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Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk

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Summary

1. The replacement of dry, fuzzy cribellar prey capture thread by viscous, adhesive capture thread was a major event in the evolution of orb-weaving spiders. Over 95% of all orb-weaving species now produce adhesive threads.
2. Adhesive thread achieves its stickiness with a much greater material economy than does cribellar thread.
3. Transformational analyses show that, relative to spider mass, adhesive orb-weavers invest less material per mm of capture thread and produce stickier capture threads than do cribellate orb-weavers.
4. The total cost of producing an orb-web that contains cribellar thread is reduced by 32% when a spider recycles its silk and another 34% when these capture threads are replaced by adhesive threads of equal stickiness.
5. The increased economy with which adhesive capture thread achieves its stickiness may have been an important factor that favoured the origin and success of modern orb-weaving spiders that produce adhesive capture threads.

Key-words: Araneidae, cribellar thread, orb-web evolution, Tetragnathidae, Uloboridae

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Introduction

Spiders have used orb-webs to capture prey for over 130 million years (Selden 1989). Today, over 4000 species produce these intricate snares (Levi 1982), whose success depends heavily on their sticky capture threads. These threads intercept insects, help absorb the force of their impact, and retain struggling prey until the spider can locate, run to and subdue them (Chacón & Eberhard 1980; Craig 1987a,b; Eberhard 1986, 1989, 1990). Ancestral orb-weaving spiders produced dry prey capture threads like those found in the less highly organized webs of non-orb-weavers. The replacement of these threads with viscous adhesive capture threads (Coddington & Levi 1991) was a pivotal event in spider evolution that was associated with an increase in the number of species, genera and families of orb-weaving spiders (Craig, Bernard & Coddington 1994). Today over 95% of all orb-weaving spider species produce adhesive capture threads (Bond & Opell 1998; Coddington & Levi 1991).

Only members of the family Uloboridae spin orb-webs that contain dry capture threads termed cribellar threads (Fig. 1a). The outer surface of this thread consists of thousands of fine, looped protein fibrils that are spun from spigots on an abdominal spinning plate termed the cribellum (Fig. 1b; Opell 1993, 1994a,b, 1995; Peters 1984, 1992). These fibrils surround a pair of larger, supporting axial fibres (Eberhard 1988;

Eberhard & Pereira 1993; Peters 1983, 1986). The Uloboridae and the Deinopidae, whose members construct highly modified webs that are derived from orb-webs (Coddington 1986), form the superfamily Deinopoidea. The sister group of this lineage, the superfamily Araneoidea, includes six families of orb-weavers that produce adhesive capture threads. These spiders have lost the cribellum and coat their axial fibres with a viscous solution as these fibres leave the spinnerets. This complex aqueous solution contains low molecular mass organic and inorganic compounds, a variety of small proteins, and high molecular mass glycoproteins (Vollrath *et al.* 1990; Townley *et al.* 1991; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast *et al.* 1993). Immediately after being deposited, this solution coalesces into a series of regularly spaced viscous droplets (Fig. 1c). Glycoprotein nodules within these droplets confer thread stickiness (Vollrath *et al.* 1990; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast *et al.* 1993; Peters 1995).

A critical functional property that may help explain the apparent selective advantage of adhesive thread over cribellar thread and the success of the Araneoidea is capture thread stickiness. This study tests the hypothesis that adhesive thread achieves a greater stickiness relative to its material cost than does cribellar thread (Lubin 1986; Vollrath 1992; Opell 1994b). It does so by comparing cribellar threads spun by eight species of the family Uloboridae with

adhesive threads spun by four species of the family Araneidae and one species of the family Tetragnathidae. Using transformational analyses, it also tests two corollaries of this hypothesis: (1) relative to spider mass, orb-weavers that produce adhesive threads invest less material per mm of capture thread than do those that produce cribellar threads and (2) relative to spider mass, adhesive threads are stickier than cribellar threads.

Greater capture thread stickiness enhances a web's ability to retain the prey that it has intercepted, allowing a spider more time to locate and subdue these struggling insects before they escape from the web (Chacón & Eberhard 1980; Eberhard 1989, 1990). If adhesive thread achieves its stickiness at a lower cost than cribellar thread, then orb-weavers that produce adhesive threads could invest less material in their threads and maintain the prey capture potential of their webs. Alternatively, they could increase the prey capture potential of their webs by producing stickier capture thread and still expend no more material than do cribellate orb-weavers.

The first part of this study tests the hypotheses that adhesive capture thread achieves its stickiness at a greater material economy than does cribellar thread and that this permits these spiders to produce, at no increase in material cost, capture thread that is stickier than that produced by cribellate orb-weavers. These hypotheses are tested using the comparative method of evolutionary biology (Harvey & Pagel 1991). This

is done by first establishing that, in each group of orb-weavers, there are functional trends that relate spider size to the volume of material invested in each mm of capture thread and to the stickiness of this thread. This study next determines that the origin of modern orb-weaving spiders that construct adhesive capture threads was associated with a reduction in the cost of capture thread and an increase in its stickiness.

Another factor that may improve the economy of orb-web use is silk recycling. Many orb-weaving spiders ingest silk as they take down their webs and recycle it when they construct future webs, thereby reducing web cost (Breed *et al.* 1964; Peakall 1971; Carico 1986; Townley & Tillinghast 1988). Silk recycling appears to be a plesiomorphic behaviour of orb-weaving spiders, as it is exhibited by both Deinopoidea and Araneoidea (Breed *et al.* 1964; Peakall 1971; Carico 1986; Lubin 1986; Townley & Tillinghast 1988). However, the energetic importance of this behaviour is unknown because the degree to which it increases the economy of orb-web use has not been evaluated.

The second part of this study uses information about the material cost of capture threads and the length of capture threads in orb-webs to quantify the relative importance of silk recycling and to model the cost of constructing an orb-web under three scenarios: (1) the use of cribellar capture thread without thread recycling, (2) the use of cribellar capture thread with recycling and (3) the use of adhesive capture thread with silk recycling. It puts this cost in perspective by estimating the mass of prey that a spider must capture to recover the material and behavioural cost of constructing a web under each of these scenarios. Only prey capture beyond this threshold is available to meet a spider's metabolic, growth and reproductive needs.

Materials and methods

SPECIES STUDIED

This study includes measurements of cribellar threads produced by eight species of the family Uloboridae and adhesive threads produced by four species of the family Araneidae and one species of the family Tetragnathidae (Table 1, Fig. 2). Species were chosen to represent the major clades within the Uloboridae and Araneidae (Coddington 1990; Levi 1985).

Uloborid representatives include four species that construct orb-webs and four species that construct reduced capture webs which contain shorter lengths of stickier prey capture threads (Lubin 1986; Opell 1994a, 1996). As cribellar fibril measurements were not available for *Philoponella arizonica*, this species is included only in comparisons of mass-specific thread stickiness.

