Web-monitoring forces exerted by orb-web and triangle-web spiders of the family Uloboridae

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Differences in web structure and cephalothorax features suggest that *Hyptiotes cavatus* should exert more force while monitoring its vertical triangle-web than *Uloborus glomosus* exerts while hanging beneath the hub of its horizontal orb-web. When this hypothesis was tested by measuring the force that instars of each species exerted on a horizontal thread, *Hyptiotes cavatus* was found to exert significantly more force throughout development than did *Uloborus glomosus*. This relationship holds when either first femur length or body weight is used as an index of spider size.

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Les différences dans la structure de la toile et les caractéristiques du céphalothorax nous amènent à conclure que *Hyptiotes cavatus* doit exercer plus de force pour tester sa toile verticale en triangle que ne le fait *Uloborus glomosus* lorsqu'il est suspendu sous le centre de sa toile horizontale circulaire. La mesure de la force qu'exercent les stades de chacune des espèces sur un fil horizontal a permis de vérifier cette hypothèse: durant tout son développement, *Hyptiotes cavatus* exerce significativement plus de force qu'*Uloborus glomosus*. Cette affirmation reste vraie, que ce soit la longueur du fémur antérieur ou la masse corporelle qui serve d'indice de la taille de l'araignée.

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Introduction

Most spiders of the family Uloboridae construct horizontal orb-webs and hang beneath their hubs as they wait for prey to become ensnared. By contrast, members of several genera spin reduced vertical webs and monitor them by tensing one of the web's attachment lines. One of these species is *Hyptiotes cavatus* (Hentz), whose members construct triangle-webs consisting of four radii, between which sticky (cribellar) threads run (Fig. 1; Comstock 1913; Opell 1982*a*; Wilder 1875). After the web is constructed, the spider assumes its monitoring position and tenses the web by pulling itself nearer the attachment point with its third and fourth legs, and, finally, by flexing its first two legs. In this manner, an adult *H. cavatus* with a body length of about 5 mm takes up 1–1.5 cm of apex line as it hangs 6–10 cm from the web's triangular prey-capture region (Fig. 1). When an insect strikes the taut web the spider releases the apex line slack, causing the web to jerk. By more rapidly taking up and releasing apex line silk in the manner described above, the spider jerks its web several more times before running down the attachment line and onto the web to wrap its prey. This accomplished, the spider returns to feed in its previous position, with the often-damaged web held taut (Opell 1982*a*).

These observations suggest that in order to effectively use its web, *H. cavatus* should exert more force than an orb-weaving uloborid. This hypothesis is supported by a comparative study of internal and external cephalothoracic features (Opell 1984). The purpose of this study is to test this hypothesis more directly by comparing the force *H. cavatus* exerts on a single thread with that exerted by a similarly sized orb-weaver, *Uloborus glomosus* (Walckenaer). Both species occur in the eastern United States and Canada (Muma and Gertsch 1964). A comparison is possible because both have similar web monitoring postures (Figs. 2, 3) and assume these postures even while hanging from a single thread (Opell and Eberhard 1983; Opell 1982*a*, 1982*b*). In both species, the first pair of legs extend directly forward and press together as they grasp the web. The tips of the fourth legs also grasp the web at a single point. Second and third legs hold slack silk but do not appear to contribute significantly to web tension. As they hang from a single thread, both species reel in and accumulate slack silk between their second and third legs and periodically flex the first legs as if to assess and adjust the thread's tension. Although similar, this posture appears to be convergent in the two genera (Opell 1979; Opell and Eberhard 1983). Posture, body shape, and setal ornamentation make both spiders cryptic (Figs. 1–3), but cephalothoracic changes and the angles at which leg articles are held should permit *H. cavatus* to exert greater force.

