

Visual fields of orb web and single line web spiders of the family Uloboridae (Arachnida, Araneida)

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Summary. In the family Uloboridae, web reduction is associated with changes in web monitoring posture and prosomal features. A spider must extend its first pair of legs directly forward to monitor the signal line of a reduced web. This posture is facilitated by shifts in prosomal musculature that cause reduced web uloborids to have a narrower anterior prosoma, a reduced or absent anterior eye row, and prominent posterior lateral eye tubercles. The eye tubercles and larger posterior eves of these uloborids suggest that web reduction may also be accompanied by ocular changes that compensate for reduction of the anterior eyes by expanding the visual fields of the posterior eyes. A comparison of the visual fields of the eight-eyed, orb web species Octonoba octonaria and a four-eyed, reduced web Miagrammopes species was made to determine if this is true. Physical and optical measurements determined the visual angles of each species' eyes and the pattern of each species' visual surveillance. Despite loss of the anterior four eyes, the Miagrammopes species has a visual coverage similar to that of O. octonaria. This is due to (1) an increase in the visual field of each of the four remaining Miagrammopes eyes, accruing from an extension of the retina and an increase in the lens' rear radius of curvature, and (2) a ventral shift of each visual axis, associated with the development of an eye tubercle and an asymmetrical expansion of the retina. Miagrammopes monitor their simple webs from twigs or moss where they are vulnerable to predation. Therefore, maintenance of visual cover may enable them to detect predators in time to assume or maintain their characteristic, cryptic posture. It may also allow them to observe approaching prey and permit them to adjust web tension or prepare to jerk their webs when prey strikes.

A. Introduction

The horizontal orb web is the most common and the most primitive web form constructed by members of the family Uloboridae (Opell 1979). However, members of one lineage spin reduced vertical webs that contain fewer silk elements and actively monitor these webs with a taut signal line. One member of this lineage is *Hyptiotes*, whose members construct triangle webs (Opell 1982). Another is *Miagrammopes*, whose members construct a capture web of either a single, horizontal line with sticky (cribellar) silk along its center or a non-stiky horizontal line from which one or several vertical or diagonal capture threads extend (Akerman 1932; Lubin et al. 1978; Opell 1984b). The posterior lateral eyes of both *Hyptiotes* and *Miagrammopes* are borne on well-developed tubercles. Opell (1984a) has shown that these lateral eye tubercles and other differences in this region of the prosoma reflect muscular reorientation which permits the first pair of legs to extend forward more directly. This leg reorientation appears to contribute significantly to *Hyptiotes cavatus*' (Hentz, 1847) ability to exert greater force on the single thread by which it monitors its triangle web (Opell 1985). Likewise, in Miagrammopes the eye tubercles displace the retinal hemispheres laterally, thus providing the space necessary for anterior passage of extrinsic leg muscles. Additionally, the presence of eye tubercles strengthens the part of the prosoma where many muscles originate. Exoskeletal infoldings at the posterior margins of eye tubercles form apodemes for anchoring both extrinsic leg muscles and endosternite suspensor muscles (Opell 1984a).

A complementary function of the posterior lateral eye tubercles of reduced web uloborids such as Miagrammopes may be a shifting of the visual fields. This would provide two advantages. These eyes are absent in Miagrammopes while those of *Hyptiotes* are very small and situated away from the anterior and lateral prosomal margins, so as to preclude ventral vision. Firstly, the tubercles could visually compensate for the diminished role of the anterior eyes. These anterior eyes in orb weaving uloborids appear to be responsible for most of the ventral vision (Opell 1984a). Secondly, reduced web uloborids may be more vulnerable to predation (as their cryptic body forms and postures suggest) and, therefore, would benefit from a ventral field of view similar to that of an orb weaver. Reduced web uloborids do not hang beneath the hub of an orb web, but at or near the monitoring line's attachment point to a twig (Lubin et al. 1978; Opell 1982, 1984b). W.G. Eberhard (personal communication) has suggested an alternative interpretation of this second advantage. The web monitoring behaviors of Hyptiotes and Miagrammopes bring them into close proximity with substrate, and so crypsis may have a greater adaptive value for them. If this is true, selection favoring crypsis may be accompanied by visual changes that permit them to detect a potential predator, assume or remain in a cryptic posture, and thereby reduce their chances of being detected.

