AUTHOR QUERY SHEET

Author(s): M.O. Gonzaga, J.F. Sobczak, A.M. Penteado-Dias and W.G. Eberhard
Article Title: Modification of *Nephila clavipes* (Araneae, Nephilidae) webs induced by the parasitoids *Hymenoepimecis bicolor* and *H. robertsae* (Hymenoptera, Ichneumonidae)
Article No.: TEEE 471305

Dear Author,

Please address all the numbered queries on this page which are clearly identified on the proof for your convenience.

Thank you for your cooperation.

Ref. no:	Query	Remarks
Q1	Can this be re-worded to read: ". . . showed that the enclosure reduced ant . . .", to avoid ambiguity?	
Q2	Is the change of 'intimates' to 'indicates' acceptable? (As 'intimates' suggests a consciousness at work.)	
Q3	Are any further details available?	
Q4	Could the "(a)"s and "(b)"s be removed from this figure legend, as they do not refer to parts of the figure?	

Ethology Ecology & Evolution 22: 1–15, 2010

Taylor & Francis
Taylor & Francis Group

Modification of *Nephila clavipes* (Araneae, Nephilidae) webs induced by the parasitoids *Hymenoepimecis bicolor* and *H. robertsae* (Hymenoptera, Ichneumonidae)

M.O. Gonzaga [1,5], J.F. Sobczak [2], A.M. Penteado-Dias [3] and W.G. Eberhard [4]

[1] *Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil*
[2] *Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São Carlos, SP, Brazil*
[3] *Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, São Carlos, SP, Brazil*
[4] *Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica*

Received 8 April 2009, accepted 14 September 2009

Some polysphinctine ichneumonid wasps induce alterations in the web construction behavior of their host spiders, and then suspend their pupal cocoons from the resulting "cocoon webs". Cocoon webs that have been described previously appear to be designed to increase the web's mechanical stability, and thus to protect the wasp's cocoon. This study describes the cocoon webs of *Nephila clavipes* that are induced by two wasp species, *Hymenoepimecis bicolor* and *H. robertsae*, and shows that the alterations induced by *H. bicolor* make the webs more resistant to destruction. The cocoon webs of both species include a hub-like platform from which the cocoon is suspended, and are usually protected by a nearby tangle of barrier lines of variable density. The web alterations induced by *H. bicolor* are apparently not a consequence of parasitized spiders being in a poorer nutritional state, because orbs spun by parasitized spiders preceding the final "cocoon webs" were not significantly smaller than those of unparasitized spiders. Cocoon webs themselves were all highly reduced, and some of those induced by *H. bicolor* resemble the "skeleton" webs that are occasionally made by unparasitized *N. clavipes*. We document a possible spider defense (molting) against polysphinctine parasitization.

KEY WORDS: behavior manipulation, cocoon-web, parasitoid, orb-web, Ichneumonidae.

[5] Corresponding author: M.O. Gonzaga, Instituto de Biologia, Universidade Federal de Uberlândia, Campus Umuarama, Bloco 2D, Uberlândia, MG, Brazil, CEP 38400-902 (E-mail: mogonzaga@yahoo.com.br).

ISSN 0394-9370 print/ISSN 1828-7131 online
© 2010 Dipartimento di Biologia Evoluzionistica dell'Università, Firenze, Italia
DOI: 10.1080/03949371003707836
http://www.informaworld.com

INTRODUCTION

Ichneumonid wasps in the *Polysphincta* genus group (= Polysphinctini sensu Townes 1969; hereafter "polysphinctines") are external parasites of spiders (Gauld & Dubois 2006). All of them are koinobionts, maintaining their hosts alive and active for appreciable periods before killing them. Polysphinctine wasps are derived from ancestors that parasitized lepidopterans in silk cocoons, and probably began attacking spiders that are associated with retreats and egg sacs as a result of their attraction to silk (Gauld & Dubois 2006). Among the polysphinctines, wasps in the "*Polysphincta* clade" attack free-living spiders on their webs (Gauld & Dubois 2006).

The typical life cycle of a wasp in the *Polysphincta* clade is the following (extracted from Nielsen 1923; Eberhard 2000a, 2000b, in press; Gonzaga 2004; Gonzaga & Sobczak 2007; Matsumoto & Konishi 2007; Weng & Barrantes 2007; M.O. Gonzaga et al. in prep.). The wasp attacks the spider in its web and stings it into a brief paralysis, glues an egg to the surface of the spider's abdomen, and leaves. The spider recovers rapidly, and its behavior is apparently normal during the subsequent week or more. It builds apparently normal webs (many species make a new web each day), and captures prey. During this period the wasp's egg hatches and the larva, which remains on the outer surface of the spider's abdomen, slowly grows, feeding on the spider's hemolymph by making small holes in the cuticle of its abdomen. When the wasp larva is nearly mature, it induces the spider to build an altered web (the "cocoon web"), grasps lines in this web with its dorsal proleg-like swellings whose tips are covered with minute hooks, kills and consumes the spider, and then builds a pupal cocoon that is suspended from the cocoon web of its host.

In all orb-weaving species in which the behavioral effects of parasitization by wasps in the *Polysphincta* clade have been observed, the alterations in host webs suggest that cocoon webs provide greater protection to the pupal cocoon against damage by weather and/or predators than would normal webs (Nielsen 1923; Eberhard 2000a, 2000b, in press; Gonzaga 2004; Gonzaga & Sobczak 2007; Matsumoto & Konishi 2007). In all six species of orb weavers previously studied, the sticky spiral is reduced or completely eliminated, and the radial and frame lines are shortened and apparently strengthened. In contrast, in two non-orb-weaving species (the theridiid *Theridion evexum*, and the agelenid *Agelena limbata*), the cocoon webs induced by the wasps (*Zatypota petronae* and *Brachyzapus nikkoensis*, respectively) are silk enclosures for the cocoon (Weng & Barrantes 2007; Matsumoto 2009). Experimental removal of the enclosure in *B. nikkoensis* showed that it reduced ant predation (Matsumoto 2009). The degree of protection provided by an orb-weaver cocoon web has never been documented directly, however, and it has been suggested alternatively that the orb reductions might simply be the result of the poorer nutritional status of parasitized spiders (Gonzaga & Sobczak 2007).

