

Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae

BRENT D. OPELL

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA, U.S.A. 24061

Received July 23, 1986

OPELL, B. D. 1987. Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. *Can. J. Zool.* **65**: 1028–1034.

Members of the genera *Uloborus*, *Hyptiotes*, and *Miagrammopes* have similar web-monitoring postures, but very different webs and tactics for monitoring them. Orb weavers of the genus *Uloborus* construct horizontal webs and hang from their hubs, whereas reduced-web uloborids construct vertical webs and monitor them from a single thread. To determine if changes in spider strength accompanied web reduction, resting and maximum force measurements were taken of a developmental series of *Hyptiotes cavatus*, *Uloborus glomus*, *Miagrammopes animotus*, *Miagrammopes pinopus*, and an undescribed Costa Rican *Miagrammopes* using a glass needle strain gauge. Both carapace length and spider weight were used as indexes of spider size. Regression analyses of forces show that *H. cavatus* exerts the greatest relative force and *Miagrammopes* species the least. This is consistent with requirements for the operation of each web type: *Hyptiotes cavatus* tenses its entire triangular web and suddenly releases this tension when a prey strikes its web, whereas a *Miagrammopes* species jerks a single thread that has captured a prey. Within the genus *Miagrammopes*, the species with the most highly modified carapace expressed the greatest resting force.

OPELL, B. D. 1987. Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. *Can. J. Zool.* **65**: 1028–1034.

Les espèces des genres *Uloborus*, *Hyptiotes* et *Miagrammopes* ont des postures semblables lors de l'inspection de leur toile, mais leurs toiles et les tactiques qu'elles emploient pour en faire l'inspection sont très différentes. Les tisseuses de toiles circulaires du genre *Uloborus* construisent des toiles horizontales et restent suspendues au milieu; en revanche, les Uloboridae qui construisent des toiles plus petites les fabriquent à la verticale et les surveillent à partir d'un fil unique. L'utilisation d'un indicateur d'effort à aiguille de verre a permis de mesurer la tension au repos et la force maximale chez des séries en développement d'*Hyptiotes cavatus*, *Uloborus glomus*, *Miagrammopes animotus*, *Miagrammopes pinopus* et une espèce encore inédite de *Miagrammopes* de Costa Rica, mesures relevées dans le but de déterminer si la réduction de la toile est reliée à un changement de force. La longueur de la carapace et la masse de l'araignée servaient d'indices de la taille de l'araignée. Les analyses de régression des forces indiquent que c'est *H. cavatus* qui exerce la plus grande force relative et les espèces de *Miagrammopes*, les forces les moins grandes. Ces données sont compatibles avec les forces requises pour l'opération de chaque type de toile: *Hyptiotes cavatus* exerce une tension sur la totalité de sa toile triangulaire et relâche brusquement cette tension lorsqu'une proie frappe la toile, alors que les espèces de *Miagrammopes* ne secouent que le fil qui a capturé une proie. Chez les espèces du genre *Miagrammopes*, celle qui possède la carapace la plus modifiée est celle qui conserve la plus grande tension de repos.

[Traduit par la revue]

Introduction

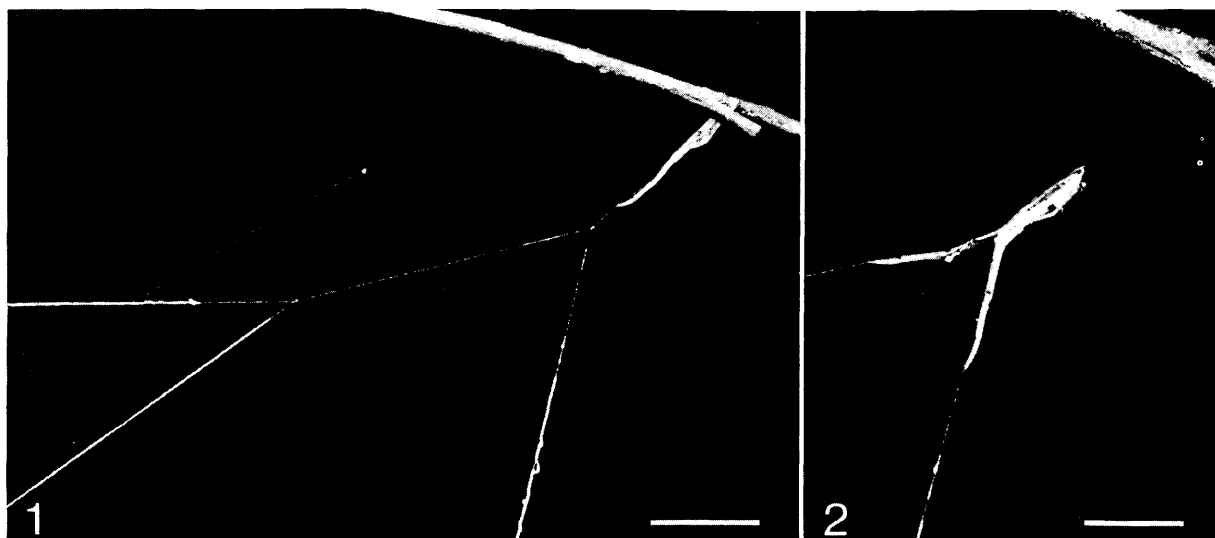
In the spider family Uloboridae, web form correlates with carapace shape and the position, size, and number of eyes (Opell 1984a). This association is explained by changes in web-monitoring tactics that accompany reduction of the family's primitive orb web (Eberhard 1972; Muma and Gertsch 1964; Opell 1979) to one of several types of simpler webs. Unlike orb-weaving uloborids that typically hang from the hubs of their webs while waiting for prey to contact their snares (Opell and Eberhard 1983), reduced-web uloborids monitor their webs near an attachment point of one of the web's taut anchor threads (Fig. 1). Here they extend their first legs directly forward and more actively monitor and manipulate their webs, and, in at least one case, exert greater force than orb weavers (Opell 1985). To facilitate these postural and force changes, prosomal muscles, particularly the extrinsic muscles of the first legs, and the endosternite plate to which they attach have been reoriented (Opell 1984a). These appear to be primary changes that facilitate both the effective paraxial movement of the legs and the exertion of force along the plane of the web's monitoring thread. Other changes in leg article lengths and leg muscles may optimize either leg strength or the total amount of leg movement. Externally, this prosomal reorganization is expressed in modified carapace features of the reduced-web genera *Hyptiotes* and *Miagrammopes*.

