

Centers of Mass and Weight Distribution in Spiders of the Family Uloboridae

BRENT D. OPELL

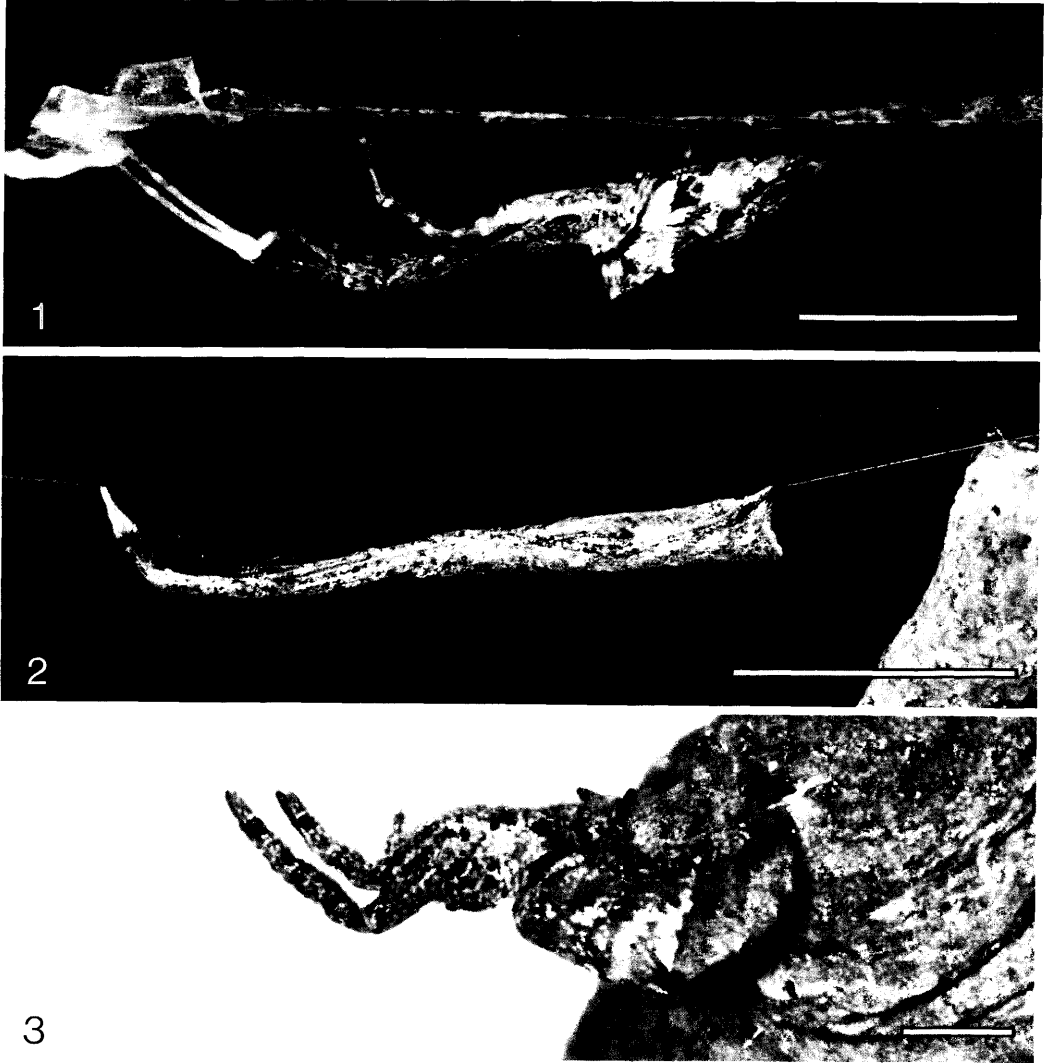
Department of Biology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061

