

Incidence of parasitoids and predators on eggs of seven species of Theridiidae (Araneae)

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Summary

Although many characteristics of the egg sacs of spiders likely evolved to reduce the effect of parasites and predators that attack their eggs, many parasite and predator insects have become specialized on spider eggs. Eggs of six of the seven species of Theridiidae included in this study were attacked by wasp parasites (*Baeus achaearaneus*, *Idris* sp., and *Comastichus zopheros*), and two by the specialized spider egg predator (Neuroptera: *Zeugomantispina minuta*). The incidence of parasites in the egg sacs varied across species. Parasites attacked more than 60% of the egg sacs of *Tidarren sisyphoides* and *Parasteatoda tepidariorum*, but none of the sacs of *Latrodectus geometricus*. The incidence of parasites in the egg sacs was higher during the dry season for *T. sisyphoides*, and during the rainy season for *P. tepidariorum*. The proportion of the eggs parasitized per egg sac varied from 0.09 (± 0.19) in *Nesticodes rufipes* to 0.50 (± 0.46) in *T. sisyphoides*. Differences in the biology of parasites, as well as in the structure of spider webs and habitat preference of spiders, may influence the incidence of parasitism and proportion of eggs parasitized in each egg sac.

Introduction

Maternal care is widespread in spiders and extremely variable even between species in the same genus. Within maternal care, construction of an egg sac and its protection is common in most spiders (Gertsch 1949). The egg sacs provide embryos with more stable environmental conditions for their development (Hieber 1985; Hieber 1992a)

and protect them against predators and parasitoids (Austin 1985; Hieber 1992a,b). The silk layers of the egg sac reduce thermal stress and maintain favourable humidity inside the egg sac because it reduces water loss and egg desiccation (Hieber 1985; Hieber 1992a). The silk layers also act as a barrier to prevent fungal invasion of eggs and embryos (Christenson & Wenzl 1980), and reduce or prevent attacks from predators and parasitoids (Austin 1985; Hieber 1992a,b).

Spiders have evolved many different behaviours to reduce predation and parasitism on their eggs. For instance, *Pozonia nigroventris* and *Micrathena* spp. (Araneidae) lay their eggs on the surface of a dead leaf which the spider then folds, forming a protective case that it drops to the ground (Moya *et al.* 2010). Wolf spiders protect their eggs by constantly carrying the egg sac attached to their spinnerets until the spiderlings emerge (Edgar 1971; Cobb & Cobb 2004). Some araneids build an egg sac and then use a thread to hang it from their web (Hieber 1992b). In the family Theridiidae, many species construct different types of retreats with silk, plant debris, remnants of prey, or folding a leaf that help camouflage the egg sacs (Nielsen 1932; Bristowe 1958; Barrantes & Weng 2007).

Despite the protection that the egg sacs provide, many parasitoid and predatory insects are capable of gaining access to the eggs within the egg sac (Auten 1925; Austin 1985). Mantisflies (Mantispinae) are obligate predators of spider eggs during their larval stage. The larva burrows into the egg sac or enters the egg sac during its construction and then feeds on the spider's eggs (Redborg & MacLeod 1985; Guarisco 1998). However, wasp and fly parasitoids are likely the major causes of destruction of spider eggs. Larvae of many of these parasitoids feed and develop exclusively within spider eggs (Auten 1925; Valerio 1971, 1975; Fitton, Shaw & Austin 1987).

Of the 13 Hymenoptera families that include egg endoparasitoids in the Neotropics, six of them have species that

