Chapter 16
Host Behavioural Manipulation of Spiders by Ichneumonid Wasps

Marcelo O. Gonzaga, Thiago G. Kloss, and Jober F. Sobczak

Abstract Modified webs constructed by spiders parasitized by Ichneumonid wasps were first mentioned in literature in 1771. These initial observations were restricted to the description of the cocoon web spun by an unidentified spider species presenting a cocoon attached. Only in the year 2000 was the subject intensively studied in another host/parasitoid system. The interaction between *Leucauge argyra* (Tetragnathidae) and *Hymenoepimecis argyraphaga* (Ichneumonidae) was carefully described by W. G. Eberhard in Costa Rica. Web modifications, in this case, are even more extensive than those previously recorded. Cocoon webs spun by *L. argyra* are composed of just a few strong lines. Spirals are absent, and the cocoon remains suspended attached to the hub of the structure. From these studies up to now, several other cases have been described in the Neotropics. The initial doubt about the generality of host manipulation involving the *Polysphincta* genus-group was solved, but many questions arise from the subsequent studies. We still know almost nothing about the mechanisms involved in manipulation, for example. Recent studies suggest that it involves the injection of some substance by the parasitoid onto its host because the removal of the attached larva leads to a restoration of the original web patterns. Another interesting aspect is the investigation of how the structure of normal webs affects the design of cocoon webs. Finally, it is important to demonstrate that specific alterations in normal webs result in benefits to the manipulative wasp. The objectives of this chapter are to present an overview of recent discoveries involving these interactions, a brief historical summary of the researching efforts in the Neotropical region, and perspectives for future studies.

M.O. Gonzaga (✉)
Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil
e-mail: mogonzaga@yahoo.com.br

T.G. Kloss
Universidade Federal do Espírito Santo, Centro de Ciências Agrárias, Departamento de Biologia, Alegre, Espírito Santo, Brazil

J.F. Sobczak
Universidade da Integração Internacional da Lusofonia Afro-Brasileira, Instituto de Ciências Exatas e da Natureza, Acarape, Ceará, Brazil

The parasite is clearly visible on Broussard's face. In X-ray, the creature is a maze of complicated biology. But the shocking thing is that, in X-ray, we can see that Broussard's jaws are forced wide open, and THE PARASITE HAS EXTRUDED SOME KIND OF LONG TUBE, WHICH IS STUFFED INTO HIS MOUTH AND DOWN HIS THROAT, ending near his stomach…

- – HUNTER: It doesn't make any sense. It paralyzes him… puts him into a coma… then keeps him alive.
- – MELKONIS: We can't expect to understand a life form like this. We're out of our back yard. Things are different here…

The X-ray reveals a spreading dark blot in the vicinity of Broussard's chest. In the centre, the stain is completely opaque…

- – ROBY: That tube must be depositing it in him…
- – MELKONIS: Could be some kind of venom, or poison…
- – HUNTER: This is horrible.

The excerpts above were transcribed from the original story 'Alien', written by Dan O'Bannon and Ronald Shusett, which was later turned into a script by Walter Hill and David Giler, replacing the characters Hunter and Melkonis with Lieutenant Ripley (Sigourney Weaver) and Ash (Ian Holm), respectively. Hunter and Melkonis were wrong in two very important ways: (1) it is quite understandable that the creature would keep its host alive while her egg (the dark stain that appears later in the X-ray) developed within it, and (2) things in space (at least in this specific situation) are not that different from what happens in our backyard. In fact, the author, Dan O'Bannon, said that the habits of parasitoid wasps that lay their eggs in caterpillars were the inspiration for the story. If Melkonis had better knowledge of the biology of these wasps then, he would already know exactly what was happening to his friend Broussard. And here, on our planet, that is what we are trying to understand in detail. The interactions between parasitoid insects (Fig. 16.1) and their hosts involve complex behaviours and physiological mechanisms, including the production of anaesthetics and other substances that alter the normal behaviour of hosts and put them under the control of their enemies. This is the subject of this chapter.

Host Behaviour Manipulation by Parasitoids

Host behaviour manipulation by parasites is a widespread phenomenon that has long aroused the curiosity of the scientific community (Cram 1931; van Dobben 1952; Holmes and Bethel 1972; Moore 1984; Barnard and Behnke 1990; Godfray 1994; Poulin 2000; Moore 2002; Thomas et al. 2005; Lafferty and Shaw 2013; Hafer 2016; Soghigian et al. 2017). For example, numerous publications report parasites of fish that alter the activity patterns and foraging locations of their intermediate hosts, making them especially susceptible to avian predators (Barber et al. 2000; Shaw et al. 2009). Thus, the parasites gain access to new avian hosts, enabling their life cycle to continue. Mice infected by *Toxoplasma gondii* lose their fear of
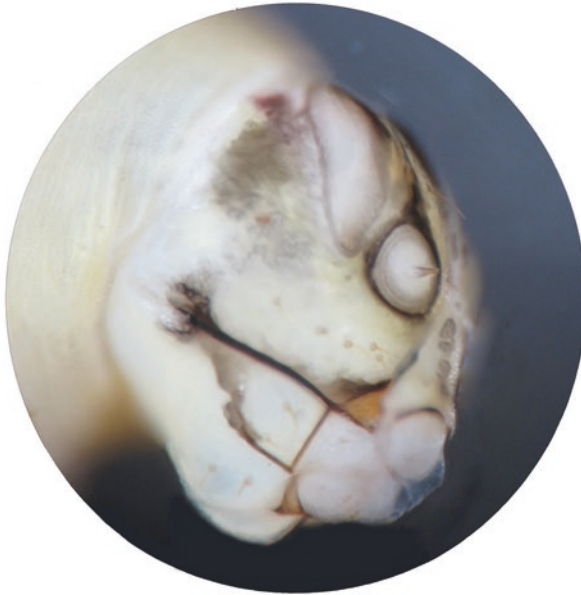
Fig. 16.1 Head of a *Hymenoepimecis bicolor* (Ichneumonidae) larva, a real version of the monster that terrorised the crew of Nostromo in the film 'Alien' (1979). This species, however, is an ecto-parasitoid (it remains attached to the body of its host, not its interior) and attacks only the spider *Nephila clavipes* (Araneidae). The larva remains attached to the body of its host, making small perforations in its abdomen and feeding on its haemolymph. When it is ready for pupation, it induces a behavioural modification in its host leading to the construction of a web with specific architectural characteristics that ensure cocoon survival for a long period. After the spider constructs this web, the larva kills the spider, consumes its entire body, and then builds a cocoon, where it will complete its development and emerge as an adult

cats. Berdoy et al. (2000) demonstrated in a laboratory experiment that infected mice do not avoid locations marked with cat urine. When a cat ingests infected prey, the parasite is released into its digestive tract. The parasite then multiplies in the intestinal wall and produces oocysts. Other remarkable examples have been reported in ants (Yanoviak et al. 2008), crickets (Biron et al. 2006), isopods (Hansen and Poulin 2005), copepods (Hafer and Milinski 2016), and snails (Wesolowska and Wesolowski 2014), among other taxa (see Hughes et al. 2012). The behavioural manipulation caused by insect parasitoids, however, is comparatively less studied, although new and interesting examples have been reported more frequently in recent years.

