

Characteristics of the capture threads of *Synotaxus* sp. (probably *S. turbinatus*) webs (Araneae, Synotaxidae)

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Summary

Synotaxus spiders have independently evolved aerial, planar webs to intercept and retain prey, but these webs differ in several respects from planar araneoid webs with similar functions. The silk capture threads of *Synotaxus* sp. (probably *S. turbinatus* Simon, 1895) webs differ markedly from the spirally arranged capture threads in araneoid webs. The sticky globules on the capture threads of *Synotaxus* sp. webs are widely spaced, and the threads are spring-like and apparently unique within spiders. This arrangement apparently allows a great extensibility, as the spring-like form is straightened under high tension, but coils again when the tension decreases. Some aspects of the feeding behaviour and habitat use of *Synotaxus* sp. are also described.

Introduction

The extensive variation in the design of spider webs is probably the result of adaptations to capture different types of prey (Turnbull, 1964), avoid predation and parasitism (Blackledge *et al.*, 2003; Agnarsson, 2004), adjust to habitat constraints, and to the expression of behavioural plasticity that alters web architecture (Eberhard, 1990a). Spiders have solved some “similar problems”, such as capturing a given prey type, with different web designs (Eberhard *et al.*, 2008). One example of such convergent functions is the independent evolution of aerial, planar rectangular webs in *Synotaxus* (see Eberhard, 1977) and orb webs in several araneoid families (Eberhard, 1990b).

To capture prey, planar webs must perform at least three different functions: interposition, stopping, and retention of the prey (Eberhard, 1990b). In other words, the web has to be positioned in the path of potential prey insects, its silk threads have to absorb the kinetic energy of the flying insect without breaking, and have to retain the insect until the spider arrives and attacks it. The first function is independent of the characteristics of the silk threads; instead it is more related to the spider's choice of building site, prey abundance, and habitat complexity (Janetos, 1986). The other two functions are related to the web design and physical characteristics of the silk threads, such as resistance and extension.

The silk of the spirally arranged capture threads of an orb must be extensible enough to absorb the momentum of prey impact without breaking. The sticky, spirally arranged threads of orb-weaving araneoids are highly extensible, owing to the physical and chemical properties of the silk and to the viscous liquid that coats the fibres (Vollrath & Edmonds, 1989; Opell & Hendricks, 2007; Opell *et al.*, 2008). The capture and retention of prey in orb webs probably results from a combination of the

stickiness, elasticity and relatively low tension of the spirally arranged capture threads (Denny, 1976).

The rectangular web of *Synotaxus* species is thought to function similarly to the orb webs of araneoids to capture prey (Eberhard, 1977). All species in this small, neotropical genus construct vertical planar webs in the understory of very wet forests (Eberhard, 1977, 1995; Agnarsson, 2003, 2004). The capture portion of the web consists of vertical, relatively thick and long non-sticky lines that extend from under a leaf that serves as the spider's retreat, to other leaves below. Additional horizontal, non-sticky lines attached to the vertical lines are included in the frame to which *Synotaxus* spiders attach their sticky lines (Eberhard, 1977, 1995). The construction of the web of two species has been described in detail (Eberhard, 1977, 1995), but the characteristics of the capture threads have not previously been studied. We describe some characteristics of the sticky threads of *Synotaxus* sp. (probably *S. turbinatus* Simon, 1895) and provide information on the natural diet of this spider. According to the geographical distribution of *Synotaxus* species, the most likely species in the study area is *S. turbinatus*. However, adult males are needed to confirm the species identification, particularly since *S. turbinatus* is considered a species complex (Agnarsson, 2003).

Methods

This research was done at La Tirimbina Biological Research station, Sarapiquí, Heredia province, Costa Rica (10°26'N, 83°59'W; 150 m elevation), in mature and old growth lowland rainforest. The annual rainfall in the region averages 3900 mm and the temperature 25.8°C. Rainfall decreases from January through March, but shows little monthly variation during the rest of the year (Sandford *et al.*, 1994). We conducted 6 nocturnal censuses (December 2007, May, June, July, August, September 2008) of *Synotaxus* sp. webs by walking for 3 h along the trails in a forested area; the census in May 2008, at the end of the dry period, lasted for 6 h. Each web was checked and insects that the spider was attacking or feeding on were collected and identified. Partial and complete attacks were observed directly; many details were clear because of the spider's slow movements.

Sections of recently constructed webs were collected in a wire frame (3.5 × 6 cm) to which double-sided sticky tape had been stuck on three sides. The frame was slowly moved toward the web until the threads adhered to the frame, and then the threads around the frame were cut. At one end of each of the short sides the frame had a 1-cm segment of wire free of tape that allowed us to load the frame into a piece of Styrofoam at the bottom of a plastic container for transportation. This collecting method allowed us to maintain undisturbed the natural tensions and positions that the threads had in the webs.

