Liocranidae, Mimetidae, Tetragnathidae, Theridiidae and Theridiosomatidae (Comstock 1913; Bristowe 1958; Austin 1985; Blackledge et al. 2009; Barrantes et al. 2014; Wheeler et al. 2017; Toft & Lubin 2018). Little is known as to whether an egg sac suspension system is actually a barrier against parasitoids, and nothing is currently known about the egg sac predators of *T. gemmosum*. The only record of a parasitoid of this species is from Guarisco (2006), who found in one egg sac of this spider, 30 empty pupal cases of an unidentified parasitic wasp. We studied egg sac parasitoids of *T. gemmosum* and we here present our findings, and discuss the interrelationship of some aspects of the architecture of its egg sac and the parasitoids of this spider.

The study was carried out in Biebrza National Park (Poland) on the site "Grzędy" (53.60794°N, 22.84036°E) in Czerwone Bagno Reserve. This site is on the boundary of the *Tilio cordatae-Carpinetum betuli* and *Ribeso nigri-Alnetum* forest communities. Egg sacs of *T. gemmosum* were collected in 2014, 2015 and 2017 (Table 1) by visual surveys. In each year, a single three-hour survey was conducted between 25 June and 17 July, during which every observed egg sac of the studied spider species was collected. Egg sacs were kept with the leaf to which they were attached, at room temperature in plastic containers. The adult parasitic wasps emerged after 7–14 days (in general in the second half of July). After the emergence of spiderlings and parasitoids, 27 cocoons without deformation and with complete stalks were measured according to the maximum diameter of each egg sac and the length of each stalk (from the egg sac to the forked part of the stalk). Parasitized ($n = 12$) as well as closed egg sacs ($n = 15$) were cut with medical scissors and examined under a microscope in order to check the contents of each egg sac. Voucher specimens were deposited at the Laboratory of Insect Evolutionary Biology and Ecology, Faculty of Biology, University of Bialystok.

The pear-shaped egg sacs of *T. gemmosum* were attached vertically about 1.0–1.7 meters above the ground, on the lower side of leaves of common hazel (*Corylus avellana* L.), small-leaved lime (*Tilia cordata* Mill.), alder buckthorn (*Frangula alnus* Mill.) and European ash (*Fraxinus excelsior* L.), with only a single egg sac recorded from a leaf of the common buckthorn (*Rhamnus cathartica* L.) and on a dry branch of spruce (*Picea abies* (L.) H. Karst), respectively. The forked stalks of the cocoons were attached to the trichomes of the leaves. The diameter of the egg sacs ranged from 1.8–2.2 mm, and the length of the stalks ranged from 18.5–39 mm (i.e., 9–19 × longer than the diameter of the egg sacs) ($n = 27$). These diameters were within the range (of 1.6–2.4 mm) reported by Hajer et al. (2009), but smaller than the diameters (of 2.4–2.7 mm) reported by Guarisco (2006). The mean length of the stalks of unparasitized and parasitized cocoons was 30.7 mm (max = 39, min = 19) and 25.1 mm (max = 35, min = 18.5), respectively. The number of eggs or spiderlings inside closed (unparasitized) cocoons ranged from 8–22 ($n = 15$).

Figure 1.—Egg sacs of *Theridiosoma gemmosum*: (a) egg sac newly constructed by a female (observation in the field, about 13:00); (b), (c) egg sacs with exit holes made by parasitoids *Gelis melanocephalus* (b) and *Pachyneuron solitarium* (c).

Although egg laying and the production of egg sacs by females of *T. gemmosum* held in the laboratory always occurred at night (Hajer et al. 2009), in the field, we observed a female who made an egg sac during the day (about 13:00) (Fig. 1a). In the laboratory, females made no more than three egg sacs each, and attached them within one suspension area (Hajer et al. 2009). We did not observe more than two egg sacs attached to a single leaf, and in these cases (7% of all observations), the sacs were never attached to the same suspension area (we do not know if they were made by one or two females). It seems that in nature a female distributes her egg sacs further apart than under laboratory conditions. This could be important in order to decrease the mortality of offspring caused by predators (e.g., parasitoids), and if so, potentially increase the fitness of female spiders.

The degree of parasitism of the analyzed egg sacs ranged from 21.4–42.9% in three different years (Table 1), and was similar to that reported for *Ero* cf. *furcata* (37.5–40.6%) and *Agroeca* spp. (0–43%) (Finch 2005), but clearly higher than in the genus *Deinopis* MacLeay, 1839 (2.9%) (Barrantes et al. 2014) (all three genera build egg sacs on a stalk and do not take active maternal care). Barrantes et al. (2014) suggested that the dense, hard outer layer of the egg sacs of *Deinopis*, resembling the layer covering the egg sacs of *T. gemmosum*, makes it more difficult for natural enemies to access to the eggs, but in our study of ray spiders, egg sac parasitoids overcame this barrier relatively easily. Indeed, from 73% of the parasitized cocoons of *T. gemmosum*, apterous (wingless) females of *Gelis melanocephalus* (Schrank, 1781) were identified. We therefore conclude that the suspension system of the egg sac of *T. gemmosum* is not a barrier to parasitoids, including wingless species.