This study compares the forces that spiders exert on a single, horizontal resting thread and not actual web-monitoring forces. The complex hub of an orb-web makes the measurement of actual web-monitoring force difficult. Therefore, resting force serves as the only easily obtainable basis for comparing the two species. This comparison serves as a conservative test of the hypothesis that morphological changes in *H. cavatus* serve to increase web-monitoring force, as it requires that these changes are so extreme as to be reflected in the force spiders exert when hanging from a single line.

Methods and materials

Hyptiotes cavatus were reared in the laboratory from field collected egg sacs. Because second instars and adult males do not construct prey capture webs (Opell 1982*a*), they were not included in this study. After each molt and after mature females had eaten four fruit flies (either *Drosophila melanogaster* or *D. virilis*), the spider was weighed on a Mettler analytical balance and the force it exerted on a single line was measured. First femur lengths were measured from exuviae and from preserved females. In Virginia, most *Uloborus glomosus* overwinter as third instars (personal observations). Juveniles were collected from shrubs on the Virginia Tech campus every 14–18 days from their first appearance in late April until spiders matured and third instars were again encountered in mid-August. As in *H. cavatus*, adult male *U. glomosus* do not construct typical capture webs and were excluded from the study. After weights, first femur lengths, and forces were measured, spiders were returned to the same shrub from which they were collected. Sampling drew alternately from two populations