Studies of host behavioural manipulation induced by parasitoid insects (especially hymenopterans) include cases of changes in habitat preferences and an increased food consumption rate of the host, care of parasitoid offspring by parasitized hosts, and construction of structures by hosts to support and protect the cocoon spun by parasitoid larvae (Wickler 1976; Godfray 1994; McLachlan 1999; Eberhard 2000a; Grosman et al. 2008; Matsumoto 2009; Sobczak et al. 2009; Gonzaga et al.

2010; Korenko and Pekár 2011). In addition, development, growth, and survival of the parasitized hosts have direct consequences for the development of immature stages of the parasitoids (Fritz 1982). Thus, parasitoids are frequently able to regulate the development of their hosts by injecting substances such as venoms and hormones, which alter host physiology and ensure that the parasitoid life cycle will not be interrupted (Vinson 1975).

Most cases of behavioural manipulation by parasitoid wasps described so far involve species of the subfamily Pimplinae (Hymenoptera, Ichneumonidae). This subfamily comprises approximately 95 genera and 1500 species, most of them ecto- or endoparasitoids of holometabolous insects (Dubois et al. 2002; Gauld and Dubois 2006). Among the several genera included in Pimplinae, the *Polysphincta* clade (sensu Gauld and Dubois 2006) (hereafter 'polysphinctine wasps') is impressive because of its spectacular way of life. This group is currently composed of 24 genera (Gauld and Dubois 2006; Pallacio et al. 2007; Matsumoto 2016) with a cosmopolitan distribution. All species are koinobiont ectoparasitoids of spiders (although there is no information on natural history for six genera — *Inbioia*, *Zabrachypus*, *Lamnatibia*, *Aravenator*, *Pterinopus,* and *Ticapimpla* — and only preliminary information on natural history of another genus, *Piogaster*). This means that the hosts, after being attacked, continue their normal activities while they are slowly being consumed by the parasitoid larvae (Dubois et al. 2002, Gauld and Dubois 2006). Immature stages of most species studied so far change some behaviour of their hosts, possibly through inoculation of substances that induce the construction of modified webs (Eberhard 2000a, b; Gonzaga and Sobczak 2007; Sobczak et al. 2009; Gonzaga et al. 2010; Takasuka et al. 2015).

The first study on parasitism of spiders by polysphinctine wasps to include the suggestion of behaviour manipulation was published by De Geer (1771). He described an orb web of an unidentified spider species, with a cocoon attached to it (Fig. 16.2). The description and illustration of this web indicate some characteristics later observed in other cases of host behaviour manipulation, such as a reduction in the number of radii and the absence of sticky spirals. After this initial description, some other authors included illustrations of modified webs in papers describing interactions between polysphinctines and spiders (e.g. Nielsen 1923); however, the first well-documented case of behavioural manipulation was described only in 2000: the construction of a simple and strong structure by *Leucauge argyra* (Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Eberhard 2000a, b).

Eberhard (2000b) observed that third instar larvae of *H. argyraphaga* were able to induce their hosts to construct a modified web on the night they would be killed and consumed. In such cases, the larvae chemically induced the expression of the early steps of one specific subroutine of orb-web construction, suppressing all the subsequent behaviours that result in a normal circular orb (Eberhard 2001). On their last night alive, parasitized individuals presented bursts of activity. They added one to several radial lines in quick succession and then spent some time (up to 30 min) immobile before another burst. These spiders presented two behavioural patterns of adding radial lines in webs. In both patterns, they basically attached a dragline at the

Fig. 16.2 Modified web
described by De Geer
(1771)
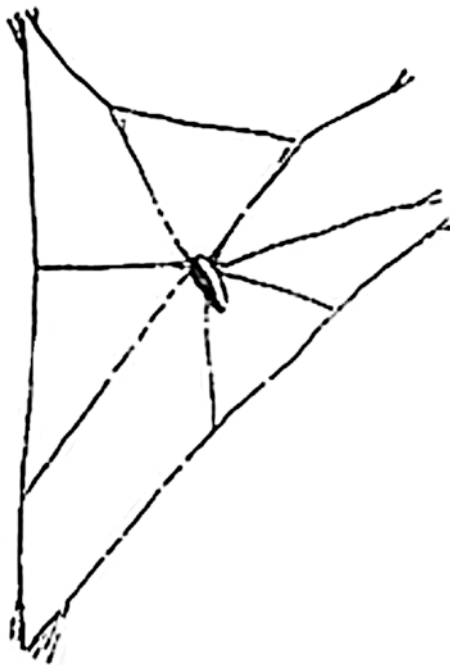
hub, walked toward the substrate along a radial line, walked along the substrate a short distance, and then attached the line that had been laid from the hub. Then they returned to the hub, walking along the same line or along another radial line that had been laid before, laying a second dragline. In the first behavioural pattern, the spider added lines without attachments to previous radial lines, and in the second, more common pattern, their draglines were attached to the radial lines on the way out and on the way back to the hub. As a result, the modified webs (cocoon webs) presented only a few strong lines, composed of approximately the same number of radial threads usually spun during the construction of normal webs (Fig. 16.3).

In the early 2000s, this was the only detailed information on a case of host manipulation by a species within the genus *Hymenoepimecis*. However, Gauld (2000) argued that *H. argyraphaga* possesses a number of plesiomorphic features, and that it possibly occupies a basal phylogenetic position within the group. He suggested that this position had important implications for understanding the evolution of biological traits within the group, making additional studies on host/parasitoid interactions involving other species of the genus critical to determining whether behavioural manipulation is a particularity of *H. argyraphaga* or a widespread trait within the genus, and perhaps, within polysphinctines. Other *Hymenoepimecis* species thus became excellent candidates for subsequent research on this subject.

