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Brent D. Opell

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## FUNCTIONAL SIMILARITIES OF SPIDER WEBS WITH DIVERSE ARCHITECTURES

BRENT D. OPELL\*

Department of Biology, Virginia Polytechnic Institute and State University,  
Blacksburg, Virginia 24061

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*Abstract.*—Spider orb webs are made of sticky prey capture threads supported by a scaffold of nonsticky threads. Capture threads produced by members of the family Uloboridae are formed of thousands of dry, proteinaceous silk fibrils. From measurements of the diameters and lengths of fibers that form the sticky and nonsticky threads of uloborids, this study determines the volume of silk these webs contain. It employs a transformational analysis to examine the relationship between spider size and the silk volume and total stickiness of webs produced by four orb-weaving species and four species that spin simpler webs. Despite differences in web design, web-monitoring behavior, and spider size, a web's total silk volume is directly related to spider weight. A web's prey capture potential, as determined by its total stickiness and total capture area, is also directly related to spider weight. The volume of silk fibrils responsible for a web's stickiness is related to spider weight, whereas the volume of its support elements is not but appears instead to be influenced by web orientation and architecture. Thus, a spider's energetic requirements appear to set the bounds within which the material investment, stickiness, and architectural details of its web are free to differ.

Orb-weaving spiders combine sticky and nonsticky threads to produce intricate aerial snares that intercept and retain prey until subdued by a spider. One of the simplest observations that can be made about these spiders and their webs is that small spiders tend to spin small webs and large spiders tend to spin large webs. This observation suggests that, in addition to being strong enough and sticky enough to catch prey, a web is designed to meet a spider's energetic needs parsimoniously. However, this hypothesis has never been tested. The total length of sticky and nonsticky threads in the orb webs of a few spider species has been measured (e.g., Witt et al. 1968; Eberhard 1986), but length does not adequately describe either the amount of silk a spider invests in its web or the web's total stickiness. This is because thread diameter differs both between the elements that form a web and among the webs produced by different species (Craig 1987*a*, 1987*b*; Opell 1994*d*) and because even spiders of similar size produce prey capture threads with different adhesive properties (Opell 1994*a*).

A number of factors affect the type and number of insects that an orb web captures, including the microhabitat in which the web is placed, its architecture (Eberhard 1986), its orientation (Eberhard 1989), its tension (Craig et al. 1985),

\* E-mail: bopell@VT.edu.

its strength (Craig 1987a, 1987b), and the degree to which it is invisible or attractive to insects (Craig 1988, 1990, 1994a, 1994b; Craig and Bernard 1990; Craig and Freeman 1991; Craig and Ebert 1994; Craig et al. 1994). However, the success of a web ultimately depends on its ability to intercept insects and hold them long enough for a spider to subdue them. Thus, if one assumes an invariant prey capture regime, the total capture area of an orb web and the total stickiness of its prey capture threads are useful indexes of its prey capture potential.

This study tests the hypothesis that spider weight governs the amount of silk this spider invests in its web and thus the web's stickiness and capture area. As a spider's weight is correlated with its metabolic rate (Anderson and Prestwich 1982), the premise of this hypothesis is that a web's prey capture potential is scaled to the energetic needs of the spider that produced it. If substantiated, these relationships provide new insight into factors that determine the physical and functional properties of spider orb webs and set the energetic boundary within which the architectural details of these webs are free to differ. This study uses measurements of thread length, diameter, and stickiness to compute the total silk volume and total stickiness of webs produced by eight species in the orb web spider family Uloboridae. Along with the Deinopidae, whose members construct highly derived webs, this family is the sister group of the more diverse araneoid spiders whose members produce viscous, adhesive prey capture threads. In addition to four species that construct horizontal orb webs, this study includes four species whose web architectures are simpler than those of their orb-weaving ancestors. It assumes that if an orb web's silk volume, total stickiness, and total area are determined by spider weight, then these relationships should also have influenced features of the reduced webs that were derived from orb webs.

The orb-weaving species included in this study belong to the distantly related genera *Octonoba*, *Siratoba*, *Uloborus*, and *Waitkera* (fig. 1). Two of the reduced-web species belong to the temperate genus *Hyptiotes* and two to its tropical sister genus *Miagrammopes*. The two *Hyptiotes* species construct vertical, triangle webs, consisting of four diverging radii between which the capture threads extend (fig. 1) (Opell 1982; Lubin 1986). The two *Miagrammopes* species produce webs that are even more reduced than those of *Hyptiotes*: they have neither a stereotypical form nor a highly integrated structure. These irregular webs are formed of a variable number of branching lines that have different lengths and diverge at different angles (fig. 1) (Lubin et al. 1978; Lubin 1986; Opell 1990). Thus, this study includes webs that have different architectures, orientations, and degrees of architectural plasticity.

These species also exhibit different prey capture behaviors. Orb-weaving species wait at the web center and, after an insect is intercepted, minimally manipulate the web. In contrast, reduced-web species more actively manipulate their webs during prey capture. Members of both *Hyptiotes* and *Miagrammopes* rest at the attachment point of one of their web's anchor lines and jerk this line when an insect strikes the web (Lubin et al. 1978; Opell 1982; Lubin 1986). These differences in prey capture behavior suggest that the more active web manipulation exhibited by reduced-web species may help compensate for the apparent reduction in the capture area of their webs (Lubin 1986). However, the discovery