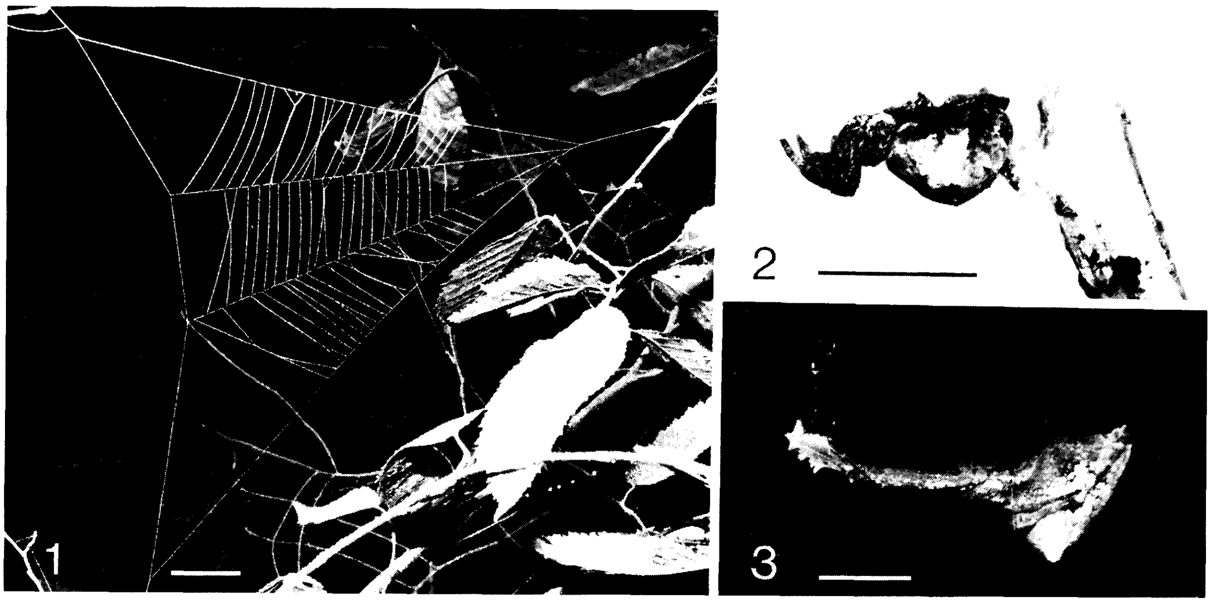


FIG. 1. Web of female *Hyptiotes cavatus*. The spider is hanging from the web's right attachment point in a typical monitoring posture. Scale bar represents 20 mm. FIG. 2. Female *Hyptiotes cavatus* monitoring a triangle-web. The spider's first pair of legs grasp the apex threat that supports the web. Immediately behind and above these legs are the second pair that hold slack silk. Tips of the third pair of legs also hold slack silk and protrude upward near the center of the spider's body. The fourth pair of legs extend posteriorly and are flexed as they grasp the thread attached to the twig. However, as they lie beside the abdomen, these legs are not easily seen. Scale bar represents 3 mm. FIG. 3. Female *Uloborus* hanging from a single, horizontal thread. The spider's first pair of legs are bent abruptly upward at the tibia–metatarsus joint and their adjacent tips grasp the thread. The two distal segments are dark, giving the illusion that the first legs terminate at the dense setal tuft located on the distal ends of the tibiae. The second pair of legs hold slack silk and rest with their tips hidden within the setal tufts of the first legs. Third and fourth legs extend along each side of the abdomen with their tips directed toward the spinnerets at its posterior tip. The tip of each shorter third leg rests at the center of the abdomen's lateral surface. The fourth legs grasp the resting thread just posterior to the spinnerets. Scale bar represents 3 mm.

of *U. glomosus*, each containing roughly 50 individuals and separated by a distance of 240 m. First femur length is an index of stepwise growth occurring as a result of molting, whereas weight is an index of continual growth. Force was measured with a glass needle strain gauge. This consisted of a 13-cm glass filament, whose deflection along a scale was calibrated with small weights and whose diameter was selected to give linear readings over the range of force being determined. Each spider was directed to spin a horizontal line between and perpendicular to the filaments's tip and a fixed wooden rod. After the spider assumed a resting posture and flexed its first legs to evaluate or adjust the thread's tension, the established deflection of the filament's tip along a scale was recorded and then converted to milligrams. Multiplication of milligrams by 9.8066×10^{-6} converts them to newtons.

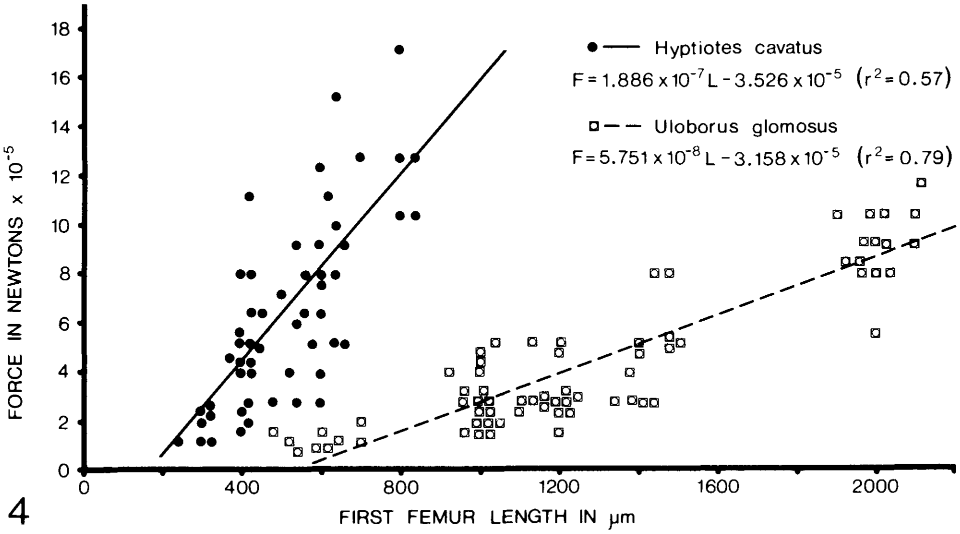
Results

Throughout development, *Hyptiotes cavatus* exerts more force on a single resting thread than does *Uloborus glomosus*. When first femur length is regressed against force (Fig. 4), the two lines' intercepts are not significantly different ($p > 0.40$), but the slope of the *H. cavatus* line is greater ($p < 0.001$), indicating a developmental increase in force about twice that of *U. glomosus*. This is particularly striking in view of the fact that the first femur of *H. cavatus* is less than half as long as that of *U. glomosus*. First femur length reflects an overall size difference between the two species and not a proportionally shorter first femur in *H. cavatus*. This is demonstrated by regressions of first femur and carapace lengths of a developmental series of 70 *H. cavatus* and 78 *U. glomosus*. The slope for *H. cavatus* ($F = 0.05\ C^{1.41}$; $r^2 = 0.92$) and that for *U. glomosus* ($F = 0.05\ C^{1.46}$; $r^2 = 0.95$) did not differ significantly ($p > 0.30$), nor did their intercepts ($p > 0.50$).