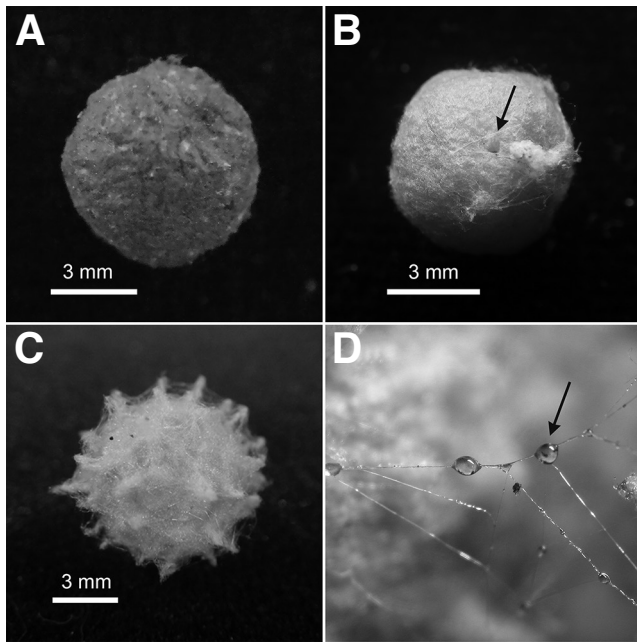


Fig. 1: Egg sacs of three species of Theridiidae. **A** *Parasteatoda tepidariorum*; **B** *Tidarren sisyphoides*, arrow points to the exit hole of spiderlings; **C** *Latrodectus geometricus*; **D** shows some sticky threads that *L. geometricus* attaches to the outer surface of the egg sac.

are specific to spider eggs: Scelionidae (Baeni); Eulophidae (some Entedonini and Tetrastichinae); Eupelmidae (some Eupelminae); Eurytomidae (just a few species; see Discussion); and Pteromalidae (*Arachnoptermalus*) (Hanson & Gauld 2006). These highly specialized wasps insert their long ovipositor several times through both the silk layer and the wall of the egg and lay one of their own eggs, which develops into a larva that feeds on a spider egg (Austin 1985); or the female wasp enters the egg sac to oviposit directly in some of the spider's eggs (*Baeus californicus*, Pemberton & Rosa 1940; *Ceratobaeus* spp., Austin 1984).

In this study, we recorded the egg parasitoids found in egg sacs of seven theridiid spiders: *Tidarren sisyphoides* (Walckenaer, 1841), *Parasteatoda tepidariorum* (C. L. Koch, 1841), *Parasteatoda tessellata* (Keyserling, 1884), *Nesticodes rufipes* (Lucas, 1846), *Latrodectus geometricus* C. L. Koch, 1841, *Theridion evexum* Keyserling, 1884, and *Anelosimus studiosus* (Hentz, 1850). We then quantified the proportion of egg sacs parasitized, the proportion of eggs parasitized in each sac, and the correlation of seasonal

climatic changes on the incidence of egg sacs parasitized. The egg sacs of these species have a papery surface, except *L. geometricus* in which the egg sac surface is slightly translucent and studded with silk pompons (Fig. 1; Kaston 1970).

Methods

We collected a total of 144 egg sacs from seven species of Theridiidae on the campus of the University of Costa Rica, San José, Costa Rica (9°54'N 84°03'W, 1200 m a.s.l.) and some nearby areas from April 2007 to November 2009. The annual average temperature is around 20°C, with a dry season from December through March. The site is urbanized with isolated patches of trees and gardens. All spider species are abundant and can be found on bushes or on external walls of buildings. For each species, we collected the following numbers of egg sacs: 47 *Latrodectus geometricus*, 40 *Parasteatoda tepidariorum*, 37 *Tidarren sisyphoides*, 8 *P. tessellata*, 7 *N. rufipes*, 4 *Theridion evexum*, and 1 *Anelosimus studiosus*. Vouchers have been deposited in the Museo de Zoología of the Universidad de Costa Rica.

Egg sacs were placed individually in a Petri dish in the laboratory at room temperature. When either spiderlings or parasitoids emerged, we removed them and left the egg sac in the Petri dish for two more weeks, waiting for other spiderlings or parasitoids to emerge. After this additional time, we opened the egg sac and examined its contents to check whether some spiderlings or wasps had failed to exit the egg sac. For wasps, we counted the total males and females to determine the sex ratio. If both parasitoids and spiderlings emerged, we determined the proportion of eggs parasitized within each egg sac. Total eggs for each egg sac was calculated as the sum of spiderlings, wasps, and unhatched eggs; if unhatched eggs had a dead wasp or wasp pupa inside they were considered as parasitized, otherwise they were considered as not parasitized.