The purpose of this study is to test the hypothesis that

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Fig. 1. Cross section through the anterior median eyes of *Octonoba* octonaria. d lens thickness; s sepration of rear lens surface and retinal cells; a pigment ring diameter; cb cheliceral bases

posterior lateral eye tubercles characteristic of reduced web uloborids ventrally extend the visual fields of the eyes they bear. It also aims to determine to what extent this compensates for reduction or loss of the anterior eyes in these spiders. Visual fields of the horizontal orb weaver *Octonoba octonaria* (Muma, 1945) were compared with those of an undescribed *Miagrammopes* species. Although eye anatomy and eye position have been used in systematic studies (e.g., Homann 1971; Levi 1980), differences in visual fields and their orientations have not. This study demonstrates some of the visual implications of shifts in eye position and orientation and suggests that they can provide productive insight into behavior and functional morphology.

B. Materials and methods

Specimens of *O. octonaria* were collected in a greenhouse on the campus of Cornell University and those of the *Miagrammopes* sp. were collected at the Organization of Tropical Study's La Selva field station near Puerto Viejo, Heredia, Costa Rica. These were anesthetized with carbon dioxide, fixed at 20–26° C for 12–18 h in 3% formaldehyde/3% glutaraldehyde buffered in 0.1 *M* sodium cacodylate buffer (pH 7.3), and rinsed and stored in 0.1 *M* sodium cacodylate buffer. Specimens used for histological study were dehydrated through a graded series of acetone and embedded in Spurr's epoxy resin. We used a Sorvall JB-4 microtome to make 1 μ m thick cross-sections and stained these with 1% toluidine blue in 1% borate buffer prior to examining them.

To determine the optical properties of each eye, we used an intact lens and cross-sections of the ocular region and employed methods described by Meyer-Arendt (1972), Homann (1950, 1971), and Land (1969). Table 1 lists the formulas used to compute these values and Table 2 the data used in their computation. Focal length was measured from an eye suspended from a hanging drop of saline and with its cornea in air, as described by Blest and Land (1977). This drop hung from the underside of a number 1 cover glass sealed with a thin film of silicone vacuum grease to the rim of the 3 mm high glass cylinder of a microscope culture slide. A piece of moist cotton placed along the cylinder's inside edge retarded evaporation of the saline. We

placed this preparation on the stage of a compound microscope whose condenser apparatus had been removed. The 20 or 40 power objective was focused on the lens' rear surface to measure the image size of a 20 mm long scale bar placed on top of the microscope light source. When the image was in sharp focus we measured the lens-to-objective distance with a pair of dividers. We then used these measurements to compute the focal length of the lens. The eyes used for this purpose were removed from fixed specimens stored in buffer. A subsequent comparison of the focal lengths of fixed and fresh Uloborus glomosus (Walckenaer, 1841) eyes showed that the effect of fixation was within the accuracy limits of this measuring technique. The mean focal length of four freshly removed U. glomosus posterior median eyes (PME's) was 55.7 µm (range 49.1-60.9 µm), compared with 62.6 µm (range 55.1-67.6 µm) for three fixed PME's. The mean focal length of three freshly removed posterior lateral eyes (PLE's) was 57.1 µm (range 54.9-61.0 μ m), compared with 57.1 μ m (range 51.3–61.1 μ m) for three fixed PLE's.

We used focal length and lens measurements from eye cross sections (Fig. 1) to compute the refractive index of the lens. When recombined with physical measurements of the lens, this value permitted us to compute the position of each lens' principal plane. Using focal length, principal planes, and retinal position, we plotted the front and rear nodal points of each lens. In order to determine the visual angle of each eye, we measured the angle formed by lines drawn from the most peripheral retinal cells to the rear nodal point. An inverted projection of this angle from the front nodal point yields the eye's visual cone. Accurate frontal diagrams of each species were produced from superimposed tracings from photographs of prosoma cross sections through the center of each eye, with the visual angle of each eye added. Slight asymmetries are artifacts both of specimen asymmetry and a slight deviation from perfect specimen alignment during sectioning. Dorsal views were drawn to the same scale from preserved specimens, with visual angles added.