Unparasitized orb-weaving spiders may modulate their construction behavior both of orbs and of associated protective lines in response to changes in their internal state (Sherman 1994; Venner et al. 2003, Nakata 2007; Kawamoto & Japyassú 2008). For example, well-fed individuals of *Argiope bruennichii* (Araneidae) were more likely to include barrier lines in their webs, while poorly fed individuals constructed only orbs, avoiding investment in a protective structure (Baba & Miyashita 2006). Witt et al. (1968) and Sherman (1994) observed an increase in the area and total thread length of prey-capturing orbs constructed by starved *Araneus diadematus* and *Larinioides cornutus* (Araneidae), and Higgins & Buskirk (1992) observed that female *Nephila clavipes* (Nephilidae) in situations of low foraging success increased orb-web radius more rapidly as they grew and maintained constant mesh sizes. Despite this increase in foraging investment reported for hungry spiders, it is possible that an extended state of food privation or a continuous exploitation of body fluids by a parasitoid might result in a weakened condition that prevents the construction of a normal-sized orb.

In the present study we describe the cocoon webs induced by *H. bicolor* and *H. robertsae* in *N. clavipes*, and compare them with those induced by other species of wasps. We also conducted a food-deprivation experiment to test whether the architecture of cocoon webs is a consequence of a condition of nutritional deficiency. Finally, we confirm empirically that the cocoon webs induced by larvae in the *Polysphincta* clade provide protection for the wasp's cocoon in the field. There is one previous study of *H. robertsae* parasitizing the spider *N. clavipes* (Fincke et al. 1990), but no description was given of the cocoon webs other than noting that the wasp's cocoon was suspended in the tangle next to the orb.

METHODS

Study sites

Observations of *H. bicolor* were made in Serra do Japi, a forest reserve located in Jundiaí (23°15′S, 46°57′W), state of São Paulo, Brazil. Adult and subadult females of *N. clavipes* were found along forest borders in the area known as DAE and the roads around the research station from January to May 2007 and 2008. Observations of *H. robertsae* were made in secondary forest near Santa Ana, San José Province, Costa Rica (el. 900 m) (9°55′N, 84°13′W) in December 2005 and January 2006.

Web description

Webs of *N. clavipes* with *H. bicolor* cocoons were coated with cornstarch and photographed in the field and in enclosures (see "*Food-deprivation experiment*"). We photographed five cocoon webs in the field and five in the enclosures.

We also measured the vertical and horizontal diameters of the sticky spiral (Fig. 1) to estimate the capture area of webs constructed by spiders carrying larvae of *H. bicolor* that were in the penultimate instar (n = 13) and by unparasitized spiders (n = 54). To control the effect of spider size, we carried out a non-parametric rank ANCOVA (Conover & Iman 1982), using spider abdominal length as a covariate.

Three cocoon webs of *N. clavipes* parasitized by *H. robertsae* (two in the field, one in captivity) were coated with cornstarch and photographed. One spider was brought into captivity and released unrestrained in a room while the wasp larva was still immature. Its building behavior was observed on the subsequent nights before the larva killed it.

Food-deprivation experiment

Unparasitized and parasitized *N. clavipes* females carrying *H. bicolor* eggs or larvae were kept individually in 15 bamboo frame enclosures (0.7 × 0.7 × 1.5 m) built around small bushes, trees or branches and covered with netting in an open area at the field station in April 2008. The spiders were divided into three groups of five individuals: (1) parasitized spiders that received one fly (*Musca domestica*) daily; (2) non-parasitized spiders kept without any food; and (3) non-parasitized spiders that received one fly daily. The number of radii (counted at the edge of the web) and maximum number of sticky spiral loops (Fig. 1) in the webs of each spider (a good indicator

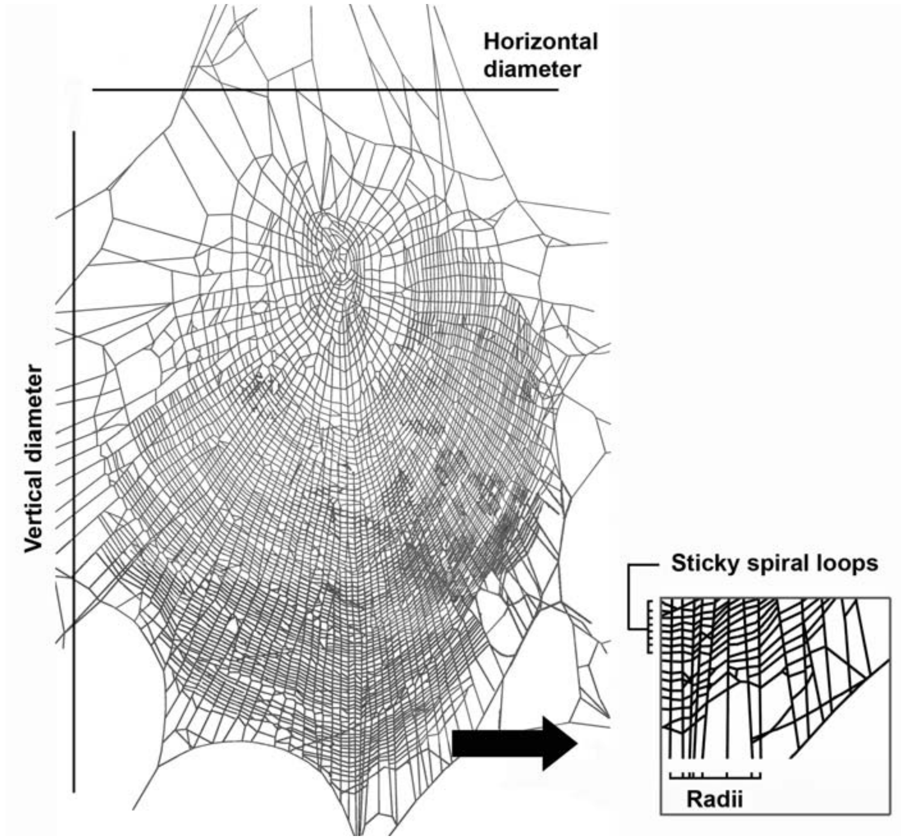

Fig. 1. — Schematic picture of *N. clavipes* web. Vertical and horizontal diameters were measured considering the area of the web covered with the sticky capture spiral. The other variables measured were the number of sticky spiral loops and the number of radii.

of the overall size of the orb in many orb weaver species: Koenig 1951; Mayer 1952; Eberhard 1972, 1986, 1988) was recorded daily for 21 days.

