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in the Spider Family Uloboridae**

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# Increased stickiness of prey capture threads accompanying web reduction in the spider family Uloboridae

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## Summary

1. The prey capture threads of a spider's orb-web retain insects that strike the web until the spider can subdue them. To determine how changes in web architecture influence thread effectiveness, the stickiness of cribellar prey capture threads produced by nine species of similarly sized spiders from the family Uloboridae was measured.
2. The weight-specific stickiness of these threads differed by as much as 5·7-fold among the species and was correlated with differences in web architecture.
3. Threads spun by representatives of five orb-weaving genera were less sticky than those spun by species that make reduced webs.
4. Two species of the simple-web genus *Miagrammopes* produced stickier threads than two species of the triangle-web genus *Hyptiotes*.
5. This suggests that the stickiness of capture threads is closely allied to web design and function.

*Key-words:* Cribellar thread, silk stickiness, spider webs, web architecture

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## Introduction

Sticky prey capture threads are important components of most spider orb-webs. After a web intercepts an insect, these threads retain the struggling prey until a spider can run to and subdue it by either envenoming the prey or wrapping it with silk, events that often take as long as 10 s (Eberhard 1989). Although the stickiness of capture thread contributes directly to successful prey capture, it has been measured in only three species (Eisner, Alsop & Ettershank 1964; Opell 1990; Opell, Roth & Cushing 1990) and never examined in a systematic way. Aspects of orb-web architecture, such as the orientation of the web in a horizontal vs a vertical plane, are known to affect web design (Eberhard 1981; Craig 1987). This study determines if changes in web design are correlated with changes in the stickiness of the web's capture threads.

Two types of sticky prey capture threads are found in spider webs: dry, fuzzy cribellar thread and moist, adhesive threads (Vollrath 1992). Cribellar thread is the more primitive type and was present in the first aerial webs made by spiders (Peters 1986; Coddington & Levi 1991). It is retained by the members of only one group of orb-weaving spiders, the Uloboridae. In this family, cribellar threads consist of a pair of supporting axial lines surrounded by a cloud of thousands of very thin, looped fibrils (Fig. 1; Peters 1984; Opell 1989).

The family Uloboridae exhibits several degrees of web reduction that make it suitable for this study. The family's plesiomorphic web form is a horizontal orb-web (Fig. 2A; Opell 1979; Coddington 1990). In the genus *Hyptiotes* this has been reduced to a triangle-web (Fig. 2B) and in its sister genus, *Miagrammopes*, to an irregular, simple-web that has no stereotypic form (Fig. 2C; Lubin, Eberhard & Montgomery 1978; Opell 1982, 1990; Lubin 1986). Spiders that construct these reduced webs may benefit in two ways: (1) they appear to invest less silk, time and energy in constructing their webs and (2) they may avoid detection by predators because they assume cryptic postures as they monitor their web from the attachment point of one of its anchor lines (Figs. 2B,C; Lubin 1986).

There is no evidence to suggest that these differences in web architecture are associated with prey specialization. Even *Miagrammopes* species, which have the most specialized web type, capture small- to medium-sized insects belonging to a number of orders (Lubin, Eberhard & Montgomery 1978; Opell 1990). However, as these studies did not evaluate total insect availability, it is possible that web architecture and placement select for certain functional groups of insects. The habitat preference (Opell 1986) may also affect the prey that strike a web.

