

Material investment and prey capture potential of reduced spider webs

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Summary. The webs of *Miagrammopes animotus* have a simple structure and variable form. However, both the length of their lines and the total surface area of their capture threads are closely associated with spider size. These spiders' ability to deposit both linear and looped cribellar capture threads along a web's diverging capture lines plays an important role in establishing these relationships. Looped capture threads have the greater surface area and are more prominent in the webs of older spiders where they increase a web's surface area and enhance its ability to retain prey. The predicted performance of these webs is supported by comparisons of the stickiness of their threads and a survey of the prey their owners capture. Cribellar thread stickiness increases with spider size, and larger spiders capture prey that have greater masses.

greater behavioral involvement in subduing prey that are caught in their webs. An orb-weaving uloborid hangs beneath the hub of its web until a prey strikes. It then jerks the web, possibly to help locate the prey or gauge its weight (Lubin 1986), before running to and wrapping it. In contrast, *Miagrammopes* more actively manipulate their webs before and during prey capture (Lubin 1986; Lubin et al. 1987; Opell 1987). While monitoring their webs, they flex their long first legs to evaluate and adjust web tension. When a prey strikes a capture line, they first respond by releasing slack silk held between their second and third legs, causing the web to shake and momentarily become slack. Next, they run to the thread that holds the prey and forcefully jerk it. This sends loops down the thread that probably serve to more tightly ensnare the prey. Finally, they run to the struggling prey and begin throwing wrapping silk onto it with their fourth legs. Like all uloborids, *Miagrammopes* lack poison glands and rely entirely on prey wrapping to subdue prey (Lubin 1986; Opell 1979).

Larger or more actively struggling prey that are caught in orb-webs are likely to encounter several capture threads. In contrast, prey that strike a *Miagrammopes* web are held by only one thread. Although *Miagrammopes* are more actively involved in prey capture than are orb-weavers, their webs must still hold prey long enough for them to subdue it. If, as spiders develop, they are to capture larger, more profitable prey, then their webs must become increasingly better able to retain this prey.

The purpose of this study is to test the null hypothesis that morphological changes in the spinning apparatus of *Miagrammopes* (Opell 1989a) alone account for developmental changes in the functional properties of these spider's webs. Alternatively, differences in web spinning behavior may contribute to qualitative and quantitative changes in web properties. This hypothesis is tested by examining the developmental changes in webs produced by *Miagrammopes*, the tenacity of their capture threads, and the prey these spiders capture.

Introduction

Orb-webs are intricate and economical prey capture devices that minimize the material a spider need invest to intercept and retain prey (Craig 1987; Denny 1976; Eberhard 1981, 1986). However, some members of orb-weaving groups exhibit web reduction (Stowe 1986). A striking example of this is the genus *Miagrammopes* of the family Uloboridae (Lubin 1986; Lubin et al. 1978). These spiders spin non-planar webs that contain from one to nine lines (Lubin 1986; this study) of various lengths that diverge at different angles (Fig. 1). The degree of intraindividual variability in web form has not been established, although it is probably governed largely by a spider's chance encounters with attachment sites during web construction.

Unlike bolas spiders (Eberhard 1977, 1980; Stowe 1986), *Miagrammopes* show no evidence of chemical attractants or prey specialization (Lubin 1986; Lubin et al. 1978; personal observations). However, their reduced investment in web material is achieved at the expense of

