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When a little is enough: cocoon web of *Kapogea cyrtophoroides* (Araneae: Araneidae) induced by *Hymenoepimecis heidyae* (Ichneumonidae: Pimplinae)

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Abstract. The final instar larvae of the koinobiont ectoparasitoids in the *Polysphincta* group of genera induce their host spiders to construct webs that protect the wasp pupa during its development. It has been hypothesized that changes in structure and design in the cocoon web correlate with the duration and characteristics of the normal web. *Kapogea cyrtophoroides* (Araneidae) construct long-lived, strong normal webs; the cocoon web induced by *Hymenoepimecis heidyae* (Ichneumonidae) is nearly identical to the normal web, providing support for the hypothesis. The larva constructs its cocoon in the centre of the host's dense web, connecting it to the spider web and following the same behavioural pattern of construction described for other wasp species in the same group. The behaviour induced in the spider as well as the cocoon construction is very stereotypic, and consistent with other species, but modifications in the cocoon web seem to be strongly determined by the characteristics and design of the spiders' normal web.

Keywords: cocoon construction, cocoon webs, ectoparasitoids, host parasitoid interaction

Zusammenfassung. Wenig ist schon genug: das Kokonnetz von *Kapogea cyrtophoroides* (Araneae: Araneidae) induziert von *Hymenoepimecis heidyae* (Ichneumonidae: Pimplinae). Das letzte Larvenstadium der koinobionten Ektoparasitoiden der *Polysphincta* Gattungsgruppe induziert bei ihren Wirten die Bildung eines Netzes, das die Puppe der Wespe während ihrer Entwicklung schützt. Es gibt die These, dass Änderungen in Struktur und Design des Kokonnetzes mit Lebensdauer und Charakteristika des normalen Netzes korrelieren. *Kapogea cyrtophoroides* (Araneidae) baut langlebige und kräftige normale Netze; dass das von *Hymenoepimecis heidyae* (Ichneumonidae) induzierte Kokonnetz fast identisch wie das normale Netz ist, unterstützt diese These. Die Larve spinnt ihren Kokon im dicht gewebten Zentrum des Wirtsnetzes, verknüpft ihn mit dem Spinnennetz und führt dabei die für andere Wespen der Gattungsgruppe bekannten Verhaltensmuster bei der Konstruktion durch. Das induzierte Verhalten der Spinne ist ebenso wie die Kokonkonstruktion sehr stereotyp und stimmt mit dem anderer Arten überein. Jedoch scheinen Modifikationen des Kokonnetzes stark von den Merkmalen und dem Design des normalen Spinnennetzes abhängig zu sein.

A large number of parasites drastically change host behaviour which increases parasite survivorship, dispersal, and reproduction (Helluy & Holmes 2005). Among spider parasitoids, all wasp species in the *Polysphincta* genus group (Ichneumonidae: Pimplinae) are koinobiont ectoparasitoids, which lay a single egg on the dorsum of the anterior section of the spider opisthosoma (Nielsen 1923). When the larva emerges, it bites through the spider cuticle to feed on the hemolymph, remaining attached to the spider to the last instar (Nielsen 1923, Eberhard 2000). Hours before moulting to the last instar, the larva induces the spider to construct a modified web (cocoon web), which provides protection to the cocoon that the last-instar larva constructs (Eberhard 2001, Weng & Barrantes 2007, Gonzaga et al. 2015, Korenko 2016).

The cocoon webs constructed by spiders under the influence of polysphinctines vary widely across different spider species (Gonzaga & Sobczak 2007, Weng & Barrantes 2007, Gonzaga et al. 2010, Barrantes et al. 2017), and often within the same spider species (Eberhard 2001, 2013). This variation correlates with the design and structure of the normal web. With few exceptions (Gonzaga et al. 2016), in normal webs with a retreat for the spider's protection, or in long-lived webs, the cocoon web induced by the parasitoid tends to be more similar to the normal web, than in cocoon webs of spiders that normally build short-lived, exposed webs (Eberhard 2000, Weng & Barrantes 2007, Korenko 2017).