THREAD STICKINESS

Capture threads were collected from newly constructed orb-webs on microscope slides to which

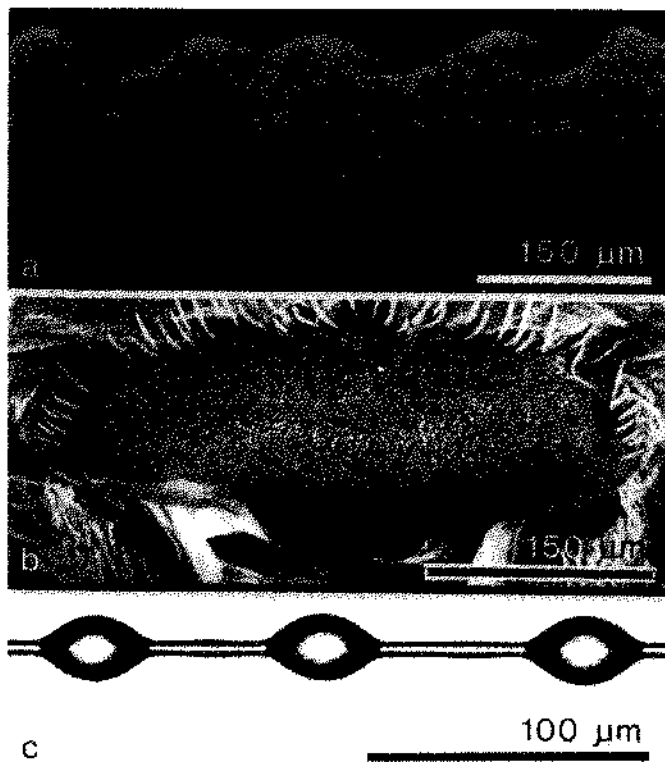


Fig. 1. (a) Cribellar thread of *Hyptiotes cavatus* (scanning electron micrograph, SEM). (b) Cribellum of *Waitkera waitakerensis* (SEM). (c) Adhesive thread of *Argiope trifasciata* (light micrograph).

raised supports were glued at 4–8-mm intervals. After a sample was taken, the spider was collected and weighed. Thread stickiness was measured with a strain gauge that incorporated a glass or stainless steel needle (Opell 1994a, 1994c) that passed over a linear scale. The deflection of both types of needle was linear relative to the force applied. This instrument was calibrated in a vertical orientation where its needle moved downward along the scale as a succes-

sion of 5-mg analytical balance riders were added to the contact plate on the needle's tip until a total of 30–60 mg (depending on the needle's sensitivity) had been added. The needle's position on the scale was then plotted against the mass on the needle's tip and a straight line was drawn through these points. For stickiness measurement, this instrument was positioned horizontally so that the mass of the needle and contact plate deflected the needle downward slightly

Table 1. Spider masses and capture thread stickiness values (means \pm 1 standard error). Values for Uloboridae are from Opell (1994a, 1996). The ancestral values for features included in transformational analyses are given in brackets. The ancestral mass used to compare thread volume precedes that used to compare thread stickiness. The stickiness of uloborid capture threads was measured between 23 and 27 °C

| Family Web type Species (sample size) | Mass (mg) | Stickiness ($\mu\text{N mm}^{-1}$) | Measurement precision (μN) % species mean | Measurement uniformity ($\mu\text{N mm}^{-1}$) % species mean | Temp. (°C) | Percentage relative humidity |
|---------------------------------------------------------|------------------------------------|-----------------------------------------|--------------------------------------------------------------|--------------------------------------------------------------------------|---------------|------------------------------------|
| Uloboridae | | | | | | |
| Horizontal orb-webs: | | | | | | |
| 1. <i>Waitkera waitakerensis</i> (38) (Chamberlain) | 8.97 \pm 0.46 [7.20, 7.16] | 15.45 \pm 0.82 [15.18] | 1.37 8.9% | 3.07 19.9% | – | 68 \pm 0.3 |
| 2. <i>Siratoba referena</i> (26) (Muma & Gertsch) | 4.42 \pm 0.22 [7.20, 7.16] | 11.46 \pm 0.80 [15.18] | 1.78 15.3% | 1.66 14.2% | – | 66 \pm 0.4 |
| 3. <i>Uloborus glomus</i> (32) (Walckenaer) | 9.39 \pm 0.49 [10.12, 9.81] | 15.38 \pm 1.02 [16.76] | 2.86 18.5% | 4.02 25.9% | – | 56 \pm 0.1 |
| <i>Philoponella arizonica</i> (27) (Gertsch) | 13.35 \pm 0.86 [–, 11.97] | 14.97 \pm 1.11 [16.25] | 1.78 11.9% | 2.55 17.0% | – | 66 \pm 0.3 |
| 4. <i>Octonoba sinensis</i> (36) (Simon) | 12.74 \pm 0.73 [10.12, 11.97] | 17.02 \pm 1.19 [16.25] | 2.68 15.7% | 4.22 24.7% | – | 55 \pm 0.1 |
| Triangle-webs: | | | | | | |
| 5. <i>Hyptiotes cavatus</i> (56) (Hentz) | 8.11 \pm 0.57 [8.42, 8.40] | 26.18 \pm 1.70 [26.67] | 1.73 7.4% | 5.37 22.9% | – | 58 \pm 0.2 |
| 6. <i>Hyptiotes gertschi</i> (32) Chamberlain & Ivie | 9.83 \pm 0.56 [8.42, 8.40] | 29.84 \pm 2.17 [26.67] | 1.78 5.9% | 6.82 22.7% | – | 55 \pm 0.4 |
| Simple webs: | | | | | | |
| 7. <i>Miagrammopes animotus</i> (101) Chickering | 4.96 \pm 0.23 [5.35, 5.33] | 31.50 \pm 1.78 [26.63] | 1.69 5.6% | 5.53 18.5% | – | 62 \pm 0.4 |
| 8. <i>Miagrammopes</i> species (24) | 3.75 \pm 0.24 [5.35, 5.33] | 24.41 \pm 2.07 [26.63] | 1.78 7.2% | 5.74 23.3% | – | 65 \pm 0.4 |
| Araneidae | | | | | | |
| Vertical orb-webs: | | | | | | |
| 9. <i>Argiope trifasciata</i> (21) (Forsk.) | 340.4 \pm 33.2 [237.5, 276.5] | 27.15 \pm 1.99 [25.56] | 2.52 9.3% | 6.89 25.4% | 23 \pm 0.3 | 60 \pm 0.5 |
| 10. <i>Araneus marmoreus</i> (22) Clerck | 646.9 \pm 63.9 [364.8, 358.5] | 34.76 \pm 4.21 [27.60] | 2.59 7.5% | 5.21 15.0% | 23 \pm 0.2 | 61 \pm 0.2 |
| 11. <i>Cyclosa conica</i> (20) (Pallas) | 7.42 \pm 0.34 [154.2, 152.1] | 11.47 \pm 1.03 [22.47] | 1.91 16.7% | 2.06 17.9% | 24 \pm 0.1 | 61 \pm 0.5 |
| 12. <i>Micrathena gracilis</i> (20) (Walckenaer) | 90.4 \pm 5.5 [154.2, 152.1] | 28.34 \pm 3.12 [22.47] | 1.76 6.2% | 5.46 19.2% | 23 \pm 0.2 | 62 \pm 0.4 |
| Tetragnathidae | | | | | | |
| Horizontal orb-web: | | | | | | |
| 13. <i>Leucauge venusta</i> (26) (Walckenaer) | 28.1 \pm 2.3 [237.5, 130.6] | 20.01 \pm 2.50 [21.93] | 3.38 16.9% | 4.25 21.3% | 25 \pm 0.1 | 61 \pm 0.5 |

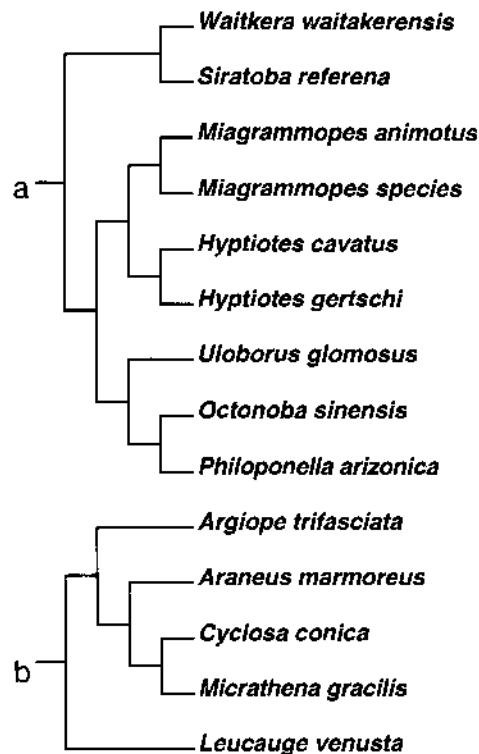


Fig. 2. Phylogeny of uloborid (a) and araneoid (b) species included in this study (after Coddington & Levi 1991; Levi 1985).

toward rather than along the scale. Thus, differences in the masses of contact plates did not affect the value registered by the needle. The needle's horizontal resting position was marked on the graph described above and a line drawn through this point and parallel to the initial calibration line. This second line was offset to the left of the first and was used to determine thread stickiness because it factored out the mass of the needle and contact plate and indicated only the mg equivalent of the force required to deflect the needle horizontally. This value was multiplied by the accelerating force of gravity, to obtain the μN of force necessary to deflect the needle to a given scale value.

