



# The material cost and stickiness of capture threads and the evolution of orb-weaving spiders

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Prey capture threads are essential to the operation of spider orb-webs because they prevent insects that have been intercepted from escaping before a spider can subdue them. The volume of material invested in a web's capture threads is related to spider weight and is the same for primitive orb-weavers that produce cribellar capture thread and modern orb-weavers that produce adhesive capture thread. However, as adhesive capture thread achieves greater stickiness relative to its volume, adhesive orb-webs have a greater total stickiness and, consequently, a greater prey capture potential than cribellate orb-webs. These differences appear to have favoured the transition from cribellate to adhesive capture threads and the success of adhesive orb-weavers, which include 95% of all orb-weaving species. Differences in the thread economy and the total stickiness of webs constructed by spiders of different weights also suggest that adhesive orb-weavers should grow more rapidly and be capable of attaining a larger size than cribellate orb-weavers.

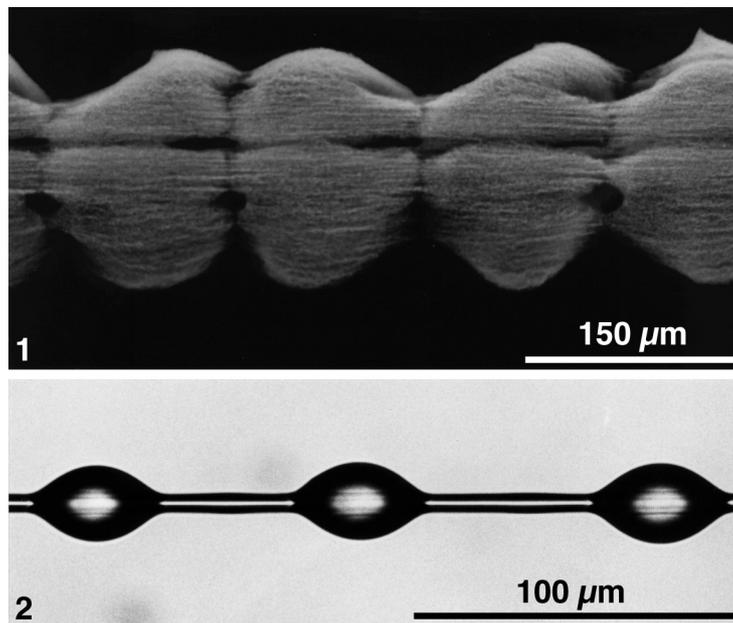
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ADDITIONAL KEY WORDS:—cribellar thread – viscous thread – Araneidae – Uloboridae – Tetragnathidae – orb-web – prey capture – key innovation.

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Figures 1 & 2. Capture threads of orb-weaving spiders. Fig. 1. Cribellar thread of *Hyptiotes cavatus* (scanning electron micrograph). Fig. 2. Adhesive thread of *Argiope trifasciata* (light micrograph).

#### INTRODUCTION

Over 4200 species of spiders use orb-webs to capture prey (Platnick, 1988). The prey capture success of these intricate aerial snares depends first on their ability to intercept insects and absorb the forces of their impacts and then on their ability to retain insects until a spider can subdue and feed on them. A number of factors may affect a web's ability to intercept prey, including its placement within a habitat (Craig, 1988, 1990), its orientation (Eberhard, 1989), its architecture (Craig, Okubo & Andreasen, 1985; Eberhard, 1986), its strength and extensibility (Craig, 1987a, b; Denny, 1976; Eberhard, 1986, 1989; Lin, Edmonds & Vollrath, 1995), its invisibility or attractiveness to insects (Craig, 1988, 1990; Craig & Bernard, 1990; Craig, Bernard & Coddington, 1994), and the visibility of a spider positioned at its hub (Craig & Ebert, 1994; Craig & Freeman, 1991). However, a web's ability to retain prey is determined principally by the stickiness and spacing of its spirally arranged capture thread. Increased thread stickiness increases prey retention (Chacón & Eberhard, 1980; Eberhard, 1989, 1990) and, consequently, should be favoured by selection if it is achieved at a cost less than the increase in prey capture that it facilitates.

Over 135 million years ago (early Cretaceous) a major change occurred in the design of spider orb-webs: dry, cribellar capture threads (Fig. 1) were replaced by viscous, adhesive capture threads (Fig. 2; Coddington, 1986, 1990a; Coddington & Levi, 1991; Selden, 1989). Today, the only orb-weaving spiders that produce cribellar threads belong to the family Uloboridae, whereas adhesive capture threads are produced by members of six families that together contain over 95% of the genera and species of orb-weaving spiders (Levi, 1982; Platnick, 1988). A null Markovian

model (Guyer & Slowinski, 1993; Slowinski & Guyer, 1989) shows that there are significantly more unbalanced clades (those whose species numbers differ by 90% or more) within the order Araneae than predicted by chance alone (Bond & Opell, unpublished data). This indicates that some of the diversity within spiders can be attributed to adaptive radiation that occurred when new features allowed lineages to enter new adaptive zones (Simpson, 1944). One of the more highly unbalanced bifurcations divides the Orbiculariae clade into the Deinopoidea that includes orb-weaving spiders that produce cribellar threads and the Araneoidea that contains 97% of the species of Orbiculariae and includes orb-weavers that produce adhesive threads. A second null model (Nee, Barraclough & Harvey, 1996; Nee & Harvey, 1994) shows that this increased diversity is significant and that it is associated with synapomorphies of the Araneoidea and not with features that appear later in this group's evolutionary history (Bond & Opell, unpublished observations).