As uloborid webs become reduced, they present a smaller prey capture area. One mechanism that may help compensate for this apparent reduction in prey

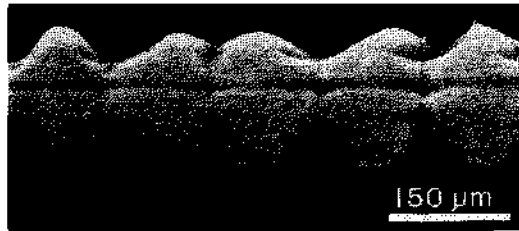


Fig. 1. The cribellar prey capture thread of *Hyptiotes cavatus*.

capture potential is increased cribellar thread stickiness. This would enhance a web's ability to retain prey that it intercepted and, thereby, increase a spider's chances of subduing the prey. Two other factors also suggest that the capture threads of reduced webs should be stickier. First, the triangle-webs of *Hyptiotes* are vertically oriented and, therefore, more likely to intercept faster-flying insects than horizontal orb-webs (Eberhard 1981, 1990; Craig 1987). Relative to their size, faster-flying prey strike a web with greater force and should be retained better by webs that have stickier capture threads. Second, the larger a prey is, the more likely it is to contact several capture threads when it strikes an orb-web or a triangle-web. If a prey pulls free from one of these web's capture threads, there is a good chance that it will contact an adjacent thread. However, it is very unlikely that an insect will strike more than a single capture thread in a *Miagrammopes* simple-web and, if it struggles free of this thread, that it will contact another thread. When combined with the very small capture area presented by these simple-webs, this factor suggests that *Miagrammopes* species should produce the stickiest capture threads of all uloborids.

The objectives of this study were:

1. To measure the stickiness of cribellar threads produced by nine species of the Uloboridae to determine how plastic capture thread stickiness is among similarly sized, closely related species.
2. To use these measurements to test the general hypothesis that spider web architecture and capture thread stickiness are closely allied and the specific

hypothesis that, relative to spider weight, the stickiness of capture threads increases as uloborid webs become simpler. This hypothesis predicts that capture thread stickiness ranges from least to greatest as follows: orb-web species, triangle-web species, simple-web species.

## Materials and methods

Measurements were made of the stickiness of capture threads spun by adult females (adult male uloborids do not construct capture webs) of nine species, representing seven of the family's 18 genera (Fig. 3). To control for the effect of phylogenetic relationship on stickiness, orb-weaving species were selected from widely separated clades. Because the reduced-web genera *Hyptiotes* and *Miagrammopes* are sister taxa, the sister orb-weaving genera *Octonoba* and *Philoponella* were also included. If web architecture and not phylogenetic position correlates with capture thread stickiness, then the stickiness of threads produced by members of *Hyptiotes* and *Miagrammopes* should differ more than those produced by members of the orb-weaving genera *Octonoba* and *Philoponella*.

This study included five orb-weaving species: *Waitkera waitakerensis* (Chamberlain) ( $\bar{x} \pm \text{SD}$  live weight  $8.79 \pm 2.99$  mg,  $n = 39$ ), from New Zealand's North Island; *Siratoba referena* (Muma and Gertsch) ( $\bar{x} \pm \text{SD}$  live weight  $4.31 \pm 1.14$  mg,  $n = 27$ ) and *Philoponella arizonica* (Gertsch) ( $\bar{x} \pm \text{SD}$  live weight  $13.35 \pm 4.49$  mg,  $n = 27$ ), both from the Chiricahua Mountains of south-eastern Arizona; *Uloborus glommosus* (Walckenaer) ( $\bar{x} \pm \text{SD}$  live weight  $9.39 \pm 2.66$  mg,  $n = 30$ ) from south-western Virginia; and *Octonoba sinensis* (Simon) ( $\bar{x} \pm \text{SD}$  live weight  $12.86 \pm 4.30$  mg,  $n = 36$ ), an introduced Asian species, collected from free-ranging populations in greenhouses at Virginia Polytechnic Institute and State University. It also included two triangle-web species: *Hyptiotes cavatus* (Hentz) ( $\bar{x} \pm \text{SD}$  live weight  $7.76 \pm 3.60$  mg,  $n = 37$ ), from south-western Virginia