A large portion of a spider's mass resides in its abdomen; therefore, total weight is greatly influenced by abdomen shape. Although *H. cavatus* is smaller than *U. glomosus*, it has a more spherical abdomen (Figs. 2, 3). This is demonstrated by a mean weight (milligrams) / first femur length (millimetres) index of 2.56 for *H. cavatus* and a significantly lower ($p < 0.002$) value of 1.74 for *U. glomosus*. For this reason, it is not surprising that when weight is used as an index of size, *H. cavatus* still exerts more force than *U. glomosus* (Fig. 5). Natural log transformation allows regression lines to be fitted to these data. The intercepts of these lines differ significantly ($p < 0.001$) but their slopes do not ($p > 0.90$), demonstrating that *H. cavatus* exerts more weight-specific force throughout its development.

Discussion

By demonstrating that *Hyptiotes cavatus* exerts more force on a single line than does *Uloborus glomosus*, these results support the hypothesis that changes in web structure require changes in web-monitoring strategies and in associated morphological features. Because both species studied spend most of their time monitoring their webs, the tension they exert is probably highly optimized. Whereas gravity helps tense and stabilize a horizontal orb-web, it serves to collapse a vertical triangle-web, making it more advantageous for *H. cavatus* to tense its web. Additionally, it would be difficult for an orb-weaver to effectively tense its web unless radii were anastomosed near the hub into four or six compound radii. Although this occurs in the family Theridiosomatidae (McCook 1889; Wiehle 1931), it is not known in the Uloboridae. When a *Hyptiotes* pulls on its web, the tension is distributed along the



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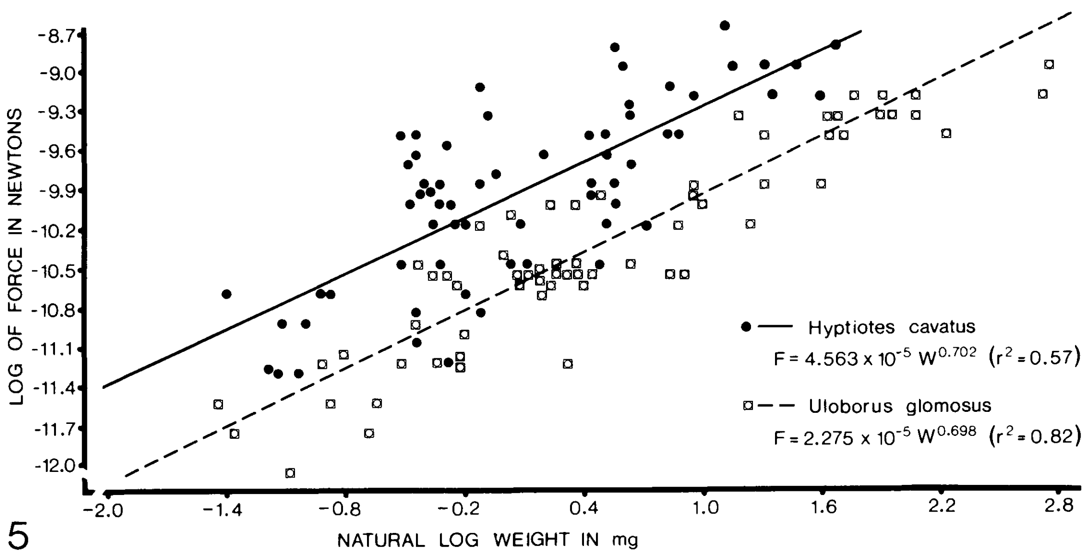