If adhesive thread provides significant functional advantages over cribellar thread, then the origin of adhesive thread may be considered a key innovation (*sensu* Liem, 1973; Larson *et al.*, 1981) that contributed to the success of modern orb-weaving spiders. Several differences between cribellar and adhesive capture threads have been documented. Compared to cribellar thread, adhesive thread is either spectrally flat or has a lower UV reflectance (Craig, Bernard & Coddington, 1994), features that reduce its visibility and make it more likely that insects will strike an orb-web that contains adhesive thread. Adhesive thread is also more extensible than cribellar thread (Köhler & Vollrath, 1995; Vollrath & Edmonds, 1989) and, therefore, enhances a web's ability to absorb the impact of a prey strike (Craig, 1987b). However, the most important role of capture thread, its ability to retain insects after they strike the web, has not been examined.

The purpose of this study is to determine if adhesive thread reduces the material cost of achieving orb-web stickiness or increases the total stickiness of an orb-web's capture threads. If this hypothesis is supported, it will provide both critical evidence for the selective advantage of adhesive thread over cribellar thread and a new perspective on the functional properties of spider orb-webs. As broad questions such as this must be addressed from an evolutionary perspective, I employ the comparative method (*sensu* Harvey & Pagel, 1991) to test the hypothesized functional differences between cribellar and adhesive threads in a phylogenetic context.

Cribellar capture threads appeared early in spider phylogeny and are present in capture webs that are less highly organized than orb-webs (Coddington & Levi, 1991; Eberhard & Pereira, 1993). These threads derive their stickiness from thousands of fine, looped fibrils which are produced by the spigots of a cribellum spinning plate located at the posterior of the spider's abdomen. These fibrils form the outer surface of a spider's composite cribellar capture threads and are supported internally by a pair of larger axial fibres (Fig. 1; Eberhard, 1988; Eberhard & Pereira, 1993; Opell, 1993, 1994a-d, 1995; Peters, 1983, 1984, 1986, 1992). In contrast, adhesive capture threads are formed of a complex chemical solution that is deposited on a pair of axial fibres as they issue from spigots on a spider's spinnerets (Tillinghast *et al.*, 1993; Townley *et al.*, 1991; Vollrath *et al.*, 1990; Vollrath & Tillinghast, 1991). This solution quickly coalesces into a series of regularly spaced viscous droplets (Fig. 2) that owe their stickiness to glycoprotein nodules that lie within (Peters, 1995; Tillinghast *et al.*, 1993; Vollrath & Tillinghast, 1991; Vollrath *et al.*, 1990).

The replacement of cribellar threads by adhesive threads was a pivotal event in spider evolution, yet little attention has been given to factors that may have favoured

this transition. One hypothesis is that adhesive capture threads achieve their stickiness at a lower material cost than do cribellar threads (Lubin, 1986; Opell, 1994b; Vollrath, 1992). If this is correct, then adhesive orb-webs should either achieve at a lower material cost the same total stickiness as cribellate orb-webs or, at the same material cost, achieve a greater total stickiness. In the first instance, a spider would benefit from a lower cost of web construction; in the second, from an increased prey capture potential (Chacón & Eberhard, 1980; Eberhard, 1989, 1990).

Tentative support for this hypothesis comes from the observation that, relative to the volume of material they contain, adhesive capture threads are stickier than cribellar threads (Opell, unpublished data). However, across species of the family Uloboridae, cribellar thread stickiness is inversely related to capture thread length (Opell, 1994a). Thus, a critical test of this hypothesis must take into account not only the cost and stickiness of capture threads, but also the total length of capture thread that orb-webs contain.

#### EXPERIMENTAL SYSTEM

A recent study (Opell, 1996) suggests a method by which the properties of cribellar and adhesive threads can be compared. This study found that, among members of the family Uloboridae, both the volume of a web's cribellar capture thread and its stickiness are correlated with spider weight. If a similar relationship exists among adhesive orb-weavers, then a comparison of the slopes of their regression lines with those of cribellate orb-weavers will determine if the capture thread component of an adhesive orb-web is indeed less costly to produce than that of a cribellate orb-web. This comparison will also determine if, relative to spider weight, adhesive orb-webs achieve a greater total stickiness than cribellate orb-webs.

By equating the material cost of capture thread with its volume, this study underestimates the cost of cribellar thread and overestimates the cost of adhesive thread, thereby providing a more conservative test of the study's hypothesis. Cribellar threads appear to be formed entirely of proteinaceous silk and have an outer surface formed of fibrils that are looped and coiled (Fig. 1). However, as the amount of coiling cannot be quantified, their volume was computed as if these fibrils were straight (Opell, 1996). This probably underestimates their volume by at least 50%, more than compensating for the possibility that cribellar fibrils may have a greater density than the viscous material of adhesive threads. Adhesive capture thread is less costly to produce than its volume would suggest for two reasons. First, water forms about 80% of an adhesive droplet's volume (Gosline, DeMont & Denny, 1986), whereas the fibrils of cribellar threads are formed of protein. Consequently, it should be less costly for a spider to produce a given volume of adhesive thread than the same volume of cribellar thread. Second, adhesive threads contain low and high molecular weight hygroscopic agents, both of which attract water at relative humidities (RH) in excess of 50% (Townley *et al.*, 1991). As I measured the dimensions of adhesive thread droplets after they were kept at 60–62% RH for 2–4 h, some of their volume originated from the atmosphere and not from the spider that produced them.

