On the sticky cobwebs of two theridiid spiders (Araneae: Theridiidae)

MARCELO O. GONZAGA1, NATÁLIA O. LEINER2 & ADALBERTO J. SANTOS3

1Departamento de Zoologia, Instituto de Biologia, Unicamp, Campinas, Brazil, 2Pós-graduação em Ecologia, Instituto de Biologia, Unicamp, Campinas, Brazil, and 3Laboratório de Artrópodes, Instituto Butantan, São Paulo, Brazil

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Abstract
In this study we describe and illustrate a new species, Chrysso intervales n. sp., based on males and females collected in Parque Estadual Intervales, an area of Atlantic Forest in the State of São Paulo, Brazil. We present data on habitat selection, web architecture, thread adhesiveness, diet, and mortality due to fungi for both Chrysso intervales and the sympatric species, Helvibis longicauda. Both species build webs on vegetation close to river margins, but they were not found in forest sites away from these shaded and extremely humid corridors. The webs of both species are entirely composed of viscid silk lines, occupying the space between two or more large leaves. The construction of this web type by Helvibis and Chrysso, and the large amount of viscid droplets in their threads, indicate that the investment in adhesive components in theridiids may be dependent on the ambient conditions. We suggest that the costs of maintaining viscid silk lines in humid areas may be relatively low, explaining the habitat restriction observed in the species studied. By selecting humid habitats, however, these spiders are susceptible to attacks by fungi. The webs constructed by both species intercepted mostly Diptera, especially tipulids, but H. longicauda was also observed consuming a wide variety of prey types.

Keywords: Habitat selection, pathogenic fungi, spider webs, Theridiidae, viscid silk

Introduction
Spiders build a great variety of web types to capture prey, from dense tangles to bi-dimensional orbs or single lines with a sticky globule at one end (Eberhard 1990, and references therein). Some of these web designs are especially efficient in intercepting and retaining one or a few prey types (Stowe 1986; Eberhard 2001), while others are used to capture a wide variety of prey (Nentwig 1983, 1985). In spite of the importance of web characteristics as protection against natural enemies (Blackledge et al. 2003) and to...
resource acquisition, and the great variety of these structures, most studies describing web types and web construction behaviors are restricted to orb-webs (Eberhard 1990). Additional studies on spider groups that build other web types are essential to the analysis of evolutionary hypotheses regarding design modifications and ecological pressures determining different architectural patterns within some spider families.

Theridiidae is one of the largest spider families, with 2214 species in 86 genera (Platnick 2005). According to Griswold et al. (1998), the gumfoot web typifies the theridiid–nesticid lineage. They described these webs as simple or complexly distorted sheets to which dry lines with sticky extremities are attached. However, although a number of theridiid species build gumfoot webs (Griswold et al. 1998; Benjamin and Zschokke 2002, 2003), other very distinct web types also occur within the family. Ariamnes attenuatus O. P.-Cambridge, 1881, for example, builds three-dimensional networks with two or three and up to seven long non-sticky threads; these webs are used to capture flies which use these lines as resting places (Eberhard 1979). Anelosimus jucundus (O. P.-Cambridge, 1896) builds non-viscid webs around branches, using leaves as protective structures (Nentwig and Christenson 1986).

In a recent revision of theridiid web architecture and construction behavior, Benjamin and Zschokke (2003) identified four major web types: an Achaearanea-type web with a central retreat, a Latrodectus-type with a peripheral retreat (both presenting gumfooted lines), a Theridion-type with viscid lines, and a Coleosoma-type without viscid lines, but with a sheet and a knock-down trap structure (the last two types lack gumfoot lines). Other types, such as the webs of A. attenuatus, were considered by them as modified. Considering the lack of information on web design of most genera in Theridiidae and the fact that some relatively well-studied genera (such as Theridion) probably are not monophyletic (Agnarsson 2004; Arnedo et al. 2004), we might expect alterations on this initial categorization of web types in the future.