Web integrity in the absence of spiders

At the end of the feeding experiment we dismantled the enclosures and removed the remaining spiders, to evaluate the longevity of normal deserted webs (control webs) and cocoon webs. Without the periodic maintenance performed by the spider, a web gradually lose its normal structure due to damage from rain, wind and the impact of insects and detritus. During the period of observations the meteorological station in Jundiaí (CIIAGRO) registered 83.6 mm of rain. We considered a web to be destroyed when the hub area, the site where the parasitoid pupa would be located, was completely gone.

Voucher specimens of *H. bicolor* are deposited in the collection of Universidade Federal de São Carlos (DCBU – curator A.M. Penteado-Dias), São Carlos, SP, Brazil, and of *H. robertsae* in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica and also The Museum of Natural History, London, UK.

RESULTS

Life cycle of the wasps

Both species of wasps followed the typical *Polysphincta* clade life cycle outlined above in many respects, including location on the host, feeding, timing of web alteration, site of cocoon construction, and morphological and behavioral adaptations of the larva to hold the lines of the spider's web (Fig. 2; M.O. Gonzaga et al. in prep.).

Webs and construction behavior

The webs of unparasitized *N. clavipes* were similar in both sites to previous descriptions of the webs of this and other species of *Nephila* (Peters 1953; Robinson & Robinson 1973a; Kuntner et al. 2008). The orb was inclined from the vertical, and was vertically asymmetrical, with the hub near its upper edge; there was a tangle of lines on one or both sides of the upper portion of the orb (Fig. 3). The areas of orb webs constructed by parasitized spiders carrying intermediate-sized penultimate-instar *H. bicolor* larvae were not significantly smaller than the areas of webs spun by unparasitized spiders (ANCOVA; $F_{1,64} = 1.24$, $P = 0.27$). The effects of *H. bicolor* on its host's web building behavior that culminated in production of a cocoon web occurred gradually over the space of 3–4 days, as host orbs gradually became smaller, with fewer radii and loops of sticky spiral (Figs 4 and 5 – repeated measures ANOVA: (a) spirals $F_{(8,16)} = 5.058$, $P = 0.003$; (b) radii $F_{(8,16)} = 5.005$, $P = 0.003$). The final structure of all cocoon webs included a dense tangle of lines and an inclined hub-like disk in the central portion of the tangle (Fig. 4). The wasp larva attached its cocoon to the lower surface of the disk, and the cocoon thus hung between the disk and a dense tangle of barrier lines.

The two cocoon webs of *N. clavipes* parasitized by *H. robertsae* found in the field were clearly orb-like, with a more or less planar array of radial lines that diverged from a hub-like area and ended on frame-like lines; two cocoon webs (Fig. 6a,b) had much less extensive hub loops than the other (Fig. 6c). Neither field web had an extensive tangle nearby, nor any sign of an abandoned or partially destroyed orb in the vicinity. Thus these spiders had apparently either moved some distance away from their former orb and tangle webs, or had completely destroyed their previous webs before building the cocoon web.

The behavior of the spider brought into captivity resembled that of spiders parasitized by *H. bicolor* in that she built a central disk in the midst of the tangle of lines next to the orb, and the changes in behavior were manifested gradually. Five days before she was killed by the larva, the spider built an apparently normal orb, with a maximum of 70 sticky spiral loops. On the next two days she built orbs that were normal in form but smaller (maxima of 56 and 37 sticky spiral loops). On the next evening the spider removed her orb, and added lines to the adjacent tangle without producing an obvious hub. The following evening (the next to last of the spider's life), the larva was very large but had not yet molted to the final instar, and the spider moved apparently "aimlessly" in the tangle. At 3 a.m. the spider was laying lines in the tangle, but no orb-like or hub pattern was discernible. At 8 a.m. the spider laid additional lines in the tangle and cut a few others. She finally stopped at a "non-hub" site, and rested facing down as if at the hub of an orb until the next evening. At 4:40 a.m. of this final night she had built a planar disk with a vaguely hub-like pattern in the tangle (Fig. 6d,e) where she rested. At 7 a.m., the spider was barely alive and the larva had