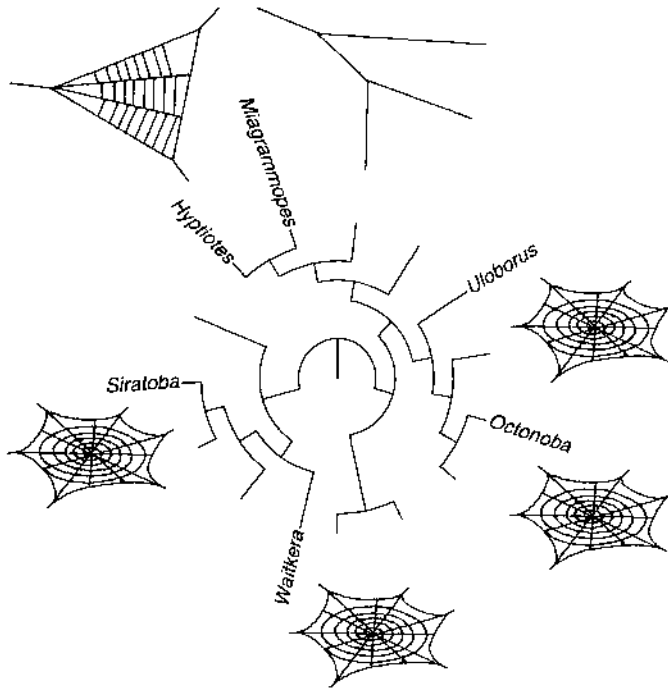


FIG. 1.—Cladogram of the family Uloboridae from Coddington (1990), showing the phylogenetic positions and web architectures of the six genera included in this study.

that web reduction is accompanied by an increase in capture thread stickiness (table 1) (Opell 1994a) suggests that web manipulation does not entirely compensate for web reduction. Only a quantitative comparison of the material and functional properties of these webs can address this question.

The primitive prey capture threads produced by uloborids lend themselves to a detailed comparison of silk volume, as they are made entirely of fibrous proteinaceous silk (fig. 2). These dry, composite strands are known as cribellar threads because their outer surfaces are formed of thousands of fine, looped silk fibrils (fig. 3) that are spun from the spigots of an oval spinning field termed the cribellum (figs. 4, 5). In uloborids, this array of fibrils is deposited on a network of 30–56 paracribellar fibers that form a superstructure around a single pair of larger, supporting axial fibers (Peters and Kovoov 1980; Peters 1983, 1984, 1986, 1992; Eberhard 1988; Kovoov and Peters 1988; Eberhard and Pereira 1993; Opell 1993, 1994b, 1995). Thus, by determining the number and diameter of strands that form a cribellar thread and the length of cribellar thread in a web, we can compute the volume of silk expended as cribellar thread. This dry, cribellar thread differs from the adhesive threads produced by more derived orb-weaving spiders, whose threads are usually formed by a pair of supporting axial fibers covered with a viscous material. This material contains low-molecular-weight organic and inorganic compounds, a variety of small proteins, and high-molecular-weight gly-

TABLE 1  
 THREAD VALUES USED TO COMPUTE THE TOTAL SILK VOLUME AND TOTAL STICKINESS VALUES OF WEBS

WEB TYPE	FRAME THREAD			AXIAL FIBER			CRIBELLAR FIBRIL			CRIBELLAR THREAD STICKINESS† ( $\mu\text{N}/\text{mm}$ contact)
	Diameter (nm)	Volume ( $\mu\text{m}^3/\text{mm} \times 10^3$ )	Diameter (nm)	Diameter ( $\mu\text{m}^3/\text{mm} \times 10^3$ )	Node Diameter (nm)	Internode Diameter (nm)	Node Spacing (nm)	Volume per Fibril ( $\mu\text{m}^3/\text{mm}$ )	Number of Cribellum Spigots	
Orb webs:										
<i>Waitkera waitakerensis</i>	694 (101, 5)	378	236 (54, 6)	87	17.4 (1.5, 6)	10.1 (.6, 6)	51.4 (8.9, 6)	107	3,905 (437, 36)	15.45 (5.03, 38)
<i>Siratoba referena</i>	699 (177, 5)	384	292 (79, 5)	134	17.5 (1.9, 4)	8.7 (2.0, 4)	63.9 (22.9, 4)	87	1,800 (150, 23)	11.46 (4.09, 26)
<i>Uloborus glomosis</i>	940 (138, 6)	694	307 (52, 5)	148	18.4 (1.4, 5)	10.4 (1.1, 5)	54.5 (14.3, 5)	116	4,717 (807, 29)	15.38 (5.75, 32)
<i>Octonoba sinensis</i>	708 (126, 5)	394	402 (60, 5)	254	18.8 (2.4, 5)	10.7 (.9, 5)	87.7 (12.9, 5)	110	4,098 (743, 34)	17.02 (7.12, 36)
Triangle webs:										
<i>Hyptiotes cavatus</i>	1,007 (221, 6)	796	443 (35, 5)	308	19.4 (1.0, 5)	10.3 (.3, 5)	63.1 (10.0, 5)	118	7,276 (1,802, 42)	26.18 (12.74, 56)
<i>Hyptiotes gertschi</i>	...	796	...	308	...	...	...	118	7,724 (1,016, 34)	29.84 (12.30, 32)
Simple webs:										
<i>Miagrammopes animotus</i>	1,051 (256, 7)	868	147 (26, 7)	34	16.2 (.5, 4)	8.6 (.7, 4)	42.3 (11.1, 4)	88	8,990 (1,504, 115)	31.50 (17.92, 101)
<i>Miagrammopes</i> sp.	695 (122, 5)	379	85 (8, 4)	11	18.4 (1.0, 4)	9.5 (1.0, 4)	52.7 (13.1, 4)	108	7,254 (824, 25)	24.41 (10.14, 24)

NOTE.—Below each mean value appears the standard deviation and sample size.

\* Combined volume of the two axial fibers of a cribellar thread.

† Values from Opell 1994a.