In the laboratory, viscid threads collected from six different webs were placed on glass slides to observe and photograph them under a compound microscope, using a digital camera Nikon Coolpix 4500. To avoid stressing the sticky threads, the wire frame was fastened to a piece

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of Styrofoam and under a dissecting microscope the glass slide was gently brought up to the threads from below; the threads were cut at the edges of the slide as they contacted the slide. Other sticky thread samples were collected on glass slides framed with strips of double-sided adhesive tape as described in Barrantes & Weng (2006). Both methods permit photographing viscid droplets without their being distorted by contact with the slide surface. Three segments of viscid threads 0.5 cm long under resting tension were attached to pieces of double-sided sticky tape that had previously been attached to the jaws of a digital calliper. To further secure the threads, we applied mimeograph correction fluid along the length of thread that contacted the tape, as described by Opell *et al.* (2008). We then observed the threads as we slowly separated the jaws of the calliper to elongate the threads until they broke. Adult female specimens have been deposited in the Museo de Zoología, Universidad de Costa Rica.

Results

All webs ($n=53$, including webs not forming part of the censuses) were constructed in the understory of mature and old growth forests, between 20–70 cm above the ground. The height of webs ranged from 16–37 cm and the width from 13–27 cm. The web contained vertical non-sticky lines that extended from a relatively long, horizontal leaf that served as the spider's retreat, downward to other leaves below (Fig. 1: a–b). Horizontal dry threads connecting the vertical lines completed the network of non-sticky lines to which the spider attached the sticky threads (Fig. 1: c–d). There was a relatively dense tangle of thick, dry threads near the lower surface of the retreat leaf. This tangle was attached along part of the border of the leaf, forming a structure similar to an upside-down canoe. When resting, these green, slender spiders hung upside-down along the central vein of the leaf, and were very difficult to see. The webs constructed by juveniles ($n=2$) were apparently similar to the adult



Fig. 1: Web (height 19 cm, width 13.5 cm) of an adult female of *Synotaxus* sp. powdered with cornstarch: **a**=leaf retreat; **b**=vertical frame thread; **c**=horizontal frame thread; **d**=sticky thread.

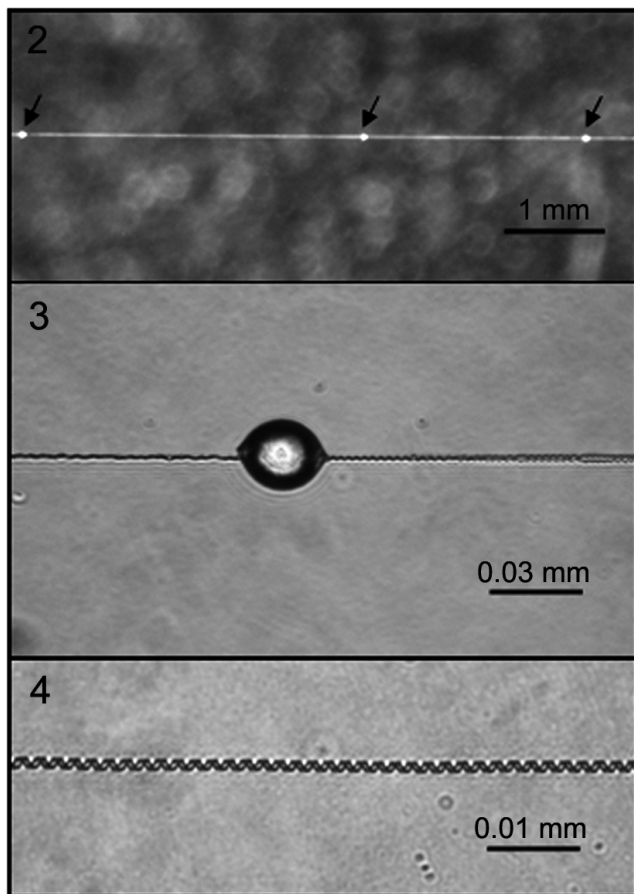
webs; one of the juveniles was one-third the size of an adult female. The only notably different web observed was that of an adult female which had two egg sacs. In addition to the tangle, this web consisted of only a small capture section (extending downward about 5 cm from the leaf retreat) that was oval rather than rectangular, as in normal webs. The same spider was observed a week later with a similar small oval web. The number of webs changed between censuses from 0 to 6 (mean=3.80, SD=2.28).