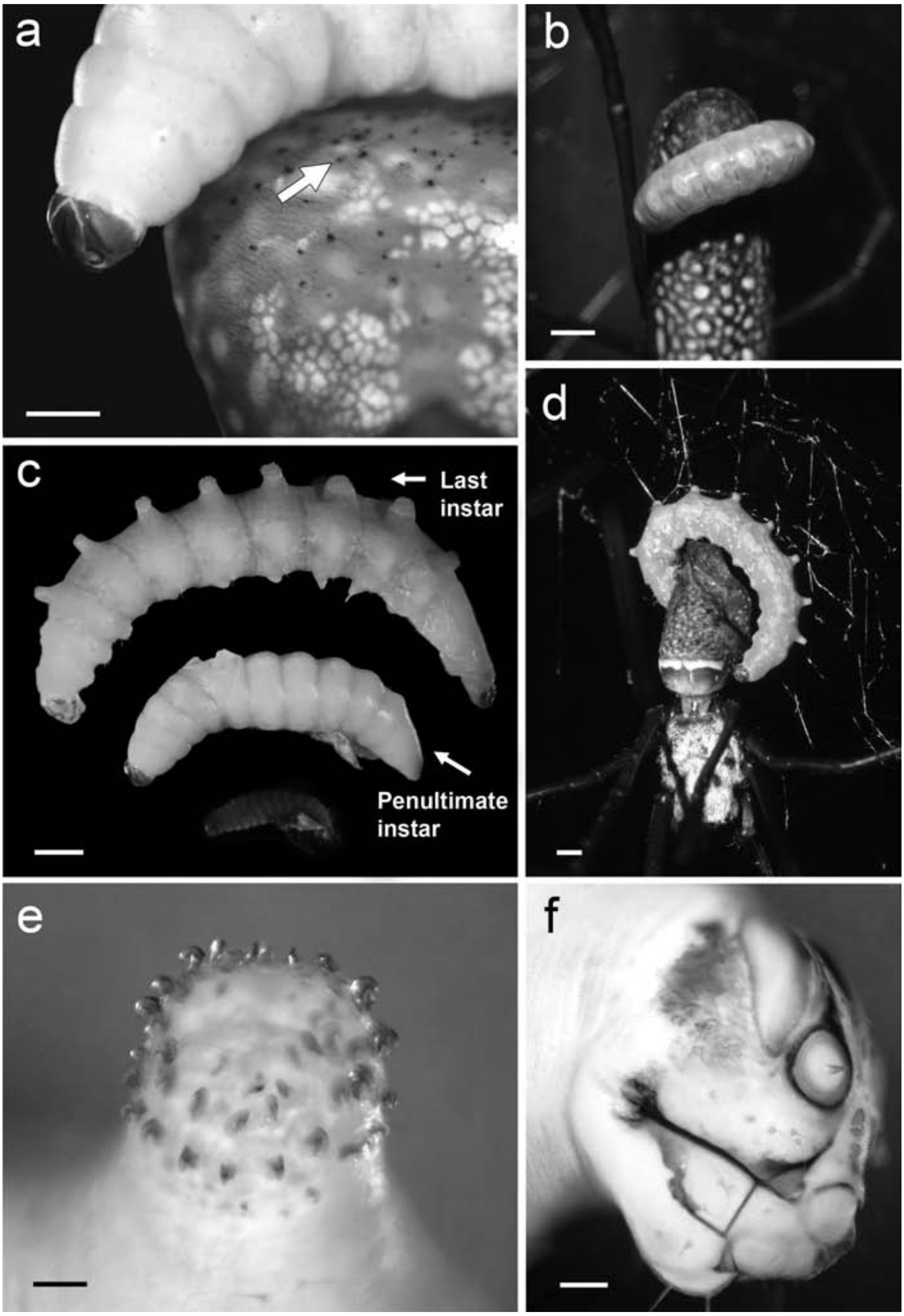

Fig. 2. — Immature stages of *H. bicolor* and their effects on their hosts. (a) Feeding scars (arrow) on spider's abdomen; (b) penultimate-instar larva attached; (c) larval instars; (d) final-instar larva consuming the spider; (e) dorsal tubercles in the final larval instar; (f) detail of the larva's head. Scales: (a) 0.5 mm; (b–d) 1 mm; (e,f) 0.1 mm.

Fig. 3. — Normal web of *Nephila clavipes*: (a) Frontal view; (b) lateral view. Scales: 10 cm.

molted to the final instar and held web lines with its dorsal "prolegs". The spider ceased moving soon thereafter, and the larva finished consuming her and dropped her carcass about 14 hr later. About 40 hr later the larva had built a cocoon, and was still visible, working inside it.

Food-deprivation experiment

The numbers of radii and spirals of webs constructed by non-parasitized spiders kept with and without food were relatively stable (Fig. 7). Even after 21 days without food the non-parasitized spiders did not construct webs with characteristics similar to those of cocoon webs. The orb web reduction in parasitized spiders appeared only a few days before the larva killed and consumed the spider (Fig. 5).

The five wasps emerged from the cocoons 19 days after their construction.

Web integrity in the absence of spiders

Seven days after the spiders were removed, six of the 10 control webs had been destroyed (presumably due to the effects of rain and wind). The four remaining control webs were all destroyed during the subsequent 6 days. The five cocoon webs remained intact during these same 13 days, and for at least 8 days after the destruction of the last normal web ($P = 0.004$ with one-tailed Fisher's exact test).

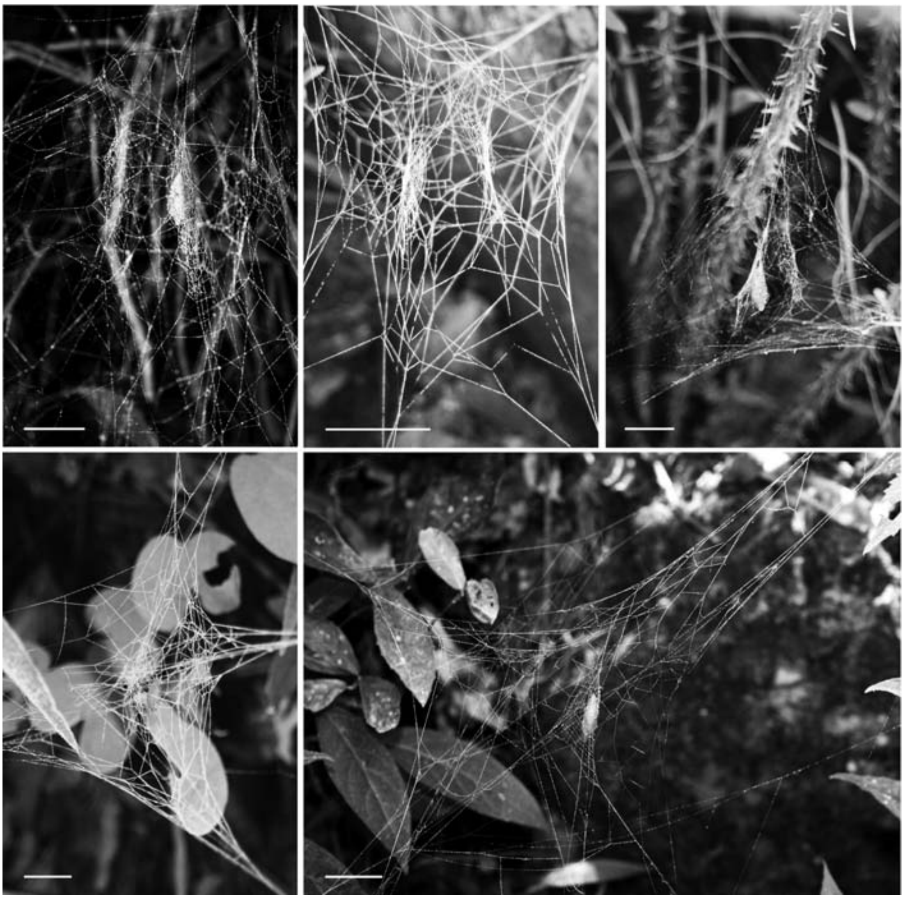

Fig. 4. — Lateral view of cocoon webs of spiders parasitized by *H. bicolor*. Scales: 2 cm.