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 1993) and these plates registered the same stickiness for both cribellar and adhesive threads as did contact plates made from fleshfly (*Sarcophaga bullata* Parker) wings (Opell 1994a, 1997). Thus, the stickiness values obtained by this method are similar to those registered by a representative insect surface.

A motorized advancement mechanism pressed the sandpaper contact plate against a thread at a constant speed (13.5 mm min^{-1} for cribellar thread and 10.7 mm min^{-1} for adhesive thread) until a force of 19.61 $\mu\text{N mm}^{-1}$ of thread contact was achieved. The sandpaper plate was then immediately withdrawn by

this mechanism at a constant speed (14.0 mm min^{-1} for cribellar thread and 10.4 mm min^{-1} for adhesive thread) until it pulled free from the thread. The force registered by the strain gauge immediately before this occurred was divided by contact plate's width (measured to the nearest 20 μm) to yield stickiness, expressed as μN of force per mm of thread contact with the sandpaper plate. The mean sensitivity of needles used to measure the stickiness of each species' threads is given in Table 1. The stickiness of four thread samples was measured for each specimen and their mean used as a spider's value. Thread stickiness was measured at 23–27 °C and 55–68% r.h. (Table 1). The mean humidity at which the stickiness of both cribellar and adhesive threads was measured was 61% r.h. Mean r.h. was normally distributed for araneoid species (Shapiro–Wilk W Statistic $P = 0.32$), but not for uloborid species ($P = 0.004$), but became so for both clades ($P > 0.11$) when r.h. was log-transformed. A t -test showed that these transformed values did not differ between the two clades ($t = 0.013$, $P = 0.99$).

The same procedures were used to measure the stickiness of cribellar and adhesive threads. However, two additional precautions were taken when measuring adhesive thread stickiness: (1) the stickiness of adhesive thread was measured within 2–8 h after collecting samples (compared with 2–40 h for cribellar threads) and (2) to avoid any effect of residue left on sandpaper plates by adhesive threads, the stickiness was measured of all adhesive threads with unused sectors of the contact plate. It is possible to document that cribellar fibrils do not accumulate on contact plates after repeated use (Opell 1993), but more difficult to determine if residue is left by adhesive threads.

The absolute sensitivity of the needles used to measure the stickiness of adhesive capture threads (Table 1) was normally distributed ($P = 0.601$), but that of needles used to measure the stickiness of cribellar threads was not ($P = 0.007$) and did not become so when log-transformed. However, a Wilcoxon rank sums test showed that the absolute sensitivities of the needles used to measure the stickiness of cribellar and adhesive threads did not differ ($Z = 1.348$, $P = 0.178$). The relative sensitivities (expressed as a percentage of the mean stickiness of the species measured) of needles used to measure the stickiness of cribellar and adhesive threads (Table 1) were normally distributed ($P = 0.221$ and 0.136, respectively) and a t -test showed that they did not differ between the two types of thread ($t = 0.22$, $P = 0.83$). Both the uniformity of stickiness measurements, expressed as the mean standard error of the mean of the four stickiness measurements taken from each individual's thread, and this mean standard error, expressed as a percentage of a species' mean stickiness (Table 1), were normally distributed for cribellar and adhesive threads ($P > 0.660$). Neither index differed between cribellar and adhesive threads (t -test, $t = 0.46$, $P = 0.65$ 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 artefacts 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 measurement.

THREAD VOLUME

The volume of a mm length of each species' cribellar thread was determined from species-specific cribellar fibril and axial fibre diameters reported in the literature (Opell 1994b,d, 1996). The total number of cribellar fibrils in a species' cribellar thread was determined from the mean number of spigots on its cribellum (Fig. 1b; Opell 1994b).

The volume of material invested in a mm length of adhesive thread was computed from measurements made less than 3 h before a thread's stickiness was measured. Threads were measured to the nearest μm at 500x 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 μm . A blind, randomized test of the repeatability of measurements of droplet and interdroplet regions was conducted during a 1-h period using 8-month-old thread samples of *Micrathena gracilis* to ensure that

droplet volume was stable. During this test, a total of 10 measurements were taken at 500x of two droplet and two interdroplet regions and, to vary the procedure, 10 measurements were taken at 250x of one droplet. Measurements of the two interdroplet regions were an invariant 4 μm and those of the droplet measured at 250x were an invariant 36 μm . The diameters and standard errors of the mean of the two droplets measured at 500x 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 μm . 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 2), this has only a small effect on the computation of total thread volume.

The volume of adhesive thread was determined from the following measurements made in μm (Fig. 3): (1) the distance (D) spanned by a series of droplets (N), (2) interdroplet diameter (I) and (3) the lengths (L , dimension parallel to thread length) and widths (W) of two droplets. Two thread sectors were measured for each spider and subscripts 1 and 2 refer to their measurements. Using the following formulas, the μm^3 of adhesive thread per mm of thread length was computed:

$$\text{Mean droplet radius (MDR)} = (\text{grand mean of } L \text{ and } W)/2, \quad \text{eqn 1}$$

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

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

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

$$\text{Total interdroplet length (TIL)} = (D_1 + D_2) - [(N_1 + N_2) \times \text{mean } L], \quad \text{eqn 5}$$

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

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

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

$$\text{Number interdroplet sectors per mm (ISPM)} = [\text{IDS}/(D_1 + D_2)] \times 1000, \quad \text{eqn 9}$$

$$\text{Interdroplet volume per mm (IVPMM)} = \text{IV} \times \text{ISPM}, \quad \text{eqn 10}$$

Table 2. Volume of adhesive capture threads produced by members of the families Araneidae and Tetragnathidae (mean \pm 1 standard error). Ancestral values are given in brackets

| Species (sample size) | Droplet length (μm) | Droplet width (μm) | Interdroplet diameter (μm) | Droplets per mm | Thread volume ($\mu\text{m}^3 \text{ mm}^{-1} \times 10^3$) | Mean interdroplet volume (%) |
|---------------------------------|----------------------------------|---------------------------------|-----------------------------------------|-----------------|---------------------------------------------------------------|------------------------------|
| <i>Argiope trifasciata</i> (20) | 36.7 \pm 2.1 | 25.2 \pm 1.4 | 4.7 \pm 0.3 | 9.7 \pm 0.8 | 178.0 \pm 30.8 [156.5] | 8.7 |
| <i>Araneus marmoreus</i> (22) | 59.0 \pm 3.5 | 46.3 \pm 3.1 | 4.7 \pm 0.2 | 7.0 \pm 0.8 | 484.1 \pm 54.5 [272.3] | 2.7 |
| <i>Cyclosa conica</i> (20) | 11.7 \pm 0.6 | 9.6 \pm 0.5 | 1.7 \pm 0.0 | 33.7 \pm 2.1 | 23.0 \pm 2.0 [139.6] | 8.0 |
| <i>Micrathena gracilis</i> (20) | 25.2 \pm 0.9 | 20.1 \pm 0.7 | 2.3 \pm 0.1 | 19.9 \pm 0.8 | 123.5 \pm 8.9 [139.6] | 1.8 |
| <i>Leucauge venusta</i> (26) | 12.5 \pm 0.5 | 10.1 \pm 0.4 | 2.0 \pm 0.0 | 41.3 \pm 2.0 | 32.9 \pm 2.4 [156.5] | 6.1 |

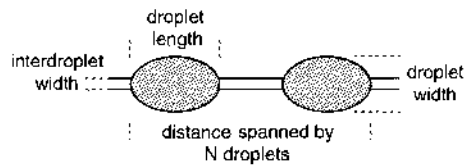


Fig. 3. Diagram of measurements used to compute adhesive thread volume.