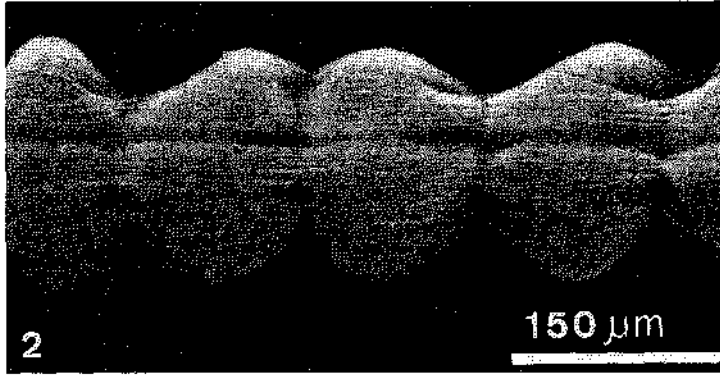


FIG. 2.—Cribellar thread of *Hyptiotes cavatus*

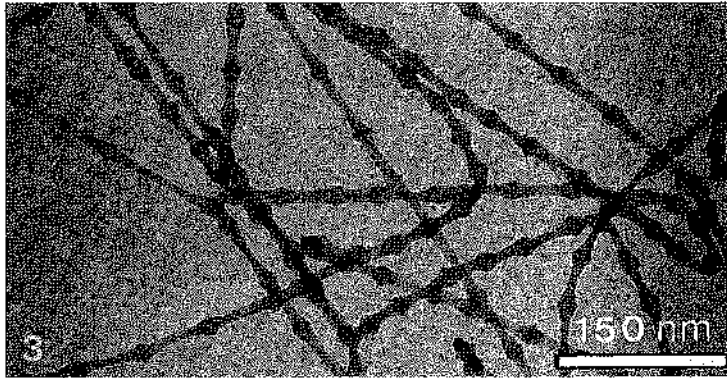


FIG. 3.—Cribellar fibrils of *Miagrammopes* species



FIG. 4.—Cribellum of *Miagrammopes animotus*

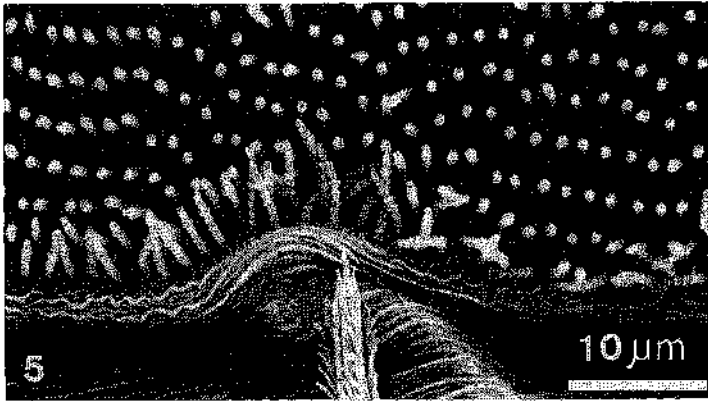


FIG. 5.—Cribellar spinning spigots of *Miagrammopes animotus*

coproteins (Vollrath et al. 1990; Townley et al. 1991; Vollrath and Tillinghast 1991; Tillinghast et al. 1993).

A successful orb web must both absorb the force of an insect's impact and retain the insect long enough for the spider to locate, run to, and subdue it (Craig 1987a). Whereas sticky prey capture threads alone retain prey, both nonsticky and sticky threads strengthen the web (Denny 1976; Craig 1987a, 1987b). The measurements described above allow a web's total silk volume to be partitioned into silk that is responsible for web support (frame and radial threads and the axial fibers of cribellar prey capture threads) and silk that is responsible for web stickiness (cribellar fibrils) (Opell 1994b, 1995). Thus, it is possible to determine whether both components are related to spider weight or whether selection affects each independently.

#### MATERIAL AND METHODS

##### *Species Studied*

I quantified the volume of silk and the total stickiness of prey capture threads in the webs produced by adult females (adult male uloborids do not construct capture webs) of eight species in six genera. These included the orb-weaving species: *Waitkera waitakerensis* (Chamberlain), *Siratoeba referena* (Muma and Gertsch), *Uloborus glomosus* (Walckenaer), and *Octonoba sinensis* (Simon). Also included were two triangle-web species—*Hyptiotes cavatus* (Hentz) and *Hyptiotes gertschi* Chamberlin and Ivie—and two simple-web species—*Miagrammopes animotus* Chickering and an undescribed species of *Miagrammopes*. Figure 1 shows the phylogenetic positions of the genera to which these species belong.

All but one species included in this study appear to replace their webs daily. The architecture of triangle and simple webs and the more active prey capture behavior used by spiders that construct these webs typically result in web damage

that requires spiders to take down and replace their webs every day (Lubin 1986). All of the orb-weaving species that I studied, with the possible exception of *O. sinensis*, also appeared to rebuild their webs every day. Their webs showed no signs of long-term damage or extensive repair that would indicate that they routinely lasted for more than a day. In contrast, the webs of *O. sinensis* more commonly showed major repairs, which suggests that a spider may use a web for several days before replacing it. The webs of this species were studied in greenhouses where most prey were small and there was little chance of wind damage. Therefore, it is difficult to form conclusions about the duration of the orb webs of *O. sinensis* under natural conditions. However, for this and all species, I photographed and measured only newly produced webs that showed no signs of damage or extensive repair.

#### *Web Measurements*

I dusted all webs with corn starch to make their threads more visible (Carico 1977) and measured to the nearest millimeter the total lengths of their cribellar prey capture thread and nonsticky radial and frame threads. I measured the webs produced by the two *Miagrammopes* species in the field. I photographed the webs produced by the other species and used a digitizing tablet to measure their areas and the lengths of their threads from enlarged photographic prints. After measuring or photographing a spider's web, I collected the spider and determined its live weight.