Within this group of ectoparasitic wasps, those in the genus *Hymenoepimecis* are known to attack orb-web spiders in

two different families (Araneidae and Tetragnathidae). Our aim here is to describe the cocoon web and behaviour of the larva of *H. heidyae* (Gauld, 1991) parasitizing the araneid *Kapogea cyrtophoroides* (F. O. P.-Cambridge, 1904). The only previous information on this interaction consists of the description of a single individual of *H. heidyae* reared by W. G. Eberhard (in Gauld 2000) from *Cyrtophora nympha* (= *K. cyrtophoroides*). In this case, the spider host was provided with some twigs in which the larva induced the spider to build a small tangle in whose centre the larva built its cocoon (W. Eberhard pers. comm.), but no further behavioural observations were taken.

The web of *K. cyrtophoroides* consists of a dense, nearly horizontal, orbicular web that has a large number of primary and secondary radii and a large number of very closely spaced non-sticky spiral loops (Levi 1997). It also includes a dense tri-dimensional thick tangle of threads above and below the horizontal web (Fig. 1a). The tangles support the orb, and probably also function to knock down prey onto the sheet as well as to defend the spider against attacks from below. Thus, considering the characteristics of the *Kapogea* web, we expect the changes induced by *H. heidyae* on the spider's cocoon web to be small, as observed in cocoon webs of the related genus *Manogea* (Sobczak et al. 2009) and other long-lived webs (Korenko 2017).

Material and methods

We collected the parasitized spiders at La Tirimbina Biological Reserve, Sarapiquí, Heredia province (10.4333°N, 83.9833°W; 150 m a.s.l.), Veragua Rainforest Eco Adventure (9.9167°N, 83.1833°W; 350 m a.s.l.) and the Indigenous Reserve Kéköldi, Talamanca (9.6325°N, 82.7867°W; 280 m a.s.l.), both in Limón province; all three sites are on the Caribbean slope of Costa Rica. The mean annual temperature ranges from 25.3 °C

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Fig. 1: Distinct aspects of the web of *Kapogea cyrtophoroides*. **a.** Natural web in the forest (the web in the picture is similar to at least other 20 webs we have seen in the field). **b.** The hub of a natural web. **c.** Cocoon web that the larva induced the spider to build after the spider was removed from its web; arrows point to cocoon web threads. **d.** Central section of the cocoon web and the wasp's cocoon

to 26.0 °C and the mean annual precipitation from 3500 to 4500 mm at these sites (Martínez 2012, Tirimbina Biological Reserve 2010). Spiders and their hosts were collected in mature and old second growth lowland rainforests.

In the laboratory each spider with its parasite was placed in a 30 cm diameter plastic container with plants of different families (e.g. Commelinaceae and Crassulaceae) which covered nearly the entire diameter of the container. We recorded daily the larval stage and the design of the web of the spider, which was fed every other day with *Lucila* sp. flies (Calliphoridae). We regularly photographed each spider and its parasitoid larva (daily in one spider) and video-recorded the behaviour of two last-stage larvae.

Results

“Cocoon web”. In the laboratory the spiders constructed webs similar to those in nature (Fig. 1a). The second-instar parasitoid larva induced the host spider to build the cocoon web and during the night it killed the spider. However, differences between the cocoon web and normal web were nearly imperceptible. The only differences between cocoon and normal webs were that the spider was induced to produce a hole through the centre of the hub and to add a few additional threads in the central section of the orb, to which the cocoon was then attached by the larva (Fig. 1b, N = 3 cocoon webs).

We did not observe the spider breaking the silk threads of the hub, but in one case a last instar larva constructed its cocoon within an open space in the hub which was intact the previous night. In the field we also observed a cocoon constructed within the space in the centre of the hub (Fig. 1d).