Parasitoids were identified using keys provided in LaSalle (1994) and Margaría, Loíacono & Gonzaga (2006), but for the identification of *Idris* (Scelionidae) species there are no keys presently available. All specimens obtained in this study belong to *Idris sensu stricto*, and not to *Ceratobaeus*, which is currently a synonym of *Idris*. While all our specimens appear to belong to a single species, it should be noted that there are an estimated 100 species of *Idris sensu*

Spider	N	% egg sacs parasitized	Wasps/total eggs	No. eggs per sac	Parasitoid species
<i>Tidarren sisyphoides</i>	37	67	0.50 (0.46)	86.5 (54.5)	<i>Baeus achaeareneus</i> , <i>Idris</i> sp., <i>Comastichus zopheros</i>
<i>Parasteatoda tepidariorum</i>	40	65	0.17 (0.17)	142.0 (62.5)	<i>Baeus achaeareneus</i> , <i>Comastichus zopheros</i> , <i>Zeugomantispa minuta</i>
<i>Parasteatoda tessellata</i>	8	12.5	?	?	<i>Baeus achaeareneus</i> , <i>Idris</i> sp.
<i>Nesticodes rufipes</i>	7	29	0.09 (0.19)	145.1 (55.3)	<i>Baeus achaeareneus</i>
<i>Latrodectus geometricus</i>	47	2.12	0	141.9 (62.4)	<i>Zeugomantispa minuta</i>
<i>Theridion evexum</i>	4	25	?	?	<i>Baeus achaeareneus</i>
<i>Anelosimus studiosus</i>	1	100	?	?	<i>Idris</i> sp.

Table 1: Percentage of egg sacs parasitized, proportion of eggs parasitized in each egg sac, number of eggs per sac, and parasitoid species collected from egg sacs of seven Theridiidae spiders. Standard deviation in parentheses. *Zeugomantispa minuta*, an egg predator, is also included.