Hyptiotes species spin triangle webs (Opell 1982a; Wilder

1875; Peters 1938) which consist of a monitoring thread from which four taut radii diverge. The outer two radii attach to surrounding vegetation and are connected by a frame thread that completes the triangle. The inner two radii attach distally to this frame thread. Evenly spaced, sticky (cribellar) prey-capture threads extend between the four radii. The carapace of *Hyptiotes* is broad and its four anterior eyes are small and offset from the anterior margin of the carapace (Opell 1979, 1984a). The four posterior eyes are large and the posterior laterals are borne on prominent tubercles.

Members of the genus *Miagrammopes* construct an even more reduced web which shows a much less stereotypic form (Akerman 1932; Lubin et al. 1978; Lubin 1986). This web usually consists of a roughly horizontal, nonsticky resting thread from which one or several vertical or diagonal prey-capture threads extend (Figs. 1, 2). In some cases, capture silk may be deposited along the resting line. Even within a single species, the number, orientation, and lengths of the capture threads are quite variable (Lubin 1986; Lubin et al. 1978; B. D. Opell, unpublished observations). *Miagrammopes* lacks anterior eyes and, like *Hyptiotes*, has large posterior eyes and prominent posterior lateral eye tubercles (Opell 1984b; Opell and Cushing 1986).

The relative leg lengths of reduced-web uloborids also differ from those of most orb-weaving members of the family: the legs of *Hyptiotes* are proportionately shorter and the legs of



FIGS. 1 and 2. *Miagrammopes animotus*. Fig. 1. Female monitoring a capture web in a typical cryptic posture. Scale bar = 1 cm. Fig. 2. The same female responding to a prey on the vertical capture line. Scale bar = 0.5 cm.

Miagrammopes, proportionately longer. These differences are consistent with requirements for the use of each type of reduced web. After constructing a triangle web, a *Hyptiotes* positions itself near the attachment point of the monitoring thread, where it pulls in and holds slack thread equal in length to three to four body lengths (Opell 1982a). The spider periodically flexes its first legs as it monitors its web. When a prey strikes the web, *Hyptiotes* instantaneously releases its grip on the apex line, causing the web to jerk as the slack thread previously held between the first and fourth legs is taken up.

By contrast, the capture lines of a *Miagrammopes* web extend at less regular and more oblique angles from the typically horizontal monitoring line, a situation that limits the spider's ability to greatly alter the tensions of these capture lines. When a *Miagrammopes* detects web vibration, it moves from the monitoring site onto its web, begins tugging on the capture line from which these vibrations emanate (Fig. 2), and then violently jerks the web, sending a wavelike loop down it (Lubin et al. 1978). This prey-capture behavior appears to be enhanced by the longer legs of these spiders, which permit greater distal displacement when they are flexed. Because the legs of *Miagrammopes* do not have distinctly greater relative diameters, this increased displacement is probably gained at the expense of mechanical advantage (strength).

An earlier study (Opell 1985) supported these predictions by showing that when it hangs from a single, horizontal resting thread, the triangle-web spider *Hyptiotes cavatus* (Hentz) exerts greater force throughout development than does *Uloborus glomus* (Walckenaer), an orb weaver with a similar web-monitoring posture (Opell and Eberhard 1983). The purpose of this study is to test further the hypothesized functional links between web form, carapace features, and leg lengths. This was done by measuring the forces exerted by *U. glomus* and *H. cavatus* and comparing them with values of three *Miagrammopes* species, representing the two subgroups of the genus (Opell 1984b). Because these *Miagrammopes* subgroups are characterized by differences in the degree of carapace modification, this study also determines if subsequent prosomal modification within this genus is associated with an increase in expressed force. Additionally, it compares the maximum force

expressed by each species and, unlike my earlier study (Opell 1985) using laboratory-reared *H. cavatus*, employs exclusively measurements taken from natural populations.