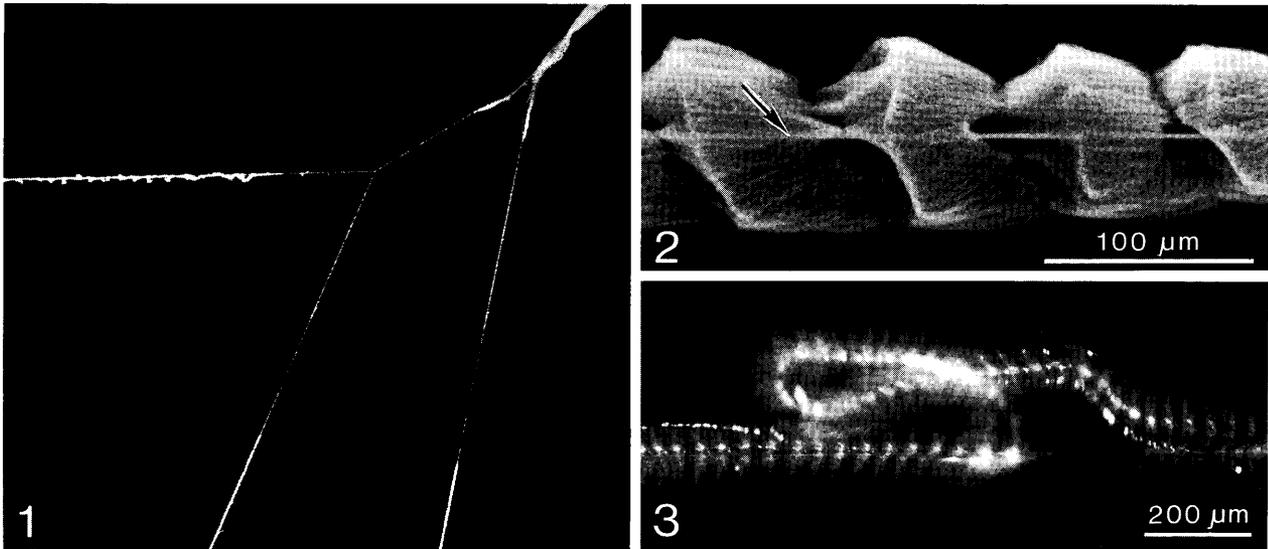


Fig. 1. Adult female *Miagrammopes animotus* (about actual size) monitoring a web with three capture lines. The horizontal line has looped capture silk and the vertical lines have linear capture silk on their lower regions. **Fig. 2.** Scanning electron micrograph of linear capture silk, showing the frame line (arrow) on which cribellar thread is laid. **Fig. 3.** Light micrograph of looped capture silk

Background

Spider orb-webs are made of frame lines that anchor them to their surroundings and support their prey capture threads. The capture threads of more derived orb-weaving spiders owe their stickiness to adhesive droplets that are deposited on them as the thread is spun from spigots. The primitive cribellar capture threads spun by members of the family Uloboridae and other cribellate families are formed of a cloud of fine, looped fibrils that issue from the spigots of an oval spinning plate, the cribellum, and are deposited as torus shaped puffs around a pair of supporting threads (Figs. 2 and 3; Opell 1979, 1989a; Peters 1983, 1984, 1986). Although the prey retention mechanism of this composite thread is not fully understood, the fibril loops that form its fuzzy surface appear to snag a prey's setae and surface irregularities.

Miagrammopes are freer than orb-weavers to regulate the lengths of their web's supporting and prey capture threads. They first spin one or several interconnected lines of varying lengths and then add cribellar prey capture thread to segments of some or all of these lines (Fig. 1; Lubin 1986; Lubin et al. 1978). Along a single frame line, prey capture thread may be deposited in both linear (Fig. 2) and looped (Fig. 3) patterns.

Looped cribellar thread has never been described in the Uloboridae, although it appears to be common in *Miagrammopes* and unique to members of this genus. All uloborids except members of *Miagrammopes* and the monotypic genus *Polenecia* produce self-supporting capture threads that are laid across rather than along frame

(radial) lines (Peters 1983, 1984, 1986). The supported capture threads of *P. producta* (Simon) do not contain looped capture threads (Peters 1983). However, I have observed these threads in the webs of *M. animotus* Chickering and an undescribed Costa Rican species (Opell 1987) that belongs to another subdivision of the genus (Opell 1984).

Developmental changes alter the properties of *Miagrammopes* webs. As these spiders grow, their cribellae increase in area and spigot number, causing them to spin wider swaths of capture threads with more fibrils (Opell 1989a).