To observe a cocoon web built from scratch, we carefully removed one spider with a second-instar larva attached to its opisthosoma from its web the night before it killed its host. We then destroyed the web, cleaned the plant, and returned the spider with its larva back to the same plant in the same container, and allowed the spider to build its cocoon web. In this case, the second-instar larva induced the spider to build a relatively sparse, horizontal tangle that did not have an orbicular design (Fig. 1c).

Larval development and behaviour. Two of the host spiders were found with wasp eggs attached to them (Fig. 2a) and in both cases the larva emerged three days later in the lab. Both larvae passed through three stages, which lasted a total of nine days (Tab. 1). We determined the number of larval stages by examining the number of shed-skins that were attached to the “saddle” (the mass of coagulated spider hemolymph which adhered to the spider's opisthosoma; Nielsen 1923, Eberhard 2000, Weng & Barrantes 2007); the last stage is characterized by the presence of dorsal tubercles.



Fig. 2: Egg and different larval stages. **a.** Egg recently attached to the spider’s opisthosoma. **b.** First instar larva recently emerged from the egg. **c.** Second instar larva. **d.** Third instar larva feeding on the recently killed spider; details of the dorsal hooklets are visible in the inset

During the first two stages, the larva only grew in size, with no obvious morphological changes (Fig. 2b). During this period the larva sometimes appeared to feed on the spider’s hemolymph: the larva’s mouth contacted the spider’s cuticle, and peristaltic contractions moved posteriorly in the anterior section of the larva’s body.

The third stage larva had a dorsal tubercle with hooklets on each of eight body segments (Fig. 2c). During this stage the larva killed the spider, grasped the web with its dorsal tubercles, and then spent nearly two days sucking out the contents of the spider; upon completion of feeding it dislod-

ged the spider’s carcass and then began cocoon construction (Tab. 1).

Cocoon construction. We video-recorded portions of cocoon construction by two larvae. In both cases the larva constructed the cocoon in the centre of the orb-web, the hub, where the larva had killed and consumed the spider. Construction began with the larva hanging by its hooklets to threads of the cocoon web (Fig. 3a). With silk threads produced from the larva’s mouth, it first constructed a fluffy mass of silk around its posterior half (Fig. 3b). During this phase we observed the larva connecting some threads to the cocoon web (Fig. 3c-d).

After several hours of continuous spinning, the larva had gradually constructed a fluffy mass of silk that encased the entire larva (Fig. 3). On several occasions, we observed the larva move down to reach the bottom of the cocoon and continue adding silk threads to the interior of the cocoon (Fig. 3e), so that the cocoon wall became denser over time (Fig. 3f). During spinning, the larva connected the threads in sequence and the next connection point was always near the previous one. The larva commonly began by connecting threads to the top of the cocoon and then in a sequence of connecting points, moved its head while curling its body about its abdominal section, to nearly reach the bottom of the cocoon (Fig.

Tab. 1: Days spent in each developmental stage by two larvae of the parasitoid wasp *Hymenoepimecis heidyae* on its host spider *Kapogea cyrtophoroides*.

Stage	Days
Egg	3
First instar larva	3
Second instar larva	4
Third instar larva	2
Cocoon construction	2
Pupa	15
Total	29