ABSTRACT In the Uloboridae, web reduction is accompanied by changes in opisthosomal shape, leg length, and web-monitoring tactics. These morphological changes make reduced-web spiders more cryptic and alter their leg leverage and centers of mass. When compared with the orb-weaver *Uloborus glomosus*, the irregular, reduced-web spider, *Miagrammopes animotus*, invests more mass in its prosoma and first legs. However, the latter species' elongate opisthosoma posteriorly shifts this region's center of mass, causing the relative position of its composite center of mass and the distribution of weight between its first and fourth legs to be similar to that of the orb-weaver. Like these species, the opisthosomal center of mass of the triangle-weaver, *Hyptiotes cavatus*, lies near its midpoint. However, the shorter first legs and rounder, heavier opisthosoma of *Hyptiotes* posteriorly shift its composite center of mass and distribute more of its weight onto its fourth legs. Consequently, the morphology of *M. animotus* can be adequately explained by its adaptiveness for web manipulation, balance, and weight distribution and the crypsis that these features confer as an ancillary advantage. In contrast, anatomical changes in *H. cavatus* are better explained as adaptations for web manipulation and crypsis.

Within the spider family Uloboridae a variety of body forms are represented (Opell, '79). These range from the more typical orb-weavers such as *Uloborus* with elliptical opisthosomae and legs of intermediate length (Fig. 1), to triangle-weavers of the genus *Hyptiotes* with nearly round opisthosomae and short, stout legs (Fig. 3), to members of the genus *Miagrammopes* that spin irregular, non-planar webs formed of diverging capture lines and have long, cylindrical opisthosomae and legs (Fig. 2). These differences in opisthosomal shape and leg length can be viewed as either cryptic or mechanical adaptations. Both hypotheses relate to the web-monitoring tactics these spiders employ.

Unlike orb-weaving uloborids that rest beneath the hubs of their horizontal webs while waiting for prey to strike (Fig. 1), uloborids that spin reduced-webs monitor these vertical webs from the attachment point of a non-sticky frame line to a twig (Lubin, '86). As they hang contiguously with a twig, the elongate opisthosoma and legs of *Miagrammopes* make these spiders appear to a human observer as a thorn or smaller twig (Fig. 2; Lubin et al., '78). Similarly, the round opisthosoma and short legs of *Hyptiotes* give them the appearance of a bud or broken twig base (Fig. 3; Opell, '82).

Differences in leg length also have important mechanical consequences for these spiders. The complexity of an orb-web precludes spiders that spin these webs from significantly changing their tension after the web has been constructed, but the simpler structure of reduced-webs permits spiders that spin these webs to alter a web's tension without damaging it by pulling on the monitoring line. After constructing a triangle-web, *Hyptiotes* tense the web's four radii by reeling in monitoring-line silk with the short first and fourth legs. The resulting slack silk is held between the second and third legs and released suddenly when a prey strikes the web, causing the entire web to shake (Lubin, '86; Opell, '82). *Miagrammopes* also tense their webs, although the irregular and oblique angles at which a web's capture lines diverge appear to restrict the web tension that can be established by pulling on the monitoring line. When a prey strikes one of their web's capture lines, a *Miagrammopes* moves to this line and jerks it by rapidly flexing one of its long first legs (Lubin, '86; Lubin et al., '78). The short legs of *Hyptiotes* give them greater mechanical advantage and the long legs of *Miagrammopes* give them greater total leg displacement. These differences are reflected by the fact that



Figs. 1-3. Web-monitoring postures of the species studied. 1. *Uloborus glomus*. 2. *Miagrammopes animotus*. 3. *Hyptiotes cavatus*. Scale bar = 5 mm.

Hyptiotes exert greater force when pulling on a resting line than do *Miagrammopes* (Opell, '87).

Opisthosoma shape and leg length also affect a spider's center of mass and the distribution of weight borne by the legs. For spiders that spend their lives suspended from threads, these are important, albeit unstudied, aspects of body design. Because leg length directly affects leg leverage, it appears to have been selected principally for the mechanical requirements of web monitoring and manipulation rather than for its ability to enhance a spider's crypsis. In contrast, opisthosoma shape may be explained either as an adap-

tation to enhance crypsis or as one to adjust a spider's center of mass.