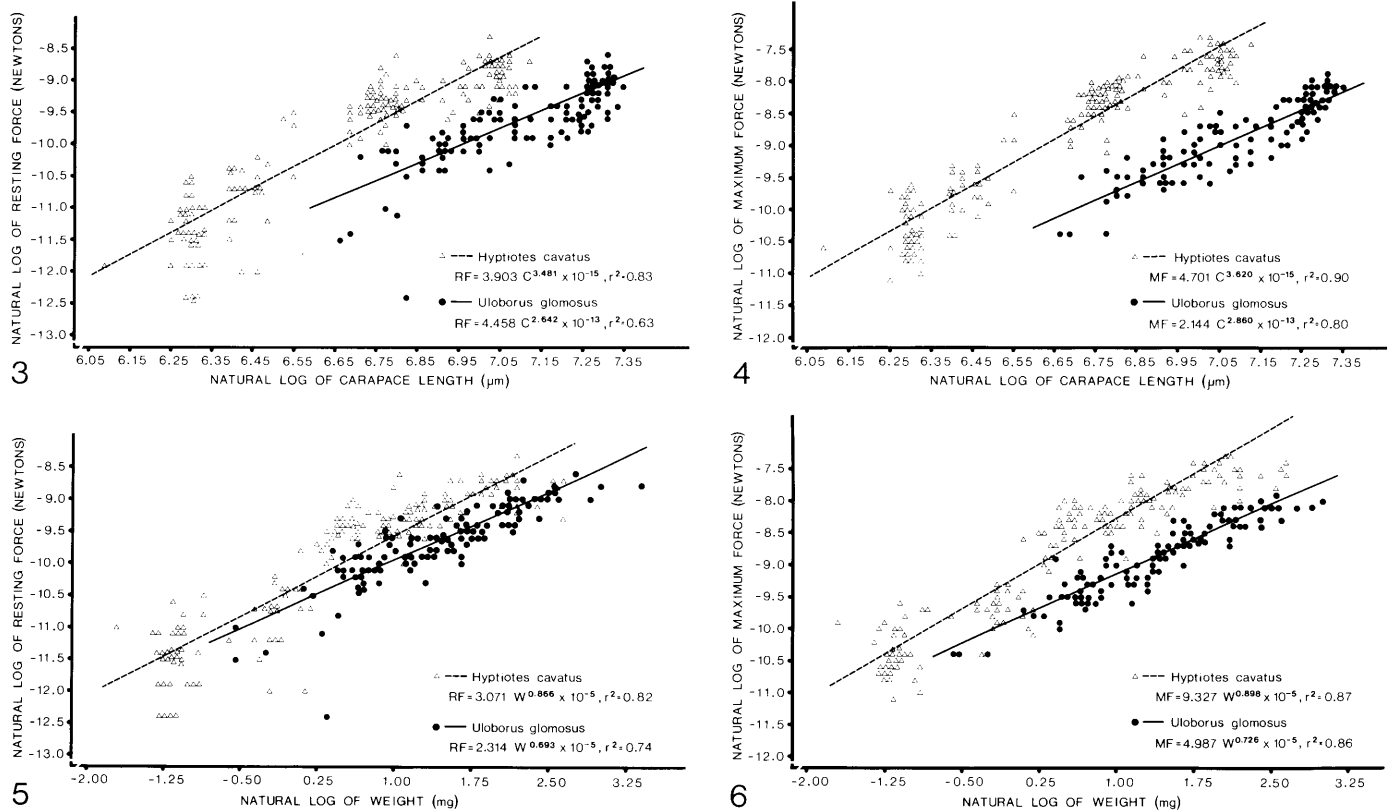
Methods and materials

All field studies were conducted during 1985. I collected *Uloborus glomus* on the Virginia Polytechnic Institute campus during May and June and *Hyptiotes cavatus* from Giles and Montgomery counties, Virginia, from May through August. I studied *Miagrammopes animotus* Chickering at the El Verde field station of the Center for Energy and Environment Research in the Luquillo National Forest of Puerto Rico during January and February and *Miagrammopes pinopus* Chickering at the Virgin Islands Ecological Research Station, St. John, U.S. Virgin Islands, during February. During late June and early July, I studied an undescribed *Miagrammopes* species at the La Selva field station of the Organization for Tropical Studies, near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica. This latter *Miagrammopes* species belongs to a different subgroup and has a more highly modified, shorter carapace with more prominent posterior lateral eye tubercles, and more widely spaced and posteriorly displaced posterior median eyes (Opell 1984b).

Adult male (sixth instar) uloborids and spiderlings newly emerged from egg sacs (second instars) either do not construct capture webs or construct atypical capture webs (Eberhard 1976; Lubin et al. 1978; Opell 1982a, 1982b). For this reason, I used only third- to fifth-instar juveniles and mature (sixth-instar) females in this study.