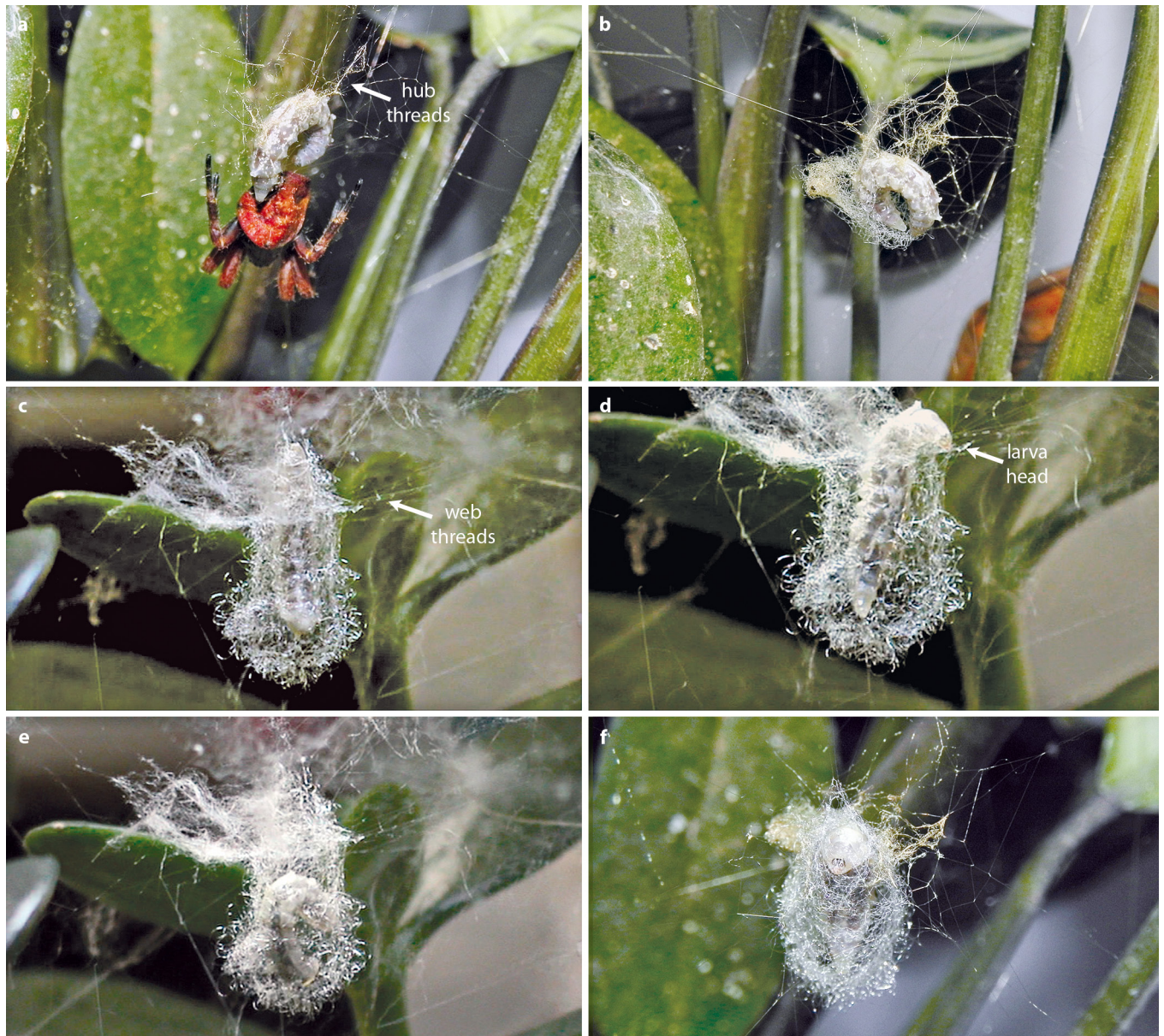


Fig. 3: Different phases of cocoon construction. **a.** Third instar larva removing the spider's carcass at the hub of the orb web. **b.** Beginning of cocoon construction around the rear section of the larva. **c.** Larva constructing the upper section of the cocoon. **d.** Larva attaching silk threads to the cocoon web. **e.** Larva adding more threads to the lower section of the cocoon. **f.** Unfinished cocoon after several hours of construction

3e). It then returned gradually to the starting point at the top of the cocoon, as it continued connecting more threads on the way up. The larva required *ca.* 20 h to construct its cocoon, which had a yellowish-white colour that darkened to orange-yellow over the next two days.

Spider behaviour. We did not notice any change in the spider behaviour during the first larval stage and most of the second stage. It was only during the last night of the second stage that the larva induced the spider to construct a sparse tangle, in the case where the spider and its larva were removed from the web. However, when the spider remained in its web, the last-instar larva only attached some threads to the centre of the hub of the orbicular web to secure the cocoon.