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

RELATIONSHIP OF SPIDER MASS TO THREAD VOLUME AND STICKINESS

A transformational analysis was used to analyse the relationships of thread features and spider size in a phylogenetic context (Huey & Bennet 1986, 1987; Harvey & Pagel 1991). The ancestral values of each character were first determined, using the minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison 1992). The changes from these ancestral states to those expressed by each species were then calculated and the relationships between these changes examined using regression techniques. Statistical tests with $P < 0.10$ are considered significant.

In addition to orb-weaving species, the family Uloboridae includes the genus *Hypitotes*, whose members construct triangle-webs, and the genus *Miagrammopes*, whose members construct irregular, simple webs that contain progressively shorter and stickier lengths of cribellar capture thread (Lubin, Eberhard & Montgomery 1978; Opell 1982, 1990, 1994a; Lubin 1986). Data for four reduced-web species (Table 1) are included in the transformational analysis, as they document the stickiness that cribellar thread can achieve and maximize the resolution of the transformational analysis used to determine the ancestral values of uloborid species that construct orb-webs.

Because the material that covers the axial threads of cribellar and adhesive threads is not homologous, independent, unrooted character tracing was used to determine the ancestral values of capture thread volume and of the spider masses used in its analysis. In contrast, the stickiness of cribellar and adhesive threads were measured in the same way and under the same conditions. Therefore, an unrooted analysis was used to determine the ancestral stickiness and mass values of the Uloboridae and then the Uloboridae was used as an outgroup in a rooted analysis of Araneoidea ancestral values.

THE MATERIAL COST OF CAPTURE THREAD PRODUCTION WITH AND WITHOUT SILK RECYCLING

This study expresses the cost of web construction by uloborids as the dry mass of a web's silk threads plus the mass equivalent of the behavioural cost of

synthesizing and deploying these threads. Cost is expressed as mg rather than joules, as this seems more appropriate for the precision of this study's methods and data and the general models that it develops.

Measurements of four species of the family Uloboridae that construct orb-webs and four species that construct simpler webs (Opell 1996) show that the total volume of sticky and nonsticky threads in a spider's web is given by the formula:

$$\text{Silk volume in mm}^3 = \text{Spider mass in mg} \times 0.563 - 0.002. \quad \text{eqn 12}$$

Silk volume was converted to silk mass based on a silk density of 1.26 (Wainwright *et al.* 1982) using the formula:

$$\text{Silk mass} = \text{mm}^3 \text{ silk} \times 1.26 \text{ mg mm}^{-3}. \quad \text{eqn 13}$$

The behavioural cost of building a web is estimated to be 20% of the material cost (Eberhard 1986) and the total material and energetic cost of web construction is given by the formula:

$$\text{Total cost of web construction} = \text{mg silk} \times 1.2. \quad \text{eqn 14}$$

It is clear that silk recycling increases the economy of web use. However, studies of the efficiency of recycling by orb-weaving spiders that produce adhesive capture threads yield very different values. These savings range from 97% (Peakall 1971), to 50% (Breed *et al.* 1964), to 32% (Townley & Tillinghast 1988). The conservative model developed here assumes that (1) 32% of the silk in an old web is recycled into a new web, (2) that this value includes the metabolic cost of silk recycling and (3) that cribellar and adhesive threads are recycled with the same efficiency. The cost of constructing a web with recycled silk is given by the formula:

$$\text{Web cost with recycling} = \text{mg silk} \times 0.68. \quad \text{eqn 15}$$

Relative to the volume of material they contain, adhesive capture threads are stickier than cribellar threads. Adhesive capture threads achieve an average of 377 503 μN of stickiness per mm^3 of material invested, compared with 28 668 $\mu\text{N mm}^{-3}$ for cribellar threads (this study). Consequently, adhesive threads could achieve the same stickiness as cribellar threads at only 8% of the material cost. However, capture threads are responsible for only part of a web's total silk volume. The volume of cribellar fibrils (the capture thread components responsible for thread stickiness; Opell 1994b, 1995) in the orb-webs of four species of Uloboridae averages 37% of the web volume (Table 3). Thus, a 92% reduction in the material devoted to establishing capture thread stickiness would lower the average total cost of web production by 34%. This saving is similar to that resulting from silk recycling and is described by the formula:

$$\text{Web cost with reduced capture thread cost} = \text{mg silk} \times 0.66. \quad \text{eqn 16}$$

Table 3. Silk volumes for four orb-weaving species of Uloboridae from Opell (1996). Mean \pm 1 standard error

| | <i>Waitkera waitakerensis</i> (<i>N</i> = 27) | <i>Siratoba referena</i> (<i>N</i> = 23) | <i>Uloborus glomusosus</i> (<i>N</i> = 27) | <i>Octonoba sinensis</i> (<i>N</i> = 24) |
|----------------------------------------------------|---------------------------------------------------|----------------------------------------------|------------------------------------------------|----------------------------------------------|
| Mass (mg) | 7.70 \pm 0.28 | 4.09 \pm 0.23 | 6.83 \pm 0.34 | 12.16 \pm 0.79 |
| Frame & radial thread volume (mm ³) | 1.20 \pm 0.08 | 1.02 \pm 0.08 | 2.94 \pm 0.15 | 3.31 \pm 0.16 |
| Cribellar thread: | | | | |
| Fibril volume (mm ³) | 1.38 \pm 0.11 | 0.38 \pm 0.04 | 2.15 \pm 0.15 | 3.70 \pm 0.20 |
| Axial fibril volume (mm ³) | 0.28 \pm 0.02 | 0.36 \pm 0.03 | 0.63 \pm 0.03 | 2.13 \pm 0.11 |
| Total volume (mm ³) | 1.63 \pm 0.13 | 0.73 \pm 0.06 | 2.77 \pm 0.17 | 5.83 \pm 0.29 |
| Total web: | | | | |
| Silk volume (mm ³) | 2.85 \pm 0.20 | 1.75 \pm 0.13 | 5.72 \pm 0.30 | 9.14 \pm 0.44 |
| Percent cribellar fibril volume | 48 | 22 | 38 | 40 |

The savings incurred by a spider that produces cheaper capture thread and practises silk recycling is the product of the savings of these two strategies. The total cost of producing a web under this scenario is given by the formula:

$$\text{Web cost with silk recycling and less costly capture thread} = \text{mg silk} \times 0.45. \quad \text{eqn 17}$$

As these computations are based on the wet mass of adhesive thread, they provide a more conservative estimate of the cost of adhesive orb-webs. However, when the wet mass of adhesive thread is converted to dry mass under the assumption of a 80% water content (Gosline, DeMont & Denny 1986), the results differ only slightly: the multiplier in equation 16 is reduced to 0.636 and that in equation 17, 0.43.