Only one set of resting and maximum force measurements was taken from each *Miagrammopes* individual. *Uloborus glomus* were collected from a population of approximately 200 individuals living on campus shrubbery and *H. cavatus* were collected from three hemlock groves each with a population of about 80 individuals. Sampling and release of these latter two species was done systematically to insure that an individual was not measured more than once in a given stadium, although this method did not preclude an individual's being used more than once during the course of this study.

After collecting specimens, I measured their carapace and first femur lengths using a dissecting microscope equipped with a micrometer and weighed them on a Cahn millibalance. Specimens were kept individually in small, cotton-stoppered glass vials for 1 to 3 days before their forces were measured. To prevent dehydration, these vials were placed in a plastic bag containing a piece of moist cotton. Using a small brush, I induced each specimen to spin a resting thread between the fixed applicator stick and the moveable glass needle of a strain gauge



FIGS. 3–6. Comparison of the resting (Figs. 3 and 5) and maximum (Figs. 4 and 6) forces exerted by the orb weaver *Uloborus glomus* and the triangle weaver *Hyptiotes cavatus* as a function of carapace length (Figs. 3 and 4) and weight (Figs. 5 and 6). RF, resting force; C, carapace length; MF, maximum force.

TABLE 1. Mean temperature values ($^{\circ}\text{C}$) at which force measurements were taken, results of Kolmogorov–Smirnov D -tests of normality of temperature values, and sample sizes

	<i>Hyptiotes cavatus</i>	<i>Uloborus glomus</i>	<i>Miagrammopes</i> sp.	<i>Miagrammopes pinopus</i>	<i>Miagrammopes animotus</i>
Mean temperature (SD)	25.2 (0.8)	24.4 (0.7)	25.2 (1.5)	25.3 (1.0)	21.8 (0.4)
Probability of normal distribution	0.92	0.98	0.89	0.99	0.92
Stadium sample size and mean temperature					
Third	37, 24.4	27, 24.1	68, 24.8	48, 25.4	20, 21.7
Fourth	24, 25.5	27, 24.2	49, 25.6	33, 25.1	27, 21.8
Fifth	53, 25.6	13, 24.0	23, 25.3	14, 24.8	14, 21.7
Sixth	42, 25.2	45, 25.0	26, 25.5	21, 25.3	37, 22.0
Total sample size	156	113	170	123	114