Members of the genus *Miagrammopes* construct their simple webs by first producing a network of nonsticky threads and then adding prey capture threads to some regions of these lines. Consequently, it is inappropriate to characterize some threads as anchor lines and others as capture threads and impossible to measure directly an enclosed capture area similar to that of an orb or triangle web. Therefore, I estimated the capture areas of these simple webs by assuming that insects that fly within 5 mm of either side of a capture thread are intercepted and by multiplying this 1-cm capture width by the total length of lines that formed a web. I included the total length of a web's lines in this calculation to compensate for two factors. First, some lines are covered by looped cribellar threads that extend farther from the line than do linear threads such as those shown in figure 2 and, thereby, increase the encounter contact region of these threads. Second, measurements of orb web capture areas include the web's hub, where there are no capture threads, and the web's perimeter, where there is often a gap between the last capture thread spiral and the web's frame line.

I photographed the webs of *W. waitakerensis* in the field and those of *O. sinensis* in greenhouses. In field photographs of the other species' webs it was difficult to distinguish threads from the web's background. Therefore, I allowed these spiders to build their webs in large plastic boxes containing wooden dowel rods and photographed these webs against a black background. As uloborids construct their webs during the early morning hours, I measured the webs of *Miagrammopes* species between 5:00 and 10:00 A.M. This reduced the chance of inadvertently measuring a simple web whose damage might not be as easily detected as that of a more highly structured orb or triangle web.



I also photographed the hub of each orb web and measured the nonsticky thread that formed its tight mesh. Some orb webs contained a linear or circular silk pattern (stabilimentum) at their hubs. These decorations are generally considered to protect spiders from predators or to attract prey to their webs (Eisner and Nowicki 1983; Lubin 1986; Craig 1990; Craig and Bernard 1990; Cushing and Opell 1990; Craig and Freeman 1991; Schoener 1992) and not to be directly associated with prey interception and retention. I observed that, even in webs produced by adult females of the same species, the presence and size of these decorations were variable. For these reasons and because it is difficult to quantify the silk that forms these dense bands, I did not attempt to measure their silk volume.

Members of the genus *Miagrammopes* deposit cribellar threads in the linear fashion typical of other uloborids (fig. 2), but on some sectors of their capture lines they deposit loops of cribellar thread that extend outward from the frame lines along which these species deposit their cribellar threads (Opell 1990). As this looped thread contains more silk and is stickier than linear thread, I measured the lengths of linear and looped threads separately and used formulas (A1) and (A2) in the appendix to compute the length of a web's capture thread as if it were formed entirely of linear thread.

#### *Thread Diameters*

Species-specific thread diameters and stickiness values were used to compute the cost and total stickiness of each species' web. These measurements were taken from thread samples collected from undusted webs. Threads were collected on microscope slides to which raised supports were glued. Double-sided adhesive tape atop these supports maintained the natural tension of these threads. I subsampled threads on Formvar-coated copper grids and examined them with a transmission electron microscope without further treatment.

From each web sample I photographed one to four radial threads, cribellar thread axial fibers, and cribellar fibrils at 50,000 $\times$ , 66,000 $\times$ , and 130,000 $\times$ , respectively, taking care to include only those strands that had a uniform diameter and showed no signs of being damaged by the microscope's electron beam. I determined the diameters of radial threads and axial fibers directly from negatives by measuring the diameter of each at its center and both ends. Although radial threads are composed of two fibers, these strands unite after being spun and appear as a single strand under the microscope. The mean diameter of each thread type was used. From enlarged photographic prints of cribellar fibrils spun by each species, I measured the diameter of three nodes and three internodes and the spacing of nodes in a fibril segment that contained 4–22 ( $\bar{X}$  = 9) nodes (fig. 3). The mean values of these features were used as a species' values.

On each of the 12 d that I examined these threads, I also photographed a grating replica (2,160 lines per millimeter) at 50,000 $\times$ , 66,000 $\times$ , and 130,000 $\times$  to calculate specimen magnification precisely and determine whether this was consistent from day to day. The standard errors of the mean width of one of the replica's 463-nm-wide lines, as measured from photographic negatives, were 2.9, 4.3, and 2.7 nm, respectively.

### *Cribellar Fibril Number*

Spiders whose threads were sampled were collected and preserved in 80% ethanol. I then removed the cribellum of each preserved spider, mounted it in water-soluble medium on a microscope slide, and examined it under a compound microscope equipped with differential phase contrast optics and connected to a computerized digitizing apparatus. I assumed that each spigot on a cribellum produces a fibril and determined the total number of spigots that form a cribellum using formula (A3) in the appendix.

### *Thread Volume*

I computed the volume of silk invested in a web's nonsticky threads as the volume of a cylinder with a diameter equal to that species' mean radial thread diameter and a length equal to the combined lengths of the web's hub, axial, and perimeter framework threads. These measurements did not include the anchor lines of orb webs or the two attachment lines of triangle webs. However, I did include the length of a triangle web's apex monitoring line, as I consider this a functioning component of the web and not simply an attachment line. I computed the volume of silk invested in a web's cribellar thread using formulas (A4)–(A9) in the appendix. I did not include paracribellar fibrils in computations of thread volume, because they do not contribute significantly to the total silk volume of cribellar threads. Paracribellar fibrils are similar to those of cribellar fibrils, but there are only 30–56 paracribellar spigots in most uloborids and none in *Miagrammopes* (Peters 1984).

By modeling cribellar threads as if they were formed of straight cribellar fibrils, these methods underestimate the volume of silk invested in the web. Cribellar fibrils are bent to form cribellar thread puffs (fig. 2), and on the surface of these puffs they assume a coiled and looped configuration (fig. 3). Consequently, the actual lengths of cribellar fibrils may be over twice that of the cribellar thread that they form. However, as there is no way to determine the actual lengths of cribellar fibrils, I treat all species as though their cribellar threads are made of straight cribellar fibrils.