THE THRESHOLD OF PROFITABILITY FOR PREY CAPTURE

Feeding data for the uloborid species *Hyptiotes cavatus* fed on *Drosophila melanogaster* fruit flies (Opell 1988) were used to determine the mass of prey a spider must capture to recover the total cost of constructing a web. This laboratory study probably determines maximum prey extraction values, as spiders fed on

small, soft-bodied insects and were neither disturbed during feeding nor presented with other prey. The mean wet mass of a *D. melanogaster* fruitfly is 0.85 mg (B. D. Opell, unpublished data) and the mean dry mass is 0.19 mg (Opell 1988). Adult female *H. cavatus* extract 0.16 mg dry mass of material from these flies (Opell 1988). Thus, the dry mass of nutrients extracted from a fly is 18.8% of the fly's live mass. To recover the material and energetic cost of constructing a capture web, a spider feeding with this efficiency must consume prey whose live mass is 5.319 times the total material and behavioural cost of its web, as described by the three scenarios.

Results

ECONOMY OF THREAD STICKINESS

Tables 1, 2 and 4 present the masses, stickiness values and capture thread volumes of the species studied and of their immediate hypothetical ancestors. Figure 4 compares the stickiness achieved per mm³ of material invested in cribellar and adhesive threads. Values are normally distributed for both cribellar and adhesive threads ($P = 0.610$ and 0.370 , respectively). The values of adhesive threads exceed those of cribellar threads

Table 4. Volume of cribellar threads produced by members of the family Uloboridae. Cribellum spigot numbers are from Opell 1994b; thread volumes from Opell 1996. Ancestral values are given in brackets

| | Volume two axial fibres ($\mu\text{m}^3 \text{mm}^{-1} \times 10^3$) | Volume each cribellar fibril ($\mu\text{m}^3 \text{mm}^{-1}$) | Cribellar spigots | Total volume of fibrils ($\mu\text{m}^3 \text{mm}^{-1} \times 10^3$) | Total volume of cribellar thread ($\mu\text{m}^3 \text{mm}^{-1} \times 10^3$) |
|-------------------------------|------------------------------------------------------------------------------|-----------------------------------------------------------------------|----------------------|------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| <i>Waitkera waitakerensis</i> | 87 | 107 | 3905 | 417.8 | 540.8 [507.4] |
| <i>Siratoba referena</i> | 134 | 87 | 1800 | 156.6 | 290.6 [507.4] |
| <i>Uloborus glomusosus</i> | 148 | 116 | 4717 | 547.2 | 695.2 [697.0] |
| <i>Octonoba sinensis</i> | 254 | 110 | 4098 | 450.8 | 704.8 [697.0] |
| <i>Hyptiotes cavatus</i> | 308 | 118 | 7276 | 858.6 | 1166.6 [1085.0] |
| <i>Hyptiotes gertschi</i> | 308 | 118 | 7724 | 911.4 | 1219.4 [1085.0] |
| <i>Miagrammopes animotus</i> | 34 | 88 | 8990 | 791.1 | 825.1 [829.3] |
| <i>Miagrammopes species</i> | 11 | 108 | 7254 | 783.4 | 794.4 [829.3] |

(*t*-test, *t* = 3.824, *P* = 0.003). The mean value of the four species' adhesive threads (377 503 $\mu\text{N mm}^{-3}$) is 13.2 times greater than that of eight species' cribellar threads (28 668 $\mu\text{N mm}^{-3}$).

The range of stickiness per thread volume among araneoid species is much greater than among uloborid species (Fig. 3). However, in both groups, interspecific differences are explained by a negative relationship between spider mass and stickiness per volume: smaller spiders produce capture threads that achieve their stickiness with a greater material economy than do the threads of larger spiders. Spearman rank-order correlations for spider mass and stickiness per thread volume for uloborid and araneoid orb-weaving species are -0.80 and -0.90, respectively. As uloborid masses range from 4 to 13 mg and araneoid masses range from 7 to 647 mg, interspecific differences are much more pronounced among araneoid than uloborid species.

THREAD VOLUME

Change in spider mass is normally distributed for both uloborid and araneoid orb-weaving species (Shapiro-Wilk *W*-Statistic *P* = 0.653 and 0.245, respectively). Although change in capture thread volume was normally distributed for araneoid orb-weavers (*P* = 0.169) it was not normally distributed for cribellate orb-weaving species (*P* = 0.037) and did not become so when log-transformed (*P* = 0.021). To normalize the data for uloborids, the analysis values for the two reduced-web species that had the greatest

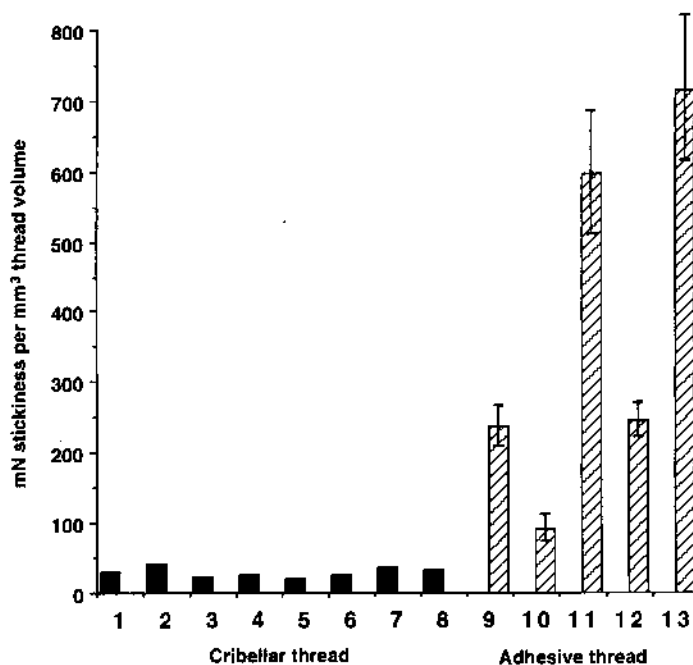


Fig. 4. Histogram comparing the relative stickiness of cribellar and adhesive prey capture threads. Numbers refer to species numbers given in Table 1. Error bars for adhesive threads represent ± 1 standard error.

thread stickiness (*M. animotus* and *H. gertschi*) were added to. This made the change in thread volume of the six uloborid species normally distributed (*P* = 0.162) and improved the normality for the change in mass of these species (*P* = 0.742). The regression of change in capture thread volume and change in spider mass is significant for both uloborids and araneoids (Fig. 5), but a test of the homogeneity of these regression slopes shows that they differ (*F* = 0.05, *P* = 0.0197). This shows that, relative to spider mass, cribellar threads contain a greater volume of material than do adhesive threads. The great difference in the slopes of these regression lines and the fact that all points for the Uloboridae lie on the regression line indicate that the inclusion of the two reduced-web uloborid species, *M. animotus* and *H. cavatus*, in this analysis does not compromise this conclusion.

THREAD STICKINESS

Both changes in spider mass and changes in capture thread stickiness were normally distributed for the five orb-weaving uloborid species (*P* = 0.392, 0.579, respectively) and the five araneoid species (*P* = 0.311, 0.513, respectively). Change in the natural log of spider mass was used instead of change in spider mass, as it improved the fit of the regression lines for both clades (for uloborids *P* 0.066 \rightarrow 0.050; for araneoids *P* 0.186 \rightarrow 0.027) and was normally distributed for both clades (*P* > 0.240). A test of the homogeneity showed that the regression slopes for change in capture thread stickiness and change in the \log_n of spider mass did not differ between uloborids and araneoids (Fig. 6, *F* = 0.06, *P* = 0.82). However, a one-tailed *t*-test showed that the *y*-intercept of the regression line for araneoids was greater than that for uloborids (*t* = 3.061, 0.010 < *P* < 0.025). This shows that, relative to spider mass, adhesive threads are stickier than cribellar threads.