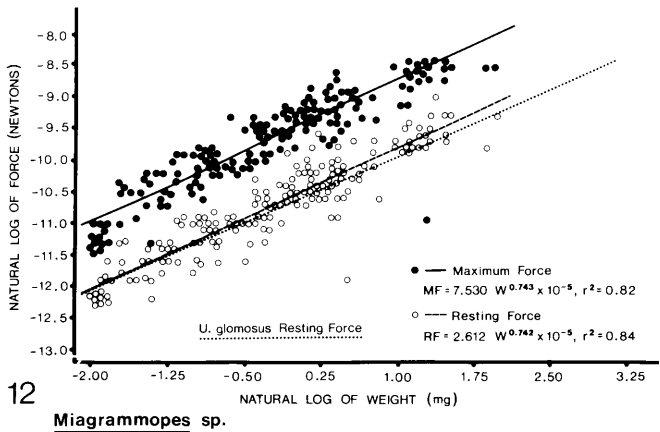
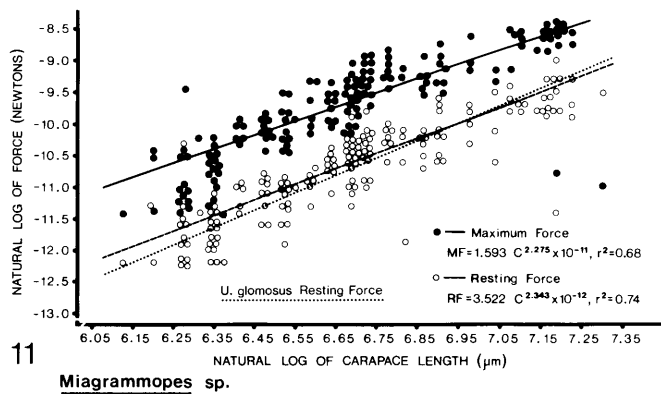
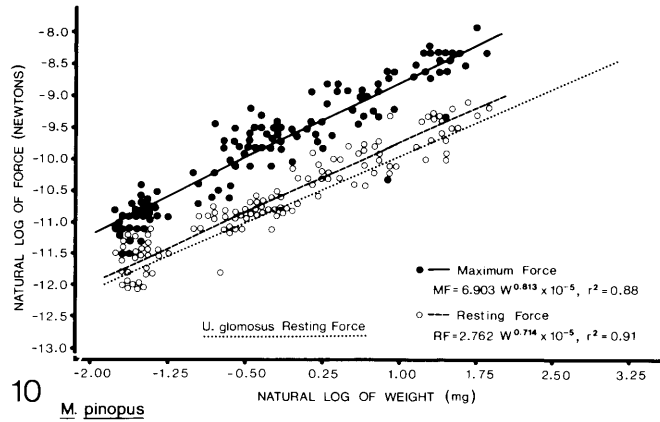
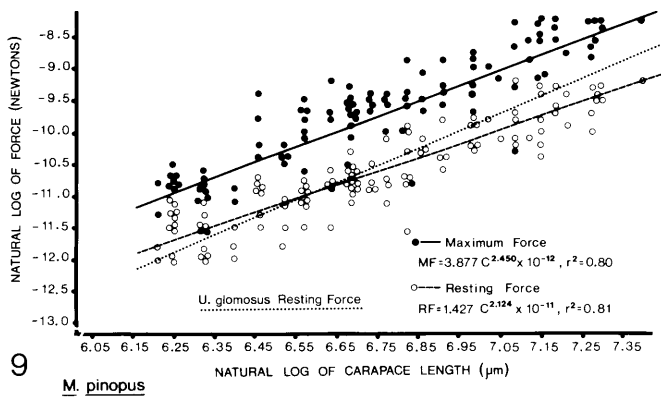
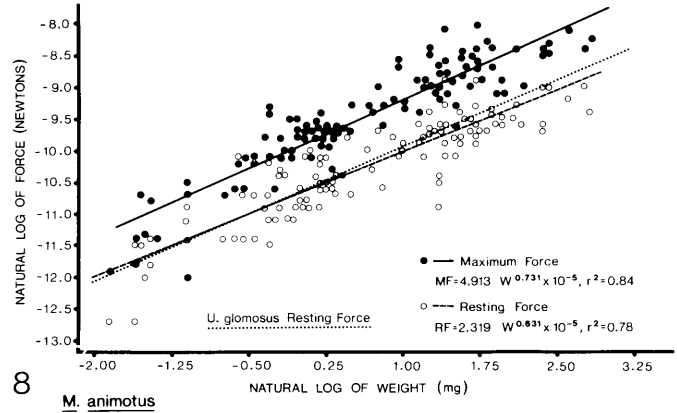
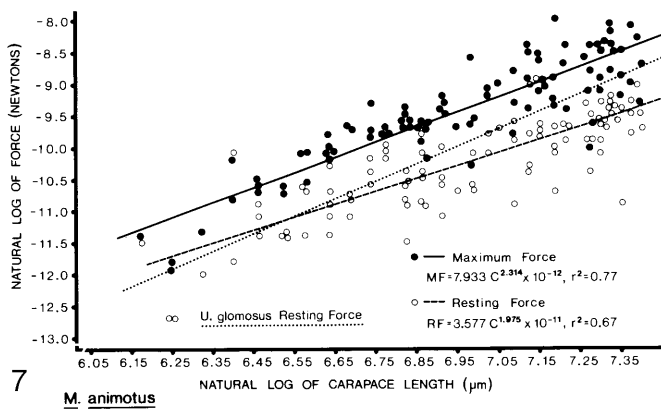
(Opell 1985). After the spider had assumed a typical resting posture, tugged on the thread to evaluate and adjust its tension, and produced a stable deflection of the glass needle, I recorded the needle's position on the scale. This value was subsequently converted to its milligram equivalent, multiplied by the accelerating force of gravity, and termed "resting force." Next, I prodded the spider with a small brush, causing it to increase the tension it exerted on the thread. I recorded the maximum deflection I could cause the spider to achieve and, after conversion, termed this "maximum force." Immediately after measuring these values for a spider, I recorded the ambient temperature.

To obtain the summary force values reported in Table 2, I assigned an instar value to each specimen. The carapace or first femur lengths used for this purpose were established by noting discontinuities in the plotted size data and are reported in Table 2. This approach was

satisfactory for all species except *Uloborus glomus*. For this species, well-defined breaks were not apparent and a cluster analysis (unweighted, pair group method using arithmetic averages and squared distances) based on abdomen, carapace, and first femur lengths was used to divide individuals into groups to which instar values were then assigned.

Results

For all species except *M. animotus*, the mean temperatures at which forces were measured differed by only 0.9°C (Table 1). The mean temperature for *M. animotus* was 2.6°C lower than that of the species with the next higher value. Kolmogorov–Smirnov D -tests showed that the temperatures for each species



FIGS. 7–12. Comparison of the resting and maximum forces exerted by *Miagrammopes animotus* (Figs. 7 and 8), *Miagrammopes pinopus* (Figs. 9 and 10), and *Miagrammopes* sp. (Figs. 11 and 12) as a function of carapace length (Figs. 7, 9, 11) and weight (Figs. 8, 10, 12). A regression line of the resting force of *Uloborus glomosis* (dotted line) has been added to these figures so that they may be related to Figs. 3–6. RF, resting force; C, carapace length; MF, maximum force.

were reasonably normally distributed and a breakdown of temperatures by instar showed that, within a species, mean values varied no more than 1.2°C across the stadia (Table 1).