Possible spider defenses against wasps

One penultimate-instar female *N. clavipes* in Costa Rica demonstrated a resistance to the wasp larva not reported in any species attacked by a polysphinctine wasp. The spider was brought into captivity with an unhatched egg on her abdomen. After 2–3 days of not building an orb, she molted, despite the fact that her abdomen was relatively thin. The still unhatched wasp egg was attached to the shed skin. One day later this spider built a small orb, the next day she made a large, apparently normal orb.

A second type of possible defense was observed when one *N. clavipes* with a *H. bicolor* and another with a *H. robertsae* larva were seen scraping and pushing on the larvae with their legs IV and III; the legs contacted both the larva and nearby portions of the spider's abdomen. In neither case, however, was the larva displaced or apparently damaged.

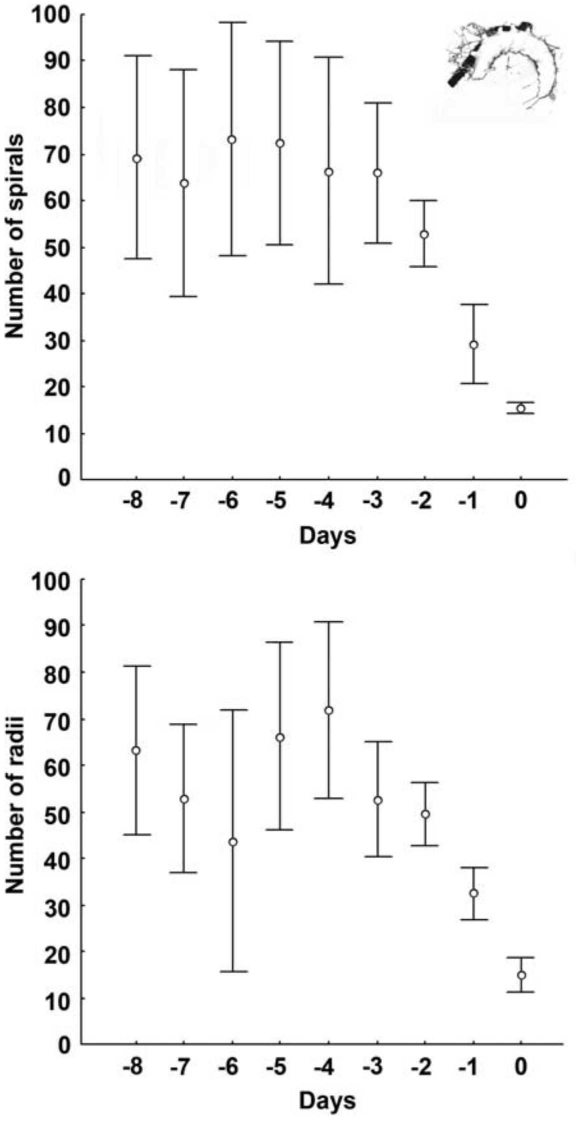

Fig. 5. — Number of radii and spirals in webs of parasitized spiders during the 8 days before the host's death.

DISCUSSION

Our observations of the cocoon webs of *N. clavipes* that are induced by larvae of *H. bicolor* and *H. robertsae* indicate that the alterations induced by the wasp larvae make these webs more resistant to destruction, and thus favor the survival of the 220
wasps. The larvae of both *H. bicolor* and *H. robertsae* affected the web construction behavior of the host spider gradually over the space of several days before the spider's

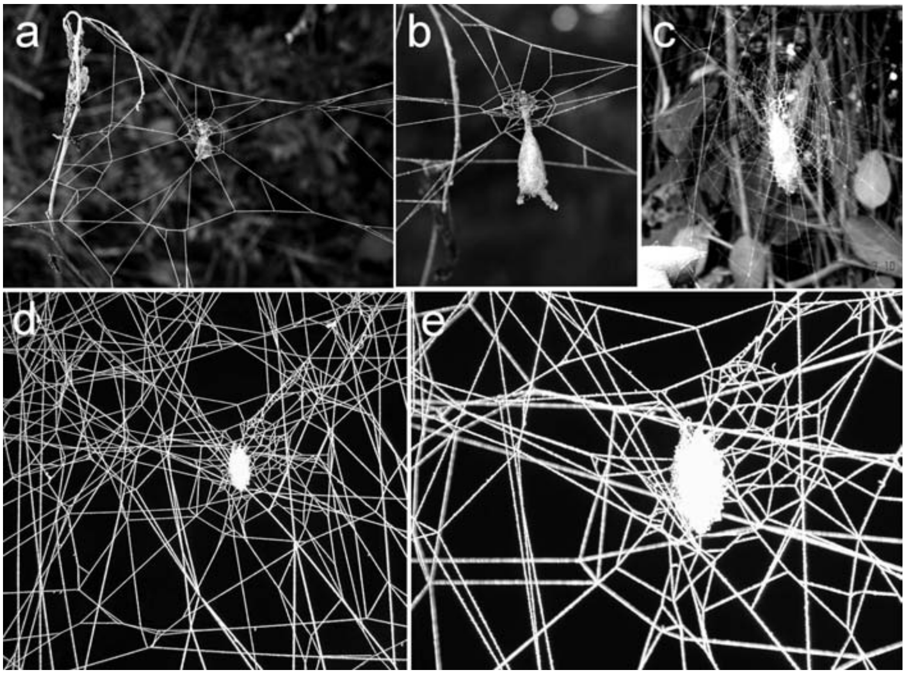

Fig. 6. — Cocoon webs of *N. clavipes* parasitized by *H. robertsae*. (a,b) Views from above and from the side of a cocoon web in the field; (c) a view from above of a second field cocoon web (photo by G. Barrantes); (d,e) views from the side and above of a cocoon web built in captivity. In all photos the maximum diameter of the cocoon is approximately 0.7 cm.