Hymenoepimecis is currently composed of 20 valid species. The genus is exclusively Neotropical, and its distribution ranges from Mexico to southern Brazil, with
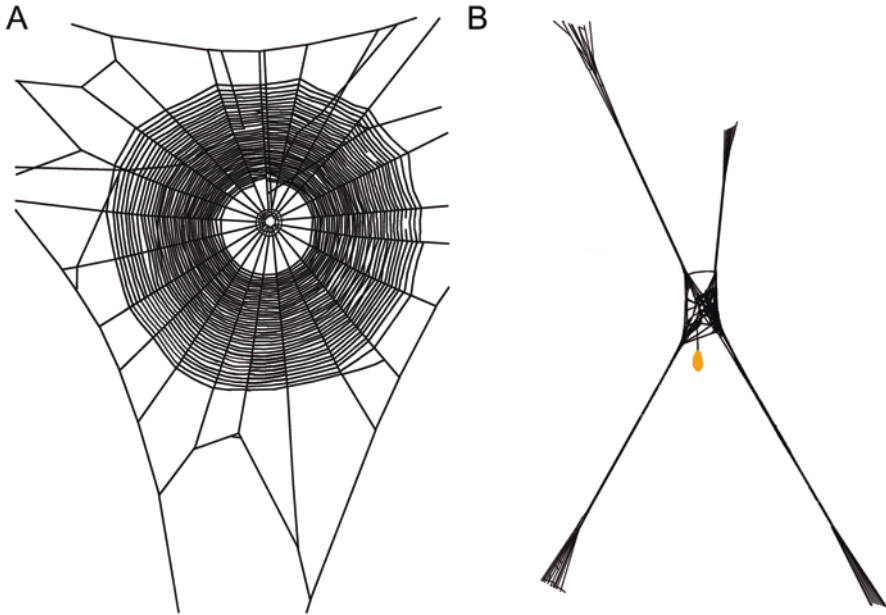
Fig. 16.3 (**a**) Web of an unparasitized adult individual of *Leucauge argyra*. (**b**) Dorsal view of the cocoon web (Modified from Eberhard (2001))

one species recorded in Cuba (*H. atriceps*). All species for which some information is available in the literature attack orb-weaver spiders of the families Araneidae and Tetragnathidae (Fincke et al. 1990; Eberhard 2000a, b; Eberhard 2001; Gauld and Dubois 2006; Gonzaga and Sobczak 2007; Sobczak et al. 2009; Gonzaga et al. 2010; Sobczak et al. 2012a, b). In the early 2000s, however, only nine species were known, and little information was available on their natural history.

The next case of behavioural manipulation involving one of these species was published by Gonzaga and Sobczak (2007). In this case, the interaction was between the spider *Araneus omnicolor* and the parasitoid *H. veranii* in southeastern Brazil. The authors described attacking and egg-laying behaviours, which included an event of infanticide, and structural differences between normal and cocoon webs. They also observed a reduction in the orb components (number of radii and spirals) of cocoon webs. Normal webs of *A. omnicolor* present an irregular three-dimensional structure attached to the orb, which is used to support a dead curled leaf that constitutes a shelter for spiders in resting positions. In cocoon webs, this three-dimensional structure remains intact; however, orbs are absent or very reduced. The authors argued that this reduction might decrease the probability of web rupture due to the interception of insects, until the emergence of the adult parasitoid.

Since these initial reports from Costa Rica and Brazil, nine other species of *Hymenoepimecis* have been observed attacking orb-weavers and inducing web modifications (Table 16.1). Sobczak et al. (2009) described two new species of *Hymenoepimecis* from southeastern Brazil attacking orb-weaver spiders. In *H. japi*,

Table 16.1 Spider hosts from the Neotropical region and their ichneumonid parasitoids

Spider host	Parasitoid wasp	Location	Source
Linyphiidae			
Dubiaranea sp.	*Eruga* sp.	Mulungu, CE, Brazil	Sobczak et al. (Unpublished data)
Tetragnathidae			
Leucauge argyra	*Hymenoepimecis argyraphaga*	Costa Rica	Eberhard (2000a, b, 2001)
Leucauge mariana	*Eruga* ca. *gutfreundi* *Hymenoepimecis tedfordi*	Costa Rica Costa Rica	Eberhard (2013)
Leucauge roseosignata	*Hymenoepimecis japi*	Jundiaí, SP, Brazil	Sobczak et al. (2009)
Leucauge volupis	*Hymenoepimecis jordanensis*	Estrela do Sul, MG, Brazil	Gonzaga et al. (2015b)
Leucauge henryi	*Hymenoepimecis manauara*	Manaus, AM, Brazil	Pádua et al. (2016)
Araneidae			
Nephila clavipes	*Hymenoepimecis bicolor* *Hymenoepimecis robertsae*	Jundiaí, SP, Brazil Santa Ana, San José, Costa Rica	Gonzaga et al. (2010)
Araneus omnicolor	*Hymenoepimecis veranii* *Hymenoepimecis neotropica*	Jundiaí, SP, Brazil Jundiaí, SP, Brazil	Gonzaga and Sobczak (2007) Sobczak et al. (2012a)
Araneus orgaos	*Hymenoepimecis veranii*	Jundiaí, SP, Brazil	Sobczak et al. (2014)
Araneus venatrix	*Hymenoepimecis silvanae*	Jundiaí, SP, Brazil	Sobczak et al. (2012b)
Manogea porracea	*Hymenoepimecis sooretama*	Linhares, ES, Brazil	Sobczak et al. (2009)
Mecynogea bigiba	*Hymenoepimecis japi*	Jundiaí, SP, Brazil	Unpublished data
Argiope argentata	*Acrotaphus chedalae*	Santa Teresa, ES, Brazil Jundiaí, SP, Brazil	Gonzaga and Sobczak (2011)
Argiope trifasciata	*Acrotaphus tibialis*		Eberhard (2013)
Eustala perfida	*Acrotaphus tibialis*	Jundiaí, SP, Brazil	Messas et al. (Unpublished data)
Cyclosa monteverdi	*Polysphincta gutfreundi*	Costa Rica	W.G. Eberhard (Unpublished data)
Cyclosa morretes	*Polysphincta janzeni*	Viçosa, MG, Brazil Ribeirão Grande, SP, Brazil Santa Teresa, ES, Brazil	Unpublished data Gonzaga et al. (2015b) Kloss et al. (2016a, b)
Cyclosa fililineata	*Polysphincta janzeni* *Polysphincta* nr. *purcelli*	Ribeirão Grande, SP, Brazil Santa Teresa, ES, Brazil	Gonzaga et al. (2015b) Kloss et al. (2016a, b)