Methods

I studied *Miagrammopes animotus* Chickering, 1968 from 4 February to 10 March 1987 at the Center for Energy and Environment Research's El Verde field station, located in a subtropical wet forest zone (Holdridge system) of Puerto Rico's Luquillo National Forest. Immatures can be identified with certainty, as this is the only species found at this locality. I used three developmental series of third (first web-spinning) through sixth (adult) instars of this species. From one series I determined cribellum and cribellar thread parameters, from another, web features, and from another the stickiness of linear cribellar thread. I collected each spider, measured the silk or web, and assigned it to a developmental stadium on the basis of its first femur length (Opell 1987): third instar <1.20 mm, fourth instar 1.20–1.64 mm, fifth instar 1.65–2.04 mm, sixth instar >2.04 mm. Mature males do not spin capture webs and were excluded from this study.

During field surveys, I dusted undamaged webs with corn starch (Carico 1977) to make their lines more visible and measured to the nearest millimeter the total length of all web lines and the lengths of their segments that were covered by linear and looped capture thread. Lines with either type of cribellar thread are designated as capture lines.

The surface of uloborid capture thread is formed of fibrils spun from cribellar spigots. This study assumes that all or a constant percentage of these spigots operate at any given time and, therefore, that the number of spigots on a spider's cribellum is an index of the material invested in the capture thread it spins. Methods used to determine the mean number of spigots in each instar's cribellum are described in Opell (1989a). Because the cribellar fi-

brils that form uloborid capture thread are coiled and deposited as puffs, multiplying the number of spigots in a spider's cribellum by the length of cribellar thread in its web underestimates the total length of cribellar fibrils spun. However, as the length-to-width ratio of *M. animotus* puffs does not change significantly during development (Opell 1989a), this index is appropriate for intraspecific comparisons.

I collected 3-cm long linear and looped cribellar thread samples on raised adhesive supports affixed to microscope slides. As an index of the prey capture potential of linear cribellar thread, I computed the mean surface area per millimeter of each instar's capture thread using the formula for a double cone:

$$\text{Area} = 2 \pi R \sqrt{R^2 + h^2}$$

where R is the cone's maximum radius (one-half the puff's width) and h is the cone's height (one half the puff's length). I multiplied the mean surface area of an instar's cribellar thread puffs by the mean number of puffs in 1 mm of its capture thread to determine the surface area per millimeter length of its linear capture thread.

To compute the surface area of a segment of looped cribellar thread, I determined the average number of loops per millimeter in a 15–30 mm long segment of continually looped cribellar thread. I then determined the actual length of cribellar thread in four of the sample's loops by first measuring the length of five cribellar thread puffs in one loop; then I determined the mean length of each puff and multiplied this value by the total number of puffs in each of four loops. To determine the length of cribellar thread invested in loops, I multiplied the mean length of these four loops by the average number of loops in a mm of looped thread. This value is an index of the increased length of cribellar thread when it is deposited as looped rather than linear capture thread. For webs containing looped capture thread, I computed an adjusted cribellar thread length by adding to the length of the web's linear capture thread the product of its looped cribellar thread length and the instar-specific index of increase just described.

I determined the stickiness of linear cribellar thread samples by measuring the force required to pull an aluminum contact plate free from the thread (Opell 1989b). A spider's cribellar thread was collected on a microscope slide sampler with five adhesive supports spaced at 4 mm-intervals. Each of the thread's four sectors was examined under a dissecting microscope to assure that it was not damaged. The 2.20 mm wide contact plate was pressed against each thread sector with a force of 3.03×10^{-5} Newtons and then slowly raised until it pulled free of the thread. The mean force required to pull the plate free from a sample's four sectors was divided by the width of the contact plate and expressed as Newtons per millimeter of contact. These stickiness measurements were taken at a mean temperature of 23° C (SD=0.9) and a mean relative humidity of 66% (SD=1.5%).