Two technical considerations should be mentioned. Firstly, determination of visual angles required the use of eyes from two specimens: one for the measurement of focal length, and one for the measurement of physical features. Table 1. Formulas used in determing optical properties of eyes. All measurements are in um

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Focal length (F):		in an
$F = \frac{i}{o}u$	i o u F	image length object length object and eye separati focal length
Refractive index (n):		
$\frac{1}{F} = (n-1) \left[\frac{1}{r_1} + \frac{1}{r_2} - \frac{d(n-1)}{n r_1 r_2} \right]$	n r ₁ r ₂ d	refractive index radius of outer curvatu radius of inner curvatu lens thickness
Power of lens surface (P):		
Front: $P_1 = \frac{\Delta n}{r_1}$	∆n	difference in refractive dex of front lens and or between rear lens a body fluids
REAR: $P_2 = \frac{\Delta n}{r_2}$	$r_1 r_2$	radius of outer curvatu radius of inner curvatu
Equivalent power (P_E) :		
$P_E = P_1 + P_2 - \frac{d}{n} P_1 P_2$	$P_1 \\ P_2 \\ d \\ n$	front surface power rear surface power lens thickness refractive index
Principal planes (VH):		
Front: $V_1H_1 = \frac{d}{n} \times \frac{P_2}{P_E}$ Rear: $V_2H_2 = \frac{d}{n} \times \frac{P_1}{P_E}$	$d \\ n \\ P_1 \\ P_2 \\ P_F$	lens thickness refractive index power of front lens surf power of rear lens surfa equivalent power
Nodal points (N) .	L	1 1
Determined by plotting.	N_{1}	front nodal point
<i>F</i> -Stop (<i>f</i>):	N_2	rear nodal point
$f = \frac{F}{F}$	f	fston
' 2a	j a	pigment ring radius

he same site were used. However, slight differences in lens diameters may have caused small errors in the results. Secondly, lenses were considered to have a uniform refractive index. As Fig. 1 shows, the lens is made of several concentric layers and we could not evaluate the refractive index of each. Although other studies of spider eyes have also assumed a uniform refractive index, this may not be the case.

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2	power of rear lens surface	the
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		the

C. Results

Primary data obtained from intact lenses and cross-sections through each eye (Fig. 1) are presented in Table 2. Visual angles and orientations of eyes, from formulas in Table 1, are given in Table 3 and presented in Fig. 2. Figure 3 is a three-dimensional reconstruction of each species' cones of vision, allowing comparison of their visual fields. The visual coverage of an eve is determined by its angle of vision and its orientation. Angle of vision can be altered by changing either lens properties (e.g., thickness and curvature) or the extent of the arc of retinal cells. Visual orientation can be altered by changing the orientation of either the eye's physical axis or its visual axis with respect to its physical axis, as occurs with an asymmetrical expansion of the retina.

As shown in Table 3, the posterior eyes of the Miagrammopes sp. each have visual fields 22° greater than those of O. octonaria. This is because the eyes of the former have more expanded retinae, thicker lenses and bigger front and rear radii of curvature (Table 2). Additionally, the retinal hemispheres of the Miagrammopes sp. have proportionally er radii. In O. octonaria the PME has a retinal radius al to 0.62 of the lens thickness or 0.57 of its diameter he pigment ring and that of the PLE is 0.49 of the thickness and 0.40 of the lens diameter. In the Mianmopes sp. values for PME retinal radius are 0.77 of lens thickness and 0.78 of the lens diameter and for E retinal radius, 0.58 of the lens thickness and 0.56 of the lens diameter. Changes in lens shape also increase the visual angles of *Miagrammopes* eyes. An increase in lens thickness and curvature posteriorly shifts the lens' nodal points (Fig. 2), bringing the rear nodal point closer to the retina. In O. octonaria the PME's rear nodal points are 0.52 of the lens thickness from the lens' outer surface and those of the PLE's are 0.57. In the *Miagrammopes* sp. these values are 0.78 and 0.73, respectively. The rear nodal point represents the theoretical point from which light diverges as it passes to the retina. Thus the nearer it is to the retina, the greater the eye's angle of vision. With respect to lens size, this distance is slightly less in *Miagrammopes* sp. than in O. octonaria. In the latter, the rear nodal point of the PME is 1.07 of the lens thickness from the center of the retinal hemisphere. The rear nodal point of the PLE is 1.24 of the lens thickness from the retinal hemisphere. These