death (Fig. 5). This contrasts with the more abrupt effect of *H. argyraphaga* on its host (Eberhard 2000a, 2000b, 2001), but resembles the gradual effects of *Polysphincta gutfreundi* on its host (Eberhard in press). The significance of gradual vs. abrupt effects is not clear. One difference between the two wasp species of this study was that the cocoon webs of spiders parasitized by *H. bicolor* consistently included a tangle next to the hub, while only one of three *H. robertsae* cocoon webs had a tangle (Figs 4 and 6).

Non-parasitized *N. clavipes* sometimes make reduced orbs or “skeleton webs”, with a small number of radii, no well-defined structural spiral and an associated tangle on which they may molt (Robinson & Robinson 1973b; Fig. 8), that resemble cocoon webs. Thus some *Hymenoepimecis* larvae may have triggered construction of such molting webs. Two cocoon webs induced by *H. robertsae* differed from skeleton webs, however, in not having associated tangles.

Gonzaga & Sobczak (2007) suggested that the orb reduction and elimination in webs of *Araneus omnicolor* containing cocoons of *Hymenoepimecis* sp. could be due either to reduced activity because parasitized spiders are weakened by lack of nutrition (due to larval feeding), or to manipulation of host behavior by the larva to produce a safer structure for the wasp’s cocoon. Similar reductions in orbs have been observed in *C. octotuberculata* (Araneidae) attacked by *R. tuberculatus* (Matsumoto & Konishi 2007), *C. fililineata* attacked by *P. janzeni* (M.O. Gonzaga in prep.), and *A. bifurca* attacked by *P. gutfreundi* (Eberhard in press). In all of these cases, however, the relatively sudden effects of the larva on the spider`s behavior suggests manipulation rather

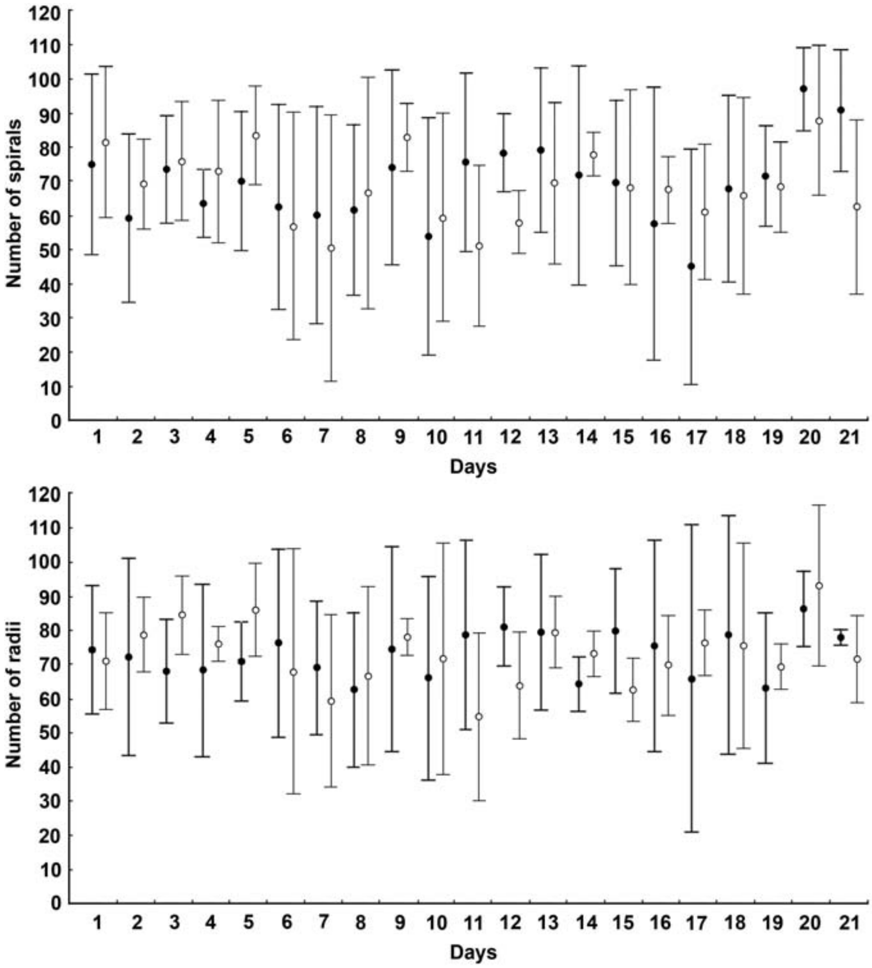

Fig. 7. — Number of radii and spirals in webs constructed by spiders in captivity with (black circles) and without (white circles) food. Repeated measures ANOVA – spirals: (a) with food $F_{(20,60)} = 1.197$ $P = 0.289$; (b) without food $F_{(20,60)} = 1.008$, $P = 0.466$; radii: (a) with food $F_{(20,60)} = 0.611$, $P = 0.889$; (b) without food $F_{(20,60)} = 1.353$, $P = 0.183$.

Q4

than gradual weakening. Both the results of experimental manipulation of food availability in this study and the very specific changes in spider behavior observed in this and other species argue against the nutrition hypothesis and in favor of the manipulation hypothesis.