### *Cribellar Thread Stickiness*

The stickiness values reported in table 1 are taken from my earlier work (Opell 1994a). As described more fully in that study, stickiness was measured by first pressing a 2-mm-wide piece of fine sandpaper against a 4-mm-long strand of cribellar thread with a standard force and then pulling the sandpaper plate away from the thread at a slow, constant rate. The force required to pull the plate from a strand of cribellar thread was then divided by the width of the plate (measured to the nearest 20  $\mu\text{m}$ ), and stickiness was reported as micronewtons of force per millimeter of thread contact with the sandpaper plate. Values obtained with a sandpaper plate are the same as those obtained with a section of a fleshfly (*Sarcophaga bullata*) wing (Opell 1994a) and, therefore, provide a reasonable estimate of a cribellar thread's performance. However, different insect surfaces result in significantly different stickiness values (Opell 1994c). A web's total stickiness

was determined by multiplying the total length of its cribellar thread by the mean stickiness value of threads spun by members of this species.

#### *Transformational Analysis*

To minimize the effect of intrafamilial phylogenetic position on the relationships among spider weight, total web silk volume, and total web stickiness (Harvey and Pagel 1991), I employed Huey and Bennett's (1986, 1987) method for evaluating the relationships among continuous variables whose states are hypothesized to be functionally linked. This method has three steps: the state of each character in a taxon's most immediate hypothetical ancestor is determined, the change in each character from this ancestral state to the state expressed by extant members is computed, and the relationship between these changes in character states are evaluated by regression. If this analysis shows that changes (either positive or negative) in two characters are significantly related, then their states are considered to have coevolved. I determined ancestral values using the rooted, minimized sum-of-squared-changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison and Maddison 1992).

#### RESULTS

Tables 1 and 2 present mean values of the eight species' thread and web features and the ancestral values of those indexes that were examined by transformational analyses. Transformational analyses show that a web's total silk volume, total stickiness, and total capture area are directly related to spider weight (figs. 6, 7, and 8, respectively). When the estimated web areas of the two *Miagrammopes* species are deleted and ancestral values recalculated, the relationship between spider weight and web area remains significant (area = 53.199 weight - 0.167,  $R^2 = 0.81$ ,  $P = .015$ ). The silk volume of a web's cribellar fibrils is also directly related to spider weight (fig. 9), although the volume of its support elements (the combined volumes of its radial and framework threads and the axial fibers of its cribellar threads) is not related to spider weight ( $R^2 = 0.003$ ,  $P = .90$ ).

#### DISCUSSION

This study shows that even among uloborid species that have different prey capture behaviors and produce webs whose architecture, orientation, and degree of stereotypy differ, spider weight is a principal determinant of both the total amount of silk invested in a web and the web's total stickiness and total capture area. These relationships portray uloborid orb webs and the reduced webs derived from them as functionally similar in many ways and yet highly constrained by the demand for economical prey capture that is related to a spider's weight. They show that the architectural details of webs can differ greatly and still satisfy these requirements.

These results make it more appropriate to describe triangle webs and simple

TABLE 2

## SILK VOLUME AND STICKINESS VALUES FOR THE WEBS PRODUCED BY EIGHT SPECIES OF ULORORIDAE

INDEX	ORB WEBS			TRIANGLE WEBS			SIMPLE WEBS	
	<i>Waitkera waitakerensis</i> (N = 27)	<i>Siratoba referena</i> (N = 23)	<i>Uloborus glomosis</i> (N = 27)	<i>Octonoba sinensis</i> (N = 24)	<i>Hyptiotes cavatus</i> (N = 27)	<i>Hyptiotes gertschi</i> (N = 41)	<i>Miagrammopes animotus</i> (N = 38)	<i>Miagrammopes Species</i> (N = 25)
Weight (mg)	7.70 + .28 (6.26)	4.09 + .23 (6.26)	6.83 + .34 (8.90)	12.16 + .79 (8.90)	8.11 + .55 (7.84)	8.17 + .23 (7.84)	6.48 + .42 (6.18)	4.83 + .30 (6.18)
Frame and radial thread: Length (cm)	317.0 + 20.4	265.4 + 20.7	424.0 + 20.9	838.9 + 41.7	91.3 + 2.5	104.5 + 3.9	98.8 + 5.9	121.1 + 7.4
Volume (mm <sup>3</sup> )	1.20 + 0.08	1.02 + .08	2.94 + .15	3.31 + .16	.73 + .02	.83 + .03	.86 + .05	.46 + 0.03
Cribellar thread: Length (cm)	329.2 + 27.5	242.2 + 25.1	392.2 + 27.3	820.9 + 45.5	169.3 + 8.4	146.1 + 6.5	81.3 + 5.2	90.8 + 4.9
Fibril volume (mm <sup>3</sup> )	1.38 + .11 (1.06)	.38 + .04 (1.06)	2.15 + .15 (2.54)	3.70 + .20 (2.54)	1.45 + .07 (1.38)	1.33 + .06 (1.38)	.64 + .04 (.90)	.71 + .04 (.90)
Axial fibril volume (mm <sup>3</sup> )	.28 + .02	.36 + .03	.63 + .03	2.13 + .11	.28 + .01	.32 + .01	.03 + .00	.01 + .00
Total volume (mm <sup>3</sup> )	1.65 + .13	.73 + .06	2.77 + .17	5.83 + .29	1.74 + .08	1.65 + .07	.68 + .04	.72 + .04
Total web: Silk volume (mm <sup>3</sup> )	2.85 + .20 (2.69)	1.75 + .13 (2.69)	5.72 + .30 (6.37)	9.14 + .44 (6.37)	2.46 + .09 (2.62)	2.48 + .09 (2.62)	1.53 + .09 (1.88)	1.18 + .07 (1.88)
Support silk volume (mm <sup>3</sup> )	1.48 (1.46)	1.38 (1.46)	.89 (.99)	.47 (.99)	3.57 (3.76)	5.44 (3.76)	1.01 (1.48)	1.15 (1.48)
Stickiness (mN)	50.86 + 4.25 (43.9)	27.75 + 2.87 (43.9)	60.31 + 4.20 (87.4)	139.72 + 7.74 (87.4)	44.33 + 2.19 (44.6)	43.60 + 1.94 (44.6)	25.61 + 1.64 (31.3)	22.17 + 1.20 (31.3)
Area (cm)	176 + 15 (164)	96 + 13 (164)	298 + 17 (405)	642 + 50 (405)	152 + 9 (186)	205 + 16 (186)	99 + 6 (140)	121 + 7 (140)
Support thread volume/ cribellar fibril vo- lume	1.07	3.63	.41	.13	2.46	4.09	1.58	1.62