Table 16.1 (continued)

Spider host	Parasitoid wasp	Location	Source
Cyclosa sp.	*Polysphincta sp. nov.*	Rio Preto do Eva, AM, Brazil	Unpublished data
Allocyclosa bifurca	*Polysphincta gutfreundi*	San Jose Province, Costa Rica	Barrantes et al. (2008), Eberhard (2010a)
Parawixia bistriata	*Hymenoepimecis sp.*	Uberlândia, MG, Brazil	Unpublished data
Theridiidae			
Achaearanea tingo	*Zatypota alborhombarta*	Ribeirão Grande, SP, Brazil	Gonzaga et al. (2016)
Achaearanea cinnabarina	*Zatypota* nr. *riverai*	Jundiaí, SP, Brazil	Unpublished data
Anelosimus baeza	*Zatypota solanoi* *Zatypota* sp. nov	Jundiaí, SP, Brazil Mulungu, CE, Brazil	Unpublished data
Anelosimus nigrescens	*Zatypota solanoi*	Jundiaí, SP, Brazil	Unpublished data
Anelosimus jabaquara	*Zatypota solanoi*	Jundiaí, SP, Brazil	Unpublished data
Anelosimus octavius	*Zatypota sp. nr. solanoi*	Bebedero, Costa Rica	Eberhard (2010b)
Anelosimus nr. *studiosus*	*Zatypota sp. nr. solanoi*	San Pedro de Montes de Oca, Costa Rica	Eberhard (2010b)
Cryptachaea migrans	*Zatypota alborhombarta*	Santa Teresa, ES, Brazil Cariacica, ES, Brazil	Unpublished data Unpublished data
Cryptachaea rioensis	*Zatypota alborhombarta*	Santa Teresa, ES, Brazil Domingos Martins, ES, Brazil Conceição da Barra, ES, Brazil	Unpublished data Unpublished data Unpublished data
Cryptachaea migrans	*Zatypota morsei*	Santa Teresa, ES, Brazil Domingos Martins, ES, Brazil	Unpublished data Unpublished data
Theridion evexum	*Zatypota petronae*	San Jose Province, Costa Rica	Barrantes et al. (2008)

a parasitoid of *L. roseosignata*, when the parasitoid larva reaches the last instar before pupation, there is a significant modification in the host web design, similar to that observed by Eberhard (2001) in parasitized individuals of *L. argyra.* The modified web is composed of only three strong threads converging to a platform, located in the hub, which holds the cocoon; viscid spirals are completely absent. In the second species, *H. sooretama*, a parasitoid of *Manogea porracea* (Araneidae), there

is no apparent modification of web architecture. However, the cocoon constructed by the parasitoid larva is attached to the web in a position far from the usual resting position of the spider. In this case, it seems that host behavioural changes are restricted to transporting the larva to a more protected area, a location covered by a denser mesh of threads (Sobczak et al. 2009).

All other studied species of *Hymenoepimecis* also change the behaviour of their hosts in some way (e.g., Eberhard 2013; Pádua et al. 2016). Gonzaga et al. (2015a), for example, observed that cocoon webs constructed by the *L. volupis* attacked by *H. jordanensis* are similar to those constructed by unparasitized, immature individuals, presenting a lower tangle that is absent in webs spun by adults. This structure may increase web stability, reducing the probability that the cocoon will fall to the ground. In this case, sticky spirals are also absent from the cocoon webs, but the reduction in spirals is not as subtle as that observed for parasitized *L. argyra*, which starts before the construction of the cocoon web. The same gradual effect on webs over the interval of several days was also observed in *Nephila clavipes* attacked by *H. bicolor* and *H. robertsae* (Gonzaga et al. 2010). Differences between the cocoon webs of *L. volupis* and the cocoon webs spun by other congeneric species suggest that the substance used for host manipulation may vary in concentration or composition (see the section "Mechanism of Manipulation" in this chapter).

Despite the great diversity within polysphinctines and the long time since the first behavioural record, and the existence of complex parasitoid–host interactions such as host behavioural manipulation by larvae, several aspects of such interactions remain poorly known. In the Neotropical region, most studies were carried out in Costa Rica and Brazil, and they involved species of *Hymenoepimecis*; however, information on certain species of *Zatypota*, *Polysphincta*, *Eruga,* and *Acrotaphus* is also available, which indicates that the phenomenon of host manipulation is widespread within polysphinctines (Table 16.1, Figs. 16.4, 16.5, and 16.6). Contributions from other geographic regions are currently mostly restricted to studies developed in Japan (Matsumoto and Konishi 2007; Matsumoto 2009; Takasuka et al. 2009, 2015; Takasuka and Matsumoto 2011a, b), the Czech Republic (Korenko and Pekár 2011; Korenko et al. 2011, 2014), Italy (Korenko and Pekár 2011; Korenko et al. 2014, 2015a, b), the Netherlands (Korenko et al. 2015b), and Canada (Bovee and Leech 2014). Most of these studies have focused on interactions involving the genus *Zatypota*, but there is also detailed information available on certain species of *Reclinervellus* (Matsumoto and Konishi 2007; Takasuka et al. 2015), *Brachyzapus* (Matsumoto 2009), and *Polysphincta* (Bovee and Leech 2014).