LIMITS TO THE STICKINESS OF CRIBELLAR THREADS

The cribellar threads of uloborids that construct reduced-webs containing shorter lengths of capture threads demonstrate that the material cost of producing cribellar thread and not spider size limits cribellar thread stickiness. The spider masses and cribellar thread stickiness values of the five orb-web species and those of the four reduced-web species are normally distributed (*P* > 0.517). Mass does not differ between orb-web species and reduced-web species (*t*-test, *t* = 1.42, *P* = 0.20), yet the reduced-web species produce cribellar threads that are, on average, 1.88 times stickier than those of the orb-weaving species (*t*-test, *t* = 7.42, *P* = 0.0001). Both species of *Miagrammopes* weigh less than half as much as these orb-weaving species (mean masses 4.36 and 9.77 mg, respectively). However, they produce threads that are 1.89 times stickier than those produced by the orb-weaving species. Furthermore,

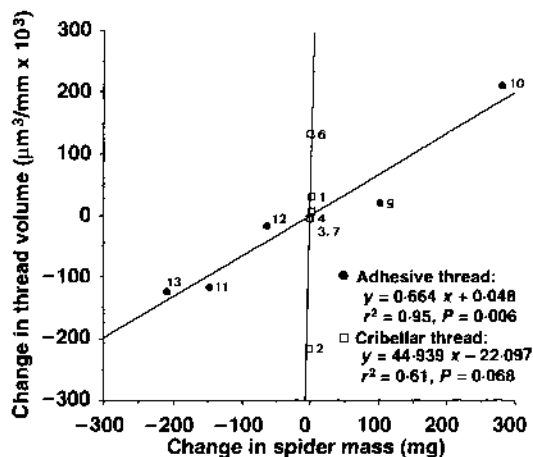


Fig. 5. Regression of changes in spider mass and changes in the volume of material invested in cribellar and adhesive capture threads (one point hidden). Numbers refer to species numbers in Table 1.

although the average mass of the four uloborid species that construct reduced-webs is only 2% that of the five araneoid species, their cribellar threads are as sticky as the adhesive threads produced by these larger spiders (*t*-test, $t = 0.77$, $P = 0.47$; stickiness values of araneoids are normally distributed, $P = 0.840$).

BENEFITS OF CAPTURE THREAD RECYCLING

Figure 7 models the combined material and behavioural costs of webs constructed by spiders of different masses. The cost of constructing a cribellate orb-web is equivalent to about 85% of a spider's mass. Silk recycling and the production of capture thread that achieves stickiness with the material economy of adhesive thread each reduce this total cost by about 33%. Thus, in constructing an orb-web with recycled silk, cribellate orb-weavers expend a silk dry mass equivalent to about 58% of their masses, whereas adhesive orb-weavers invest material equivalent to only 35% of their masses.

Discussion

This study supports the hypothesis that adhesive capture threads are less costly to produce than cribellar threads. Relative to the volume of material they contain, adhesive threads are 13 times stickier than cribellar threads produced by orb-weaving uloborids. Relative to spider mass, adhesive orb-weavers invest less material in their capture threads, but produce stickier threads than cribellate orb-weavers. These differences may have favoured the origin of adhesive orb-weavers and contributed to the success of these spiders.

Comparison of the material that covers the axial fibres of cribellar and adhesive capture threads result in a conservative test of these hypotheses. This

comparison tends to underestimate the volume of material invested in cribellar threads and overestimate the volume of material invested in adhesive threads. The fibrils that form a cribellar thread's outer surface are looped and coiled (Fig. 1a). However, as the amount of coiling cannot be quantified, their volume is computed as if these fibrils were straight, thereby probably underestimating their volume by at least 50%. This more than allows for the fact that cribellar fibrils may have a greater density than the viscous material of adhesive threads.

The stickiness of adhesive capture thread is less costly to achieve than its volume indicates for three reasons. First, water forms about 80% of an adhesive droplet's volume (Gosline *et al.* 1986), whereas the fibrils of cribellar threads are formed entirely 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, the stickiness of cribellar threads is directly related to the number and therefore the volume of cribellar fibrils they contain (Opell 1994b, 1995), whereas the stickiness of adhesive threads resides in their glycoprotein nodules which constitute only a part of each droplet's volume (Peters 1995; Tillinghast *et al.* 1993; Vollrath 1992; Vollrath & Tillinghast 1991). Although the solution that surrounds these nodules enhances thread extensibility (Vollrath & Edmonds 1989), it does not appear to contribute directly to thread stickiness. This solution does contribute indirectly to stickiness, as it serves as the vehicle by which glycoproteins are deposited and maintains an aqueous environment for these nodules. Third, adhesive threads contain low and high molecular mass hygroscopic agents, both of which attract water at relative humidities (r.h.) in excess of 50% (Townley *et al.* 1991). As the dimensions of adhesive thread droplets were measured after they were kept at 60–62% r.h. for 2–4 h, some of their volume originated from the atmosphere and not the spider that produced them.

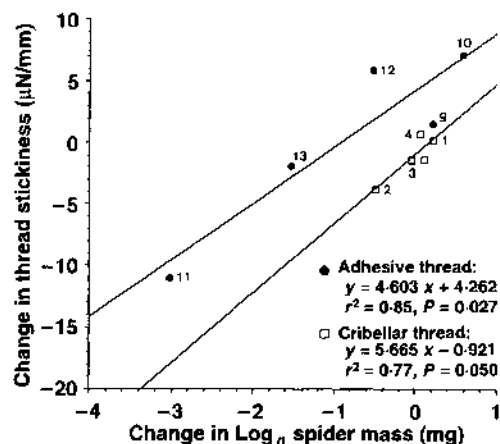


Fig. 6. Regression of changes in spider mass and changes in the stickiness of cribellar and adhesive capture threads.

The stickiness of cribellar threads produced by orb-weaving uloborids appears to be constrained by the material cost of producing this thread and not by spider size or spinning anatomy. Small *Miagrammopes* species produce cribellar threads that are not only stickier than those of larger cribellate orb-weavers, but are as sticky as the adhesive threads produced by the largest orb-weaving species. This is energetically possible because their reduced webs contain much shorter lengths of cribellar thread than do orb-webs constructed by other uloborids. Within the Uloboridae, the total stickiness and total volume of cribellar threads in uloborid webs are, regardless of their architecture, directly related to spider mass (Opell 1996). Species that construct reduced webs maintain the prey capture potential of these webs by producing stickier but more costly cribellar threads.

The greater cost of achieving capture thread stickiness may have constrained the size of orb-weaving spiders that produce this type of capture thread. Uloborid species are all rather small. The species included in this study are characteristic of this family and the two larger species representative of its upper size limit (Opell 1979). Conversely, the lower cost of achieving adhesive capture thread stickiness and the relationship between the masses of these orb-weavers and the volume of material they invested in their

threads suggest that their size is not as highly constrained by the cost of producing capture threads as is that of cribellate orb-weavers.

For both uloborid and deinopoid orb-weavers, silk recycling significantly improves the economy of web use. These differences are reflected in the mass of prey that spiders must capture to recover the cost of constructing an orb-web. Without web recycling a cribellate orb-weaver must capture an insect whose mass is 4.5 times greater than its own; with recycling, 3 times greater; and, with both recycling and the production of less costly capture thread, 2 times greater. Although these values provide a useful general perspective on the economy of orb-web use, the data and assumptions used in their computation warrant empirical confirmation. As orb-webs capture insects that belong to different size and taxonomic groups (Eberhard 1990), the energetics of orb-web use are probably influenced significantly by the nutrient content, degree of sclerotization and size of the insects captured.