In addition to accommodating changes in web-monitoring tactics, the longer first legs of *Miagrammopes* and the shorter first legs of *Hyptiotes* shift these spiders' centers of mass anteriorly and posteriorly, respectively. In contrast, the longer opisthosoma of *Miagrammopes* and the shorter opisthosoma of *Hyptiotes* have the potential to shift their centers of mass posteriorly and anteriorly, respectively. If these changes cause *Miagrammopes* and *Hyptiotes* to have centers of mass and distributions of weight

across their legs that are similar to those of an orb-weaving uloborid, then a mechanical hypothesis is sufficient to explain differences in opisthosoma shape. If these anatomical differences do not conserve a spider's center of mass and weight distribution, then they support the hypothesis that opisthosomal shape changes serve principally to enhance a spider's crypsis. The purpose of this study is to test these hypotheses by quantifying and comparing the centers of mass and weight distributions of uloborids with different opisthosoma shapes and leg lengths.

MATERIALS AND METHODS

This study employs two Uloboridae from eastern North America, the orb-weaver *Uloborus glomosus* (Walckenaer) and the triangle-weaver *Hyptiotes cavatus* (Hentz), and the Puerto Rican irregular web-weaver *Miagrammopes animotus* (Chickering). The postures of each species with their first legs extended in a typical web-monitoring posture and with their first legs flexed to shorten their reach by half were established from enlarged 35 mm photographs of adult females. Except for the larger *Miagrammopes* whose opisthosoma is illustrated in Figure 6, these specimens had opisthosomas typical of recently matured females. That is, they were neither conspicuously swollen with eggs nor obviously shriveled from recent egg-laying.

For laboratory studies, specimens were anesthetized with carbon dioxide, fixed in 3% glutaraldehyde/3% formaldehyde for 16-18 hours, and stored in 0.1 M cacodylate buffer (pH 7.3). This coagulated hemolymph and prevented its loss when a specimen's opisthosoma and legs were removed and weighed to the nearest 0.01