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FIGS. 4 and 5. Regressions of web forces exerted by *Hyptiotes cavatus* and *Uloborus glomosus* against first femur length (Fig. 4) and body weight (Fig. 5).

apex attachment line and the web's four radii. By contrast, the complex hub of a *Uloborus* orb-web (Eberhard 1972, 1981) distributes tension over many radii, making even sizable forces much less important in altering overall web tension than in a triangle-web. For these reasons, it was not surprising to find that the maximum force exerted by *H. cavatus* prior to establishing a lesser, resting force was greater than the maximum force exerted by *U. glomosus*.

It is interesting that the presumably greater web-monitoring force used by *H. cavatus* is also expressed by spiders resting on single lines where this greater force has no clear advantage. The only possible benefit may be that it permits the spider to escape a predator more effectively when the spider releases one end of its line. In the laboratory, nearly all *H. cavatus* that had no capture web rested on a single line rather than on a wooden support. However, this was also true for *U. glomosus*. A more likely explanation is that the greater force expressed by *H. cavatus* reflects behavioral and anatomical modifications associated with effective web use. Comparison of postures assumed by each species (Figs. 2, 3) indicates that *H. cavatus* flexes its first leg articles at angles that should serve to more effectively transfer force to the line. Coupled with changes in cephalothoracic muscles attached to the bases of the legs (Opell 1984), this probably explains part of the observed difference in force. However, it does not fully account for this difference, as a significant part of the force exerted by both species is generated when the spiders reel in silk with the posterior legs. Only after this is done are the first legs flexed to evaluate and adjust the line's tension. As neither species exerts maximum force on a single line, the difference observed in this study must be explained in part as a difference in the resting line tension acceptable to each species. In *H. cavatus*, the greater threshold for acceptable tension could be explained by a reduction in the amount of resting line tension transferred to stress receptors, by reduced sensitivity of the stress receptors, or by changes in the central nervous system. The former explanation is probably the simplest, as it could occur as an artifact of shortening of the distal leg articles of *H. cavatus* in order to exert greater force on a single line. This leg shortening would also reduce the mechanical amplification of force transferred from the line to stress receptors at the leg bases. Conversely, if orb-weavers like *U. glomosus* have slightly longer legs, it is probable that force transferred to their proximal stress receptors would be more greatly amplified. If this is the case, both species may have similar thresholds for forces received by stress receptors. Resolution of this problem is beyond the scope of this study. However, the difference in resting line force documented here suggests that further study of leg article lengths and angles of flexion is important for a fuller understanding of morphological changes associated with web reduction in the Uloboridae.

COMSTOCK, J. H. 1913. The spider book. Doubleday, Page, & Co., Garden City, New York.

EBERHARD, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). J. Zool. Soc. London, **166**: 417–465.

——— 1981. Construction behavior and distribution of tensions in orb-webs. Bull. Br. Arachnol. Soc. **5**: 189–204.

MCCOOK, H. D. 1889. American spiders and their spinningwork. Vol. 1. Published by the author, Philadelphia.

MUMA, M. H., and W. J. GERTSCH. 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**: 443–549.

——— 1982*a*. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). J. Arachnol. **10**: 185–191.

——— 1982*b*. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). Bull. Br. Arachnol. Soc. **5**: 338–343.

——— 1984. Comparison of the carapace features in the family Uloboridae (Araneae). J. Arachnol. **12**: 229–240.

OPELL, B. D., and W. G. EBERHARD. 1983. Resting postures of orb-weaving uloborid spiders. J. Arachnol. **11**: 369–376.

WIEHLE, H. 1931. Araneidae. Tierwelt Deutschlands, **23**: 1–136.

WILDER, B. G. 1875. The triangle spider. Pop. Sci. Monthly, 1875(April): 1–15.