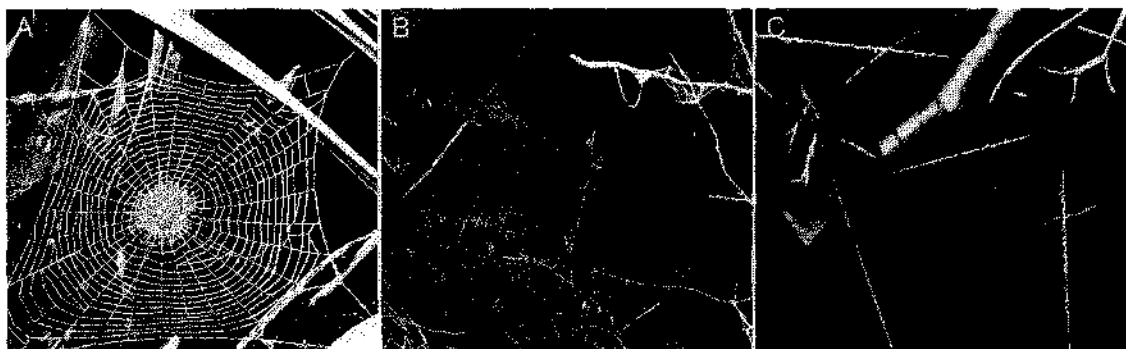


Fig. 2. (A) The orb-web of *Waitkera waitakerensis*. (B) The triangle-web of *Hyptiotes cavatus*. (C) The simple-web of *Miagrammopes animotus*.

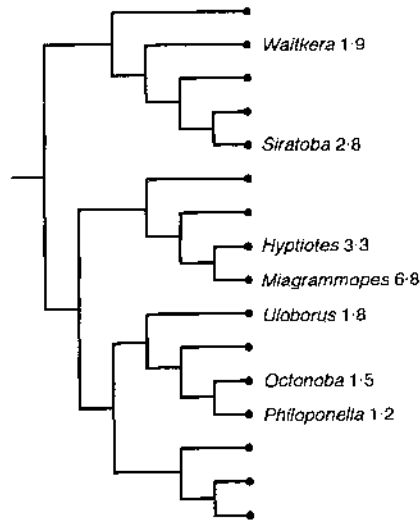


Fig. 3. A cladogram of the genera of Uloboridae from Codrington (1990), showing the phylogenetic positions of the seven genera included in this study. The number following each name is the mean weight-specific stickiness ( $\mu\text{N mm}^{-1}$  contact  $\text{mg}^{-1}$  spider weight) of that genus.

and *H. gertschi* Chamberlin and Ivie ( $\bar{x} \pm \text{SD}$  live weight  $9.68 \pm 2.95$  mg,  $n = 34$ ), from north-western Washington. Two simple-web species were studied: *Miagrammopes animotus* Chickering ( $\bar{x} \pm \text{SD}$  live weight  $5.26 \pm 2.09$  mg,  $n = 118$ ), from the Luquillo National Forest of Puerto Rico and an undescribed green *Miagrammopes* species ( $\bar{x} \pm \text{SD}$  live weight  $3.92 \pm 1.36$  mg,  $n = 24$ ) from north central Costa Rica.

All uloborids deposit cribellar thread in the linear fashion shown in Fig. 1. However, *Miagrammopes* species increase the surface area of some segments of their prey capture lines by depositing cribellar threads in a looped fashion (Opell 1990). The stickiness of only the linear cribellar threads produced by *Miagrammopes* species was measured in this study. This provides a conservative measure of the stickiness of *Miagrammopes* threads and a more conservative test of the hypothesis that capture thread stickiness increases as spider webs become reduced.

Because uloborids construct their webs in the early morning, thread samples were collected between 05.00 and 10.00 h to obtain fresh threads that were not contaminated by dust or pollen or damaged by prey. Threads were collected on microscope slides to which five raised, parallel, 4.8-mm wide, 2-cm long brass supports were glued at 4.8-mm intervals. Double-sided tape atop each support securely anchored the threads and maintained their original tensions. After obtaining a thread sample from a spider's web, the spider was collected and its live weight determined. The stickiness of four strands of thread from each spider's web was measured 2–40 h after collection and the mean stickiness of these strands was used as the value for that spider's capture thread. All threads were examined under a dissecting microscope before

their stickiness was measured to assure that only intact threads were included in this study.