Feeding spiders and their prey were collected. Spiders were measured and their silk-wrapped prey were dried in a desiccator, weighed to the nearest 0.01 mg on a Cahn Millibalance model 7500 DTL, unwrapped, and identified. Only spiders feeding on single prey items are included in the analysis; the prey of two spiders, each with two insects wrapped together, were excluded from the analysis. I also weighed the prey's silk wrapping when it was not contaminated by debris.

Only webs with looped cribellar thread are included in comparisons of looped parameters. All statistical tests were performed with SAS V (compiled by the Statistical Analysis System Institute, SAS Circle, P.O. Box 8000, Cary, NC, 27511, USA). I used a one factor analysis of variance (ANOVA) to determine whether development (instar) significantly influenced web parameters and, if so, a Kruskal-Wallis k-sample test (K-W) to determine whether instar designations significantly ranked mean web parameters.

Results

Cribellar thread and web properties are given in Table 1 for each *Miagrammopes animotus* instar. The number

of capture lines in webs varies greatly within each instar (third instar, 2–9; fourth, 2–8; fifth, 1–7; sixth, 2–7) but does not change significantly during development (ANOVA: $P > 0.53$). The total lengths of a web's frame lines, exposed frame lines, and frame lines covered by cribellar thread, as well as the percentage of frame lines covered by cribellar thread, increase significantly throughout development (ANOVA: $P < 0.0001$; K-W: $P < 0.0014$).

The length of linear cribellar thread does not change during development (ANOVA: $P > 0.17$), but looped cribellar thread becomes more common and increases in length in the webs of older spiders. The percentage of webs containing looped thread increases 2.8 fold during development. Both the percent of a web's capture lines having looped cribellar thread and the total measured length of a web's looped cribellar threads increase during development (ANOVA and K-W: $P < 0.0001$).

By depositing capture thread in a looped rather than a linear fashion, *M. animotus* achieves three things. (1) It maintains a high ratio between adjusted capture thread length and frame thread length (grand mean = 0.87) that does not change through development (ANOVA: $P > 0.18$). (2) It shortens by 25% the length of cribellar thread that would otherwise have been available to intercept prey (the index in Table 1 computed as: looped + linear capture thread/adjusted capture thread length). Among those webs that contain looped cribellar threads, this index does not change during development (ANOVA: $P > 0.27$). (3) It increases the ratio of a web's cribellar thread surface area to the measured length of its cribellar thread. Webs with greater indexes have cribellar threads that have, on average, greater surface areas and, therefore, a greater ability to retain prey. This index increases during development, as shown by ANOVA and K-W tests of instar means ($P < 0.0001$) and by a significant linear regression ($P < 0.0001$, $R^2 = 0.76$) of the index against first femur length (Fig. 6). This regression, like those reported hereafter, is not confounded by interinstar differences in slope or intercept, since within instars regressions are not significant ($P > 0.06$).

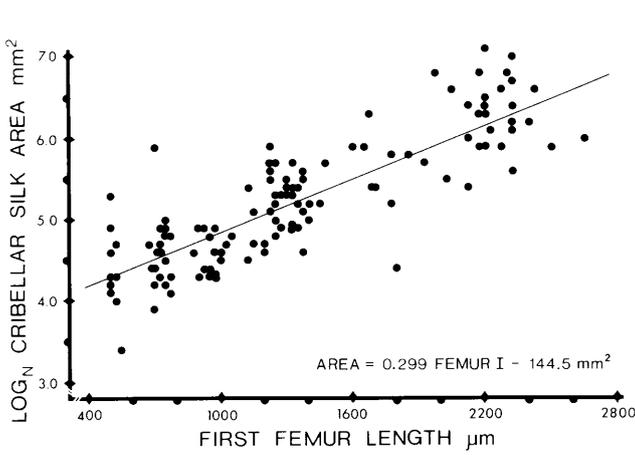
Both mean total capture thread surface area and total cribellar fibril length increase during development (ANOVA and K-W: $P < 0.0001$). Linear regressions of the log of a web's total capture thread surface area and the log of total cribellar fibril length against its owner's first femur length (Figs. 4 and 5) are significant ($P < 0.0001$) and have R^2 values of 0.71 and 0.83, respectively.