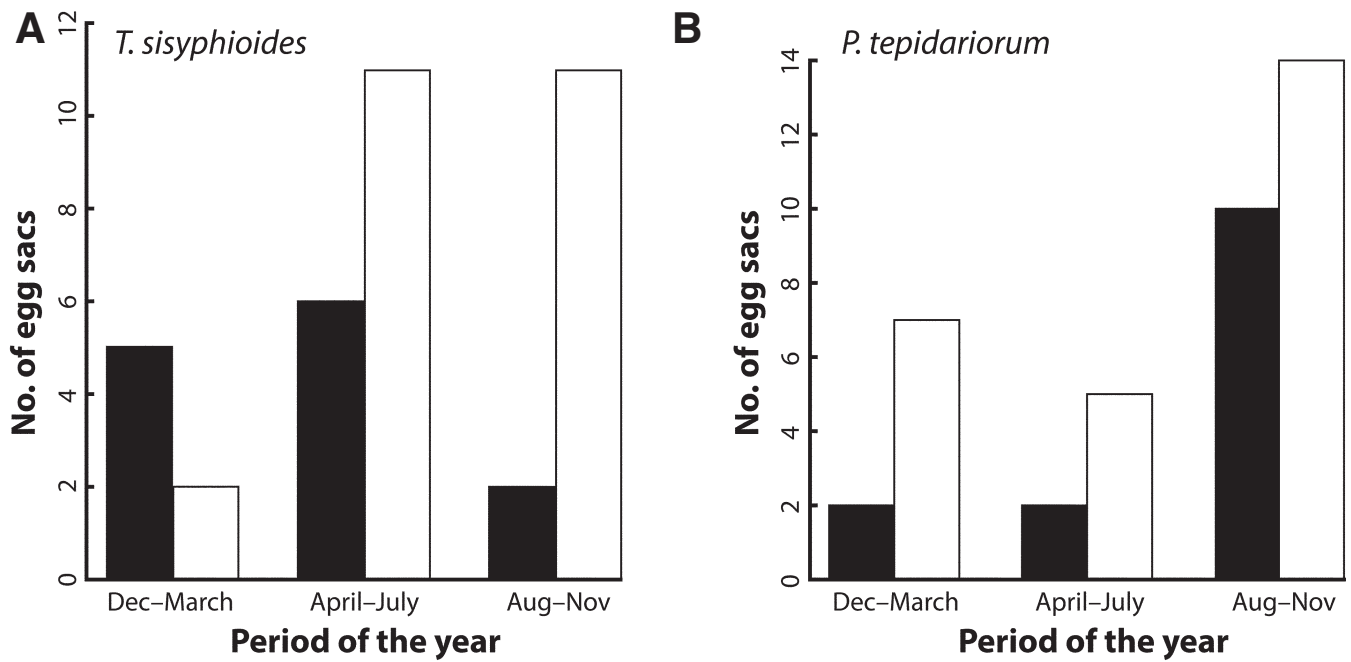


Fig. 2: Number of egg sacs of *Tidarren sisypoides* (A) and *Parasteatoda tepidariorum* (B), parasitized (black bars) and not parasitized (white bars) during three different seasons. December–March is the driest period of the year, August–November the rainiest, and April–July is a transitional period.

lato, in Costa Rica, most of which are undescribed (Masner 1995).

We divided the year into three periods according to the rainfall pattern: dry period, from December through March; transition period, from April through July; and rainy period, from August through November. We analysed the effect of seasonality on the incidence of parasitism of egg sacs and on the proportion of eggs parasitized within each egg sac for those spider species with more than 30 egg sacs, using chi-squared, Kruskal–Wallis, and Mann–Whitney tests. We also examined the effect of the number of eggs in each egg sac and seasonality (and interaction of both factors) on the probability of an egg to be parasitized, using a generalized linear

model (with binomial distribution). All statistical analyses were performed with R statistical Language (version 2.13.2: <http://cran.r-project.org>).

Results

Egg endoparasitism varied widely among the seven species of Theridiidae (Table 1). *Tidarren sisypoides* was the species with the highest percentage (67%) of egg sacs parasitized by wasps, while *L. geometricus* had none of their egg sacs parasitized (*A. studiosus* was not included in the analysis due to insufficient sample). Three different species