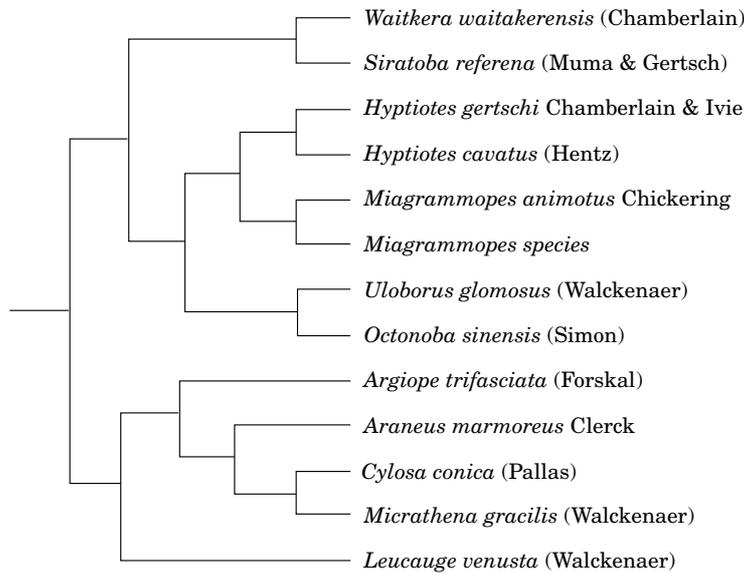


Figure 3. Phylogeny of species included in this study (based on Coddington, 1990b; Coddington & Levi, 1991; Levi, 1985).

MATERIAL AND METHODS

*Species studied*

The species included in this study and their phylogenetic relationship are given in Figure 3. I measured the total volume and stickiness of adhesive capture threads in orb-webs constructed by mature females of five adhesive orb-weaving spider species found in southwestern Virginia (Table 1). I compared these with the values of cribellar threads in webs constructed by females of eight species of the family Uloboridae, as reported by Opell (1996). Adhesive orb-weavers include four species of the family Araneidae (each representing one of this large family's four clades: the Argiopinae, Araneinae, *Acanthepeira* clade, and *Gasteracantha* clade; Levi, 1985) and one species of the family Tetragnathidae. All of the species included in this study, with the possible exception of the uloborid species *Octonoba sinensis* (Opell, 1996), construct a new web every night.

*Thread stickiness*

Capture threads were collected from newly constructed orb-webs on raised supports that were glued to microscope slides at 4.8 mm intervals. After a thread sample was taken, I collected and weighed the spider that produced it. I measured thread stickiness with a strain gauge that incorporated a stainless steel needle (Opell, 1993, 1994a). A contact plate made from a 2 mm wide piece of 320 grit, 3M waterproof silicon carbide sandpaper was glued to the tip of this needle. The particles on the surface of these sandpaper plates are of uniform size and distribution (Opell,

TABLE 1. Spider weights, capture thread stickiness, and conditions under which stickiness was measured. Mean  $\pm$  1 SE. Cribellar thread stickiness was measured at 23°–27°C. Values for cribellar threads are from Opell (1996)

FAMILY species (sample size)	weight mg	stickiness $\mu\text{N}/\text{mm}$	precision $\mu\text{N}/\text{mm}$ % species $\bar{X}$	uniformity $\mu\text{N}/\text{mm}$ % species $\bar{X}$	temperature C°	percent RH
ULOBORIDAE						
<i>Waiikera waitakerensis</i> (38)	8.97 $\pm$ 0.46	15.45 $\pm$ 0.82	1.37 8.9	3.07 19.9	—	68 $\pm$ 0.3
<i>Siratoba referena</i> (26)	4.42 $\pm$ 0.22	11.46 $\pm$ 0.80	1.78 15.3	1.66 14.2	—	66 $\pm$ 0.4
<i>Hyptiotes gertschi</i> (32)	9.83 $\pm$ 0.56	29.84 $\pm$ 2.17	1.78 5.9	6.82 22.7	—	55 $\pm$ 0.4
<i>Hyptiotes cavatus</i> (56)	8.11 $\pm$ 0.57	26.18 $\pm$ 1.70	1.73 7.4	5.37 22.9	—	58 $\pm$ 0.2
<i>Miagrammopes animotus</i> (101)	4.96 $\pm$ 0.23	31.50 $\pm$ 1.78	1.69 5.6	5.53 18.5	—	62 $\pm$ 0.4
<i>Miagrammopes species</i> (24)	3.75 $\pm$ 0.24	24.41 $\pm$ 2.07	1.78 7.2	5.74 23.3	—	65 $\pm$ 0.4
<i>Uloborus glomosus</i> (32)	9.39 $\pm$ 0.49	15.38 $\pm$ 1.02	2.86 18.5	4.02 25.9	—	56 $\pm$ 0.1
<i>Octonoba sinensis</i> (36)	12.74 $\pm$ 0.73	17.02 $\pm$ 1.19	2.68 15.7	4.22 24.7	—	55 $\pm$ 0.1
ARANEIDAE						
<i>Argiope trifasciata</i> (21)	340.4 $\pm$ 33.2	27.15 $\pm$ 1.99	2.52 9.3	6.89 25.4	23 $\pm$ 0.3	60 $\pm$ 0.5
<i>Araneus marmoreus</i> (22)	646.9 $\pm$ 63.9	34.76 $\pm$ 4.21	2.59 7.5	5.21 15.0	23 $\pm$ 0.2	61 $\pm$ 0.2
<i>Cyclosa conica</i> (20)	7.4 $\pm$ 0.3	11.47 $\pm$ 1.03	1.91 16.7	2.06 17.9	24 $\pm$ 0.1	61 $\pm$ 0.5
<i>Micrathena gracilis</i> (20)	90.4 $\pm$ 5.5	28.34 $\pm$ 3.12	1.76 6.2	5.46 19.2	23 $\pm$ 0.2	62 $\pm$ 0.4
TETRAGNATHIDAE						
<i>Leucauge venusta</i> (26)	28.1 $\pm$ 2.3	20.01 $\pm$ 2.50	3.38 16.9	4.25 21.3	25 $\pm$ 0.1	61 $\pm$ 0.5