Increased cribellar thread surface area is associated with increased thread stickiness, as demonstrated by an increase in the stickiness of linear cribellar threads spun by subsequent instars (Table 1; ANOVA and K-W: $P < 0.0001$). A linear regression of data from Opell (1989a) shows that the surface area of a given length of linear cribellar thread is related to the size of the spider that produced it (area in $\mu\text{m}^2 = 270.45 \times [\text{first femur length in } \mu\text{m}] - 13493$; $P < 0.0001$; $R^2 = 0.50$). When this formula is used to estimate the surface area of the linear cribellar thread samples whose stickiness was measured,

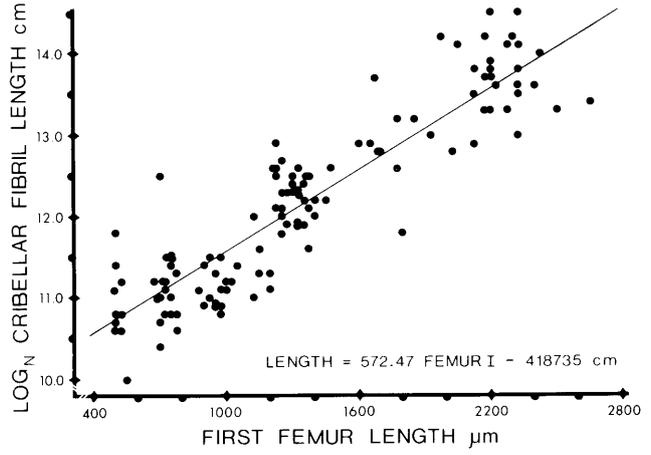
Table 1. *Miagrammopes animotus* cribellum, cribellar silk, and web values

	Stadium											
	Third			Fourth			Fifth			Sixth		
	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD
Cribellum: ^a												
Number of spigots	23	1824	795	23	4128	2285	7	6852	1890	17	10454	2103
Linear												
Cribellar Thread: ^a												
Puff area μm^2	30	11 506	8850	25	16851	6996	7	24 181	4048	22	40724	10827
Puffs/mm	37	25.8	8.3	25	20.6	3.7	7	17.5	3.2	22	15.5	3.8
Area $\mu\text{m}^2 \times 10^3/\text{mm}$	37	265	168	25	386	242	7	425	108	22	618	203
Looped												
Cribellar Thread: ^a												
Loop length μm	13	112	38	12	121	29	4	178	25	12	168	32
Loops/cm	13	6.9	1.8	12	6.7	1.3	4	6.7	0.5	12	4.2	1.3
Length increase	13	1.74	0.23	12	1.82	0.26	4	2.19	0.21	12	1.72	0.30
Web Measurements:												
Capture lines	54	3.5	1.5	33	3.4	1.4	10	3.5	1.7	26	3.7	1.4
% Capture lines with looped thread	54	18	34	33	48	39	10	58	39	26	64	37
Total length of frame lines cm	54	50.0	20.5	33	64.4	21.0	10	78.6	37.5	26	117.4	57.9
Length of exposed frame lines cm	54	12.7	8.7	33	19.4	9.6	10	24.0	18.7	26	45.2	34.3
Linear capture thread cm	54	32.8	16.7	33	31.0	21.4	10	34.3	22.7	26	39.8	25.9
% Spiders with looped thread	54	30		33	73		10	90		26	85	
Looped capture thread cm	16	15.3	17.6	24	19.3	12.1	9	22.6	29.7	22	38.3	19.7
% Looped thread	16	44	35	24	48	31	9	35	31	22	56	25
Adjusted capture thread length cm	54	40.7	19.7	33	56.4	19.2	10	78.8	54.6	26	95.3	40.4
% Adjusted capture thread comprised of looped thread	16	52	33	24	58	29	9	48	31	22	66	22
Looped + linear capture thread												
Adjusted capture thread length	16	0.78	0.14	24	0.74	0.13	9	0.74	0.16	22	0.73	0.09
Adjusted capture thread												
Frame thread	54	0.83	0.18	33	0.89	0.21	10	0.98	0.32	26	0.86	0.22
Cribellar fibril length m	54	7417	3596	33	23290	7925	10	53958	37392	26	99635	42235
Total capture surface area mm^2	54	107.6	52.2	33	217.8	74.1	10	334.3	231.7	26	589.1	249.7
Total surface area capture thread length	54	2.90	0.54	33	4.97	1.07	10	5.86	1.58	26	8.26	1.34
Linear cribellar thread stickiness:												
Linear cribellar thread stickiness Newtons $\times 10^{-5}$ per mm width of contact plate	65	1.79	1.78	16	1.40	1.18	10	3.56	2.87	14	5.14	2.75