Mechanism of Manipulation

The exact mechanism(s) of behavioural manipulation of spider hosts remains to be described in detail, but some recent studies have indicated that it may involve the direct injection of hormones by the parasitoid larva when it reaches the last instar (Takasuka et al. 2015; Kloss et al. 2017). The idea that psychotropic substances promote alterations in web building behaviours has been around for a long time.
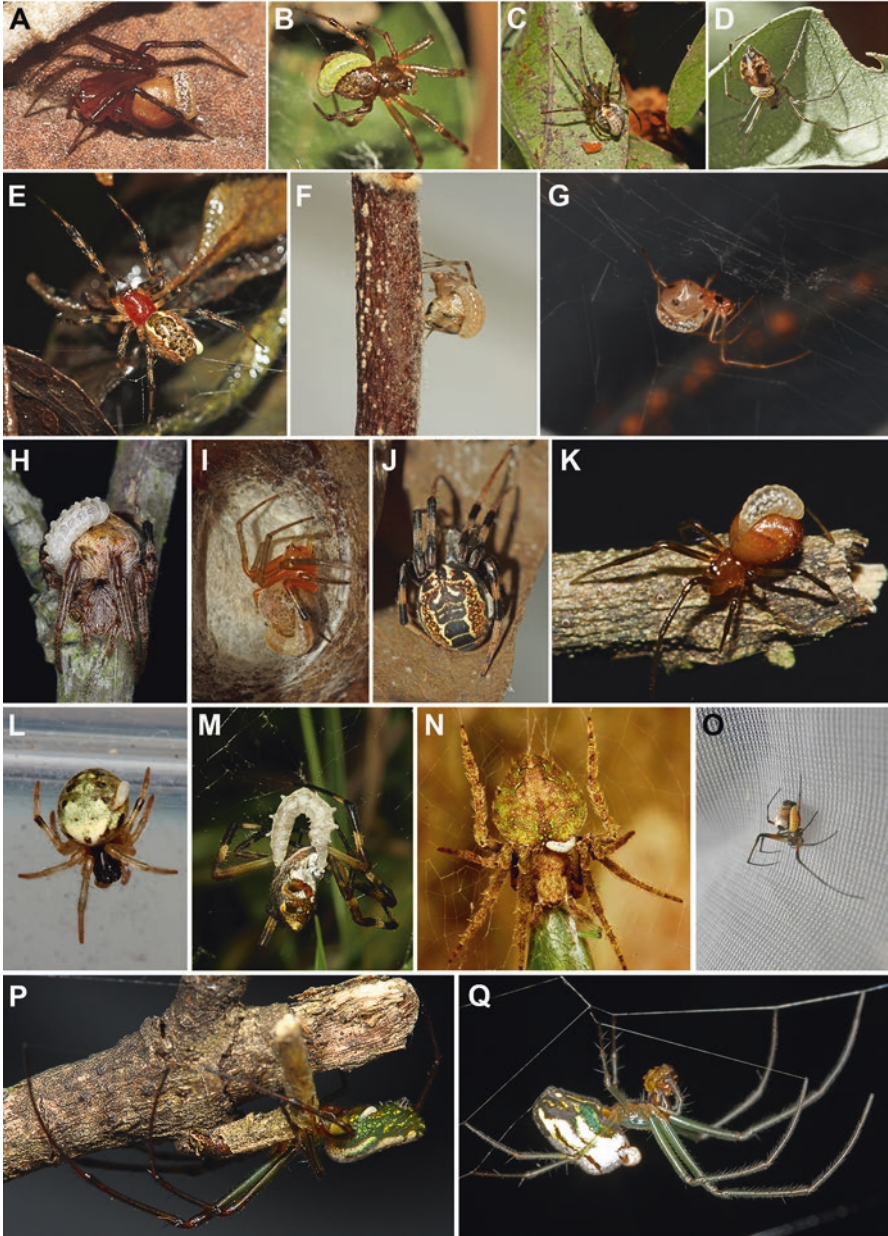
Fig. 16.4 Spider hosts carrying larvae or eggs of polysphinctines. (**a**) *Achaearanea cinnabarina*, (**b**) *Anelosimus baeza*, (**c**) *Steatoda* sp., (**d**) *Dubiaranea* sp., (**e**) *Anelosimus jabaquara*, (**f**) *Cryptachaea* sp., (**g**, **k**) *Achaearanea tingo*, (**h**) *Araneus omnicolor*, (**i**) *Araneus orgaos*, (**j**) *Araneus venatrix*, (**l**) *Araneus workmani*, (**m**) *Argiope argentata,* (**n**) *Eustala perfida*, (**o**) *Leucauge henryi*, (**p**) *Leucauge roseosignata*, (**q**) *Leucauge volupis*
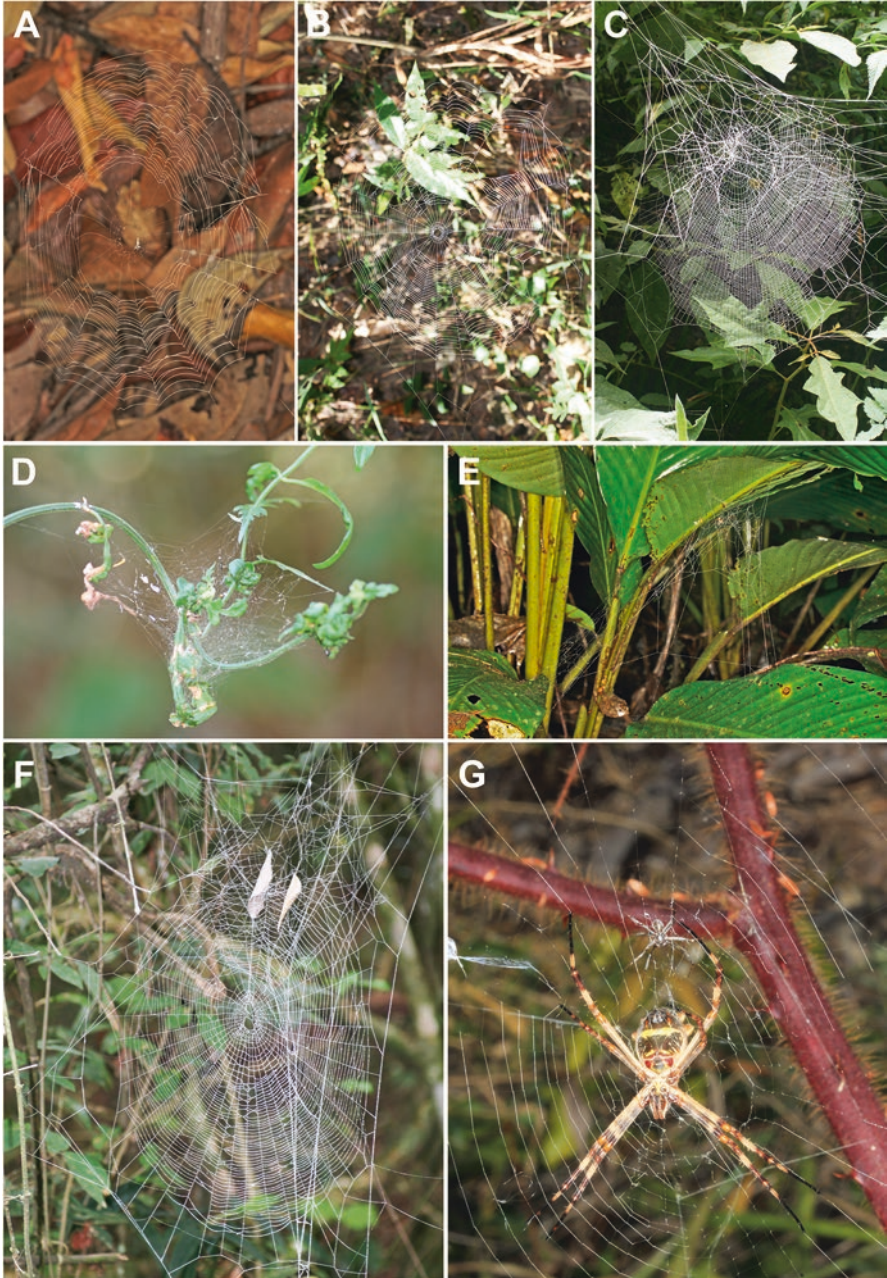
Fig. 16.5 Normal webs of some spider hosts. (**a**) *Leucauge volupis*, (**b**) *Leucauge roseosignatha*, (**c**) *Nephila clavipes*, (**d**) *Anelosimus nigrescens*, (**e**) *Achaearanea tingo*, (**f**) *Araneus omnicolor*, (**g**) *Argiope argentata*
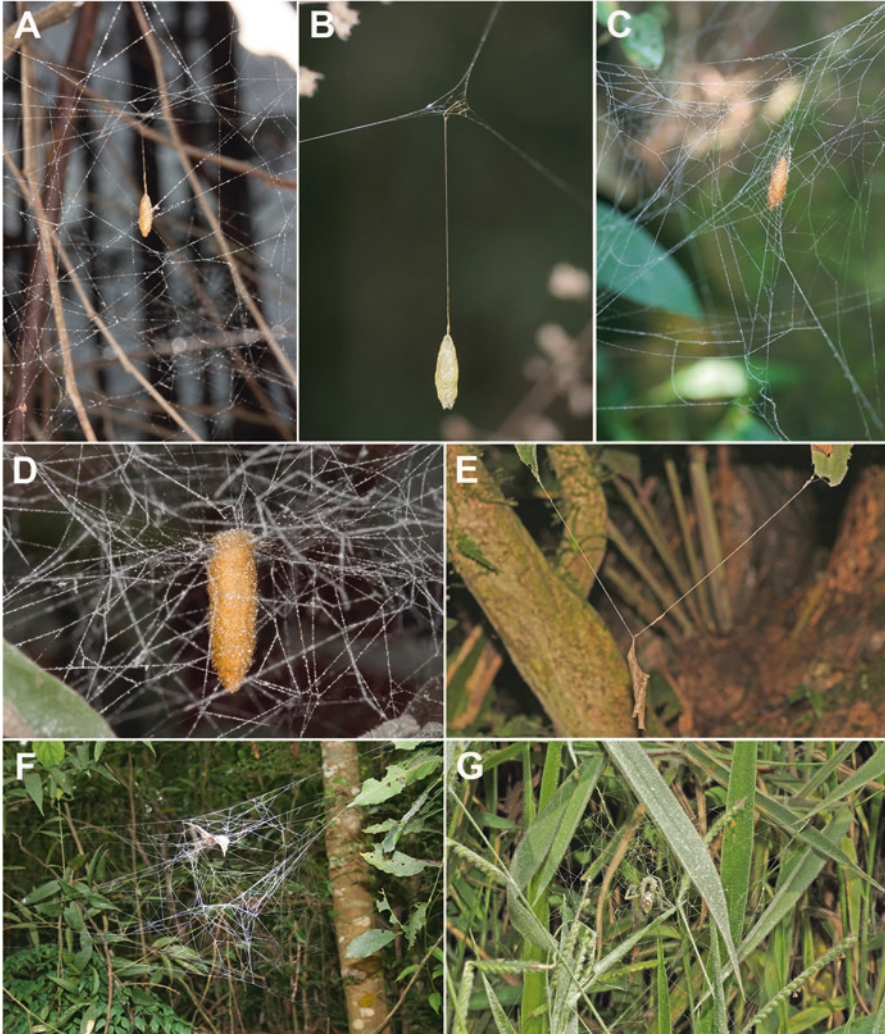
Fig. 16.6 Cocoon webs of (**a**) *Leucauge volupis*, (**b**) *Leucauge roseosignatha*, (**c**) *Nephila clavipes*, (**d**) *Anelosimus nigrescens*, (**e**) *Achaearanea tingo*, (**f**) *Araneus omnicolor*, (**g**) *Argiope argentata*