NOTE.—Mean value + 1 SE; numbers in parentheses are ancestral values.

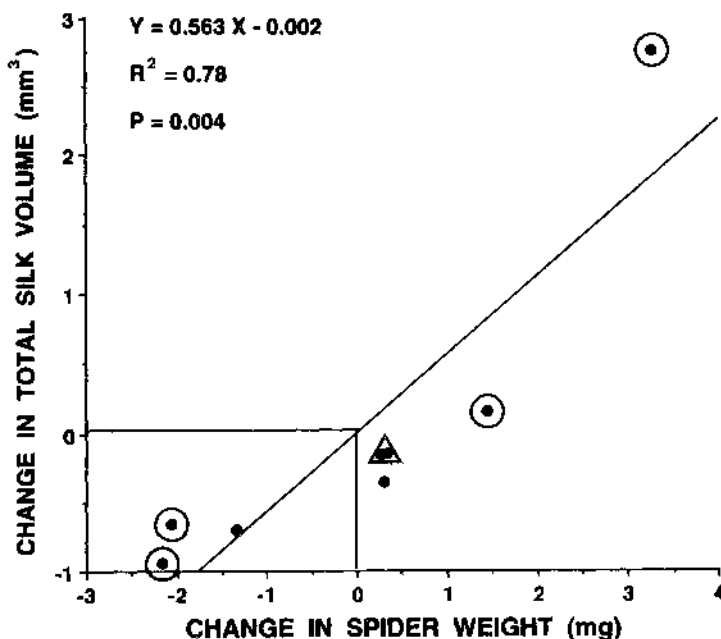


FIG. 6.—Regression of spider weight on total silk volume. Points denoting the values of orb-weaving species are surrounded by circles, those denoting the values of *Hyptiotes* species are surrounded by triangles, and those denoting the values of *Miagrammopes* species are not enclosed.

webs as restructured webs rather than as reduced webs. Even the simple webs constructed by species of *Miagrammopes* are more easily understood when viewed in terms of their total silk volume and total stickiness. These webs contain shorter lengths of both nonsticky and cribellar threads than do the orb webs produced by similarly sized orb weavers (table 2). However, compared to these orb-weaving species, they produce nonsticky threads that have greater diameters and cribellar threads that are stickier, owing to the greater number of cribellar fibrils that they contain (table 1). Consequently, both the total silk volume and total stickiness of these simple webs are similar to those of cribellate orb webs.

Two hypotheses have been proposed to explain the restructured webs of *Hyptiotes* and *Miagrammopes* (Lubin 1986): they allow spiders to monitor their webs from the attachment point of an anchor line, where they are less vulnerable to predation, and their construction requires the expenditure of less silk, for which more active web monitoring and manipulation compensate. The results of this study do not bear on the first hypothesis, but they do not support the second hypothesis. Additionally, the shorter lengths of both nonsticky and cribellar threads that form triangle and simple webs (table 2) suggest that the time and energy spent constructing a restructured web are less than those spent constructing an orb web. Consequently, when the smaller energetic cost of constructing a restructured web is added to the apparently greater energetic cost of

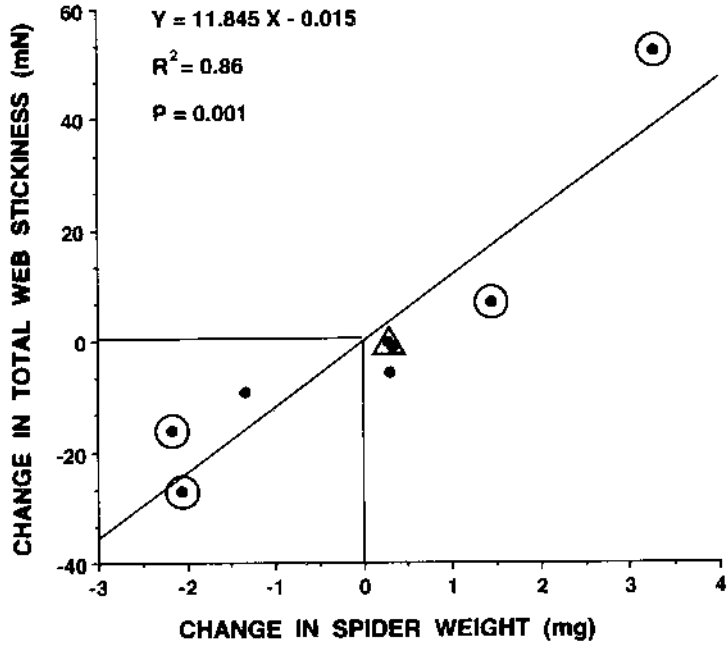


FIG. 7.—Regression of spider weight on total web stickiness. Notation is as in figure 6