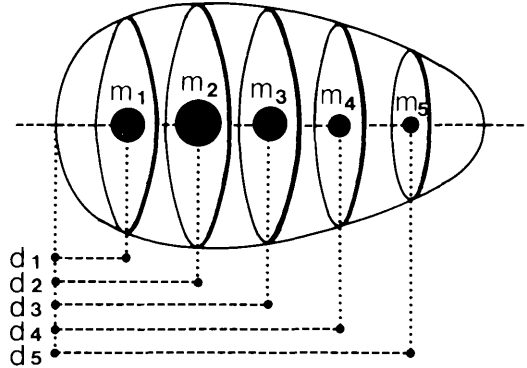


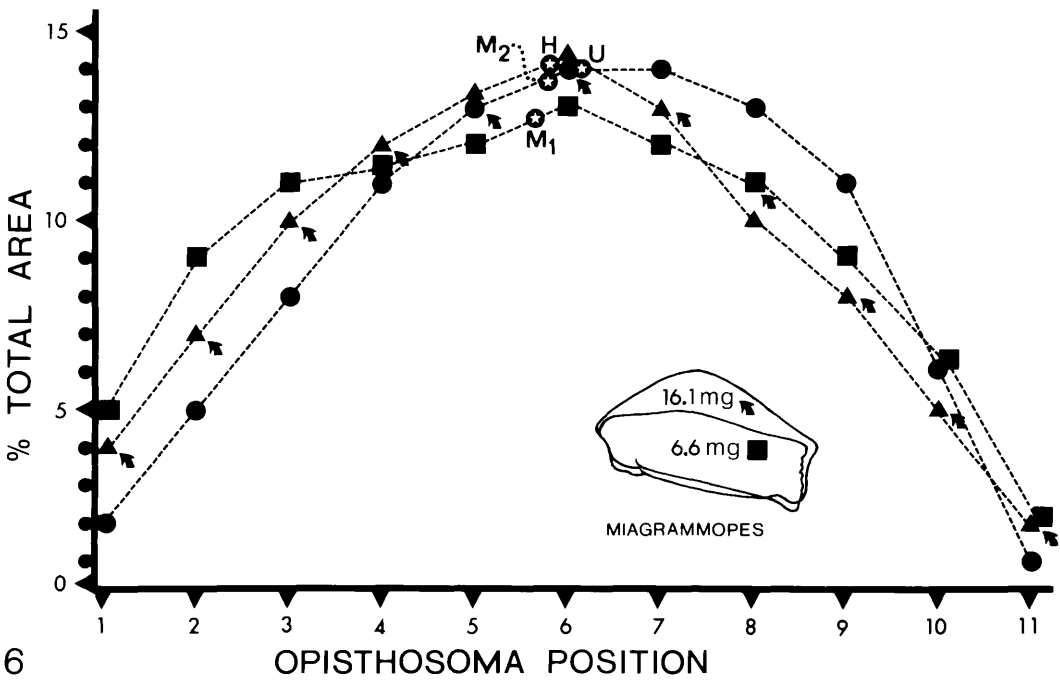
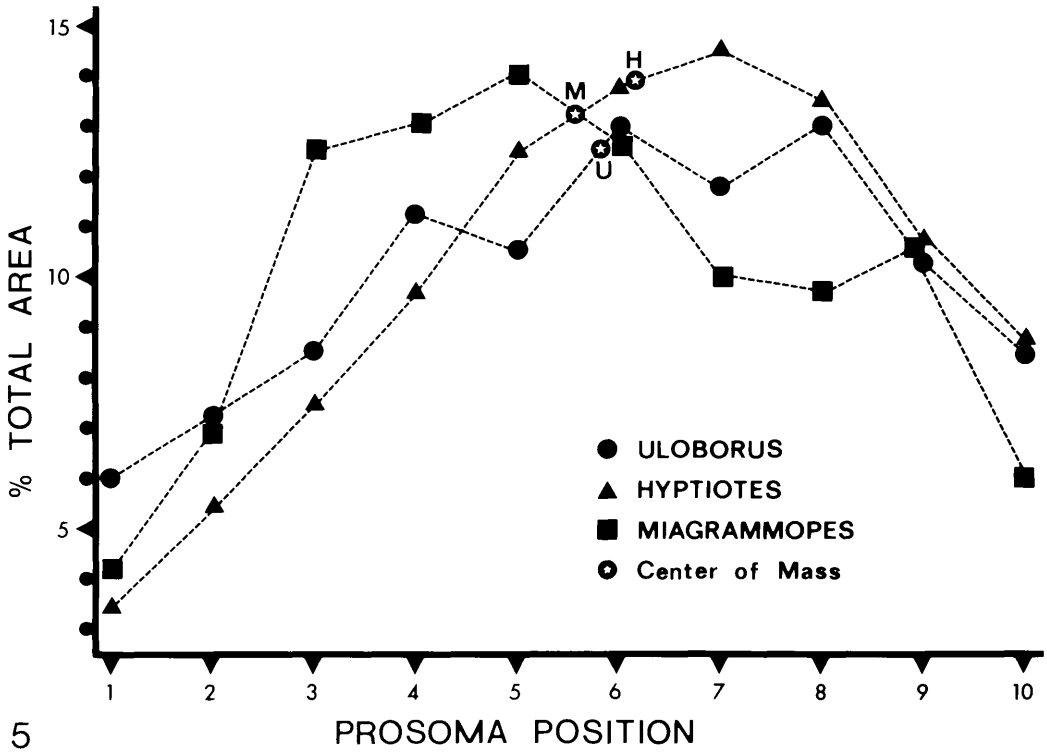
Fig. 4. The method and measurements used to determine the position of prosomal and opisthosomal centers of mass (d_{cm}) from the distances (d_1 - d_5) and masses (m_1 - m_5) of representative points along each region's midline.

mg. Formulated for use in electron microscope study of cell organelles, this fixative and buffer leaches very little material from tissues and, consequently, has a negligible effect on their mass. When compared to their live weights, the weights of eight fixed *M. animotus* females that were stored in buffer and blotted dry before being weighed ranged from 94.7% to 105.0% and averaged 100.3% of live weights.