Witt (1971) and Eberhard (2000b, 2001) suggested that substances produced by the larva were responsible for the unusual structure of cocoon webs constructed by parasitised individuals of *L. argyra*. The similarities between cocoon webs spun by some host species (but not all of them — see Korenko and Pekár 2011 for exceptions) and the resting (or 'moulting') webs constructed before moulting were clues indicating that the manipulative compounds might be ecdysteroids or some precursor of moulting hormones.

The first experimental evidence suggesting that some chemical substance produced by the parasitoid larva is responsible for host behavioural alteration during web building was obtained by Eberhard (2010a). He observed that behavioural modification of *Allocyclosa bifurca* (Araneidae) by the ichneumonid wasp *Polysphincta gutfreundi* is gradual, and that the spider is able to recover its normal behaviour when the parasitoid larva is experimentally removed. These results suggest that the effects on spiders may depend on a cumulative or dose-dependent process rather than on injection of several distinct substances that are each responsible for influencing specific behaviours. Gonzaga et al. (2010) and Kloss et al. (2016a) tested an alternative hypothesis, considering that reduction in web investment might result from nutritional restrictions imposed by the parasitoid. They found no evidence supporting the idea that modification in web design arises as a by-product of nutritional deficiencies, and agreed that alterations in spider behaviour are probably caused by the injection of some substance by the larva.

Recently, Takasuka et al. (2015), studying the behavioural modifications of *Cyclosa argenteoalba* (Araneidae) induced by *Reclinervellus nielseni* (Ichneumonidae), analysed, in detail, the similarities between cocoon webs spun by parasitised individuals and the moulting webs. They hypothesised that the parasitoid larva evokes the innate moulting web construction behaviour of *C. argenteoalba*, suggesting that injection of chemical components corresponding to moulting hormones (ecdysteroids) into the spider body may be responsible for behavioural changes. They found a number of similar characteristics between the two types of webs (e.g., presence of fibrous thread decorations on the radii, absence of stabilimenta, and reduction in radii number), confirming that presence of the same substance(s) leading to moulting web and cocoon web construction is a valid possibility. However, they also found some important differences, such as repeated thread weavings that occur during cocoon web construction but not during moulting web construction. The authors attributed these differences to the distinct hormone concentrations in each situation.