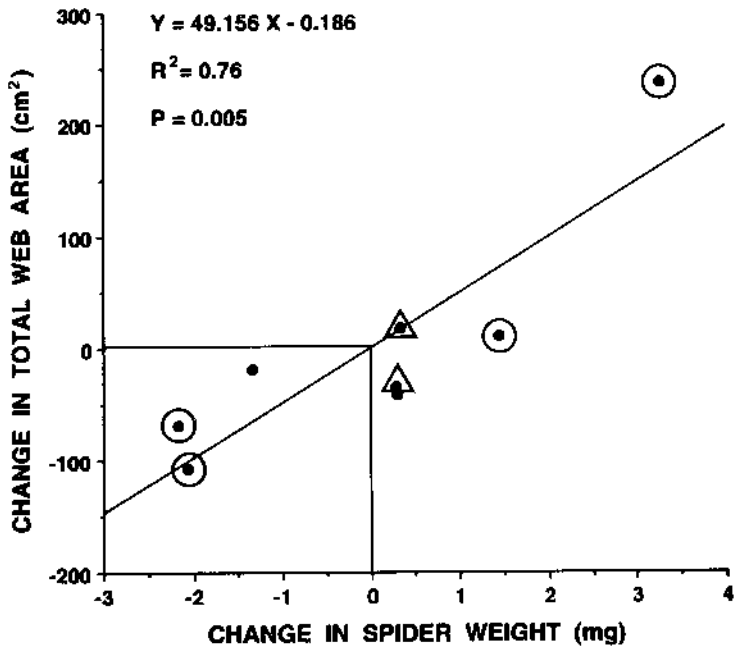


FIG. 8.—Regression of spider weight on total web area. Notation is as in figure 6

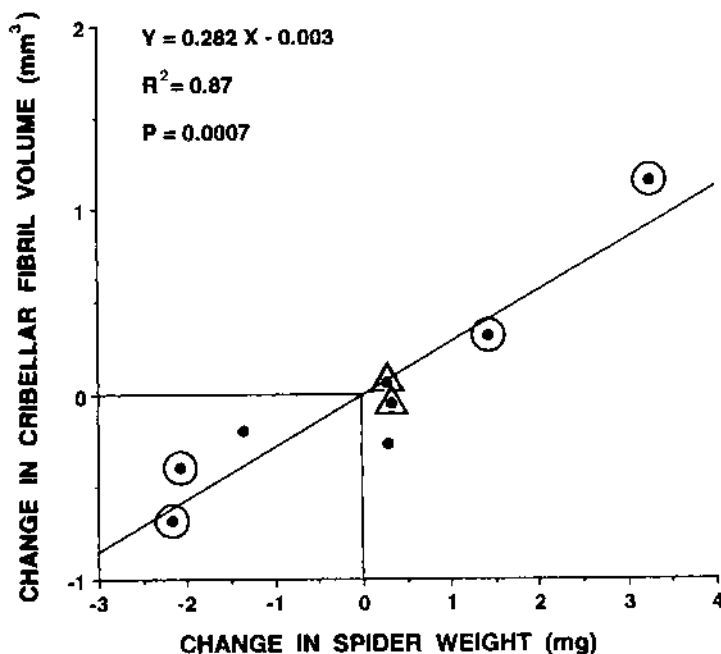


FIG. 9.—Regression of spider weight on total cribellar fibril volume. Notation is as in figure 6.

using this type of web, the total energetic cost of prey capture may not differ greatly between restructured webs and orb webs. Given that energetic costs of these web types appear to be similar, differences in their architectures may adapt them to capture insects with particular flight or visual capabilities, as suggested by Craig's studies (Craig 1987*b*, 1990; Craig and Barnard 1990; Craig and Freeman 1991; Craig et al. 1994).

In uloborids, capture thread stickiness is determined principally by the number of cribellar fibrils that form a thread (Opell 1994*b*, 1995). Therefore, as total web stickiness is associated with spider weight, it is not surprising that so too is the total volume of a web's cribellar fibrils. Although the architecture and orientation of a web do not affect the volume of its cribellar fibrils, they do appear to influence the volume of the web's support threads. This is suggested by the absence of an association between spider weight and support thread volume and by differences in the ratio of a web's support thread volume to cribellar fibril volume (table 2). Vertical, planar webs are more likely to intercept faster-flying insects than are horizontal webs and, therefore, must be stronger to absorb the greater impact forces generated by these insects (Eberhard 1986, 1989; Craig 1987*b*). This observation is borne out by the greater volume of support thread in the vertical triangle webs produced by *Hyptiotes* species as compared to that in horizontal orb webs. Relative to their cribellar fibril volumes, *Hyptiotes cavatus* and *Hyptiotes gertschi* produce an average of six times more support thread volume than do the more-or-

less horizontal orb web-spinning species *Waitkera waitakerensis*, *Uloborus glomus*, and *Octonoba sinensis*. In contrast, the obliquely angled orb webs produced by *Siratoba referena* ( $\bar{X}$  angle to horizontal =  $37^\circ$ , SE = 3,  $N = 23$ ; B. D. Opell, unpublished data) have a ratio of support thread volume to cribellar fibril volume that is similar to that of the triangle webs of *Hyptiotes*.