1993) and these plates registered the same stickiness for cribellar threads as did contact plates made from fleshfly (*Sarcophaga bullata* Parker) wings (Opell, 1994a). Likewise, the mean stickiness of adhesive capture threads of adult female *Argiope trifasciata* measured with contact plates made of fleshfly wings (25.70  $\mu\text{N}/\text{mm}$ , SE = 3.52,  $n = 19$ ) and that measured with sandpaper contact plates (26.65  $\mu\text{N}/\text{mm}$ , SE 1.96,  $n = 22$ ) did not differ ( $t$ -test:  $t = 0.244$ , 39 df,  $P = 0.81$ ). Each set of measurements was made at a mean temperature of 23°C and a mean RH of 60%. Thus, for both cribellar and adhesive capture thread, a sandpaper contact plate registers stickiness values similar to that of a representative insect surface.

Each sandpaper contact plate was pressed against a thread at a speed of 10.7 mm/min until a force of 19.61  $\mu\text{N}/\text{mm}$  of thread contact was achieved. It was then immediately withdrawn at a speed of 10.4 mm/min until the sandpaper plate pulled free from the thread. The force registered by the strain gauge immediately before this occurred was divided by the contact plate's width (measured to the nearest 20  $\mu\text{m}$ ) to yield stickiness, expressed as  $\mu\text{N}$  of force per mm of thread contact with the sandpaper plate. The mean sensitivities of the needles used to measure the species' stickiness, expressed as an absolute value and as a percent of each species mean stickiness value were: *Argiope trifasciata* 2.52  $\mu\text{N}/\text{mm}$ , 9.3%; *Araneus marmoreus*

2.59  $\mu\text{N}/\text{mm}$ , 7.5%; *Cyclosa conica* 1.91  $\mu\text{N}/\text{mm}$ , 16.7%; *Microthema gracilis* 1.76  $\mu\text{N}/\text{mm}$ , 6.2%; *Leucauge venusta* 3.38  $\mu\text{N}/\text{mm}$ , 16.9%.

I measured the stickiness of four thread samples from each individual's web and used their mean as that spider's value. Each measurement was made with an unused sector of a contact plate to avoid the possible effects of residue left by previous contact with a thread. The stickiness of all threads was measured 2–8 h after they were collected. The mean temperature at which each species threads were kept and measured was 23–25°C and the mean humidity was 60–62% RH.

*T*-tests showed that there were no differences between either the absolute sensitivities of needles or the relative sensitivities (expressed as a percentage of the mean stickiness of the species measured) of needles used to measure cribellar and adhesive threads (Table 1;  $t=1.62$ ,  $P=0.13$  and  $t=0.22$ ,  $P=0.83$ , respectively). Likewise, neither the consistency of stickiness measurements, expressed as the mean standard error of the mean of the four stickiness measurements taken from each individual's thread, nor this mean standard error expressed as a percentage of a species' mean stickiness, differed between cribellar and adhesive threads (Table 1;  $t=0.46$ ,  $P=0.65$  and  $t=0.58$ ,  $P=0.57$ , respectively).

The standard error of the mean stickiness of four different sectors of a spider's thread provides an index of the uniformity of these measurements. However, this value is not in the strict sense a measure of repeatability, because measuring the stickiness of a span of thread alters its surface properties and tension and precludes a second measurement of this strand from being taken. Duplicate measurements of an individual's thread may differ for at least three reasons: (1) thread features may not be absolutely uniform along the length of a thread, (2) cribellar threads are not symmetrical around the axial fibres and may present a slightly different surface area or configuration to a contact plate depending on their rotation, and (3) although the particles on the surface of sandpaper contact plates have a very uniform size and distribution (Opell, 1993), the number and configuration of the particles that a thread contacts varies slightly from measurement to measurement. These factors are not simply artifacts of the technique employed in this study, as they also affect the strength with which capture threads hold insect surfaces. Therefore, the mean of the four stickiness measurements of an individual spider's thread provides a more representative value of the thread's typical performance than does a single stickiness measurement.

#### *Capture thread volume*

I used formulas given in the Appendix to compute the volume of material invested in a mm length of adhesive thread from measurements made under a compound microscope. These measurements were made 2–4 h after a thread was collected and no more than 3 h before its stickiness was measured. Measurements were made at the same elevation and under very similar temperatures and relative humidities (Table 1), although it was not possible to control for differences in atmospheric pressure.