For most species and size indexes (carapace length and body weight), maximum force measurements had r^2 values that were equal to or greater than those of resting force (Figs. 3–12). Mean maximum force was always greater than mean resting force (Table 2). When t -tests were used to compare regressions of the natural logs of these two force measurements, using the natural log of carapace length as an index of spider size, only the Costa Rican *Miagrammopes* species showed no significant difference ($0.10 < p < 0.05$) between resting and maximum force. In *U. glomosis* and *H. cavatus* the y -intercepts of the

regression lines were not significantly different, although the slopes were. When weight was used as an index of size, the maximum force of each species exceeded its resting force, although in *U. glomosis*, *H. cavatus*, and the Costa Rican *Miagrammopes* species, these differences were significant for the y intercept but not the slope.

Relative to carapace length, *H. cavatus* and *Miagrammopes* sp. had the greatest differentials between maximum and resting forces, with maximum force being 2.9 and 3.0 times, respectively, that of resting force. In the remaining species, maximum force was 1.8 to 2.1 times that of resting force.

Hyptiotes cavatus exerted greater force relative to both its carapace length and weight than the other species studied (Figs.

TABLE 2. Carapace and first femur lengths used to assign specimens to stadia and the mean (and standard deviation) weight and force values for each stadium

	<i>Hyptiotes cavatus</i>	<i>Uloborus glomus</i>	<i>Miagrammopes</i> sp.	<i>Miagrammopes pinopus</i>	<i>Miagrammopes animotus</i>
Third instar					
Carapace length (μm)	440–560	780–1120	—	—	—
Femur I length (μm)	—	840–1420	532–980	480–920	520–1200
Weight (mg)	0.34 (0.09)	1.72 (0.52)	0.36 (0.20)	0.34 (0.18)	0.54 (0.33)
Resting force (N)	1.221×10^{-5}	3.541×10^{-5}	1.201×10^{-5}	1.285×10^{-5}	1.677×10^{-5}
Maximum force (N)	3.509×10^{-5}	7.373×10^{-5}	3.391×10^{-5}	2.871×10^{-5}	3.030×10^{-5}
Fourth instar					
Carapace length (μm)	600–700	1000–1300	—	—	—
Femur I length (μm)	—	1260–1800	988–1178	1000–1350	1240–1640
Weight (mg)	0.98 (0.29)	3.39 (1.00)	1.05 (0.32)	0.99 (0.40)	1.23 (0.41)
Resting force (N)	2.701×10^{-5}	5.928×10^{-5}	2.832×10^{-5}	2.810×10^{-5}	2.833×10^{-5}
Maximum force (N)	7.283×10^{-5}	1.199×10^{-4}	8.786×10^{-5}	7.244×10^{-5}	6.525×10^{-5}
Fifth instar					
Carapace length (μm)	800–960	1200–1420	—	—	—
Femur I length (μm)	—	1780–2200	1254–1520	1400–1900	1720–2040
Weight (mg)	2.45 (0.93)	4.71 (0.85)	1.53 (0.40)	2.04 (0.83)	3.07 (0.98)
Resting force (N)	8.905×10^{-5}	6.865×10^{-5}	3.849×10^{-5}	4.364×10^{-5}	5.183×10^{-5}
Maximum force (N)	2.565×10^{-4}	1.666×10^{-4}	1.125×10^{-4}	1.122×10^{-4}	1.276×10^{-4}
Sixth instar					
Carapace length (μm)	1000–1250	1300–1550	—	—	—
Femur I length (μm)	—	1750–2400	1710–2094	1920–2720	2160–2840
Weight (mg)	6.76 (3.06)	9.93 (4.65)	3.59 (1.11)	3.55 (1.11)	6.39 (3.36)
Resting force (N)	1.342×10^{-4}	1.072×10^{-4}	6.619×10^{-5}	6.938×10^{-5}	7.092×10^{-5}
Maximum force (N)	4.543×10^{-4}	2.555×10^{-4}	1.720×10^{-4}	2.020×10^{-4}	1.825×10^{-4}

3–6, Table 3). Relative to carapace length, *U. glomus* exerted significantly more resting force than *M. animotus* and *M. pinopus*, but not than *Miagrammopes* sp. (Figs. 7–12, Table 3). Relative to carapace length, *U. glomus* exerted significantly more maximum force than the three *Miagrammopes* species. When first femur length was used as an index of size of the three *Miagrammopes* species studied, results support those obtained for carapace length: *Miagrammopes* sp. exerted significantly greater ($p < 0.05$) resting force than both *M. pinopus* and *M. animotus*, but there was no significant difference in the maximum force expressed by the three *Miagrammopes* species.

Relative to body weight, there were no significant differences between the resting and maximum forces expressed by *U. glomus* and *M. animotus*. Both *M. pinopus* and *Miagrammopes* sp. expressed significantly greater weight-specific resting and maximum forces than did *U. glomus*.

Because a large part of a spider's weight resides in its abdomen, abdomen shape influences spider weight.

$$[1] \quad \text{Relative weight} = \frac{\text{Spider weight (mg)}}{\text{Carapace length (μm)}} \times 1000$$

When relative weight (eq. 1) is used as an index, *U. glomus* has a mean value of 4.30, which is significantly greater ($p < 0.0001$) than that of both *H. cavatus* (2.93) and *M. animotus* (2.38). In turn, these latter two species have relative weights that are significantly greater ($p < 0.0001$) than those of both *M. pinopus* (1.23) and *Miagrammopes* sp. (1.25), which do not differ significantly from one another ($p > 0.79$). The low relative weight values of the latter two species result from their more cylindrical abdomens. The superior strength of *H. cavatus* is emphasized by the fact that, even with only 68% the relative weight of *U. glomus*, it expresses significantly more weight-specific resting and maximum force.