Webs of the two *Miagrammopes* species have support-thread-to-cribellar-thread ratios that are intermediate between those of horizontal orb webs and vertical triangle webs. However, this does not necessarily indicate that they are functionally intermediate between horizontal and vertical webs. As elements of these simple webs are less highly integrated than those of planar webs, one or more capture lines may break without damaging the web's other lines (B. D. Opell, personal observation). Thus, the lines of these simple webs may not require the same strength as vertical planar webs, in which the failure of a single frame or attachment thread may render a large part or all of the web useless. Alternatively, *Miagrammopes* may build their simple webs in microhabitats where they tend to intercept smaller or more weakly flying insects that require less force to be absorbed by the web (Craig 1987b) or where oscillations of the web's capture lines enhance their ability to intercept insects (Craig et al. 1985). The effect of these differences in support thread volume on total web silk volume appears to be constrained by the association between spider weight and total web area. Consequently, even though web orientation and architecture affect the volume of a web's support thread, the association between spider weight and total silk volume transcends differences in web architecture.

This study makes two simplifying assumptions that warrant closer examination: all uloborid webs have similar useful lives, and all uloborid species feed on a diverse assemblage of prey. All the webs included in this study, with the possible exception of those produced by *O. sinensis*, appear to satisfy the first assumption by having a useful life of less than 24 h. The tendency for *O. sinensis* to repair its web may indicate that these webs typically last longer than 1 d. If correct, this point may explain why this species produced webs whose total silk volume, stickiness, and area fell above the regression lines in figures 6, 7, and 8. Thus, the broader application of the models developed in this study must consider the longevity of a spider's web. For example, a spider that produces an orb web that has a useful life of 3 d might be expected to spin a web that has much greater silk volume, stickiness, and area than predicted by figures 6, 7, and 8, respectively.

Many orb webs catch insects from a range of size and taxonomic categories and do not appear to be fine-tuned to capture specific prey (see Eberhard 1990 for a review). Even simple webs appear to supply *Miagrammopes* with a range of insects (Lubin et al. 1978; Opell 1990). This tendency for uloborids to be generalist predators may explain why the volume of silk their webs contain is related to spider weight. However, a few spiders construct modified orb webs that are designed to capture a specific type of prey. For example, members of the genus *Scoloderus* (family Araneidae) spin ladder webs with an expanded upper region, adapted to capture night-flying lepidoptera (Stowe 1986). The construction of these webs appears to require a greater amount of silk than typical orb webs, which suggests that these spiders should build webs less frequently than do most orb weavers. General support for this comes from Stowe's (1986)



observation that spiders that construct specialized webs do so only under very favorable environmental conditions.

This study introduces a new approach for evaluating the economy of spider web use. Indices of web cost and prey capture potential promise to be useful for both fine- and coarse-grain comparisons. When combined with additional information on prey availability in the microhabitat where a species places its web and on a spider's ability to subdue and extract nutrients from prey of different types, these indexes will provide a more complete picture of a species' feeding ecology. They also promise to provide insight into broader issues in spider evolution (Coddington and Levi 1991), such as the origin of orb webs that contain viscous adhesive capture threads rather than cribellar threads. This transition was a pivotal event in spider evolution: today, over 95% of the species and genera of orb-weaving spiders produce adhesive capture threads (determined from totals given in Levi 1982). This transition may be explained by the untested hypothesis that adhesive threads are less costly to produce than are cribellar threads (Lubin 1986; Vollrath 1992; Opell 1994b). If this is the case, then adhesive orb webs should either achieve, at a lower cost of production, the same stickiness as cribellate orb webs or, at the same cost of production as cribellate orb webs, achieve a greater stickiness.

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#### APPENDIX

##### FORMULAS USED TO COMPUTE THREAD LENGTH AND SILK VOLUME

The total length of cribellar thread in the webs of *Miagrammopes* species ( $T$ ) is calculated as

$$T = C1 + C2 \times I, \quad (A1)$$

where  $C1$  is the total length of linear cribellar thread in a web,  $C2$  is the total length of looped cribellar thread, and  $I$  is the species-specific index of increase (1.72 for *Miagrammopes animotus* and 1.57 for *M* species).

The index of increase ( $I$ ), based on a sample size of 10 for each species, is calculated as

$$I = \frac{NLP}{l \text{ mm}}, \quad (A2)$$

where  $N$  is the mean number of loops per millimeter in a 15–30-mm-long segment of continuously looped cribellar thread;  $L$  is the mean number of cribellar thread puffs (fig. 1) per loop in four loops; and  $P$  is the mean length in millimeters of a puff, as determined from the lengths of five puffs from each of four loops.

Total spigot number ( $S$ ) is determined as

$$S = CA \frac{N1 + N2 + N3}{A1 + A2 + A3}, \quad (\text{A3})$$

where  $CA$  is cribellum area,  $N1$ – $N3$  are the number of spigots in regions at the cribellum's anterior midline, on its posterior lateral margin, and midway between these two regions, and  $A1$ – $A3$  are areas of the three representative cribellum regions.

The volume of silk invested in a web's cribellar thread ( $CV$ ) is

$$CV = AV + FV, \quad (\text{A4})$$

where  $AV$  is the volume of the thread's two axial fibers and  $FV$  is the total volume of cribellar fibrils. We calculate  $AV$  as

$$AV = 2(Pi \times FR^2) \times CL, \quad (\text{A5})$$

where  $FR$  is the radius of a single axial fiber and  $CL$  is the total length of cribellar thread in the web. We determine  $FV$  as

$$FV = CL \times S \times V, \quad (\text{A6})$$

where  $V$  is the volume of silk per millimeter in a single cribellar fibril. This value is calculated specifically as

$$V = UN \times UV, \quad (\text{A7})$$

where  $UN$  is the number of node-internode units per millimeter and  $UV$  is the volume of a single node-internode unit. In turn,

$$UN = 1 \text{ mm}/ND \times NS, \quad (\text{A8})$$

where  $ND$  is node diameter in millimeters and  $NS$  is node separation in millimeters, and

$$UV = (1/6 \times Pi \times ND^3) + (NS \times Pi \times INR^2), \quad (\text{A9})$$

where  $INR$  is the radius in millimeters of a fibril's internode region.

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