Threads were measured to the nearest  $\mu\text{m}$  at  $500\times$  under a light microscope. The microscope objective used to measure these threads had a numerical aperture of 0.70 and provided a resolution of  $0.4\mu\text{m}$ . A blind, randomized test of the repeatability of measurements of droplet and interdroplet regions was conducted

TABLE 2. The weights, capture thread volumes, capture thread lengths, total capture thread volumes, and total capture thread stickiness of uloborid (from Opell, 1996) and araneoid spiders. Values are presented as mean  $\pm$  1 SE. Computed ancestral values are given in brackets; for weights, value determined by independent, rooted analyses/value determined by combined, unrooted analysis

FAMILY species (sample size)	weight mg	thread volume $\mu\text{m}^3/\text{mm} \times 10^3$	thread length cm	total thread volume $\text{mm}^3$	total thread stickiness $\mu\text{N}$
<b>ULOBORIDAE</b>					
<i>Waitkera waitakerensis</i> (27)	7.7 $\pm$ 0.3 [6.3/26.4]	540.8	329 $\pm$ 28	1.65 $\pm$ 0.13 [1.44]	50.9 $\pm$ 4.3 [75.8]
<i>Siratoba referena</i> (23)	4.1 $\pm$ 0.2 [6.3/26.4]	290.6	242 $\pm$ 25	0.73 $\pm$ 0.06 [1.44]	27.8 $\pm$ 2.9 [75.8]
<i>Hyphotes gertschi</i> (41)	8.2 $\pm$ 0.2 [7.8/11.7]	1219.4	146 $\pm$ 7	1.65 $\pm$ 0.07 [1.71]	43.6 $\pm$ 1.9 [50.7]
<i>Hyphotes cavatus</i> (27)	8.1 $\pm$ 0.6 [7.8/11.7]	1166.6	169 $\pm$ 8	1.74 $\pm$ 0.08 [1.71]	44.3 $\pm$ 2.2 [50.7]
<i>Miagrammopes animotus</i> (38)	6.5 $\pm$ 0.4 [6.2/10.0]	825.1	81 $\pm$ 5	0.68 $\pm$ 0.04 [1.05]	25.6 $\pm$ 1.6 [37.4]
<i>Miagrammopes species</i> (25)	4.8 $\pm$ 0.3 [6.2/10.0]	794.4	91 $\pm$ 5	0.72 $\pm$ 0.04 [1.05]	22.27 $\pm$ 1.2 [37.4]
<i>Uloborus glomosus</i> (27)	6.8 $\pm$ 0.3 [8.9/17.9]	695.2	392 $\pm$ 27	2.77 $\pm$ 0.17 [3.69]	60.3 $\pm$ 4.2 [101.6]
<i>Otonoba sinensis</i> (24)	12.2 $\pm$ 0.8 [8.9/17.9]	704.8	821 $\pm$ 46	5.83 $\pm$ 0.29 [3.69]	139.7 $\pm$ 7.7 [101.6]
<b>ARANEIDAE</b>					
<i>Argiope trifasciata</i> (25)	474.0 $\pm$ 51.6 [352.9/335.5]	178.0 $\pm$ 30.8	2321 $\pm$ 173	4.13 $\pm$ 0.31 [4.01]	630.4 $\pm$ 47.0 [474.9]
<i>Araneus marmoreus</i> (15)	677.1 $\pm$ 75.0 [397.9/391.4]	484.1 $\pm$ 54.5	2204 $\pm$ 139	10.67 $\pm$ 0.67 [5.76]	766.0 $\pm$ 48.4 [529.5]
<i>Cyclosa conica</i> (23)	8.9 $\pm$ 0.8 [163.7/161.5]	23.0 $\pm$ 2.0	692 $\pm$ 55	0.16 $\pm$ 0.01 [2.60]	79.4 $\pm$ 6.3 [347.4]
<i>Micrathena gracilis</i> (21)	84.3 $\pm$ 5.0 [163.7/161.5]	123.5 $\pm$ 8.9	1529 $\pm$ 81	1.89 $\pm$ 0.10 [2.60]	433.3 $\pm$ 22.9 [347.4]
<b>TETRAGNATHIDAE</b>					
<i>Leucauge venusta</i> (18)	20.6 $\pm$ 1.7 [186.7/141.2]	32.9 $\pm$ 2.4	859 $\pm$ 69	0.28 $\pm$ 0.02 [2.15]	171.8 $\pm$ 13.9 [265.1]

during a 1 h period using 8-month-old thread samples of *Micrathena gracilis* to insure that droplet volume was stable. During this test, a total of ten measurements of two droplets and two interdroplet regions were taken at  $500\times$  and, to vary this exercise, ten measurements of one droplet were taken at  $250\times$ . The diameter measurements of the two interdroplet regions were an invariant  $4\ \mu\text{m}$ . The diameters and standard errors of the mean of the two droplets measured at  $500\times$  were  $34.2 \pm 0.4\ \mu\text{m}$  and  $31.2 \pm 0.5\ \mu\text{m}$ . Thus, both the repeatability and resolution of measurement of adhesive thread features are about  $0.4\ \mu\text{m}$ . This level of precision has the greatest effect on measurements of interdroplet diameter. However, as interdroplet volume constitutes only 2–9% of total volume (Table 3), this has only a small affect on the computation of total thread volume.

#### Capture thread length

Using the formulas given in the Appendix, I computed the length of each web's capture thread as if it were a series of concentric circles, rather than a continuous spiral (Eberhard, 1986). Measurements used in these calculations were taken from

enlarged photographic prints of webs that were dusted with corn starch to make their threads more visible (Carico, 1977). After photographing a spider's web, I recorded several reference measurements for use in determining photograph magnification and then collected and weighed the spider. The large webs of *A. trifasciata*, *A. marmoreus*, and *M. gracilis* were photographed in the field with a black cloth as a background. *Cyclosa conica* and *L. venusta* constructed their smaller webs in denser vegetation where a black background could not be used. Therefore, I allowed members of these species to construct their webs in 25 × 37 cm plastic boxes with wooden dowel rods glued to their perimeters. These boxes were kept in an environmental chamber with a light, temperature, and humidity regime similar to that of the spiders' habitat. Boxes were large enough to accommodate the webs that members of these two species constructed in the field, as indicated by the fact that none of the webs constructed by *C. conica* and only three of the webs constructed by *L. venusta* had outermost spirals that came within 1 cm of a box's dowel rods.