Results of this study agree with those of my earlier investigation (Opell 1985) by showing that, relative to both carapace length and body weight, *H. cavatus* expressed significantly more resting force than *U. glomus*. To avoid problems resulting from differences in relative leg lengths, the current study uses carapace length rather than first femur length as a linear index of spider size. However, when regressions of first femur length (L) and resting force (F) are computed from the current data (eqs. 2 and 3), neither their slopes nor their intercepts differ significantly ($p < 0.05$) from those of the previous study when tested with a two-tailed t -test.

$$[2] \quad \text{Uloborus glomus:} \\ F = (6.878 \times 10^{-8} L) - (4.553 \times 10^{-5}) \text{ N} \\ (r^2 = 0.61)$$

$$[3] \quad \text{Hyptiotes cavatus:} \\ F = (2.233 \times 10^{-7} L) - (5.941 \times 10^{-5}) \text{ N} \\ (r^2 = 0.73)$$

When regressions of the natural log of spider weight and the natural log of resting force of these two studies are compared, neither the slopes nor the intercepts of *U. glomus* differ significantly. However, the intercept of *H. cavatus* differs significantly ($p < 0.001$) between the two studies, with the earlier study having a greater y -intercept.

Mean relative first femur length (eq. 4) and its standard deviation were computed for five mature females of each species studied:

$$[4] \quad \text{Relative femur length} = \frac{\text{Femur length (μm)}}{\text{Carapace length (μm)}}$$

Listed in order of increasing values, the species are *H. cavatus* (0.71 ± 0.08), *Miagrammopes* sp. (1.29 ± 0.17), *M. pinopus*

TABLE 3. Results of one-tailed *t*-tests comparing regressions of resting and maximum forces

	<i>H. cavatus</i> vs. <i>U. glomus</i>	<i>U. glomus</i> vs. <i>M. animotus</i>	<i>U. glomus</i> vs. <i>M. pinopus</i>	<i>U. glomus</i> vs. <i>Miagrammopes</i> sp.
Resting force				
Carapace length				
Intercept	***	***	+	—
Slope	***	***	+	—
Weight				
Intercept	***	—	—	—
Slope	***	—	—	—
Maximum force				
Carapace length				
Intercept	***	+	+	+
Slope	***	+	+	+
Weight				
Intercept	***	—	—	—
Slope	***	—	—	—

NOTE: +, the force of the first species is greater than that of the second; —, the force of the first species is less than that of the second. —, $p > 0.05$; *, $0.05 > p > 0.01$; **, $0.01 > p > 0.005$; ***, $0.005 > p > 0.0005$.

(1.31 ± 0.27), *U. glomus* (1.38 ± 0.13), and *M. animotus* (1.55 ± 0.21). Although these values do not include the four distal leg articles, they suggest differences in leg leverage and show that even within the genus *Miagrammopes*, mechanical advantage may differ.

Discussion

Results of this study support the hypothesis that, within the family Uloboridae, web reduction is accompanied by changes in strength that are compatible with web monitoring and operation. As predicted by this hypothesis, the triangle weaver *Hyptiotes cavatus* expresses more force than the orb weaver *Uloborus glomus*. As a group, the three *Miagrammopes* species expressed less force than *U. glomus*. However, the *Miagrammopes* species with the most highly modified carapace did not exert significantly less resting force relative to carapace length than did *U. glomus*.

Although the results of this study agree with those of my earlier comparison of the resting forces of *H. cavatus* and *U. glomus* (Opell 1985), they show that my interpretation of those results overemphasized the role of prosomal change in increasing spider strength. If leg reorientation and the carapace modification that facilitates it were the primary mechanisms for increasing a spider's strength, then *Miagrammopes* species, with their extremely modified carapaces, should exert the greatest force. Their expression of the least force indicates that, after effective paraxial leg movement is established, changes in leg musculature and leg article lengths are of great importance in altering the force a spider can exert. The relatively flatter prosomas of *Miagrammopes* species may result in their having smaller intrinsic leg muscles. However, as these muscles operate only the coxa and trochanter, the differences in their masses probably do not explain the large force differences between *Hyptiotes* and *Miagrammopes*.

Because *H. cavatus* expresses the greatest force, mechanisms for reorienting its legs should be at least as well developed as those in *Miagrammopes* species. Therefore, it is likely that the more extreme carapace modifications of this latter genus serve an additional function. I have never observed much retrolateral movement of *H. cavatus* first legs, although I have seen an individual of *M. animotus* move its extended first leg both

almost directly dorsal to and almost directly lateral to its carapace to pull on one of its capture threads. Rather than simply enhancing paraxial movement of the first legs, the more extreme carapace modifications of *Miagrammopes* may facilitate this greater range of leg movements.