We collected six prey from *Synotaxus* webs: 2 small moths, 3 nematocerous flies, and 1 muscoid fly (and an additional cicadellid was collected from a web of possibly a different *Synotaxus* sp. in Intervales, São Paulo, Brazil). The descent of the spider toward the prey retained on the sticky threads was slow and interrupted by short pauses. The spiders used the vertical and horizontal dry threads to walk toward the prey and frequently stopped at the intersections of threads. After each brief pause the spiders re-oriented and continued approaching the prey while slowly waving their front legs. Eventually the spider gently tapped the prey with one of her legs I, turned around approximately 90°, and from a nearly horizontal position, facing the prey, began her wrapping attack. This species and the other *Synotaxus* species from Intervales, São Paulo, Brazil applied threads to the prey with both simultaneous and alternate movements of both legs IV (Barrantes & Eberhard, 2007).

Sticky threads were under low tension in the web and the sticky droplets were small and widely spaced (Figs. 2 and 3; mean=2.47 mm, SD=1.28 mm, $n=36$ spaces between contiguous droplets from 2 webs of mature females). The sticky droplets were very sensitive to changes in humidity. They nearly disappeared after being exposed for five minutes to air at room temperature at 20°C and 70% RH, and had completely disappeared after two hours, leaving only a whitish, small crust. This process was reversible and the sticky droplets reappeared after exposing the capture threads to saturated humidity environments. The capture threads were very extensible and the 5-mm thread segments had to be stretched by more than 100% their initial length (same tension as in the web) before breaking (mean=14.01 mm, SD=3.51, $n=4$). In the web these threads were coiled helically along their entire length (Fig. 4). However, when threads were stretched they straightened and the coiled form disappeared. The horizontal dry threads of the webs are not coiled and their extensibility was only about half (mean=8.10 mm, SD=0.30 mm, $n=2$) the extensibility of coiled threads.

Discussion

The function of the capture threads in webs of *Synotaxus* sp. is probably similar to that of the sticky, spirally arranged capture threads in orb-weaving araneoids. The low tension at which this spider attaches these lines and their highly extensible nature make them well adapted to absorb the kinetic energy of flying prey. The stopping and retention of prey by the slack sticky threads is



Figs. 2–4: Characteristics of capture threads of webs of *Synotaxus* sp. **2** Distance between contiguous sticky globules: black arrows point to nearly dry sticky droplets after being exposed for a few minutes to light of dissecting microscope; **3** Sticky globule on a capture thread; **4** Detail of spring-like arrangement of a capture thread.

apparently efficient for a wide range of prey, including moths which are difficult prey for sticky spider webs to catch (Eisner *et al.*, 1964). Moths easily escape from most orb webs as scales that fully cover their body stick to the viscid globules, allowing the moth to slide out of the web (Eberhard, 1975; Eisner *et al.*, 1964; Foelix, 1996). The sagging and extensibility conditions of the capture threads possibly increase the retention time of the prey in the web of *Synotaxus* sp. Holding prey long enough is very important to allow this slow-moving spider to arrive and attack the prey.

The high extensibility of the capture threads in *Synotaxus* sp. is the result, at least in part, of the spring-like form of the thread. In contrast to the sticky, spirally arranged capture threads of some orb-weaving araneoids in which extensibility and high hysteresis are due to their constituent proteins and surrounding coating of aqueous glue (Denny, 1976; Work, 1981; Vollrath & Edmonds, 1989; Blackledge & Hayashi, 2006; Savage & Gosline, 2008), in *Synotaxus* sp. the spring-like structure of the individual sticky threads seems to increase the extensibility of these threads. The widely spaced, small viscid droplets on the capture threads suggest that the core fibres are not evenly coated with viscid material as they are produced, as occurs in araneoid orb-weavers (Foelix, 1996). The high humidity of the forest inhabited

by this species and its habit of constructing nocturnal webs may compensate for the possible lack of a continuous aqueous coating on the core fibres, providing additional extensibility as in some orb-weaving spiders (Vollrath & Edmonds, 1989). More information on amino-acid composition and more precise analyses of the mechanical properties of the capture threads of *Synotaxus* are necessary to understand fully the functional performance of these threads.

The viscid droplets on the capture threads seem to contain a large quantity of water. This was indicated by the rapid reduction in their size when exposed to an ambient low relative humidity, their nearly complete disappearance after a few hours of exposure to this condition, and their re-hydration at high humidity. Consequently, it is possible that short periods of drought reduce the stickiness of the viscid droplets and thus reduce the capture success of the web. This may have been the cause of the absence of webs in one of the censuses, in May. This census was conducted at the end of an uncommon, very long dry period.

The attack behaviour of *Synotaxus* sp. on different prey, characterised by its slow approaching movements, is similar to the attack behaviour of another *Synotaxus* species from Brazil (Barrantes & Eberhard, 2007). Furthermore, the wrapping attack of *Synotaxus* sp. is similar to the wrapping attack of species in the families Nesticidae and Theridiidae, the sister clade of Synotaxidae (Agnarsson, 2004; Barrantes & Eberhard, 2007).

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