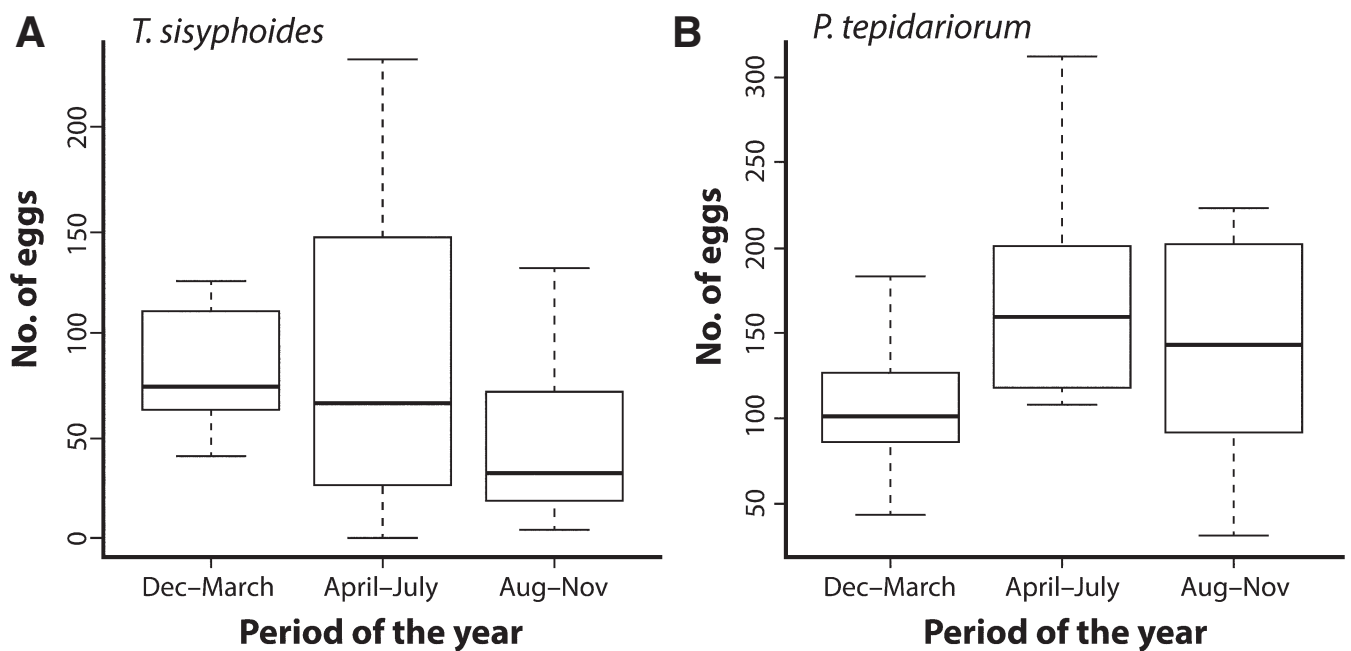


Fig. 3: Number of eggs per egg sac for *Tidarren sisypoides* (A) and *Parasteatoda tepidariorum* (B) during three different seasons. December–March is the driest period of the year, August–November the rainiest, and April–July is a transitional period.

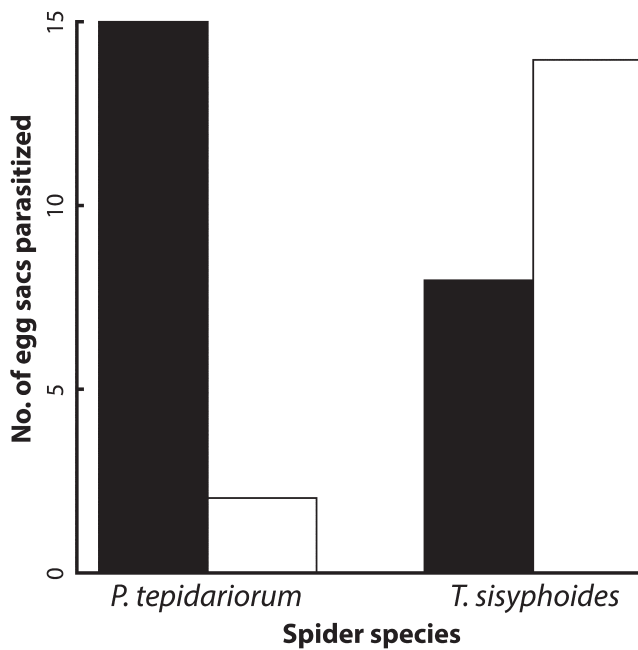


Fig. 4: Number of egg sacs of *Parasteatoda tepidariorum* and *Tidarren sisyphoides* parasitized by *Baeus achaeareneus* (black bars) and *Comastichus zopheros* (white bars).

of wasp (Scelionidae: *Baeus achaeareneus*, *Idris* sp.; and Eulophidae: *Comastichus zopheros*) and an egg predator (Mantispinae: *Zeugomantispa minuta*) emerged from egg sacs of the seven theridiids ($N = 144$ egg sacs). The most common parasitoid was *Baeus achaeareneus*, which was found in egg sacs of five spider species, *Idris* sp. in three species, and *C. zopheros* in two species (Table 1). The egg predator, *Z. minuta*, fed on eggs of two different spiders: *P. tepidariorum* and *L. geometricus*. On two occasions, two parasitoid species emerged from the same egg sac. From a single egg sac of *T. sisyphoides* and *P. tessellata* emerged *C. zopheros* and *Idris* sp., and *Baeus achaeareneus* and *Idris* sp., respectively. On one occasion, two groups of *C. zopheros* emerged from one egg sac of *T. sisyphoides* 16 days apart, suggesting that two different wasps laid eggs in the same spider sac.