The length of capture thread in each individual's orb-web was multiplied by the mean capture thread volume and stickiness values for its species (Table 1) to obtain the total capture thread volume and stickiness of its web (Table 2).

#### *Transformational analysis*

As the species included in this study are related to different degrees (Fig. 3), their weights and web features are not entirely independent, making it inappropriate to examine their relationships with traditional regression techniques (Harvey & Pagel, 1991). Therefore, I used a transformational analysis (Huey & Bennet, 1986, 1987) to analyse the relationships of these features in a phylogenetic context. To do this, I first determined the probable ancestral values of each species' features using the minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison, 1992). I then calculated the changes from these ancestral states to those expressed by each species and examined the relationships between these changes using regression techniques. The axial fibres of cribellar and adhesive threads are homologous, but the material that covers these fibres is not. Therefore, the ancestral spider weights and thread volumes used to compare the material invested in these two types of threads was determined independently for each type of thread, using the rooted option. As the stickiness of each type of capture thread was measured with the same methods and under the same conditions, the ancestral weights and stickiness values used to compare total web stickiness were determined from a phylogeny that included all species (Fig. 3) using the unrooted option.

#### RESULTS

Table 1 gives the stickiness and volume of a mm of each species' capture thread and Table 2 gives the total length of capture thread in each species' web and the web's total capture thread volume and total stickiness. Change in spider weight was log transformed because this improved the normality of weight data used in the analysis of thread volume (Shapiro-Wilk-W-Statistic  $P=0.43$  and  $0.56$  for adhesive

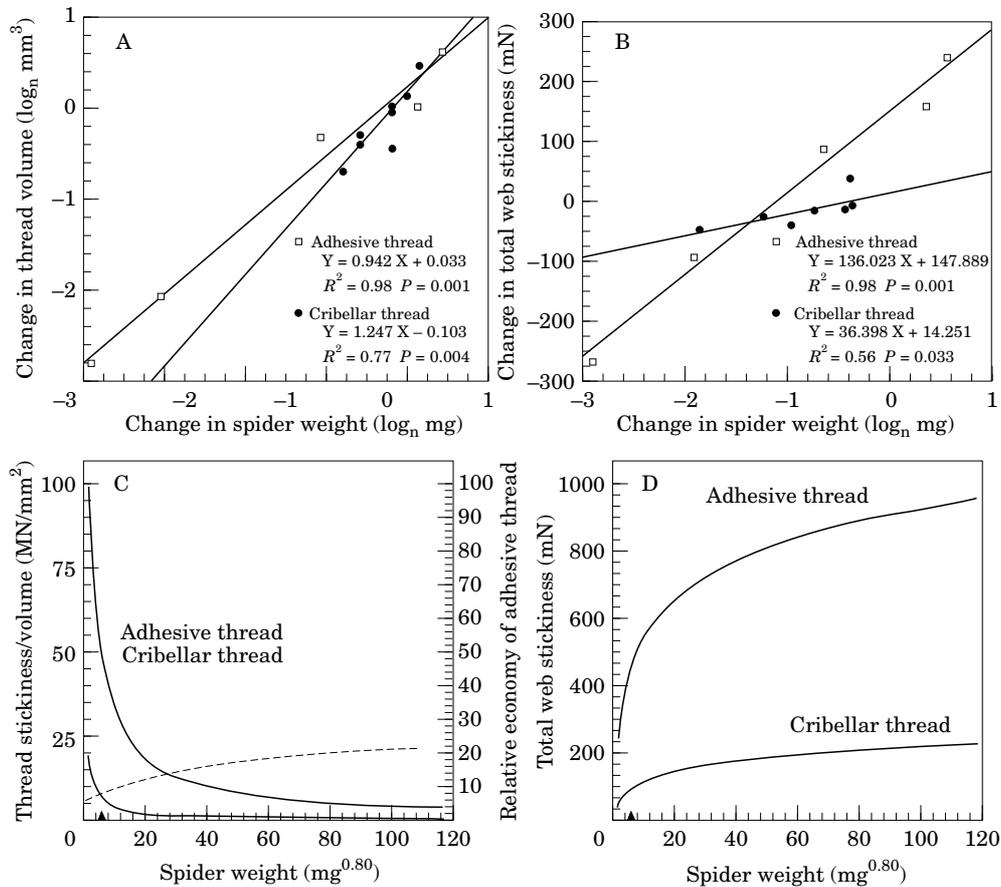


Figure 4. Relationships between spider weight and capture thread volume and total capture thread stickiness for webs containing cribellar and adhesive threads and models of thread economy and web stickiness based on these regressions. A, changes in spider weight and capture thread volume. B, changes in spider weight and total capture thread stickiness. C, comparison of the material cost of achieving capture thread stickiness. The upper line depicts webs with adhesive thread and the lower line webs with cribellar thread. The dashed line describes the economic benefit of adhesive thread, as determined by dividing its stickiness per volume by that of cribellar thread. D, comparison of the total stickiness of adhesive and cribellate orb-webs. In C and D spider weight is raised to a power of 0.80 to reflect spider metabolic rate (Anderson & Prestwich, 1982). Triangles denote a weight of 12 mg, the upper size of cribellate orb-weaving spiders.

and cribellate spiders, respectively) and thread stickiness ( $P=0.53$  and  $0.07$  for adhesive and cribellate spiders, respectively). Change in capture thread stickiness was normally distributed for both adhesive and cribellate orb-weavers ( $P=0.71$  and  $0.36$ , respectively), but change in thread volume did not become normal until log-transformed ( $P=0.48$  and  $0.96$ , respectively).