The genus Helvibis currently includes 10 species, distributed in Central and South America. Most of the South American species were described based on specimens collected in humid regions of Peru and/or Brazil (Levi 1964; Platnick 2005). This genus was revised by Levi (1964) and since then no new species have been described. There are no published data on the ecology and natural history of any Helvibis species, except the mention that they probably are restricted to humid areas (Levi 1964), and the suggestion that two species—H. brasiliiana (Keyserling, 1884) and H. chilensis (Keyserling, 1884)—are ant mimics (Reiskind and Levi 1967). Specimens collected in Guyana and identified as Helvibis cf. longicauda Keyserling, 1891 were used in a recent phylogenetic analysis of theridiids based on nuclear and mitochondrial genes (Arnedo et al. 2004). In this analysis H. cf. longicauda appears closely related to an unidentified Chrysso species from Colombia, in the “Lost Colular Setae” (LCS) clade. In the morphological phylogeny presented by Agnarsson (2004), H. cf. longicauda is sister to a clade that contains Theridion and Coleosoma, while Chrysso cf. nigriceps Keyserling, 1884 (specimens collected in the same locality as the material analysed by Arnedo et al. 2004) appears in a basal position within the Theridiinae clade (=LCS). The genus Chrysso is currently composed of 64 species, 33 occurring only in the Americas, 29 in Asia, one distributed from Europe to Asia and North America, and one with pantropical distribution (Levi 1957, 1962, 1967; Platnick 2005). This genus was originally described based on American species (Levi 1957, 1962) and Benjamin and Zschokke (2003) suggested that the inclusion of Asian species might have rendered the genus polyphyletic.

Webs of Helvibis species were not previously described, but there is detailed information on two species of Chrysso. Benjamin and Zschokke (2003) described the webs of Chrysso
*Cambridgei* (Petrunkevitch, 1911), an American species with known distribution from Mexico to Venezuela, and *C. spiniventris* (O. P.-Cambridge, 1869), from Sri Lanka. The web of *C. cambridgei* was described as a two-dimensional structure composed of dry and viscid threads (similar to *Theridion* webs), without gumfooted lines. The webs of *Chrysso spiniventris*, on the other hand, were similar to those of *Achaearanea tepidariorum* (C. L. Koch, 1841), with a three-dimensional tangle, a retreat connected to vegetation by anchor threads, and presenting gumfoot lines. The authors suggested that this intrageneric variation between an Asian and an American species may reflect the polyphyly of the genus.

In the present study we describe for the first time the web architecture of *Helvibis longicauda* and present information on a new American species of *Chrysso*. In addition, we present data on habitat selection, prey spectrum, web adhesiveness (number and distribution of viscid droplets), and mortality by fungi.

**Material and methods**

The study was done in the Parque Estadual Intervales (24°16′S, 48°25′W), a state park that is part of a large protected Atlantic Forest continuum (120,000 ha), located in the State of São Paulo in southeastern Brazil. Mean annual rainfall in Parque Estadual Intervales is 1625 ± 190 mm and mean annual temperature is 16.4 ± 0.8 °C (data from 1994 to 2004).

We searched for *H. longicauda* and *C. intervales* in 12 study sites of 200 × 5 m, along six trails located away from water courses (1–6) and six along river margins (7–12) (Figure 1). Site 7 was inspected in June and July 2004 and in March 2005, while all the others were

![Figure 1. Map of the study area indicating the position of the transects: 1–6, transects in dry lands; 7–12, transects in river margins.](image-url)
inspected only once (either July 2004 or March 2005). During inspections at each site, data on relative humidity were collected using a digital hygrometer. These data were collected at approximately the same time (16:00–17:00 h) on sunny days. For site 7 we also present monthly measurements from August 2003 to June 2004 taken with the same instrument. The mean value for each month was based on three measurements (one each morning, afternoon, and night) taken during 3–5 days, at the margin of the river.

We collected threads close to the spider’s resting position and in the middle segment between the two leaves used to support the webs by touching the threads with a frame of wire and enclosing the frame in a plastic container. In the laboratory, we measured the diameter and counted the number of viscid droplets in 0.5 mm segments using a microscope with an ocular micrometer. This procedure was done with 10 webs of *H. longicauda* and 12 webs of *C. intervales*.

The prey of *H. longicauda* and *C. intervales* were assessed by collecting partially consumed items adhered to the webs located at site 7. All the prey items found in the webs were carefully removed, stored in 70% ethanol, and transported to the laboratory to be measured and identified. The prey body length was measured to the nearest 0.01 mm using a dissecting microscope with an ocular micrometer. We excluded prey items missing major body parts or in poor preservation conditions.