Table 2. Comparison of Octonoba octonaria and Miagrammopes sp. primary ocular properties. All values except refractive index are in µm. A anterior; M median; E eye; L lateral; P posterior

Species	Eye	Lens thickness (d)	Radius of curvature (r_1/r_2)	Refractive index (n)	Focal length (F)	\bar{X} retinal cell separation (p)	Pigment ring radius (a)	Depth of focus (ΔF)
Octonoba octonaria	AME	92.3	68.1/43.2	1.49	73.7	0.4	44.9	0.4
	ALE	56.3	41.5/33.5	1.51	48.9	1.2	38.2	0.8
	PME	78.7	53.7/47.2	1.57	61.3	1.3	39.3	1.0
	PLE	65.0	55.0/45.6	1.53	60.9	1.1	38.8	0.9
<i>Miagrammopes</i> sp.	PME	89.9	63.8/50.0	1.59	67.6	1.1	33.8	0.9
	PLE	88.6	66.2/53.1	1.54	73.7	1.3	47.4	1.0

Table 3. Comparison of *Octonoba octonaria* and a *Miagrammopes* sp. visual angles and visual overlaps (1 = AME, 2 = ALE, 3 = PME, 4 = PLE). *A* anterior; *M* median; *E* eye; *L* lateral; *P* posterior

Species	Eye	Total visual angle	Visual axis from physical axis	Visual axis from frontal plane (0°=lateral)	Visual axis from sagittal plane (90°=lateral)	F-stop	Eye overlap
Octonoba octonaria	AME	182°	4° ventral	13° dorsal	32°	0.82	1, 2, 3, 4
	ALE	53°	34° ventral	35° ventral	66°	0.64	1, 4
	PME	101°	0°	64° dorsal	90°	0.78	1, 3, 4
	PLE	62°	34° ventral	8° ventral	90°	0.78	1, 2, 3
Miagrammopes sp.	PME	123°	1° ventral	51° dorsal	90°	1.00	4
- • •	PLE	84°	37° ventral	52° ventral	90°	0.78	3



Fig. 2. Reconstruction of the eyes of *Octonoba octonaria* and *Mia-grammopes* sp., showing dorsal and ventral angles of vision at the left of each eye and the extent of retinal cells at the right. Parallel, vertical, *dotted lines* imposed on each eye represent front and rear principal planes; the two *dots* on the eye's axis are the front and rear nodal points. The distance from the front nodal point to the arc denoting visual angle is equal to the eye's focal length. A anterior; *M* median; *E* eye; *L* lateral; *P* posterior

values are 0.99 and 1.03, respectively in the *Miagrammopes* sp.

The visual coverage of an eye can also change with shifts in its physical and visual axes. Relative to the physical axis of its lens, the visual axis of each *Miagrammopes* eye is directed more ventrally than is its homolog in *Octonoba* (Table 3). However, this accounts for only 8% of the total ventral visual shift in the PME's and for only 7% in the PLE's. This leaves shifts in the physical axes of the *Miagrammopes* sp. eyes as the most important mechanism for the 13° ventral visual shift in the PME's and the 44° one in the PLE's. These changes occur without altering the anterior-posterior orientation of the eyes' visual axes (Table 3).