Prosomal and opisthosomal centers of mass were determined separately but in a similar manner. Within each region, tissue density was assumed to be uniform. Cross-sectional areas were

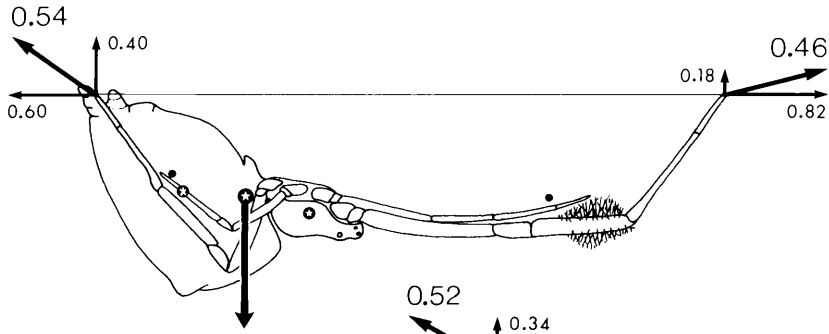
TABLE 1. Relative prosomal, opisthosomal, and leg masses, and first and fourth leg article volumes

	<i>Uloborus glomosus</i>			<i>Hyptiotes cavatus</i>			<i>Miagrammopes animotus</i>		
	N	Mean	SD	N	Mean	SD	N	Mean	SD
Relative mass									
(% of opisthosoma)									
Prosoma	5	23	15	7	17	7	8	31	11
Leg I	5	16	12	7	4	2	8	37	17
Legs II + III	5	6	5	7	3	1	8	5	5
Leg IV	5	7	6	7	5	2	8	9	4
% contribution									
to leg volume									
LEG I									
Coxa + trochanter	5	8	2	5	8	2	5	8	1
Femur	5	31	5	5	16	2	5	34	2
Patella + tibia	5	20	4	5	13	2	5	23	2
Metatarsus + tarsus	5	41	8	5	63	4	5	36	3
LEG IV									
Coxa + trochanter	5	10	4	5	7	1	5	10	1
Femur	5	18	3	5	16	2	5	14	2
Patella + tibia	5	14	3	5	17	2	5	11	2
Metatarsus + tarsus	5	59	5	5	60	4	5	65	4

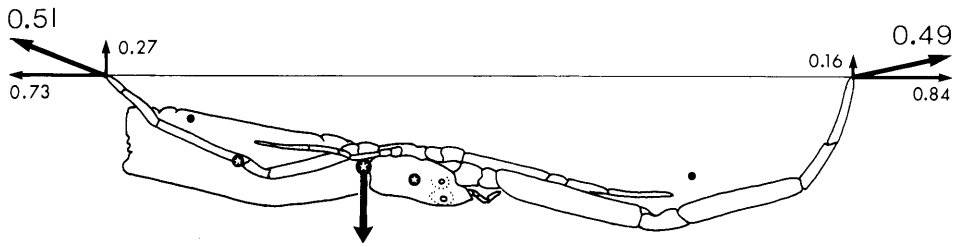
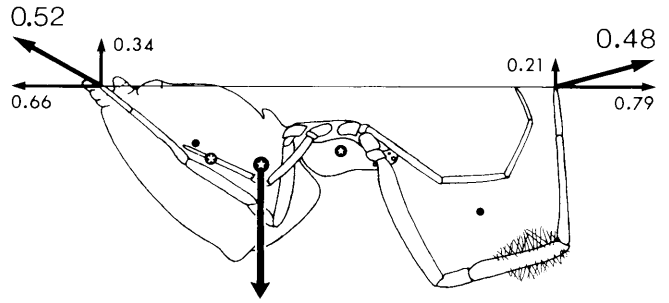