Cribellar thread stickiness was measured by a modification of Opell's (1989) technique. The instrument used incorporated a glass needle strain gauge with a contact plate glued to the needle's free tip. The thread sampler was secured to a holder that could be both rotated and moved along  $x$ - and  $y$ -axes, permitting the threads to be oriented perpendicularly to the width of the contact plate. A motorized advancement moved the sampler toward the contact plate at a speed of  $13.5 \text{ mm min}^{-1}$  and away from it at  $14.0 \text{ mm min}^{-1}$ . The glass needle strain gauge was mounted in a horizontal plexiglass frame and was positioned so that the contact plate on the protruding tip of its needle could be pressed against a cribellar thread. The distal end of the needle passed over a scale that was calibrated in mg, making it possible to determine the force required to displace the needle.

The first step in measuring stickiness was to advance the web sampler until a thread was pressed against the contact plate with a force of  $19.61 \mu\text{N mm}^{-1}$  of thread contact. Following this, the direction of the sample's movement was reversed and the position of the strain gauge's needle observed as the cribellar thread was pulled away from it. The value registered on the scale at the instant the thread pulled free of the contact plate was recorded and, by multiplying this mg value by the accelerating force of gravity, the force in Newtons required to pull the thread from the contact plate was determined. This was divided by the width of the contact plate (measured to the nearest  $20 \mu\text{m}$  under a dissecting microscope) to calculate stickiness, expressed as  $\mu\text{N mm}^{-1}$  of thread contact with the plate. Weight-specific stickiness is expressed as  $\mu\text{N mm}^{-1} \text{ mg}^{-1}$  spider live weight. Depending on the needle used, this technique had a sensitivity of  $1.33$ – $2.70 \mu\text{N mm}^{-1}$  of contact. This sensitivity was less than 16% of the mean stickiness recorded for the cribellar thread of each species. After determining the stickiness of a spider's cribellar thread, the relative humidity (r.h.) at which these measurements were taken was recorded.

The contact plate glued to the tip of the strain gauge's needle was a 2-mm wide rectangle of 320 grit 3M waterproof silicon carbide sandpaper. This material was chosen for two reasons. First, the silicon carbide particles on its surface are of uniform size and distribution and the fibrils that form the thread's surface do not pull free and accumulate on these particles (Opell 1993). Second, the surface of a sandpaper contact plate appeared to be analogous to that of an insect's wing. To confirm this, I measured the stickiness of threads spun by 20 adult female *U. glomosus* using two 2-mm wide contact plates: one made from sandpaper and another made from the dorsal surface of a fleshfly (*Sarcophaga bullata* Parker) wing. The stickiness of a set of four separate strands of thread produced by each spider was measured with each of