^a Values from Opell 1989



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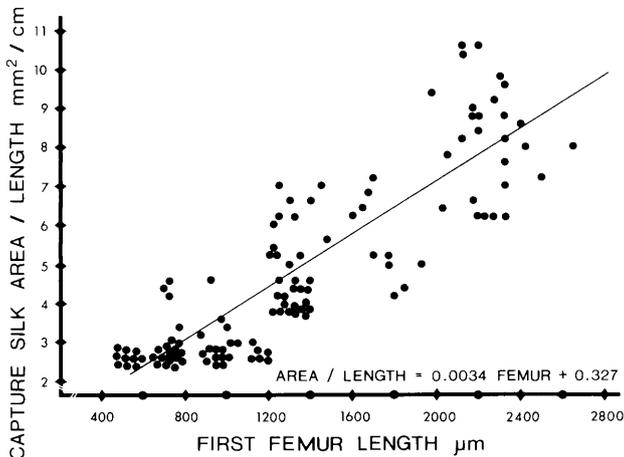


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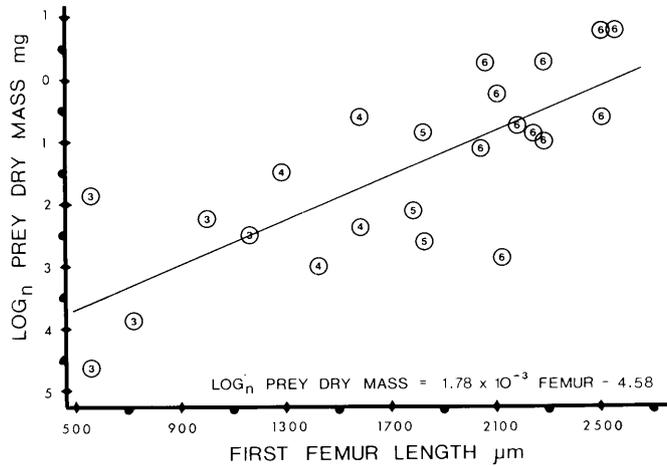
Figs. 4, 5. Plots of first femur length against total web cribellar silk area (4) and total cribellar fibril length (5). The formula for each plot's regression line appears above its lower axis

Table 2. Prey captured by the four web-spinning instars of *Miagrammopes animotus* (mean \pm standard deviation)

Taxon	Number	Mean dry mass mg	Number captured by each instar			
			Third	Fourth	Fifth	Sixth
Unidentified	6	0.07 \pm 0.03	2	1	2	1
Araneae	3	0.28 \pm 0.44	1	1	—	1
Coleoptera	6	0.65 \pm 0.79	1	1	1	3
Diptera	4	0.57 \pm 0.51	1	1	—	2
Hymenoptera	4	1.07 \pm 0.77	—	—	—	4
Total prey			5	4	3	11
Mean dry mass of prey (mg)			0.07 \pm 0.06	0.23 \pm 0.23	0.20 \pm 0.19	0.89 \pm 0.73



6



7

Figs. 6, 7. Plots of first femur length against the ratio of total web capture silk area to measured capture silk length (6) and the natural log of dry mass of prey captured (7). The formula for each plot's regression line appears above its lower axis. The circled numbers in 7 designate the spider's instar

estimated cribellar thread surface area is correlated with mean measured stickiness ($r = 0.62$, $P < 0.0001$).