The mortality caused by fungi was evaluated by counting the number of spiders infected at site 7, in July 2004 and March 2005. We collected all spider cadavers still in good enough condition to identify the spider species.

The description of *C. intervales* was based on specimens collected during the inspections at site 7. Specimens were examined, measured, and illustrated immersed in 70% alcohol in a dissecting microscope with a camera lucida attached. Female genitalia were excised and immersed in clove oil for examination and illustration of internal structure. The description format and anatomical terminology follow Levi (1962) and Agnarsson (2004), with measurements in mm. Voucher specimens of both species have been deposited in Instituto Butantan, São Paulo, Brazil (IBSP, curator A. D. Brescovit).

**Results**

**Chrysso intervales** new species

(Figures 2–7)

**Type material**

Male holotype from Parque Estadual Intervales, Ribeirão Grande, State of São Paulo, 24°16’S, 48°25’W, 10 March 2005, M. O. Gonzaga and N. Leiner coll., in IBSP 52232. Female paratype from the same locality and collectors, 20 March 2005, in IBSP 52233.

**Diagnosis**

*Chrysso intervales* shares with several other species currently assigned to *Chrysso* the abdomen with a posterior hump and the male palpus with a large subtegulum, a retrolaterally positioned tegulum, and a long embolus and conductor (Figures 2–4, see also Levi 1962). The males can be distinguished from other species by the cymbium which is narrower in the apical half, the embolus with a large base and a thin apex, and the presence of two small sclerites close to the subtegulum (Figures 3, 4, see comments below). Females
can be recognized by the epigynum which is widely excavated medially, and with a ventrally projecting posterior margin (Figures 5, 6). The internal female genitalia shows two spermathecae close to the copulatory openings, which are located at the anterior corners of the medially excavated area (Figure 5), and a long, sinuous and posteriorly closed cavity (Figure 6).

Comments
Judging by their position, at least one of the small sclerites in the male palpus is certainly a median apophysis; the other is probably homologous to the radix of other species of Chrysso (Levi 1962). The radix is currently recognized as a structure exclusive to Araneidae (Griswold et al. 1998), and the sclerites commonly referred to as a radix in theridiid palps are certainly homologous to other structures, mainly the Theridiid Tegular Apophysis (see Agnarsson 2004). In the case of C. intervale, it is possible that the two sclerites are actually part of a median apophysis with two large branches, deeply connected inside the bulb, as occurs in Chrysso nigriceps (Agnarsson 2004, Figure 39B).
Description

Male (holotype). Carapace oval, orange. Thoracic groove longitudinal, conspicuous. Anterior median eyes subequal to other eyes, 2.0 diameters apart, 1.0 from anterior lateral eyes. Posterior median eyes 2.0 diameters apart, 1.5 from posterior laterals. Lateral eyes contiguous. Clypeus orange. Chelicerae, labium, and endites cream coloured. Chelicerae with two posterior teeth. Sternum orange. Palpi cream coloured, cymbium brown. Legs cream, metatarsi and tarsi orange. Legs III and IV with a retrolateral dusky stripe on the apical half of femur, patella, and tibia. Abdomen white dorsally, covered with dark grey spots and with a black posterior mark. Epigastric plate and spinnerets orange. Total length 2.6. Carapace 1.0 long, 1.0 wide. Femur I 1.8, tibia-patella 1.6, metatarsus 1.5, tarsus 0.9. Tibia-patella II 1.1, III 0.8, IV 1.3. Abdomen 1.6 long, 1.0 wide. Cymbium narrowed apically, folded over the fovea. Subtegulum large, with the prolateral posterior corner unsclerotized (Figure 3). Tegulum restricted to the retrolateral side of the bulb, with sperm duct visible by transparency (Figure 4). Theridiid tegular apophysis not visible. Conductor hyaline, wrapping the embolus apex. Embolus base large, partially hidden under the tegulum (Figure 3).