Tidarren sisyphoides had a significantly larger proportion of egg sacs parasitized during the driest period of the year ($\chi^2 = 6.27$, $df = 2$, $P = 0.043$; Fig. 2A), whereas *P. tepidariorum* had a similar proportion of egg sacs parasitized in all three time-periods ($\chi^2 = 1.24$, $df = 2$, $P = 0.537$; Fig. 2B). *T. sisyphoides* also had a significantly larger proportion of eggs parasitized in their egg sacs than *P. tepidariorum* (Mann–Whitney test = 340, $P = 0.0013$; Table 1); other species were not included due to small sample size. For *P. tepidariorum* the proportion of eggs parasitized was significantly higher during the rainiest period of the year (Kruskal–Wallis test = 8.43, $P = 0.015$), but the proportion of eggs parasitized was similar during the three time periods for *T. sisyphoides* (Kruskal–Wallis test = 3.34, $P = 0.188$). The generalized linear model indicated that both the number of eggs per sac ($Z = -2.51$, $P = 0.012$) and the seasonal period ($Z = 2.09$, $P = 0.037$) were significantly associated with the probability that egg sacs of *T. sisyphoides* were parasitized: the probability that a wasp parasitized an egg sac increased as the number of eggs in the sac decreased, and that probability was significantly lower during the rainy season (Fig.

3A); interaction between the two factors was not significant. For *P. tepidariorum*, the probability that a wasp parasitized an egg sac was significantly higher during the rainy season ($Z = 2.28$, $P = 0.027$; Fig. 2B), but the number of eggs per egg sac did not significantly affect this probability (Fig. 3B).

Baeus achaeareneus and *Comastichus zopheros* were the most common parasitoids in egg sacs of *P. tepidariorum* and *T. sisyphoides*. *Baeus* parasitized a larger number of egg sacs of *P. tepidariorum* than *C. zopheros*, while *C. zopheros* parasitized more egg sacs of *T. sisyphoides* than *Baeus* (Fig. 4). *Idris* sp. parasitized only one egg sac of *T. sisyphoides* but none of *P. tepidariorum*.

The sex ratio (males/total) of *C. zopheros* and *Baeus* that emerged from egg sacs of *P. tepidariorum* and *T. sisyphoides* was strongly female biased. The sex ratio for *C. zopheros* in egg sacs of *P. tepidariorum* was $0.13 \pm sd = 0.13$ ($N = 13$, no. egg sacs) and 0.09 ± 0.04 ($N = 2$) in *T. sisyphoides*. *Baeus* had a similar sex ratio: 0.15 ± 0.14 ($N = 15$) in sacs of *P. tepidariorum* and 0.19 ± 0.34 ($N = 6$) in egg sacs of *T. sisyphoides*.

Discussion

All wasp species in the tribe Baeni use spider eggs as a food source for their parasitic larvae (Steven & Austin 2007). Within this tribe, wasps of the genera *Baeus* and *Idris* have a wide spectrum of host spider species in different families that vary in their life history strategies, from wandering spiders (e.g. Lycosidae) to web-building spiders (e.g. Araneidae and Theridiidae) (Austin 1985; Cobb & Cobb 2004). In this study, the theridiids parasitized by *Baeus* also varied in habitat use and web design (Eberhard 1972; Barrantes & Weng 2006, 2007; Eberhard, Agnarsson & Levi 2008; Madrigal-Brenes & Barrantes 2009). *P. tepidariorum* and *N. rufipes* are synanthropic species that construct isolated, three-dimensional, meshed webs outside and inside buildings; webs of these species are seldom found on structures other than buildings. *T. sisyphoides* build their domed-sheet webs on isolated treelets and bushes with rigid leaves for web building, primarily in open areas (Madrigal-Brenes & Barrantes 2009), and *P. tessellata* construct their sheet webs on similar plants, also in open areas, and often in colonies (Eberhard 1972; Barrantes & Weng 2006). *T. evexum* construct their webs on undergrowth herbs and bushes of secondary and mature forests, and the webs consist of a retreat built by a folded leaf from which the spider lays straight sticky threads that it attaches mostly to leaves and twigs below the retreat (Barrantes & Weng 2007).

Our results suggest that neither the web architecture nor the habitat used by spiders to build their webs hinder *Baeus* in gaining access to the spiders' eggs. *Baeus* attacked eggs of spiders with very different web design (e.g. *P. tepidariorum* versus *T. sisyphoides*) and contrasting habitats (e.g. *P. tepidariorum* versus *T. evexum*). It has been suggested that these tiny wasps rely on airborne and chemical signals to locate their host eggs (Austin, Johnson & Downton 2005). However, information on the mechanisms used by the tiny wingless *Baeus* females to move across complex landscapes (e.g. understory of secondary and mature forests) are

unknown. *Idris* parasitized eggs of the three spider species that built sheet webs in open areas.