Cribellate and adhesive orb-webs differ in many respects, including their orientation and the extensibility and spectral properties of their capture threads. Therefore, other factors in addition to the lower cost and greater stickiness of adhesive threads have probably also contributed to the success of adhesive orb-webs. The vertical orientation of most of these webs (Bond & Opell 1998) allows them to intercept more prey than the typically horizontally oriented cribellate orb-webs (Eberhard 1989). However, vertical orb-webs tend to intercept faster flying insects than do horizontal orb-webs and therefore must absorb greater kinetic energies (Eberhard 1986, 1989; Craig 1987a,b). Adhesive capture threads have a unique windlass mechanism that increases their extensibility (Vollrath & Edmonds 1989; Köhler & Vollrath 1995) and may increase a web's overall elasticity, thereby enhancing its ability to dissipate energy through aerodynamic dampening (Lin, Edmonds & Vollrath 1995). The flat or low ultraviolet light reflectance spectra of adhesive threads increases an adhesive orb-web's ability to intercept prey by making it less visible to insects (Craig 1988, 1990; Craig & Bernard 1990; Craig *et al.* 1994). Thus, the success of adhesive orb-weaving spiders appears to result from a combination of the greater material economy and stickiness of their capture threads and the architectural, mechanical and spectral properties of their orb-webs.

Spiders that construct cribellate orb-webs appear to persist because their webs continue to function effectively in some habitats and because they experience only partial niche overlap with most adhesive orb-weaving species. In some habitats, cribellate orb-weavers may actually have advantages over vertical orb-webs. For example, in a number of lowland forests on New Zealand's North Island, *Waitkera waitakerensis* is much more common than are araneoid orb-weavers (B. D. Opell, unpublished observations). For

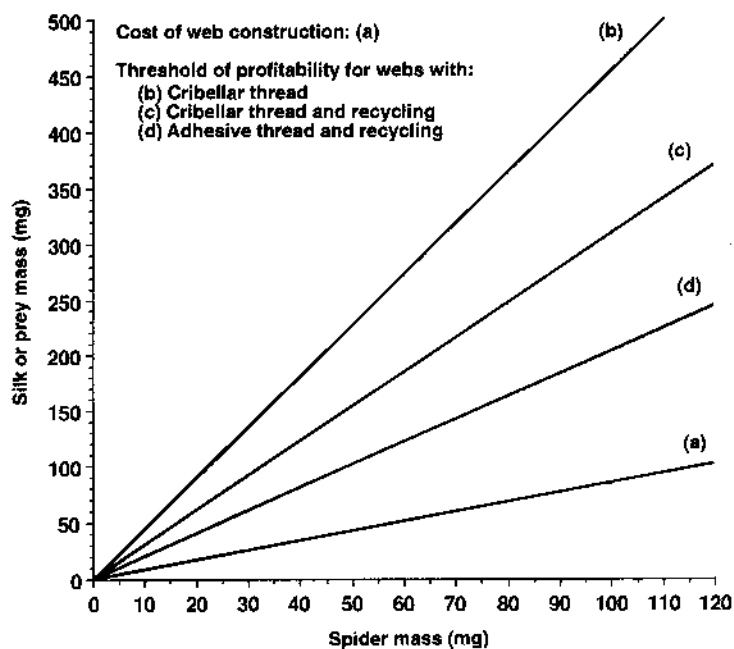


Fig. 7. The combined material and behavioural cost of constructing spider orb-webs and the mass of prey that spiders must capture to recover this cost. (a) Silk mass equivalent to the material and behavioural cost of constructing a cribellate orb-web if silk is not recycled ($Y = 0.851X - 0.003$). (b) The live mass of prey that a spider must capture to recover the total cost of constructing a cribellate orb-web ($Y = 4.528X - 0.016$). (c) The live mass of prey that a spider must capture to recover the total cost of constructing a cribellate orb-web using silk recycled from a previous web ($Y = 3.079X - 0.011$). (d) The live mass of prey that a spider that recycles its silk must capture to recover the cost of constructing an orb-web with adhesive thread whose stickiness is equal to that of cribellar thread ($Y = 2.038X - 0.007$).

insects that fly upward from the forest floor, horizontal orb-webs that reflect ultraviolet light may either be invisible against patches of sunlight that filter through the forest canopy (Eberhard 1990) or these webs may attract insects that fly toward the canopy or toward open patches of forest. As horizontal orb-webs are typically less taut than vertical orb-webs, they oscillate more in wind currents and are better equipped to capture insects that fly parallel to their planes (Craig, Akira & Andreasen 1985). Horizontal orb-webs may also provide access to microhabitats that offer abundant prey but insufficient space to accommodate vertical orb-webs (Eberhard 1990). For example, on closely trimmed shrubbery, *Uloborus glomus* is more abundant than araneoid orb-weavers (B. D. Opell, unpublished observations), presumably because the smaller spaces of this habitat can better accommodate their small, horizontal, cribellate orb-webs than they can the larger, vertical adhesive orb-webs of araneoids.

Several features that contribute to araneoid diversity also reduce the competition between cribellate and adhesive orb-weaving spiders. The low ultraviolet light reflectance of adhesive threads produced by some araneoids allows these spiders to build their web in more brightly lighted habitats where cribellate orb-webs would be more conspicuous to insects and, therefore, less effective (Craig *et al.* 1994). Adhesive orb-weavers also mature over a larger size range than do cribellate orb-weavers. Adult female uloborids do not exceed a mass of about 12 mg, whereas araneoid orb-weavers range in mass from a few mg to over 600 mg. In temperate regions where orb-weaving spiders mature during a single growing season, the increased material economy with which adhesive orb-webs achieve their stickiness may be a key factor enabling these species to reach larger adult sizes (Opell 1997). The larger, vertically oriented orb-webs constructed by these araneoids require attachment sites with different characteristics than those used by uloborids.