Female (paratype). Carapace oval, cream coloured, with pars cephalica orange. Anterior median eyes subequal to other eyes, 1.0 diameters apart, 0.5 from anterior laterals. Posterior median eyes 2.0 diameters apart, 1.0 from posterior laterals. Lateral eyes contiguous. Clypeus, chelicerae, labium, and endites orange. Chelicerae with two teeth on posterior margin. Sternum cream, palpi orange. Legs orange, with a retrolateral dark stripe on apical fourth of femur and patella IV. Abdomen cream, with a dorsal longitudinal band of dark grey spots and a median and a lateral pair of white spots on anterior and posterior thirds. Spinnerets cream. Total length 3.6. Carapace 1.0 long, 1.1 wide. Femur I 2.1, tibia-patella 2.0, metatarsus 1.6, tarsus 1.4. Tibia-patella II 1.3, III 0.9, IV 1.4. Abdomen 2.6 long, 1.7 wide. Copulatory openings in the lateral corners of the epigynum, marked by discrete sclerotized rims (Figure 5). Copulatory ducts short, with copulatory openings almost directly connected to spermathecae. Spermathecae spherical, fertilization ducts thin, medially directed and gently curved (Figure 7).

Variation

Females, total length 3.8–4.6, carapace width 1.0–1.2 (N=10).

Etymology

The specific name is a noun in apposition taken from the type locality.

Distribution

Known only from the type locality.

Additional material examined

Brazil: São Paulo: Ribeirão Grande, Parque Estadual Intervales, February 2004, M. O. Gonzaga coll., nine females (IBSP 52234).
We did not find any specimens of *H. longicauda* or *C. intervales* at the sites located away from the rivers. However, both species were especially abundant at site 7 and were also present on other sites located close to the water courses (Table I). The measurements at site 7 showed that the relative humidity in that area remained constantly high (>90%), even during the winter (dry season) (Figure 8). In addition, our measurements at the other sites indicate that relative humidity is generally higher close to the rivers (Table II). One-tailed Fisher’s exact tests comparing the presence of each species at humid versus dry places showed that preference for humid areas was significant (*H. longicauda*, *P*=0.03; *C. intervales*, *P*<0.01).

Webs of *H. longicauda* and *C. intervales* were always under large more or less horizontal leaves (X±SD=343.6±276.9 cm², *n*=23 for *H. longicauda*; X±SD=465.6±299.7 cm², *n*=18 for *C. intervales*). The webs consisted of an area with a relatively high thread density close to the spider’s resting position, and several more or less vertical threads extending to other leaves directly below (Figures 9–12). The distance between the upper and the lower leaves to which the web was attached was higher in *C. intervales* (X±SD=29.5±8.5 cm, *n*=18) than in *H. longicauda* (X±SD=21.0±8.4 cm, *n*=23) (*t* test, *t* =−3.18, df=39, *P*=0.003). The webs of both species consisted entirely of viscid silk lines.

The density of viscid droplets was slightly higher on the threads located close to the spider’s position (X±SD=8.1±1.29 droplets per 0.5 mm of thread) than in the middle segment between the two leaves (X±SD=7.0±0.94) in *H. longicauda* (*t* test, *t* =−1.88, df=9, *P*=0.047). The same pattern was observed in *C. intervales* (X±SD=7.5±1.83 droplets per 0.5 mm of thread, X±SD=6.5±1.98; *t* test, *t* =−1.82, df=11, *P*=0.048). The mean diameter of droplets did not differ between the two

Table I. Number of individuals observed in the study sites located at river margins.