Figures 5 and 6

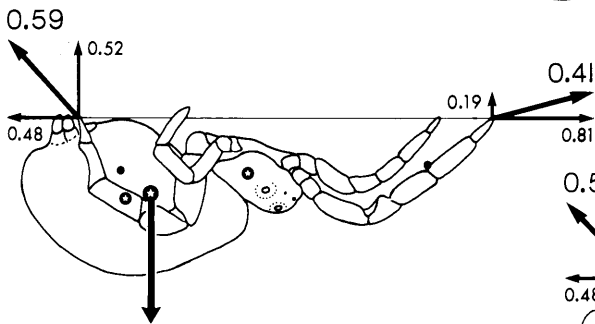
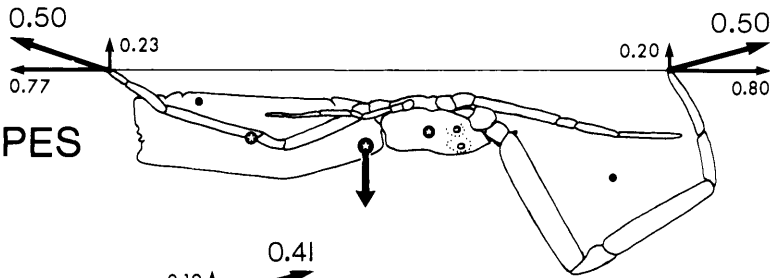
Figs. 5 and 6. Distribution of prosomal (5) and opisthosomal (6) cross-sectional areas at equal, anterior-posterior (1-10 or 1-11) intervals along each region's midline and the position of each species' center of mass. Figure 6 plots the slender opisthosoma (squares) of a 6.6 mg *Miagrammopes* (used in Fig. 7 reconstructions) and the robust opisthosoma (arrows pointing to occupied points) of a 16.1 mg female whose center of mass is denoted by M_2 .



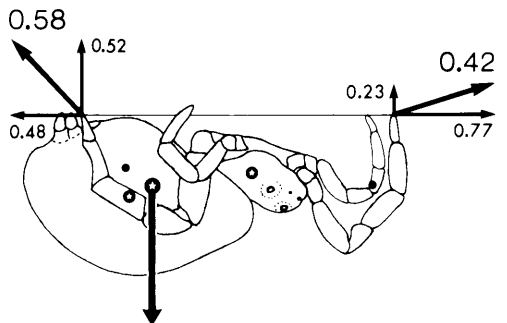
ULOBORUS



MIAGRAMMOPES



HYPTIOTES



Center of Mass of:

- Legs, ☆ Prosoma & Opisthosoma, ⚡ Spider

Figure 7

determined at evenly spaced intervals along the length of each region and each interval's percent contribution to that region's summed areas was equated with its contribution to the region's mass. Using the formula shown in Figure 4, these relative distances and masses were used to determine the centers of mass of each region.

Prosomal cross sections were prepared from specimens embedded in Spurr's epoxy resin, serially sectioned at 1 μm thickness, and stained with toluidine blue. Cross sections that fell at ten, evenly spaced ($\pm 19 \mu\text{m}$) intervals along the prosoma's length were photographed and enlarged, and their surface areas were measured with a digitizing tablet connected to a computer. At 11 evenly spaced intervals, the opisthosoma's height and width perpendicular to a line drawn from its pedicel to its posterior tip were measured from enlarged ventral and lateral photographs of living spiders. From these measurements the area of each elliptical cross section was determined (area = $\pi \times \text{half of height} \times \text{half of width}$). Because the prosoma hid the opisthosoma's anterior two intervals, their widths were estimated by multiplying the mean width-to-height ratio of the two following intervals by their measured heights.

As the second and third legs have short lengths and small masses (Table 1), only first and fourth legs were used in this study. The volumes of these legs' articles were equated with their masses and were determined by multiplying their mean cross-sectional areas by their lengths. Diameters used to compute cross-sectional areas were determined as follows: coxa, trochanter, and patella, mean central width and height; femur and tibia, mean width and height at proximal 25% of length, center, and distal 25% of length; metatarsus, mean width and height at proximal 33% and distal 33% length. Leg articles were grouped into four units (coxa-trochanter, femur, patella-tibia, and metatarsus-tarsus) and the total mass of each unit was considered to reside at the midpoint of its length.