Transformational analyses show that in adhesive orb-weaving spiders, as in cribellate orb-weavers (Opell, 1996), both the total volume and total stickiness of a web's capture thread are correlated with spider weight (Fig. 4A, B). A test of the homogeneity of the regression slopes for the natural logs of capture thread volume

and spider weight shows that they are the same for cribellate and adhesive orb-weaving spiders (Fig. 4A;  $F=0.96$ ,  $P=0.35$ ). An analysis of the covariance test shows that the intercepts of these lines do not differ ( $F=1.48$ ,  $P=0.25$ ). The common regression for deinopoid and araneoid orb-weavers is described by the formula:  $\text{Log}_n \text{ thread volume} = \text{Log}_n \text{ spider weight} \times 0.918 - 0.067$  ( $r^2=0.96$ ,  $P=0.0001$ ). However, the slope of the regression line describing the relationship between spider weight and the total web stickiness of adhesive orb-webs is greater than that describing this relationship for cribellate orb-webs (Fig. 4B;  $F=26.93$ ,  $P=0.0006$ ). Thus, relative to spider weight, cribellate and adhesive orb-weavers invest a similar volume of material in the capture threads of their webs, but adhesive orb-webs achieve a greater total stickiness.

Using the regression formulas given in Figure 4A & B, Figure 4C presents a model of the relative economics of cribellate and adhesive orb-webs, as judged by the total stickiness they achieve relative to the material invested in their capture threads. In this model, weight is raised to a power of 0.80 to reflect spider metabolic rate (Anderson & Prestwich, 1982). Figure 4D compares the total stickiness of the capture threads of cribellate and adhesive orb-webs, one index of the prey capture potential of these webs.

#### DISCUSSION

The results of this study support the hypothesis that adhesive capture thread achieves its stickiness with a greater material economy than does cribellar thread (Fig. 4C). As adhesive and cribellate orb-weavers of the same size invest a similar total volume of material in their capture threads, this results in adhesive orb-webs having a greater total stickiness than cribellate orb-webs (Fig. 4D). Consequently, by employing adhesive capture threads, araneoids construct orb-webs that are better equipped to retain prey after they have been intercepted and the forces of their impacts have been absorbed by the web. This reduces the chance of a prey struggling from the web before a spider can locate, run to, and subdue it. This is borne out by studies of artificial spider webs which show that increased thread stickiness increases the number of prey retained by a thread network (Chacón & Eberhard, 1980). Additionally, both spiders that produce cribellate threads and those that produce adhesive threads produce stickier capture threads as they develop (Opell, 1995, unpublished observations). This appears to be one of the factors responsible for the ability of more mature spiders to capture larger and presumably more profitable prey (Eberhard, 1990, 1989; Opell, 1990).

Araneoid orb-weavers of all sizes benefit from the greater material economy with which adhesive capture thread achieves its stickiness. Additionally, as spider weight increases, so too does the economic advantage of producing adhesive thread (Fig. 4C). Likewise, the total stickiness of orb-webs increases more rapidly among spiders that produce adhesive threads than among those that produce cribellar threads. Thus, there appear to be more severe limits on the size of cribellate than adhesive orb-weavers. This may help explain why large body size has evolved only among the latter. The largest cribellate orb-weavers weigh little more than 12 mg, whereas adhesive orb-weavers may weigh in excess of 400 mg. By the time a uloborid reaches a weight of 12 mg, the economy with which its cribellar thread achieves stickiness

has dropped precipitously and the total stickiness of its web will increase at a much slower rate. Consequently, the efficiency of producing and using a cribellate orb-web appears to decline after a spider reaches a weight of about 12 mg.

If the models presented in Figures 4C, D apply to developing spiders as well as to adult spiders of different weights, they suggest that adhesive orb-weavers are capable of developing more rapidly than cribellate orb-weavers. In temperate regions, where orb-weavers complete their life cycle during a single spring-fall growing season, the greater economy and stickiness of adhesive orb-webs would allow these spiders to capture more prey at a lower cost and, thereby, enable them to develop more rapidly and reach a larger adult size than orb-weavers that produce cribellar threads. This increase in the range of weights at which adhesive orb-weaving species can mature appears to be another factor that contributes to the greater diversity of these spiders.

The important role that the economy of capture thread production plays in spider evolution is further emphasized by differences in thread stickiness among the Uloboridae. A small increase in the stickiness of these spiders' cribellar threads is achieved by an increase in the density of a spider's cribellar spinning spigots and changes in the configuration of the cribellar fibril puffs that form their threads (Opell, 1995). However, major increases in thread stickiness are associated with an increase in the number of cribellar fibrils that a spider invests in its thread (Opell, 1994b, 1995). In uloborids, this is accomplished by an increase in cribellum size and spigot number and has occurred in species that spin reduced webs containing much shorter lengths of cribellar thread (Opell, 1994b, 1996). As a result of these changes, small uloborid species that spin simple webs produce cribellar threads that are much stickier than those of much larger orb-weavers and nearly as sticky as adhesive threads of the largest araneids included in this study (Opell, 1994a). Thus, the stickiness of uloborid cribellar threads is limited not by the proximate factors of spider size or spinning anatomy, but by the ultimate factor of silk economy. Species that construct reduced webs can produce stickier and more costly capture threads only because they deposit shorter lengths of these threads than found in an orb-web constructed by a spider of similar mass (Opell, 1996). This conclusion is further supported by studies indicating that both adhesive orb-weavers (Eberhard, 1986; Peters, 1937; Witt, Reed & Peakall, 1968) and cribellate orb-weavers (Eberhard, 1972, 1986) use nearly all of their capture thread reserve in constructing an orb-web, but not all of their non-sticky thread reserve (Koenig, 1951; Eberhard, 1986).