Three species, as solitary parasitoids, were reared from *T. gemmosum* egg sacs: two ichneumonids of the subfamily Cryptinae, *Gelis mangeri* (Gravenhorst, 1815) and *G. melanocephalus*, and one specimen of a pteromalid of the subfamily Pteromalinae, *Pachyneuron solitarium* (Hartig, 1838). Both ichneumonids reared from *T. gemmosum* egg sacs are ectoparasitoids which develop by feeding on spider eggs (Schwarz & Shaw 1999). *Gelis mangeri* has also been recorded from three species of Coleoptera (Yu et al. 2012), but these host records are probably erroneous. *Gelis melanocephalus* is known as a parasitoid of the egg sacs of a broad range of spider families without active parental care, including Agelenidae, Araneidae, Dictynidae, Linyphiidae, Liocranidae and Tetragnathidae (Schwarz & Shaw 1999; Yu et al. 2012). The exception is a single record from *Pardosa pullata* (Clerck, 1757), a representative of Lycosidae. Known host species from these spider taxa live in both woodland and open habitats, and they attach egg sacs to trees and other plant stems (Bee

Table 1.—Egg sac parasitism of *Theridiosoma gemmosum*. *n*, number; +, present; –, absent.

			Species, number of egg sacs parasitized (*n*) and number of specimens that emerged [*n*]		
Year	*n* of studied egg sacs	*n* and (%) of parasitized egg sacs	*Gelis melanocephalus*	*Gelis mangeri*	*Pachyneuron solitarium*
2014	14	3 (21.4%)	+ (2) [2]	–	+ (1) [1]
2015	25	6 (24.0%)	+ (4) [4]	+ (2) [2]	–
2017	7	3 (42.9%)	+ (3) [3]	–	–
Total	46	12 (26.1%)	(9)	(2)	(1)

et al. 2017). In the above-mentioned habitats, *G. melanocephalus* has been recorded as one of the most numerous parasitoids of spider egg masses; this species and *G. discedens* (Förster, 1850) together parasitized 20.4–28.7% of egg sacs of *Pachygnatha* spp. (Tetragnathidae) occurring on abandoned grassland (Finch 2005). The second ichneumonid species which emerged from *T. gemmosum* egg sacs, *G. mangeri*, has hitherto been recorded only from an egg sac of a linyphiid (either *Gongylidium rufipes* (Linnaeus, 1758) or *Hypomma cornutum* (Blackwall, 1833)) (Schwarz & Shaw 1999).

Gelis melanocephalus is known mainly as a gregarious parasitoid of spider egg masses, for example from all egg sacs of *Pachygnatha* spp. and *Agroeca* spp. studied by Finch (2005), an average of 6.5 individuals were recorded per egg sac. However, Schwarz & Shaw (1999) also recorded *G. melanocephalus* as a solitary parasitoid from the same host species. In the present study, *G. melanocephalus* always emerged as a solitary parasitoid from egg sacs of *T. gemmosum*. In the case of this species, it may be that the size of the spider egg sac is implicated in the ovipositional decision of the parasitoid female to lay one or more eggs. Indeed, the egg sacs of *Agroeca* spp. are about 3 times larger than those of *T. gemmosum* (Hajer et al. 2009; Bee et al. 2017), and *Agroeca* spp. produce on average 13–57 eggs per egg sac (Finch 2005), while the number of eggs recorded in cocoons of ray spiders ranged from 29–30 (see Guarisco 2006), 8–22 (present data) and 4–17 (see Hajer et al. 2009). Furthermore, from egg sacs of *Ero* cf. *furcata* (which has egg sacs of a similar physical size to those of *T. gemmosum*), all parasitoids (other species of *Gelis*) were also reared as solitary records (Finch 2005; Bee et al. 2017), although the contents of sacs differed between the above-mentioned spider species: the number of eggs in sacs of *T. gemmosum* found in our study was two-fold higher than reported by Finch (2005) for *Ero* cf. *furcata*.

The third recorded parasitoid of egg sacs of *T. gemmosum*, *P. solitarium,* is known as a parasitoid of more than 35 species of Coleoptera (Coccinellidae), Diptera (Asilidae), Hemiptera (Aphididae, Coccidae, Pseudococcidae, Psyllidae) and Lepidoptera (Erebidae, Lasiocampidae), as well as a hyperparasitoid of about 20 species of Hymenoptera belonging to Aphelinidae, Braconidae, Encyrtidae, Scelionidae and Trichogrammatidae (Noyes 2017). Although *P. solitarium* has a broad host range, its association with spiders has been reported only once from an unidentified spider egg sac in China (Xiao et al. 2009). Because the remains of other parasitoids in the egg sacs of *T. gemmosum* were absent, we consider *P. solitarium* as a primary parasitoid of the eggs of the studied spider. However, there is also a possibility that it fed on small larvae of *Gelis*, thus acting as a hyperparasitoid.

Schwarz & Shaw (1999) recorded a few surviving spiderlings from most of the egg sacs of *Larinioides cornutus* (Clerck, 1757) and *Singa nitidula* C. L. Koch, 1844 parasitized by *G. melanocephalus*. Similarly, Finch (2005) found unconsumed eggs in the cocoons of *Agroeca* spp. from which this parasitoid was reared. In our study, 70% of the parasitized egg sacs contained undeveloped eggs or the remains of spider eggs. Rollard (1990) reported that 1–15% of eggs in the studied spider egg sacs failed to develop, probably because they had not been fertilized. However, irrespective of the cause, in all studied parasitized egg sacs of *T. gemmosum*, the reproductive success of females was zero.

Nymphs of *T. gemmosum* and adult specimens of *Gelis* left the egg sacs by the exit slit made on the interface between the egg sac and the stalk (Fig. 1b). Here, the outer layer of silk is visibly thinner than on other parts of the egg sac (Hajer et al. 2009). In contrast, *P. solitarium* made an exit hole in the proximal part of the egg sac (Fig. 1c), where the outer silk layer is thicker. The use of the thinnest part of the egg sac for creating an exit slit by parasitoids in the genus *Gelis* may reflect their specialization in the utilization of spider egg sacs.

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