Discussion

Our observations support the hypothesis that the structure and design of normal webs of host spiders of koinobiont pa-

rasitoids in the *Polysphincta* genus group affect the designs of cocoon webs. The orb web of *K. cyrtophoroides* is a strong, long-lasting structure constructed of dry threads that remain undamaged for many days, even after the spider abandons the web (GB unpubl. data). The dense tangle above and below the dense orb-web gives strong support to the entire structure as in the webs of the sister genera, *Cyrtophora* and *Manogea* (Lubin 1974, Sobczak et al. 2009). The intact natural web of *K. cyrtophoroides* therefore gives enough support and protection from predation and environmental conditions to the *H. heidyae* cocoon (Eberhard 2000, Weng & Barrantes 2007, Sobczak et al. 2009, Korenko 2017).

It has been proposed that inhibition of adhesive spiral production in cocoon webs could save spider biomass for the larva wasp to ingest (Eberhard 2010a, Korenko et al. 2018). In *K. cyrtophoroides* silk investment in the cocoon web is minimum (if any) so that the larva has a larger proportion of the spider's biomass for development, relative to other spe-

cies that use more substantial amounts of silk to construct the cocoon web. This seems to be a widespread fine-tuning adjustment between the parasitoid larva and the spider host, since only small changes occur in the cocoon web of spiders in several families that build long-lived normal webs and are parasitized by wasps in different genera (Weng & Barrantes 2007, Eberhard 2010a, Korenko et al. 2018).

The second-instar larva induced *K. cyrtophoroides* (when separated from its web) to construct a cocoon web that consisted of a sparse horizontal tangle. The design of this cocoon web is totally different from the design of the natural orb-web built by the spider, and cannot be recognized as part of the normal web. The second instar larva of *H. heidyae* seems to be capable of inducing the spider to build a new design of cocoon web in response to unpredictable situations. Similarly, *Anelosimus* under the influence of *Zatypota solanoi* was also capable of building a cocoon web from scratch with a completely new design (Eberhard 2010b). This suggests that the response of polysphinctine larvae to unexpected situations may be more flexible than previously thought.

The general sequence of changes induced in this host spider by the parasitoid larva and the larva's behaviour differ to some extent from those described for other species in the *Polysphincta* genus group (Nielsen 1923, Eberhard 2000, Weng & Barrantes 2007). The second-stage larva *H. heidyae* only induces its host spider to construct a sparse tangle when the spider is removed from its web before the larva kills the spider. The larva then moults to its last instar, kills the spider and constructs the cocoon, and this sequence of events is quite stereotypical and apparently retained across this group of parasitoid wasps. If the spider is not removed from its web, the last instar larva secures the cocoon with some of its own silk threads to the centre of the web at the beginning of construction, but no further modifications are observed in the spider web.

The sequence of events during cocoon construction of *H. heidyae* is, in general, similar to that of *H. argyraphaga* (Eberhard 2000) and *Zatypota petronae* (Weng & Barrantes 2007), but differs in some respects. Attaching the cocoon by its upper portion to the spider web differs from *H. argyraphaga* whose cocoon hangs freely from the centre of the cocoon web (Eberhard 2001), but is similar to *Zatypota solani* in that the cocoon is attached by its upper portion to the web of its host *Anelosimus* (Eberhard 2010b).

Hymenopimecis heidyae's manipulation of its spider host is finely tuned to the design and structure of *K. cyrtophoroides*'s web. In this case changes in the cocoon web are barely perceptible, in contrast to the cocoon web of other *Hymenopimecis* species (and other species of the *Polysphincta* genus group) induced in host spiders with short-lived webs (Eberhard 2000, Gonzaga et al. 2010, Barrantes et al. 2017). Thus, strong, long-lived webs with some particular design (e.g. dry threads and dense tangles) requires only a few modifications to provide protection to the cocoon wasp (Sobczak et al. 2009).

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