As spiders are silk-producing predators, it is not surprising that their evolution is associated with the origin of new types of silk and new methods of capturing prey. The origin of both cribellar thread and aerial webs that were capable of capturing flying insects established the Infraorder Araneomorphae, a clade that contains 86% of all spider families and 94% of all living spider species (Coddington & Levi, 1991). The origin of the orb-web marked the beginning of the Orbiculariae clade (orb-weaving spiders and their descendants, Coddington & Levi, 1991). However, as only about 5% of the orb-weaving species produce cribellar thread, the full potential of this web architecture appears not to have been realized until adhesive thread replaced cribellar thread and marked the beginning of the Araneoidea clade that contains modern orb-weaving spiders.

Adhesive capture thread has several functional advantages over cribellar thread. These include: (i) its lower cost and greater stickiness that increase web stickiness

without increasing web cost (this study), (ii) its unique windlass mechanism that increases thread extensibility (Köhler & Vollrath, 1995; Vollrath & Edmonds, 1989), thereby permitting a web to better absorb the force of a prey strike (Craig, 1987a; Eberhard, 1989), and (iii) its altered spectral properties that reduce its visibility to insects and increase the likelihood that they will strike the web (Craig *et al.*, 1994). Without the combined benefits of these features, orb-weavers may not have become the large and diverse group that they are today.

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## APPENDIX

*Formulas used to compute thread volume and length*

*Volume of adhesive capture thread in  $\mu\text{m}^3/\text{mm}$  length*

D = distance spanned by a series of droplets

N = number of droplets in series

I = interdroplet diameter

$L_{a,b}$  = lengths of two droplets (dimension parallel to thread length)

$W_{a,b}$  = widths of two droplets

Subscripts 1 and 2 refer to the two thread sectors that were measured for each spider.

$$\text{Mean droplet radius (MDR)} = (L_{1a} + L_{1b} + L_{2a} + L_{2b} + W_{1a} + W_{1b} + W_{2a} + W_{2b})/16. \quad (1)$$

$$\text{Droplet volume (DV)} = 4 \times \pi \times \text{MDR}^3/3. \quad (2)$$

$$\text{Droplets per mm (DPMM)} = ((N_1 + N_2)/(D_1 + D_2)) \times 1000. \quad (3)$$

$$\text{Droplet volume per mm (DVPMM)} = \text{DV} \times \text{DPMM}. \quad (4)$$

$$\text{Total interdroplet length (TIL)} = (D_1 + D_2) - ((N_1 + N_2) \times \text{Mean L}). \quad (5)$$

$$\text{Number interdroplet sectors (IDS)} = N_1 + N_2 - 2. \quad (6)$$

$$\text{Mean interdroplet length (IL)} = \text{TIL}/\text{IDS}. \quad (7)$$

$$\text{Interdroplet volume (IV)} = \pi \times (I/2)^2 \times \text{IL}. \quad (8)$$

$$\text{Number interdroplet sectors per mm (ISPMM)} = (\text{IDS}/(D_1 + D_2)) \times 1000. \quad (9)$$

$$\text{Interdroplet volume per mm (IVPMM)} = \text{IV} \times \text{ISPMM}. \quad (10)$$

$$\text{Total volume of adhesive thread per mm} = \text{DVPMM} + \text{IVPMM}. \quad (11)$$

*Length of adhesive capture thread*

All measurements were taken in mm and corrected for photographic enlargement.

Maximum diameter of central region of web encompassed by its innermost capture thread spiral (CD1).

Minimum diameter of central region of web (CD2).

The number of spirals intercepted by four radii ( $NS_{1-4}$ ) that divide the web into approximately equal quadrants. In the vertical webs of *A. trifasciata*, *A. marmoreus*, *C. conica*, and *M. gracilis*, two of these radii were vertically oriented and two horizontally oriented, as radii below the hub tend to be longer than those above the hub.

The distance between the first and last spiral of these four radii ( $DS_{1-4}$ ).

$$\text{Mean diameter of central region (MCD)} = (\text{CD1} + \text{CD2})/2. \quad (12)$$

$$\text{Mean spiral number (SN)} = (NS_1 + NS_2 + NS_3 + NS_4)/4. \quad (13)$$

$$\text{Mean spiral spacing (SS)} = (DS_1 + DS_2 + DS_3 + DS_4)/ \quad (14)$$

$$(NS_1 + NS_2 + NS_3 + NS_4).$$

$$\text{Total capture thread length} = \quad (15)$$

$$(\pi \times \text{MCD}) + (\pi \times \text{MCD} + 2\text{MS}) + (\pi \times \text{MCD} + 4\text{MS}) + (\pi \times \text{MCD} + 6\text{MS}) \dots,$$

where each parenthetical expression represents the circumference of a successive capture thread spiral until a web's SN is reached.