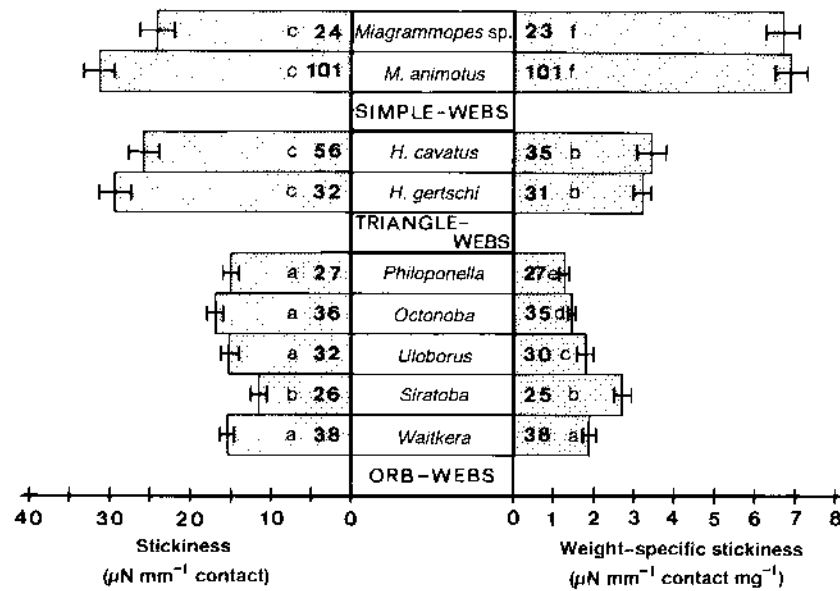


Fig. 4. Comparison of the absolute (left) and weight-specific (right) stickiness of capture threads of nine uloborid species. Numbers within each box indicate sample size; species with the same letter have values that do not differ statistically; error bars denote  $\pm 1$  SE.

the two contact plates and the mean of each set served as the two values for that individual. The stickiness measurements made with the two plates were made at the same r.h. (for each surface  $\bar{x} \pm \text{SD}$   $56.7 \pm 0.7\%$  r.h.,  $n=20$ ) and yielded the same values: sandpaper  $\bar{x} \pm \text{SD}$   $21.0 \pm 9.3 \mu\text{N mm}^{-1}$ ,  $n=20$ ; blowfly  $\bar{x} \pm \text{SD}$   $17.4 \pm 5.8 \mu\text{N mm}^{-1}$ ,  $n=20$ ; Wilcoxon two-sample test,  $Z=-1.258$ ,  $P=0.208$ . Thus, sandpaper contact plates provide uniform surfaces for measuring stickiness and yield values similar to those obtained from an insect wing.

All values were tested with a Shapiro-Wilk  $W$ -statistic to determine if they were normally distributed ( $P>0.05$ ). If they were,  $t$ -tests ( $t$ ) were used for pairwise comparisons and analysis of variance tests (ANOVA) for multiple comparisons. If one or more values being compared were not normally distributed, Wilcoxon two-sample tests ( $W$ ) were used for pairwise comparisons and Kruskal-Wallis  $K$ -sample tests ( $KW$ ) for multiple comparisons. Values were considered to be significantly different if  $P<0.05$ .

## Results

The mean r.h. at which the stickiness of the nine species' capture threads was measured ranged from 55 to 68%. A regression model whose dependent variable was stickiness and whose independent variables were web type, species and r.h. showed that both web type and species were significant predictors of stickiness ( $P<0.006$ ), but that humidity was not ( $P=0.957$ ). Therefore, these small differences in r.h. need not be considered when comparing thread stickiness.

The capture thread stickiness of the nine species is

presented in Fig. 4. Weight-specific stickiness differed among the orb-weaving genera *Waitkera*, *Siratoba*, *Octonoba*, *Uloborus* and *Philoponella* ( $KW$ ,  $\chi^2=42.198$ ,  $P=0.0001$ ) and for all species except *S. referena* (where  $W$ ,  $Z=-1.071$ ,  $P=0.284$ ), was less than the pooled values of the two species of the triangle-web genus *Hyptiotes* ( $W$ ,  $-6.134 < Z < -4.452$ ,  $P=0.0001$  for each of the four orb-weaving species). Weight-specific stickiness did not differ between the two triangle-web species ( $W$ ,  $Z=0.642$ ,  $P=0.521$ ) or the two simple-web species ( $W$ ,  $Z=0.656$ ,  $P=0.512$ ). The pooled mean  $\pm$  SD value of *Hyptiotes* ( $3.31 \pm 1.78 \mu\text{N mm}^{-1} \text{mg}^{-1}$ ) was less than that of *Miagrammopes* ( $6.86 \pm 4.02 \mu\text{N mm}^{-1} \text{mg}^{-1}$ ) ( $W$ ,  $Z=-7.186$ ,  $P=0.0001$ ).