After the centers of mass of each species' prosoma, opisthosoma, and first and fourth legs were established, they were combined to determine each species' composite center of mass. Although the first and fourth legs lie on either side of the spider's midsagittal plane, the center

of mass of each pair lies on the midsagittal plane, as does that of the prosoma and opisthosoma.

To determine the force borne by each spider's first and fourth legs and to resolve the components of these forces, a free body diagram was constructed by drawing a line from the spider's center of mass (M) to the tip of its first and fourth legs (L1 and L4, respectively). Another line (PMA) was drawn anteriorly and posteriorly through the center of mass and perpendicular to the gravitational force acting on the spider's mass. (PMA was parallel to the thread extending between the spider's first and fourth legs.) The cosines of angles L1-M-A and L4-M-P describe the forces the first and fourth legs, respectively, exert parallel to the thread they hold, and sines of these angles describe the forces they exert perpendicular to the thread.

The forces borne by a stationary spider's first and fourth legs were determined by solving the two simultaneous scalar equations: 1) horizontal force of first legs + horizontal force of fourth legs = 0, and 2) vertical force of first legs + vertical force of second legs + downward force of gravity acting on the spider's mass = 0. The combined forces borne by each spider's first and fourth pairs of legs were set equal to 1 and the amount borne by each pair of legs expressed as a fraction of this value.

RESULTS

Table 1 presents the relative masses of body components used in center of mass determinations. Prosomal and fourth leg masses form a relatively constant proportion of these three species' masses (13–17% and 4–5%, respectively). In contrast, opisthosoma and first leg masses are more variable, with *Miagrammopes*, *Uloborus*, and *Hyptiotes* having increasingly greater relative opisthosomal masses (55%, 66%, and 78%, respectively) and smaller relative first leg masses (20%, 10%, and 3%, respectively). Consequently, *Miagrammopes* is more front-loaded, with 37% of its mass residing in its prosoma and first legs, *Hyptiotes* is more rear-loaded, with only 16% of its mass invested in these components, and *Uloborus* is intermediate, with 25% of its mass distributed in these components.

Despite differences in their shapes (Fig. 7), the three species' prosomal centers of mass lie near their physical centers (50–55% of the distance from the prosoma's anterior margin, Fig. 5). More striking are similarities in the distribution of opisthosomal cross-sectional areas that appear when areas are plotted along relative opisthosoma length (Fig. 6). The center of mass of each species' opisthosoma also lies near its physical center (47–51% the distance from its anterior

Fig. 7. Spiders with their legs extended in typical web-monitoring postures and flexed, shortening their reach by half. Symbols denote the centers of mass of the body and its components. Large arrows and numbers describe the force borne by each leg. Small arrows and numbers resolve this force into its horizontal and vertical components.

margin). Comparisons of standard and enlarged (gravid) opisthosomae of *M. animotus* (Fig. 6) show that the added mass is distributed in such a way as not to alter the opisthosoma's center of mass and to make the opisthosoma's cross-sectional area profile more nearly resemble that of *Hyptiotes cavatus* than it does a more slender specimen of its own species.

Figure 7 illustrates the positions of each body component's center of mass, each species' composite center of mass, and the forces borne by first and fourth legs. In their typical web-monitoring postures, the centers of mass of both *Uloborus* and *Miagrammopes* lie at the base of their opisthosomas, slightly behind the pedicel's attachment. In contrast, the center of mass of *Hyptiotes* lies near the opisthosoma's center, only slightly forward of the opisthosoma's center of mass. When the first legs are flexed, the spiders' centers of mass shift posteriorly and dorsally in *Uloborus* and *Miagrammopes* and dorsally in *Hyptiotes*.