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References

- Bond, J.A. & Opell, B.D. (1998) Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution* **52**, 403–414.
- Breed, A.L., Levine, V.D., Peakall, D.B. & Witt, P.N. (1964) The fate of the intact orb web of the spider *Araneus diadematus* Cl. *Behaviour* **23**, 43–60.
- Carico, J.E. (1986) Web removal patterns in orb-weaving spiders. *Spiders: Webs, Behavior, and Evolution* (ed. W. A. Shear), pp. 306–318. Stanford University Press, Stanford, CA.
- Chacón, P. & Eberhard, W.G. (1980) Factors affecting numbers and kinds of prey caught in artificial spider webs with considerations of how orb-webs trap prey. *Bulletin of the British Arachnological Society* **5**, 29–38.
- Coddington, J.A. (1986) Orb webs in 'non-orb weaving' ogre faced spiders (Araneae: Deinopidae): a question of genealogy. *Cladistics* **2**, 53–67.
- Coddington, J.A. (1990) Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneocla: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology* **496**, 1–52.
- Coddington, J.A. & Levi, H.W. (1991) Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22**, 565–592.
- Craig, C.L. (1987a) The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *American Naturalist* **129**, 47–68.
- Craig, C.L. (1987b) The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biological Journal of the Linnean Society* **30**, 135–162.
- Craig, C.L. (1988) Insect perception of spider orb webs in three light habitats. *Functional Ecology* **2**, 277–282.
- Craig, C.L. (1990) Effects of background pattern on insect perception of webs spun by orb weaving spiders. *Animal Behavior* **39**, 135–144.
- Craig, C.L. & Bernard, G.D. (1990) Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71**, 616–624.
- Craig, C.L., Akira, O. & Andreasen, V. (1985) Effect of spider orb-web and insect oscillations on prey interception. *Journal of Theoretical Biology* **115**, 201–211.
- Craig, C.L., Bernard, G.D. & Coddington, J.A. (1994) Evolutionary shifts in the spectra properties of spider silks. *Evolution* **48**, 287–296.
- Eberhard, W.G. (1986) Effects of orb-web geometry on prey interception and retention. *Spiders: Webs, Behavior, and Evolution* (ed. W. A. Shear), pp. 70–100. Stanford University Press, Stanford, CA.
- Eberhard, W.G. (1988) Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. *Bulletin of the British Arachnological Society* **7**, 247–251.
- Eberhard, W.G. (1989) Effects of orb-web orientation and spider size on prey retention. *Bulletin of the British Arachnological Society* **8**, 45–48.
- Eberhard, W.G. (1990) Function and phylogeny of spider webs. *Annual Review of Ecology and Systematics* **21**, 341–372.
- Eberhard, W.G. & Pereira, F. (1993) Ultrastructure of cribellate silk of nine species in eight families and possible taxonomic implications (Araneae: Amaurobiidae, Deinopidae, Desidae, Dictynidae, Filistatidae, Hypochilidae, Stiphidiidae, Tenggellidae). *Journal of Arachnology* **21**, 161–174.
- Gosline, J.M., DeMont, M.E. & Denny, M.W. (1986) The structure and properties of spider silk. *Endeavour* **10**, 37–43.

- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, New York.
- Huey, R.B. & Bennet, A.F. (1986) A comparative approach to field and laboratory studies in evolutionary biology. *Predator-Prey Relationships: Perspectives and Approaches for the Study of Lower Vertebrates* (eds M. E. Feder & G. V. Lauder), pp. 82–96. University of Chicago Press, Chicago.
- Huey, R.B. & Bennet, A.F. (1987) Phylogenetic studies of co-adaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41**, 1098–1115.
- Köhler, T. & Vollrath, F. (1995) Thread biomechanics in the two orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *Journal of Experimental Zoology* **271**, 1–17.
- Levi, H.W. (1982) *Arthropods. Synopsis and Classification of Living Organisms*, Vol. 2 (ed. S. P. Parker), pp. 71–110. McGraw-Hill, New York.
- Levi, H.W. (1985) The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* **150**, 429–618.
- Lin, L.H., Edmonds, D.T. & Vollrath, F. (1995) Structural engineering of an orb-spider's web. *Nature* **373**, 146–148.
- Lubin, Y.D. (1986) Web building and prey capture in the Uloboridae. *Webs, Behavior, and Evolution* (ed. W. A. Shear), pp. 132–171. Stanford University Press, Stanford, CA.
- Lubin, Y.D., Eberhard, W.G. & Montgomery, G.G. (1978) Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. *Psyche* **85**, 1–23.
- Maddison, W.P. & Maddison, D.R. (1992) *MacClade: Analysis of Phylogeny and Character Evolution, Version 3*. Sinauer Associates, Inc., Sunderland.
- Opell, B.D. (1979) Revision of the genera and tropical American species of the spider family Uloboridae. *Bulletin of the Museum of Comparative Zoology* **148**, 443–549.
- Opell, B.D. (1982) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *Journal of Arachnology* **10**, 185–191.
- Opell, B.D. (1988) Prey handling and food extraction by the triangle-web spider *Hyptiotes cavatus* (Uloboridae). *Journal of Arachnology* **16**, 272–274.
- Opell, B.D. (1990) The material investment and prey capture potential of reduced spider webs. *Behavioral Ecology and Sociobiology* **26**, 375–381.
- Opell, B.D. (1993) What forces are responsible for the stickiness of spider cribellar threads? *Journal of Experimental Zoology* **265**, 469–476.
- Opell, B.D. (1994a) Increased stickiness of prey capture threads accompanying web reduction in the spider family Uloboridae. *Functional Ecology* **8**, 85–90.
- Opell, B.D. (1994b) Factors governing the stickiness of cribellar prey capture threads in the spider family Uloboridae. *Journal of Morphology* **221**, 111–119.
- Opell, B.D. (1994c) The ability of spider cribellar prey capture thread to hold insects with different surface features. *Functional Ecology* **8**, 145–150.
- Opell, B.D. (1994d) Factors affecting the diameters of axial fibers in cribellar threads of the spider family Uloboridae. *Journal of Arachnology* **22**, 12–18.
- Opell, B.D. (1995) Ontogenetic changes in cribellum spigot number and cribellar prey capture thread stickiness in the spider family Uloboridae. *Journal of Morphology* **224**, 47–56.
- Opell, B.D. (1996) Functional similarities of spider webs with diverse architectures. *American Naturalist* **148**, 630–648.
- Opell, B.D. (1997) The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. *Biological Journal of the Linnean Society* **62**, 443–458.
- Peakall, D.B. (1971) Conservation of web proteins in the spider *Araneus diadematus*. *Journal of Experimental Zoology* **176**, 257–264.
- Peters, H.M. (1983) Struktur und Herstellung der Fangfäden cribellater Spinnen (Arachnida: Araneae). *Verhandlungen des naturwissenschaftlichen Vereins, Hamburg* **26**, 241–253.
- Peters, H.M. (1984) The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida, Araneida). *Zoomorphology* **104**, 96–104.
- Peters, H.M. (1986) Fine structure and function of capture threads. *Ecophysiology of Spiders* (ed. N. Nentwig), pp. 187–202. Springer-Verlag, New York.
- Peters, H.M. (1992) On the spinning apparatus and structure of the capture threads of *Deinopis subrufus* (Araneae, Deinopidae). *Zoomorphology* **112**, 27–37.
- Peters, H.M. (1995) Ultrastructure of orb spiders' gluey capture threads. *Naturwissenschaften* **82**, 380–382.
- Selden, P.A. (1989) Orb-web weaving spiders in the early Cretaceous. *Nature* **340**, 711–713.
- Tillinghast, E.K., Townley, M.A., Wight, T.N., Uhlenbruck, G. & Janssen, E. (1993) The adhesive glycoprotein of the orb web of *Argiope aurantia* (Araneae, Araneidae). *Materials Research Society, Symposium Proceedings* **292**, 9–23.
- Townley, M.A. & Tillinghast, E.K. (1988) Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, Gabamide. *Journal of Arachnology* **16**, 303–319.
- Townley, M.A., Bernstein, D.T., Gallanger, K.S. & Tillinghast, E.K. (1991) Comparative study of orb-web hydroscopicity and adhesive spiral composition in three areneid spiders. *Journal of Experimental Zoology* **259**, 154–165.
- Vollrath, F. (1992) Spider webs and silks. *Scientific American* **266**, 70–76.
- Vollrath, F. & Edmonds, E.T. (1989) Modulation of the mechanical properties of spider silk by coating with water. *Nature* **340**, 305–307.
- Vollrath, F. & Tillinghast, E.K. (1991) Glycoprotein glue beneath a spider web's aqueous coat. *Naturwissenschaften* **78**, 557–559.
- Vollrath, F., Fairbrother, W.J., Williams, R.J.P., Tillinghast, E.K., Bernstein, D.T., Gallagher, K.S. & Townley, M.A. (1990) Compounds in the droplets of the orb spider's viscid spiral. *Nature* **345**, 526–528.
- Wainwright, S.A., Briggs, W.D., Currey, J.D. & Gosline, J.M. (1982) *Mechanical Design in Organisms*. Princeton University Press, Princeton, NJ.

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