The latest evidence in this direction was reported by Kloss et al. (2017). They also observed that moulting web structures of *C. morretes* and *C. fililineata* are similar to cocoon webs spun by these spiders when parasitized, respectively, by *P. janzeni* and *P.* sp. nr. *purcelli* (probably a new species). The authors compared the levels of 20-OH-ecdysone (20E) in unparasitized spiders, second-stage larvae, parasitized spiders carrying second-stage larvae, third-stage larvae, and parasitized spiders carrying third-stage larvae. The results indicated that the levels of the hormone in parasitized spiders carrying third-instar larvae (those with cocoon webs) were much higher than those observed in the other groups. They suggested that parasitoid larvae may directly inject the hormone into the spider body, or produce and inject a precursor chemical that is responsible for 20E synthesis in the spider host. However, the generality of this mechanism must be investigated, considering other cases of host behavioural alterations that result in webs that are very different from moulting webs (e.g., Eberhard 2000a, 2010a, b, 2013; Sobczak et al. 2009).

Host Selection

Little information is available on host selection and cues used for host location in most species of polysphinctines. Most reported cases are restricted to few observations, and a large data set is required to determine whether there is a preference for a restricted range of host body sizes and/or spider species used for egg laying. Thus, an analysis of records currently available in the literature indicates that most Neotropical polysphinctines are specialists, using only one or two host species (Table 16.1); however, this result is probably an artefact of limited investigation of habits of the great majority of these species. Some parasitoid species, such as *Zatypota solanoi*, are able to attack congeneric host species that occur in sympatry or in different locations across their distribution range. In the same way, some host species are attacked by distinct parasitoid species; however, additional studies are still needed to confirm the patterns that can be identified from the dataset presented in Table 16.1.

Lack of information is also a problem with regard to host size preferences in most cases. For a few, however, it is possible to recognise that wasps actively selected specific host ranges. Gonzaga and Sobczak (2007), for example, reported that *H. veranii* attacked relatively small individuals at a frequency higher than that expected based on the abundance of those individuals in the field, whereas large spiders are ignored. Similarly, Sobczak (2013) observed that large females of *N. clavipes* are rarely attacked by *H. bicolor*. Eventual attacks on these spiders often result in predation by the host. Finally, Fincke et al. (1990) showed that *H. robertsae* also selects intermediate-sized individuals of *N. clavipes* in Panama. Large individuals may provide more resources for the larvae, but immobilisation of a large spider may be associated with a high risk of failure. On the other hand, *H. jordanensis* prefers relatively large hosts (Gonzaga et al. 2015b). The authors argued that the range of host sizes used by polysphinctines is probably determined by their own body size (specifically, by the relationship between the size of the wasp and the spider), attacking behaviours, and venom characteristics and nutritional requirements of their developing larvae. In addition, distinct host species (and distinct instars within species) may have particular nutritional compositions, and host size selection may be influenced by the balance of lipid and proteins available. This last hypothesis, however, remains to be tested in further studies.

Host Immobilisation and Egg-Laying Processes

In the Neotropical region, attacks on host spiders and oviposition behaviours of polysphinctines have been described for eight species, representatives of the genera *Hymenoepimecis*, *Polysphincta,* and *Zatypota*. Observations suggest that attack strategies depend on the specific reactions of hosts to threats and the particular architectures of host webs, such as the presence of stabilimenta and barrier threads.

Within the genus *Hymenoepimecis*, the attacking behaviours of four species have been witnessed by researchers. *H. bicolor* attacking *N. clavipes* tend to hover around a target spider before executing a direct attack and then dart rapidly at the spider, grasping it with their legs (Eberhard 2000b; Sobczak 2013) (Fig. 16.7a). *Hymenoepimecis argyraphaga* attacks *Leucauge argyra* in a similar way; however, it has also been observed hanging immobile in a web radius in the free zone near the web hub, waiting until a spider that had left the web returned to its resting position (Eberhard 2000b). This is probably an alternative behaviour to gain access to spiders that had escaped the initial attack. *H. veranii* also uses web threads spun by the host to perform the attack. In this case, a female wasp stands immobile on barrier threads and waits until the target spider leaves its retreat to capture prey (Fig. 16.7b). At that moment, the wasp performs a direct attack (Gonzaga and Sobczak 2007). It inserts the tip of its ovipositor into the host spider's mouth, probably reaching the suboesophageal ganglion, and then inspects the host abdomen, searching for the presence of eggs previously deposited by other wasps. The venom has an immediate effect, rendering the attacked spider motionless for at least 18 min. After removing any egg of another female, the wasp lays its own egg on the dorsal surface of host's abdomen. Finally, there has been an observation of *H. sooterama* invading a web of *M. porracea* and walking on the web threads to the position occupied by the spider (Sobczak et al. 2009), but there is no record of an attack.

Attacks by *P. janzeni* on *C. morretes* and *P.* sp. nr. *purcelli* on *C. fililineata* are quite different from those of *Hymenoepimecis* spp. Females start the attacks by landing on the web hub, near the position occupied by the spider, but never directly on the spider. The spider jumps off the web immediately or moves quickly towards the web edge. After the initial attack, the wasp remains motionless at the web hub until the spider returns and touches the body of the wasp. Wasps wait for the hosts to return for periods ranging from 30 min to 14 h. The attack starts immediately after the spider touches the body of the wasp. After a struggle lasting a few seconds, the wasp remains positioned with its head facing the posterior part of the spider's abdomen and inserts its ovipositor into the spider's mouth, leading to immediate paralysis of the host. The wasp then inserts and withdraws its ovipositor from the spider's mouth repeatedly for approximately 5 min. Subsequently, the wasp appears to inspect the spider's body, repeatedly rubbing and jabbing the base of its ovipositor all over the host's abdomen (near the location where the egg will be attached) for approximately 4 min. After this behaviour, the wasp again proceeds to insert and withdraw its ovipositor into and out of the spider's mouth repeatedly for another 3 min. Finally, the wasp deposits a single egg on the anterodorsal surface of the host's abdomen and returns to the hub of the web, where it remains for at least 1 h. The function of this behaviour is not known; however, the wasp may remain on the web after oviposition as a strategy to detect possible egg removal by the spider after its recovery from paralysis (Kloss et al. 2016b).