In typical legs-extended web-monitoring postures, the first legs of *Uloborus* bear 46% of the spider's mass, those of *Miagrammopes* 49%, and those of *Hyptiotes* 41%. When the first legs are flexed, shortening their reaches by half, the forces borne by the first legs increase by 1–2%. In *Miagrammopes* and *Uloborus* 83% and in *Hyptiotes* 81% of the force borne by the extended first legs is directed along rather than perpendicular to the threads they hold (x axes), but only 73%, 60%, and 48%, respectively, of the fourth legs' forces are so directed. When the first legs are flexed, the fourth legs of *Uloborus* and *Miagrammopes* direct 2–6% more force along the threads they hold, but in *Hyptiotes* the distribution of these forces remains unchanged.

DISCUSSION

Of the three species studied, *Uloborus glomus* best typifies the body form of the Uloboridae. Compared with this species, more mass resides in the carapace and first legs of *Miagrammopes animotus*. However, the latter species' elongate opisthosoma posteriorly shifts its composite center of mass, causing it to lie only slightly forward of that of *U. glomus*. Likewise, the forces borne by these species' first and fourth legs are more similar than their leg lengths and opisthosoma shapes at first suggest. Therefore, the mechanical hypothesis alone satisfactorily explains the opisthosomal shape of *Miagrammopes* as compensating for those changes in the prosoma and legs that adapt these spiders to monitor their reduced webs. The enhanced cryp-

sis conferred by their elongate opisthosomae can be explained as an ancillary benefit.

In contrast, the heavier, rounder opisthosoma and lighter first legs of *Hyptiotes cavatus* posteriorly shift the spider's center of mass and distribute more of its weight onto its fourth legs. In this species, the failure of opisthosoma shape to maintain an approximately equal distribution of weight across the spider's legs suggests that these changes serve principally to enhance crypsis.

Differences in web tensions and monitoring tactics may help explain why *Hyptiotes*, unlike *Uloborus* and *Miagrammopes*, does not appear to be constrained by the need to maintain relatively uniform weight distribution across the first and fourth legs. Unlike *Uloborus*, which hangs beneath the hub of its orb-web, both *Miagrammopes* and *Hyptiotes* accumulate slack monitoring line between their second and third legs and are, therefore, suspended by their first and fourth legs between the taut ends of their monitoring line. As the horizontal force exerted by this monitoring line's tension increases relative to the downward force of gravity acting on the spider's mass, a spider becomes strung between rather than hung from the ends of its monitoring line. As this occurs, a spider's opisthosomal shape should become less constrained by the need to help maintain an equal weight distribution across the legs and freer to respond to other selective pressures, such as those favoring crypsis.

When data presented by Opell ('87) are used to compare the force of gravity on the bodies of mature females with the "resting" force they exert on the horizontal threads from which they hang, the mean ratios of exerted force (resting line tension) to gravitational force for *U. glomus*, *M. animotus*, and *H. cavatus* are, respectively, 1.22 (N = 40, SD = 0.30), 1.27 (N = 34, SD = 0.51), and 2.27 (N = 42, SD = 0.71). A Duncan's multiple range test shows that the mean *H. cavatus* value is significantly greater ($P < 0.05$) than those of *U. glomus* and *M. animotus*, which do not differ significantly. This may explain why the masses of *U. glomus* and *M. animotus* are nearly equally distributed between the first and fourth legs and why *H. cavatus* appears not to have been so constrained and freer to respond to other selective pressures.

ACKNOWLEDGMENTS

Paula Cushing and Gabrielle Roth helped section, photograph, and measure specimens. National Science Foundation grant BSR-8407979 partially supported this work.

LITERATURE CITED

- Lubin, Y.D. (1986) Web building and prey capture in Uloboridae. In W.A. Shear (ed): Spiders: Webs, Behavior, and Evolution. Stanford: Stanford Univ. Press, pp. 132-171.
- Lubin, Y.D., W.G. Eberhard, and G.G. Montgomery (1978) Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. *Psyche* 85:1-23.
- Opell, B.D. (1979) Revision of the genera and tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.* 148:433-549.
- Opell, B.D. (1982) Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae, Uloboridae). *J. Arachnol.* 10:185-191.
- Opell, B.D. (1987) Changes in web-monitoring forces associated with web reduction in the spider family Uloboridae. *Can. J. Zool.* 65:1028-1034.