Absolute stickiness differed among the five orb-weaving species ( $KW$ ,  $\chi^2=17.373$ ,  $P=0.002$ ), but when *S. referena* was excluded, the remaining four showed no difference ( $KW$ ,  $\chi^2=1.749$ ,  $P=0.626$ ); their pooled mean  $\pm$  SD ( $19.76 \pm 5.99 \mu\text{N mm}^{-1}$ ) was greater than that of *S. referena* ( $W$ ,  $Z=-3.985$ ,  $P=0.0001$ ). Absolute stickiness did not differ among the four reduced-web species ( $KW$ ,  $\chi^2=6.1458$ ,  $P=0.1047$ ) and their pooled mean  $\pm$  SD ( $29.07 \pm 15.39 \mu\text{N mm}^{-1}$ ) was greater than that of the four orb-weavers ( $W$ ,  $Z=-9.654$ ,  $P=0.0001$ ).

## Discussion

The weight-specific stickiness of capture threads produced by uloborid spiders differs greatly. Among orb-weavers it differs by as much as 2.3-fold; among species that construct different web types, by as much as 5.7-fold. Web architecture appears to be the major factor that correlates with stickiness: as webs become

more reduced, their capture threads become stickier. On average, triangle-weavers produce threads whose weight-specific stickiness is 1.8 times that of orb-weavers and simple-web weavers produce threads whose weight-specific stickiness is 2.0 times that of triangle-weavers.

Regardless of their phylogenetic position, orb-weaving species have stickiness values that are more similar to one another than to those of the reduced-web genera *Hyptiotes* and *Miagrammopes* (Fig. 4). Thus, changes in stickiness appear to be functional, reflecting changes in web architecture and not strictly phylogenetic relationships within the family. Further support for this comes from comparisons of the sister orb-web genera *Octonoba* and *Philoponella* and the sister reduced-web genera *Hyptiotes* and *Miagrammopes*. Weight-specific thread stickiness differed by only  $0.23 \mu\text{Nmm}^{-1}\text{mg}^{-1}$  between the orb-weavers, whereas the two simple-web species produce thread that was, on average,  $3.46 \mu\text{Nmm}^{-1}\text{mg}^{-1}$  stickier than that of the two triangle-web species.

In addition to producing stickier cribellar capture threads, members of the genera *Hyptiotes* and *Miagrammopes* also more actively monitor their reduced webs and more aggressively manipulate them when they intercept a prey than do orb-weaving uloborids (Lubin *et al.* 1978; Opell 1982, 1990; Lubin 1986). Thus, both greater behavioral investment and increased cribellar thread stickiness appear to compensate for the reduced capture areas presented by the simpler webs of *Hyptiotes* and *Miagrammopes*.

The only non-uloborid spider whose capture thread stickiness has been measured is *Nephila clavipes* (Eisner, Alsop & Ettershank 1964). When measured with a 2-mm wide contact plate made from a fly (*Tabanus* sp.) wing, the adhesive threads of these large females ( $\bar{x}$  weight = 848 mg; Anderson & Prestwich 1982) had a mean stickiness of  $152 \mu\text{Nmm}^{-1}$  contact. This value is 4.8 times greater than the maximum stickiness recorded for any uloborid species.

Unfortunately, nothing is known about the relationship between the weight of an orb-weaving spider and the stickiness of the capture thread it produces. The weights of *N. clavipes* and orb-weaving uloborid species differ so greatly that this study does not resolve this relationship. However, by showing that capture thread stickiness can differ greatly among species and that it changes in consort with web architecture, this study emphasizes the crucial role that thread stickiness plays in both web design and web function. It also illustrates the importance of considering this variable when comparing the construction and performance of spider webs.

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