The modified cocoon webs that *H. argyraphaga* induce in *P. argyra* are stronger than the fragile orbs constructed by non-parasitized individuals of this species, and constitute a more durable support for the pupal cocoons (Eberhard 2000b). The orb webs of non-parasitized *N. clavipes* are, in contrast, relatively resistant. Our results show, nevertheless, that the changes in host building behavior induced by the larvae of *H. bicolor* further protect their cocoons, probably both by having a stable hub-like platform from which they are suspended, and possibly by having additional or reinforced

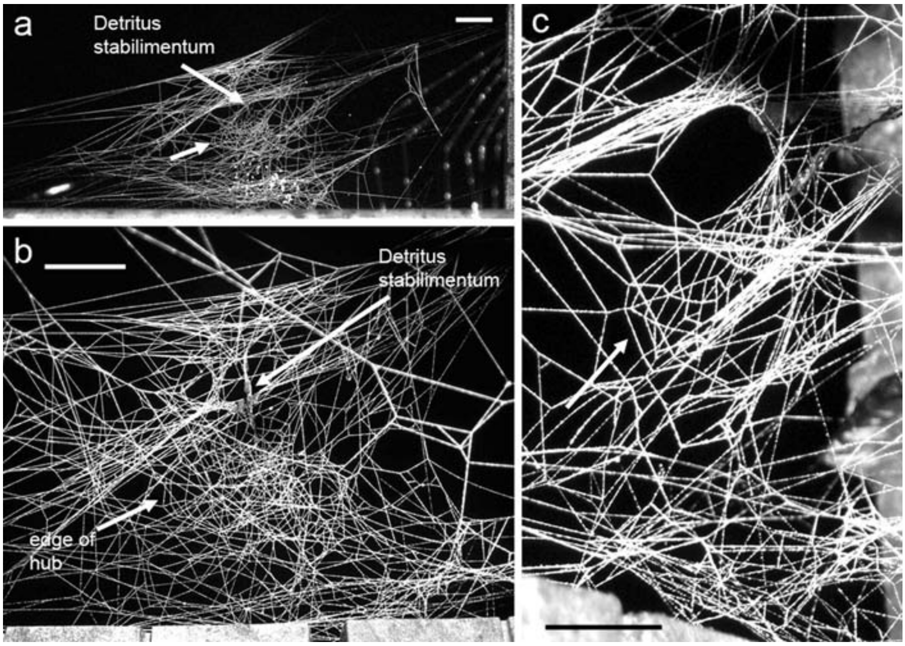

Fig. 8. — A small tangle web with a hub-like disc in the midst of the tangle made by an unparasitized, late-instar *N. clavipes* on a bridge in Costa Rica. (a) View from directly above, showing the tangles on either side of the hub-like disk where the spider rested (white spots in lower portion of photo are reflections from the water surface below). (b) View from above and side, more or less perpendicular to the hub-like area. (c) Close-up view of hub area in dorso-lateral view. Scales: 6 cm.

barrier threads nearby. Part of this stability may result from the fact that the smaller size of the web reduces the possibility that flying insects or debris will damage the cocoon web. Spiders parasitized by *H. robertsae* also built reduced webs in which sticky spirals were also completely lacking, but the webs in the field lacked a tangle. The spider in captivity, in contrast, reinforced the tangle beside the orb before making a hub-like structure.

Adult females of *N. clavipes* occur during the rainy season in Serra do Japi, when the reinforced cocoon webs provide increased protection against the cocoon being knocked to the substrate, where it would be more susceptible to pedestrian predators such as ants. Adult females of *N. clavipes* occur at different seasons in Costa Rica; all of the wasps were observed during the early months of the dry season, which are typically windy, but systematic searches were not performed at other times of the year. It is also possible that the tangles of the cocoon webs provide protection against possible aerial predators such as birds, as the cocoon is suspended away from the substrate. Cocoon webs provide protection against predators such as ants in other non-orb weaving spiders (Weng & Barrantes 2007; Matsumoto 2009).

Sticky spiral lines were completely missing from the cocoon webs of all *N. clavipes*, and indeed they are severely reduced or absent from the cocoon webs of all orb weavers parasitized by polysphinctines that have been observed to date (Nielsen 1923; Eberhard 2000a, 2000b, in prep.; Gonzaga & Sobczak 2007; Matsumoto & Konishi

2007). There are several possible advantages to the larva of suppressing sticky spiral production. The mechanical stability of an orb is probably largely determined by the numbers and degree of reinforcement of the tense, non-sticky lines, rather than by the highly elastic sticky spiral lines (Eberhard 1986; Craig & Riekel 2003), and sticky lines may in fact reduce mechanical stability by increasing the likelihood that unwanted prey or detritus will damage the web. In addition, the sticky spiral of an orb constitutes a large fraction of the mass of an orb web, and the wasp larva may obtain additional food from the host if the host is prevented from adding sticky spiral lines to the web.

The molt by an immature *N. clavipes* that left a parasite egg attached to the shed skin suggests that immature spiders may sometimes escape wasp attacks by molting. We have seen this only once in *N. clavipes*, and once in *P. argyra* (W. Eberhard unpub.), so further observations are obviously needed; the relatively thin abdomen of the *N. clavipes* spider when it molted indicates that the molt may have been designed to rid the spider of the wasp's egg. These observations indicate a possible danger to the wasp from parasitizing smaller, immature rather than mature spiders (this danger is counterbalanced in *H. bicolor* by the dangers of being captured by mature female *N. clavipes* – Gonzaga et al. in prep.).

Our observations reinforce the impression from previous work that spider and wasp species do not show a one-to-one correspondence. As in the spider *C. octotuberculata* (Matsumoto & Konishi 2007), *N. clavipes* is attacked by two congeneric species of wasps. Some wasp species also attack more than one host. *R. nielseni* attacks both *C. conica* and *C. argenteoalba* (Matsumoto & Konishi 2007), and *Polysphincta gutfreundi* attacks both *Allocyclosa bifurca* and the closely related *C. monteverdi* (W. Eberhard unpub.).