Twenty-three spiders and their prey were collected throughout this 35-day study (4, 4, 9, and 6, in the first-fourth quarters, respectively; chi square = 2.95, $P > 0.30$). Neither prey mass nor spider instar is correlated with the day of collection ($P > 0.56$), indicating that these results were not biased by progressive changes in the size of available prey or spiders.

Identifiable prey include spiders and three insect orders (Table 2). The mean dry masses of these prey taxa do not differ significantly (ANOVA: $P > 0.51$); however, the sample size is small. The four instars of *M. animotus* do not differ in the prey taxa they capture (ANOVA: $P > 0.53$), although prey dry mass increases with instar (ANOVA: $P < 0.0001$; K-W: $P < 0.016$). This is also demonstrated by a significant linear regression ($P < 0.0001$, $R^2 = 0.59$) of the log of prey dry mass and spider first femur length (Fig. 7).

Silk contributed very little to the mass of wrapped prey. For six Coleoptera, one Diptera, and four Hymenoptera, it averaged only 5.7%, 6.7%, and 6.7%, respectively, of the prey's dry mass.

Discussion

This study demonstrates that the web-spinning behavior of *Miagrammopes animotus* is characterized by both geometric plasticity and size-related changes in silk investment. Older (larger) spiders spin greater lengths of thread and have larger cribellae that increase the surface areas of their cribellar capture threads. However, the null hypothesis that these changes alone enhance the prey capture potential of webs spun by older spiders is proven false. As spiders grow, they incorporate more looped cribellar threads in their webs. This increases the surface area and width of a web's cribellar threads and, therefore, its ability to retain prey. Consequently, the webs of older spiders have capture threads that appear increasingly better adapted to retain larger, stronger, more profitable prey.

This conclusion is supported by studies of cribellar thread stickiness that show that threads with greater surface areas resist greater forces pulling on objects they hold. It is also consistent with prey records showing that larger spiders capture prey with greater masses. The short time span during which this study was conducted and the lack of correlation between the size of either spiders or their prey and the date on which they were collected make it difficult to attribute these results to an increase in the average size of available prey. Likewise, there is no evidence that larger spiders select web sites that expose them to larger prey. Individuals from all instars were commonly found clustered on fallen palm fronds, short bamboo plants, and dead tree branches, but demonstrated no obvious stratification that might expose them to different prey (personal observations). However, when collecting feeding spiders and their prey, I did not record data, such as height above ground, that would be useful in assessing potential microhabitat differences among instars.

In addition to increasing surface area, the looped cribellar threads of *M. animotus* webs also enhance their ability to capture prey by functioning in a manner analogous to the "sliding connections" between the dry radii and adhesive prey capture spirals of Araneidae orb-webs (Eberhard 1976). When sections of looped cribellar thread pull free of the frame line, they elongate, both as they straighten and as the coiled fibrils that form their surfaces are pulled taut (the "unreeling" described by Eberhard 1976). Thus, the effective length of a segment of looped cribellar thread increases without pulling completely free of the frame line. Because a thread's breaking elongation is directly proportional to its length and tension (Langer 1969), looped cribellar thread is better able to withstand the force of an initial prey strike or the thrashing of a struggling prey than is linear cribellar thread. This attribute of looped cribellar thread is more difficult to quantify than is its increased contribution to a web's total surface area. However, like increased surface area, it better equips a web to capture larger and stronger prey.

This study does not document the contributions of web manipulation and prey handling to prey capture success. From the instant a prey strikes the web, its chances of struggling free are affected by the spider's behavior. The initial web slackening that occurs at this time probably helps the web absorb the impact of a large prey without rupturing. Larger spiders are better equipped to capture larger prey because they can flex their legs more forcefully (Opell 1987) and to a greater extent, run more quickly to a struggling prey, produce more wrapping silk, and manipulate wrapping silk better with their longer legs.

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