| Site | June 2004 | July 2004 | March 2005 | June 2004 | July 2004 | March 2005 | June 2005 | March 2005 | March 2005 |
|------|-----------|-----------|------------|-----------|-----------|------------|-----------|------------|------------|
| **Helvibis longicauda** | | | | | | | | | |
| Juveniles | 4 | 14 | 15 | 2 | 1 | – | – | 3 |
| Subadult females | 14 | 6 | 0 | 4 | – | – | – | – |
| Adult females | 117 | 123 | 30 | 39 | 1 | – | – | 25 |
| Adult females with eggsac | 2 | 10 | 42 | 5 | 2 | – | – | 27 |
| Adult females with spiderlings | 7 | 2 | 12 | – | – | – | – | 19 |
| Subadult males | 6 | 7 | – | – | – | – | – | – |
| Adult males | 19 | 29 | 4 | 5 | – | – | – | 1 |
| Total | 169 | 191 | 103 | 55 | 4 | – | – | 75 |
| **Chrysso intervales** | | | | | | | | | |
| Juveniles | 8 | 6 | 2 | – | – | – | 2 | 2 |
| Subadult females | – | 9 | – | 1 | 1 | – | – | – |
| Adult females | 21 | 42 | 15 | – | – | – | 1 | – |
| Adult females with eggsac | – | 9 | 1 | 14 | – | – | – | 9 |
| Adult females with spiderlings | 1 | 1 | 6 | – | – | – | 3 | 3 |
| Subadult males | 1 | 2 | – | – | – | – | – | – |
| Adult males | 3 | 7 | – | – | – | – | 1 | – |
| Total | 34 | 68 | 37 | 1 | 1 | – | 16 | 7 |
areas of the webs in either *H. longicauda* ($X_1 \pm SD = 20.6 \pm 6.9 \mu m$ and $X_2 \pm SD = 20.0 \pm 1.9 \mu m$) or *C. intervales* ($X_1 \pm SD = 31.9 \pm 14.0 \mu m$ and $X_2 \pm SD = 33.8 \pm 11.4 \mu m$).

Most prey items intercepted by the webs of both spider species were Diptera, especially small (mean body length $\pm SD = 5.1 mm \pm 0.9$, $n=6$) tipulids. These tipulids were frequently found resting on the bottom surface of the same leaf types used by *H. longicauda* and *C. intervales* at site 7. The relatively higher diversity of prey types found in webs of *H. longicauda* is probably a consequence of the higher number of items found on the webs of this species (60 against only nine in webs of *C. intervales*). Prey captured by *H. longicauda* included the harvestman *Jussara* sp., ants, moths, beetles, wasps, and other insects (Table III).

We found 33 spiders attacked by fungi at site 7, all of them on the inferior surface of leaves (Figure 13). From these we identified 14 females and seven males of *H. longicauda*. Considering the total number of uninfected males and females, the number of females attacked represent at least 9.4% of total (probably more if we suppose that some of the

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**Table II.** Measurements of relative humidity on study sites.

| Site | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|------|---|---|---|---|---|---|---|---|---|----|----|----|
| Relative humidity (%) | 71 | 57 | 69 | 70 | 77 | 76 | 89 | 85 | 80 | 76 | 79 | 84 |
| Temperature (°C) | 17.7 | 20.6 | 17.3 | 26.0 | 24.9 | 22.6 | 13.3 | 14.5 | 15.7 | 23.0 | 22.8 | 21.9 |
| Date | July | July | July | March | March | March | July | July | March | March | March | March |
|      | 2004 | 2004 | 2004 | 2005 | 2005 | 2005 | 2004 | 2004 | 2005 | 2005 | 2005 | 2005 |
Figures 9–12. Photographs of webs and details of viscid silk lines. (9, 10) Webs of *Helvibis longicauda* mature females: (A) a viscid line collected in the denser area around spider resting position; (B) a viscid line which was extended until the lower leaf. (11, 12) Webs of *Chryso intervale* mature females and detail of a viscid line at the mid-point between the upper and the lower leaves. Scale bars: 5 cm.
unidentified cadavers were also individuals of *H. longicauda*. The number of adult males attacked represent 19.4% of total. The fungus on the cadaver of one *H. longicauda* female was identified as *Gibellula pulchra* Cavara, 1894 (Hyphomycetes).

**Discussion**

The webs of *Helvibis* and *Chryso* described here do not fit easily in any of the four categories of theridiid webs described by Benjamin and Zschokke (2003). These webs are structurally similar to the *Latrodectus*-type of web, as described by Benjamin and Zschokke (2003, Figure 8B), by the presence of a retreat surrounded by structural threads, close to the substratum, and several gumfoot lines connected to other attachment points. Nevertheless, the webs of *C. intervales* and *H. longicauda* differ from this basic type by having the viscid, sticky droplets not restricted to the tips of gumfoot lines, but distributed throughout the web. Theridiid webs composed mostly or entirely of viscid silk lines had previously been described for just a few other species. Whitehouse (1986) described the