Comastichus zopheros and *Baeus* parasitized eggs of *P. tepidariorum* and *T. sisypoides*, species with different web architecture but similar habitat preference. *C. zopheros* was previously reported from *T. sisypoides* (Knoflach & van Harten 2006), but this is the first report of *Baeus* for this spider. We found *C. zopheros* in two egg sacs of *P. tepidariorum*, but *T. sisypoides* was its most common host (Fig. 4). Valerio (1971) reported *Baeus achaeareanus* as the only egg parasitoid of *P. tepidariorum* in the same locality (the parasitoid was cited as *Baeus* sp. but Valerio's specimens were subsequently described by Loiácono 1973 as *B. achaeareanus*). The high occurrence of *C. zopheros* in egg sacs of *T. sisypoides* may be the result of a preference of this parasitoid for *T. sisypoides* or, alternatively, it is possible that the anthropogenic habitat used by *P. tepidariorum* makes it difficult for the parasitoid to locate this spider.

Parasitoids were present in egg sacs of *T. sisypoides* and *P. tepidariorum* during all three time periods. The occurrence of parasitoids year round may be related to the year-round presence of host spiders and egg sacs. A similar pattern was found for koinobiont spider parasitoids of other spider species in the same study area (Barrantes, Eberhard & Weng 2008). The seasonal changes in the incidence of parasitoids in the egg sacs of these two spider species is more difficult to explain. This, however, may be the effect of changes in abundance and distribution of either hosts, parasitoids or both, but this result may also be affected by the relatively small sample size included in the analysis.

The proportion of eggs parasitized in each egg sac was higher for *T. sisypoides* than in *P. tepidariorum*. This may be related to the flying capacity of female *C. zopheros* which allows more females to gain access to the egg sacs (see Results). Another possibility is that females of *C. zopheros* carry a larger number of eggs than the wingless females of *Baeus*, the main parasitoid of *P. tepidariorum* (but information on number of eggs that females of these species carry are lacking).

It is very surprising that parasitoid wasps, including the apparently extreme generalist *Baeus*, did not attack eggs of *L. geometricus*. Only the egg predator, *Z. minuta* (Peny & da Costa, 1983), emerged from a single egg sac. It is possible that the structure of the adult web, which consists of a dense-walled silk retreat constructed in a sheltered place from which a sloping sheet extends forward with gumfoot lines extending from the border of the sheet to the ground below (see Eberhard, Barrantes & Madrigal-Brenes 2008 for a detailed description of the web), limits the attack of parasitoids on *L. geometricus* eggs. Adult females of *L. geometricus* produce and maintain the egg sacs within the dense silken retreat and the spiders also add sticky threads to the external wall of some of their egg sacs (Fig. 1), which may prevent *Baeus* and other wasp parasitoids from gaining access to the eggs inside the sac. However, in various parts of the world, including the Neotropics, the eggs of *L. geometricus* are often parasitized by certain species of Eurytomidae; these species were previously placed in *Desantisca*, then in *Eurytoma* (e.g. in Hanson & Gauld 2006), but are now placed in *Philolema* (Lotfalizadeh, Delvare & Rasplus 2007). Parasitoids in this genus have also been found in egg

sacs of *L. geometricus* in Costa Rica, but not in this study (PH unpublished data).

For successful development of a parasitoid larva inside a spider egg, wasp oviposition should occur within the first days after the spider has laid her eggs (Austin 1984). This short window of time likely reduces the number of parasitoid females that can gain access to a single spider egg sac, and female biased sex ratios are to be expected in haplodiploid insects in which siblings emerge in proximity (Hamilton 1967).

Our results provide information on new host spiders parasitized by *Baeus achaeareanus*, *Idris*, and *Comastichus zopheros*, and on web and habitat features of the hosts that seem to correlate with parasitoid species preferences. It is also notable that much more information on natural history and behaviour of the wasp parasitoids (e.g. how the wingless females of *Baeus* locate and access their host webs) is required to fully understand the impact of egg parasitoids on their spider hosts.

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