ACKNOWLEDGEMENTS

We thank Gilbert Barrantes for allowing us to use his photo of a cocoon web, and two anonymous referees for comments on the manuscript. We were supported financially by Instituto Nacional de Ciência e Tecnologia dos Hymenoptera Parasitóides da Região Sudeste Brasileira (HYMPAR/Sudeste – CNPq/CAPES/Fapesp), Fundação de Amparo a Pesquisa do Estado de São Paulo (proc. 06/59810-8 and 07/50731-0 – MOG), Katherine McLennan Brown Charitable Foundation and CAPES (JFS), and the Smithsonian Tropical Research Institute and the Universidad de Costa Rica (WGE). We also thank Prefeitura Municipal de Jundiai and the staff of Base de Estudos de Ecologia e Educação Ambiental da Serra do Japi.

REFERENCES

Baba Y. & Miyashita T. 2006. Does individual internal state affect the presence of a barrier web in *Argiope bruennichii* (Araneae: Araneidae)? *Journal of Ethology* 24: 75–78.

Conover W.J. & Iman R.L. 1982. Analysis of covariance using the rank transformation. *Biometrics* 38: 715–724.

Craig C.L. & Riekel C. 2003. The mechanical functions of silks and their correlated structural properties, pp. 51–83. In: Craig C.L., Ed. Spider webs and silk tracing evolution from molecules to genes and phenotypes. *New York*: *Oxford University Press*.

Eberhard W.G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). *Journal of Zoology* 166: 417–465.

Eberhard W.G. 1986. Effects of orb-web geometry on prey interception and retention, pp. 70–100. In: Shear W.A., Ed. Spiders, webs, behavior, and evolution. *Stanford*: *Stanford University Press*.

Eberhard W.G. 1988. Behavioral flexibility in orb web construction: effects of silk supply in different glands. *Journal of Arachnology* 16: 303–320.

Eberhard W.G. 2000a. The natural history and behavior of *Hymenoepimecis argyraphaga* (Hymenoptera: Ichneumonidae) a parasitoid of *Plesiometa argyra* (Araneae, Tetragnathidae). *Journal of Hymenoptera Research* 9: 220–240.

Eberhard W.G. 2000b. Spider manipulation by a wasp larva. *Nature* 406: 255–256.

Eberhard W.G. 2001. Under the influence: webs and building behavior of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae). *Journal of Arachnology* 29: 354–366.

Eberhard W.G. (in press). Recovery of spiders from the effects of parasitic wasps: implications for fine-tuned mechanisms of manipulation. *Animal Behaviour.* Q3

Fincke O.M., Higgins L. & Rojas E. 1990. Parasitism of *Nephila clavipes* (Araneae, Tetragnathidae) by an ichneumonid (Hymenoptera, Polysphinctini) in Panama. *Journal of Arachnology* 18: 321–329.

Gauld I.D. & Dubois J. 2006. Phylogeny of the *Polysphincta* group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids. *Systematic Entomology* 31: 529–564.

Gonzaga M.O. 2004. Funções e variabilidade estrutural dos stabilimenta construídos por *Cyclosa* spp. (Araneae: Araneidae). *PhD Thesis,Universidade Estadual de Campinas, Campinas, SP,* Brazil.

Gonzaga M.O. & Sobczak J.F. 2007. Parasitoid-induced mortality of *Araneus omnicolor* (Araneae, Araneidae) by *Hymenoepimecis* sp. (Hymenoptera, Ichneumonidae) in southeastern Brazil. *Naturwissenschaften* 94: 223–227.

Higgins L.E. & Buskirk R.E. 1992. A trap-building predator exhibiting different tactics for different aspects of foraging behavior. *Animal Behaviour* 44: 485–499.

Kawamoto T.H. & Japyassú H.F. 2008. Tenacity and silk investment of two orb weavers: considerations about diversification of the Araneoidea. *Journal of Arachnology* 36: 418–424.

Koenig M. 1951. Beiträge zur Kenntnis des Netzbaues orbiteiler Spinnen. *Zeitschrift fur Tierpsychologie* 8: 462–492.

Kuntner J., Coddington J.A. & Hormiga G. 2008. Phylogeny of extant orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24: 147–217.

Matsumoto R. 2009. "Veils" against predators: modified web structure of a host spider induced by an ichneumonid parasitoid, *Brachyzapus nikkoensis* (Uchida) (Hymenoptera). *Journal of Insect Behavior* 22: 39–48.

Matsumoto R. & Konishi K. 2007. Life histories of two ichneumonid parasitoids of *Cyclosa octotuberculata* (Araneae): *Reclinervellus tuberculatus* (Uchida) and its new sympatric congener (Hymenoptera: Ichneumonidae: Pimplinae). *Entomological Science* 10: 267–278.

Mayer G. 1952. Untersuchen ueber Herstellung und Struktur des Radnetzes von *Aranea diadema* und *Zilla x-notata* mit besonderer Beruecksichtigung des Untershiedes von Jugend- und Altersnetzen. *Zeitschrift fur Tierpsychologie* 9: 337–362.

Nakata K. 2007. Prey detection without successful capture affects spider's orb-web building behavior. *Naturwissenschaften* 94: 853–857.

Nielsen E. 1923. Contributions to the life history of the Pimpline spider parasites (*Polysphincta, Zaglyptus, Tromatobia*) (Hym. Ichneum.). *Entomologiske Meddelelser* 14: 137–205.

Peters H.M. 1953. Beiträge zur vergleichenden Ethologie und Ökologie tropischer Webespinnen. *Zeitschrift fuer Morphologie und Oekologie der Tiere* 42: 278–306.

Robinson M.H. & Robinson B. 1973a. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* 149: 1–76.

Robinson M.H. & Robinson B. 1973b. The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. *Psyche* 80: 277–288.

Sherman P.M. 1994. The orb-web: an energetic and behavioral estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour* 48: 19–34.

Townes H. 1969. The genera of Ichneumonidae, part 1. *Memoirs of the American Entomological Institute* 11: 1–300.

VENNER S., BEL-VENNER M.C., PASQUET A. & LEBORGNE R. 2003. Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften* 90: 269–272.

WENG J.-L. & BARRANTES G. 2007. Natural history and larval behavior of the parasitoid *Zatypota petronae* (Hymenoptera: Ichneumonidae). *Journal of Hymenoptera Research* 16: 326–335.

WITT P.N., REED C.F. & PEAKALL D.B. 1968. A spider's web. *New York*: *Springer*.