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| Table III. Prey found being fed on by *Helvibis longicauda* and *Chryso intervales* in the field. |
|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|
| Prey taxa                                       | *H. longicauda* | *C. intervales* | Average body length (mm) |
|-------------------------------------------------|-----------------|-----------------|--------------------------|
| **Arachnida**                                   |                 |                 |                          |
| Opiliones                                       |                 |                 |                          |
| Sclerosomatidae—*jussara* sp.                  | 1               | –               |                          |
| **Insecta**                                     |                 |                 |                          |
| Diptera                                         |                 |                 |                          |
| Tipulida                                        | 25              | 5               | 5.1                      |
| Chironomidae                                    | 1               | –               | 1.6                      |
| Drosophilidae                                   | 2               | 1               | 2.2                      |
| Sciarida                                        | 2               | –               |                          |
| Stratiomyidae                                   | –               | 1               | 8.4                      |
| Nematocera                                      | 1               | –               |                          |
| Brachycera—Acalyptrata                          | –               | 1               | 2.6                      |
| Unidentified specimens                          | 13              | 1               |                          |
| **Hymenoptera**                                 |                 |                 |                          |
| Formicida                                       |                 |                 |                          |
| Ectoniniae—*Labidus* sp.                       | 2               | –               | 3.4                      |
| Myrmecinae—*Crematogaster* sp. a                | 1               | –               | 4.3                      |
| Myrmecinae—*Cyphomyrmex* sp. a                 | 1               | –               | 3.5                      |
| Myrmecinae—sp. 1                               | 1               | –               |                          |
| Myrmecinae—sp. 2                               | 1               | –               |                          |
| Unidentified specimens                          | 1               | –               |                          |
| Vespida                                         | 1               | –               | 6.0                      |
| **Homoptera**                                   |                 |                 |                          |
| Cicadellida                                     | 1               | –               | 4.6                      |
| Fulgoroidea                                     | 2               | –               | 3.5                      |
| Lepidoptera                                     | 1               | –               | 7.3                      |
| Coleoptera                                      |                 |                 |                          |
| Scydmaenida                                     | 1               | –               | 2.5                      |
| Pscoptera                                       | 1               | –               | 2.1                      |
| **Ephemeroptera**                               |                 |                 |                          |
| Leptophlebiidae                                 | 1               | –               | 2.9                      |
| Total                                          | 60              | 9               |                          |

aWinged individuals.
webs of *Argyrodes antipodiana* as a central mass composed of a three-dimensional network of threads covered with droplets of sticky glue, with supporting threads attached to the branches. This species, however, also forages as a kleptoparasite in webs of *Eriophora pustulosa* (Walckenaer, 1842) (Araneidae) and its solitary web may be just a temporary structure, where juveniles spend the winter (Whitehouse 1986, 1997). *Argyrodes flavipes* Rainbow, 1916 (Whitehouse and Jackson 1998) and *Theridion evexum* Keyserling, 1884 (Garcia and Japyassú 2005), on the other hand, were observed constructing webs with the same characteristics as those built by *H. longicauda* and *C. intervales*: an irregular structure of threads positioned on the inferior surface of a leaf, with some lines reaching the upper surface of another leaf located directly below, and viscid droplets on all the threads.

An interesting similarity among these theridiids with webs entirely composed of viscid silk is that they seem to occur associated with water bodies. Whitehouse and Jackson (1998) found webs of *A. flavipes* in places stationed away from sunlight, close to a stream in a rain forest near Cairns, Queensland, Australia. Garcia and Japyassú (2005) collected *T. evexum* in two areas in southeastern Brazil, at vegetation around a lake at Ibiúna, State of São Paulo, and close to waterfalls in Parque Nacional de Itatiaia, State of Rio de Janeiro. We could not find *H. longicauda* and *C. intervales* at sites located away from the rivers, while these species were abundant at the relatively humid sites. Levi (1964) had already noted that *Helvibis* seems to be associated with humid areas. In the material examined by him, there were specimens of at least four species (*H. tingo* Levi, 1964; *H. germani* Simon, 1895; *H. monticola* Keyserling, 1891, and *H. longicauda*). The specimens of *Chrysso* cf. *nigriceps* used by Agnarsson (2004) in the phylogenetic analysis of theridiids were also collected near the water, at the margin of a lake at Iguaque, Colombia.