Likewise, the greater carapace modification that distinguishes *Miagrammopes* sp. from the other two *Miagrammopes* of this study may not be responsible for the greater force expressed by this species. Other studies (Opell and Cushing 1986; B. D. Opell and A. D. Ware, manuscript submitted for publication) show that the larger eye tubercles of *Miagrammopes* sp. contribute to its having a more extensive visual surveillance than the less highly modified *M. animotus*. This, rather than strength enhancement, may be the function of larger eye tubercles. Changes in the lengths of leg articles and in leg musculature may contribute to the differences in force observed within the genus *Miagrammopes*.

Although all of the uloborids studied used their first legs to monitor and adjust the final tensions of their resting threads, *H. cavatus* was the only species whose members typically used their fourth legs in the initial stages of thread tensing. These observations indicate that the forces measured in the other species of this study represent first leg strength and that the fourth legs of *H. cavatus* are probably also stronger than those of the other species studied. There is no clear anatomical or behavioral evidence for a "locking" or "catch mechanism" in the legs of any of the uloborids studied. In fact, the leg flexions which they exhibit in an apparent effort to evaluate web tension and vibration seem inconsistent with the existence of such a locking mechanism.

"Resting force" probably approximates the sustained web-monitoring force of a spider, whereas "maximum force" may represent the limit of a spider's strength, expressed for only short periods during prey capture. During this study, spiders seldom maintained maximum force for more than about 10 or 15 s after they were prodded with a brush, although immediately after reducing this force, they often established a force that exceeded their previously measured resting force.

There are no definitive studies to evaluate the relative importance of uloborid web reduction in protecting these spiders from visually hunting predators, making their webs less

conspicuous to potential prey, and reducing the cost of constructing a prey-capture device. Lubin and Dorugl's (1982) study suggests that reduced webs may be more economical prey-capture devices than orb webs. However, they found that, unless a struggling prey is quickly subdued, it more easily escapes from a reduced web. Selection for such active and immediate web manipulation would favor the anatomical and strength changes that characterize reduced-web uloborids. The appearances and web-monitoring postures of these spiders serve, even if only secondarily, to make them more cryptic (Figs. 1 and 2). Indeed, the principal adaptive value of some features, such as the first leg setal tufts and green color of some *Miagrammopes* species (B. D. Opell 1986), seems to be enhanced protective resemblance.

Acknowledgments

Comments by William G. Eberhard helped improve this paper. National Science Foundation grant No. BSR-8407979 awarded to the author supported this study.

- AKERMAN, C. 1932. On the spider *Miagrammopes* sp. which constructs a single-line snare. *Ann. Natal Mus.* **7**: 137–143.
- EBERHARD, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). *J. Zool.* **166**: 417–465.
- . 1976. The webs of newly emerged *Uloborus diversus* and a male *Uloborus* sp. (Araneae: Uloboridae). *J. Arachnol.* **4**: 201–206.
- LUBIN, Y. D. 1986. Web building and prey capture in Uloboridae. In *Spiders: webs, behavior, and evolution*. Edited by W. A. Shear. Stanford University Press, Stanford, California. pp. 132–171.
- LUBIN, Y. D., and DORUGL, S. 1982. Effectiveness of single-thread webs as insect traps: sticky trap models. *Bull. Br. Arachnol. Soc.* **5**: 399–407.
- LUBIN, Y. D., EBERHARD, W. G., and MONTGOMERY, G. G. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. *Psyche*, **85**: 1–23.
- MUMA, M. H., and GERTSCH, W. J. 1964. The spider family Uloboridae in North America north of Mexico. *Am. Mus. Novit.* No. 2196. pp. 1–43.
- OPELL, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.* **148**: 433–549.
- . 1982a. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *J. Arachnol.* **10**: 185–191.
- . 1982b. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *Bull. Br. Arachnol. Soc.* **5**: 338–343.
- . 1984a. Comparison of the carapace features in the family Uloboridae (Araneae). *J. Arachnol.* **12**: 105–114.
- . 1984b. Phylogenetic review of the genus *Miagrammopes sensu lato* (Araneae: Uloboridae). *J. Arachnol.* **12**: 229–240.
- . 1985. Web-monitoring forces exerted by orb-web and triangle-web spiders of the family Uloboridae. *Can. J. Zool.* **63**: 580–583.
- . 1986. The choice of web-monitoring sites by a green *Miagrammopes* (Araneae: Uloboridae). *Psyche*. In press.
- OPELL, B. D., and CUSHING, P. E. 1986. Visual fields of orb-web and single-line-web spiders of the family Uloboridae. *Zoomorphology* (Berlin), **106**: 199–204.
- OPELL, B. D., and EBERHARD, W. G. 1983. Resting postures of orb-weaving uloborid spiders. *J. Arachnol.* **11**: 369–376.
- PETERS, H. M. 1938. Über das Netz der Drieckspinne, *Hyptiotes paradoxus*. *Zool. Anz.* **121**(3–4): 49–59.
- WILDER, B. G. 1875. The triangle spider. *Pop. Sci. Monthly*, 1875 (April): 1–15.