Records of *Zatypota* in the Neotropics are restricted to a study published by Weng and Barrantes (2007) on *Z. petronae* behaviour, and some unpublished observations conducted by J. Sobczak and M. Gonzaga on *Z. solanoi* in Brazil. *Z. petronae* invades the retreat of the host spider *Theridion evexum* and attacks the spider
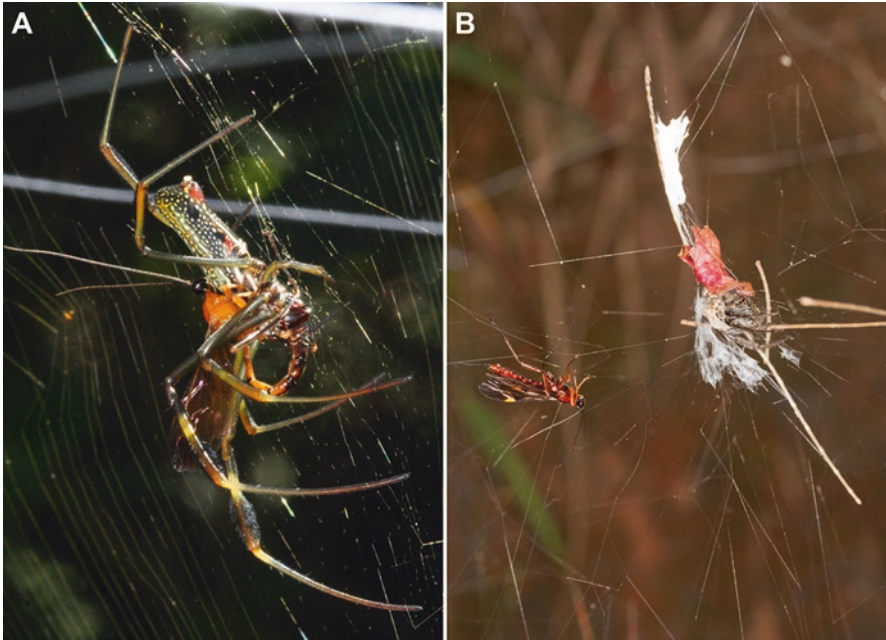
Fig. 16.7 (**a**) *Hymenoepimecis bicolor* immobilising its host, a female of *Nephila clavipes*. (**b**) *Hymenoepimecis veranii* waiting for the host to leave its shelter

inside its retreat. Details regarding *Z. petronae* behaviour during the host immobilization and egg-laying processes are not available in the literature (Weng and Barrantes 2007). *Z. solanoi* attacks *Anelosimus* species by invading their tridimensional webs and walking through the dense mesh of threads until it reaches a spider. A similar process of immobilisation, insertion of the ovipositor into the spider mouth, and inspection of the abdominal region was observed prior to egg laying. In one attack, we observed *Z. solanoi* killing a second instar larva attached to an *Anelosimus baeza* adult female.

Consequences for the Parasitoid

Modification in web architecture yields an increase in pupal survival (Kloss et al. 2016a; Sobczak 2013), because the modified structure is more stable and less efficient at intercepting insects than the normal web structure. Few studies, however, have compared the efficiency of modified and normal webs at preserving the integrity of the cocoons from their construction to the emergence of the adult wasp. Evidence obtained from the interaction between *H. bicolor* and *N. clavipes* and between *C. fililineata* and *P.* nr. *purcelli* indicate that host behavioural manipulation is important to ensure parasitoid survival during this period.

Sobczak (2013), for example, established three spider groups in individual enclosures in the field. The first group was composed of parasitized spiders that built modified webs, the second group was composed of parasitized spiders used for manipulation, and the third group was composed of unparasitized individuals. Just after their modified web construction, spiders in group 2 were transferred to the normal webs constructed by spiders in group 3. The original owners of those webs had been previously removed. Thus, the larvae had no option but to construct their cocoons in normal webs. After that, the enclosures were opened and the webs were exposed to normal field conditions, including strong winds and frequent heavy rains, which occur from January to May in the study area. Most cocoons (18 of 20) from group 1 (cocoons in modified webs) remained intact after 16 days of observations, whereas only one of 20 cocoons attached to normal webs were intact after the same period. The author observed that the collapse of normal webs and the cocoons falling to the ground were the main causes of pupal mortality in the latter group.

Kloss et al. (2016a) conducted a similar experiment with parasitized and unparasitized *C. fililineata* and *C. morretes* females in another area of Atlantic forest, also in southeastern Brazil. Survival of parasitoid individuals reintroduced to the same cocoon webs was higher than that of parasitoid larvae transferred from the original cocoon webs to unmodified webs, for both species. The author observed several mortality factors during the experiment, including web rupture due to rain resulting in cocoons falling to the ground and subsequent predation by indeterminate predators, web rupture due to falling branches, predation by araneophagic spider species (Mimetids), and predation by ants in damaged webs in which the cocoons came in contact with vegetation. Of these factors, the highest difference between groups was in mortality resulting from web rupture by the rain, indicating that web modification improves the stability of the structure holding the cocoon.

Conclusions

Systematic investigation on the subject of host behavioural manipulation involving spider hosts and polysphinctine wasps is a relatively new area of investigation, and many aspects such as host selection and the mechanism(s) involved in the phenomenon of manipulation are currently poorly understood. However, during the few years since the description of the cocoon webs spun by parasitized individuals of *L. argyra*, significant discoveries have been made. We know now, with reasonable confidence, that some substance injected by the larva into the host induces the construction of modified webs, which present structural characteristics that confer to them an increased stability and a reduced probability of rupture due to insect interception. Wasp survival during the pupal stage is certainly higher in cocoon webs as a direct result of this new architecture. We also know that cocoon webs, at least in some cases, are very similar to moulting webs, and the first evidence that moulting hormones may be involved in the process of manipulation has arisen in recent studies.

These and other recent discoveries are part of the initial efforts to clarify the patterns, origins, and ecological consequences of interactions between spiders and parasitoids. Certainly, there are many other cases (including genera without any available information to date) to be discovered and described. We hope to discover, in the next years, how these further findings will influence the patterns presented in this chapter. Being more optimistic than the character Melkonis mentioned at the beginning of this chapter, we believe that there is no reason not to expect to understand (at least partially) these life forms. Contribution from other research groups, especially within the highly biodiverse Neotropical region, is very important in this endeavour.

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