The selection of habitats near the water may be related to characteristics of vegetation, presence of specific prey types, prey abundance, or to the higher humidity of those places. In Parque Estadual Interaules we found some of the same plant species often used by *H. longicauda* and *C. intervales*, including *Dichorisandra* sp. (Commelinaceae) and an unidentified species of Marantaceae (M. O. Gonzaga and N. O. Leiner, unpublished data), were abundant at sites away from the rivers. Thus the absence of these spiders in relatively dry places cannot be explained by the lack of appropriate vegetation for web
construction. Although most prey items captured by *Helvibis* and *Chrysso* belonged to Diptera, especially tipulids (which are often collected in humid places; Borror et al. 1989), at least *H. longicauda* also captured a wide diversity of other prey types, indicating that their web types are able to intercept insects not necessarily associated with water bodies. Therefore, we suggest that selection of web sites near water may function to maintain the adhesive properties of the viscid silk used for web construction.

Benjamin and Zschokke (2003) suggested that the high cost of producing and maintaining viscid silk might have led to web reduction and to web structures lacking any viscid elements (i.e. gumfooted lines and viscid droplets). This hypothesis implies the assumption that webs with viscid lines should precede phylogenetically the webs entirely composed of non-sticky threads. The analyses presented by Agnarsson (2004) and Arnedo et al. (2004), however, indicate that this is not the case. Instead of the evolutionary trend from extensive to reduced amounts of viscid elements, suggested by Benjamin and Zschokke (2003), the positions of *Argyrodes*, *Chrysso*, *Helvibis*, and *Theridion* in the theridiid phylogeny indicate that webs with large amounts of viscid silk probably evolved from structures composed mainly of dry silk. We suggest that the costs of maintaining webs with viscid material are probably dependent on the humidity of the habitat and that these costs may not be so high in moist areas.

The viscid droplets present in webs of araneids—and at least one theridiid (*Latrodectus mactans*), the only species of this family with web composition investigated so far (see Tillinghast and Christenson 1984)—are composed in great part of water-soluble compounds with low molecular weight (LMW) (Tillinghast and Townley 1987; Vollrath et al. 1990). The water absorption promoted by the LMW portion of the web is essential to maintain the adhesiveness, extensibility and elasticity of the capture threads (Vollrath and Edmonds 1989; Edmonds and Vollrath 1992; Higgins et al. 2001). Edmonds and Vollrath (1992) showed that in dry atmospheres (RH, 45%) droplet formation on *Araneus diadematus* Clerck, 1757 (Araneidae) webs may take several hours to complete, or even never take place. On the other hand, under high humidity the capture thread forms large droplets and reaches optimum stickness in minimum time.

Although apparently allowing the maintenance of viscid silk, permanence in humid areas may imply a high incidence of attack by fungi. Spiders are infected by a number of fungal genera (Evans and Samson 1987). The pathogenic genus *Gibellula*, for example, was collected on dead spiders over a wide geographic range, including temperate, subtropical, and tropical regions (Evans 1974; Strongman 1991; Samson and Evans 1992; Tzean et al. 1997). Samson and Evans (1992) had difficulty cultivating *Gibellula* species, indicating that these fungi have specialized nutrient requirements and are probably obligate pathogens of spiders. However, most studies on fungal pathogens do not include data on the identity of spider hosts or the impact of infection on spider populations. Thus, we cannot be sure if the prevalence of infection in the humid habitats investigated in this study is especially high. Haupt (2000) studied fungi attacking *Latouchia* sp. (Ctenizidae) in Japan and found four individuals infected by the hyphomycete *Nomuraea atypicola* (Yasuda, 1915) in a sample of 22 spiders, representing a proportion of 18%. This proportion is similar to our results for males of *H. longicauda*, but higher than the proportion of females attacked in our study. It is interesting that we could not identify any attacked specimen of *C. intervales*, in spite of their similarity in body size, web placement, and habitat selection. Additional work is needed to determine whether this difference is due to fungi nutritional requirements or some characteristic (morphological, physiological, or behavioural) that makes *H. longicauda* more susceptible to infection than *C. intervales*. 
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