Together, the increased visual angles and ventral shifts



Fig. 3. Dorsal and anterior views of *Octonoba octonaria* and *Mia-grammopes* sp. showing cones of vision. Although loss of the anterior eye row in *Miagrammopes* results in loss of anterior vision and complex visual overalp, they are still capable of full lateral and ventral visual surveillance. In dorsal views, ellipses of all dorsally directed cone apertures, except those of the posterior median eyes, are *stippled*; the lower rim of a ventrally directed cone is shown as a *dotted line*. In anterior views, anteriorly directed visual cones are denoted by ellipses whose widths are proportional to their anterior orientation. The axis of the visual cone is directed forward at an angle proportional ot the width of the ellipse. In dorsal views the visual cone is directed dorsally if its lower rim is visible and ventrally if its lower rim is eclipsed by the upper rim

in visual fields of the *Miagrammopes* sp. contribute to the maintenance of the spiders' visual coverage in the absence of their anterior eyes. Thus, although the visual axes of their PME's have been shifted ventrally by 13°, the wider angles of their visual fields ventrally extend their visual coverage by 24° with no loss of dorsal coverage (Fig. 3). Likewise, the 22° increase in the visual angle of each of their PLE's and the 44° ventral shift of each visual axis extend ventrally the eye's visual coverage by 53°. This is

accomplished without loss of lateral visual coverage. As shown in Figure 3, the net result of these changes is the maintenance of good coverage, despite the loss of anterior eyes. However, the *Miagrammopes* sp. does lose some of the anterior visual coverage and complex visual overlap found in *O. octonaria*. In the latter, each of the posterior eyes overlap visually with three other eyes, whereas in *Miagrammopes* sp. they overlap only with one another (Table 3). Despite these differences, the overall visual coverages are similar. The *Miagrammopes* sp. even has more extensive posterior ventral visual coverage. Its PLE's have approximately the same visual coverage as the combined fields of the AME's and ALE's of *O. octonaria's*, as does its PME's with the combined fields of the other's PME's and PLE's.

Miagrammopes sp. eyes are larger relative to spider size than those of *O. octonaria*, as demonstrated when lens thickness is expressed as a percentage of maximum thoracic width. The following values were obtained for *O. octonaria*: AME 7.6, ALE 4.7, PME 6.5, PLE 5.4. Higher values were obtained for the other species: PME 9.3, PLE 9.2. Only in the PME's of the *Miagrammopes* sp. does this increased lens size result in a greater f-stop value (Table 3).

D. Discussion

Results of this study support the hypothesis that the development of posterior lateral eye tubercles and other characteristic ocular changes enables the Miagrammopes sp. to maintain its ventral vision, despite loss of the anterior eye row. Anatomical changes at several levels are responsible for shifts in its visul fields: (1) eye tubercles result in major ventral shifts in visual axes, (2) extension of the arc of the retina results in major increases in visual angles, (3) asymmetrical expansion of the retina is associated with minor ventral shfts in visual axes of the PLE's, and (4) increased radii of curvature of the lenses is responsible for minor increases in visual angles. The congruity of these changes and the ensuing similarity of the visual fields of Miagrammopes and Octonoba indicate that these are not simply artifacts of prosomal remodelling designed to accommodate muscle reorganization. Instead, they have most likely been specifically selected to accompany and compensate for them.

The f-stop values of both Octonoba and Miagrammopes are much less than those of the visually active, diurnal salticids whose values range from 2.68 to 5.90 (Land 1969). They more closely match those of the nocturnal, ogre-faced spider Dinopis subrufus, in which the large PME's have a value of 0.58 (Blest and Land 1977) and are used to locate prey (Baum 1938; Roberts 1955; Robinson and Robinson 1971). Therefore, we conclude that Octonoba and Miagrammopes, like Dinopis, are adapted to the low-light conditions in forests and at night. However, this similarity does not indicate how uloborid eyes are used.

Behavioral studies such as those summarized by Forster (1982) have not been conducted to evaluate the visual acuity of reduced web uloborids or determine the role their eyes play in predator or prey detection. Unpublished observations on several *Miagrammopes* species do not clearly support one hypothesis over another. Predation on uloborids, as for most spiders, is poorly documented. In habitats where *Miagrammopes* are found, the first author has seen both wasps and damselflies slowly flying up and down branches apparently searching for prey. An *Anolis* lizard has been

observed attempting to eat a *Miagrammopes* specimen that was being transferred from one vial to another. Therefore, it is probable that these spiders are subjected to predation by both vertebrate and insect predators. The webs of most Miagrammopes consist of a non-sticky horizontal or diagonal resting thread from which several sticky threads extend. Spiders monitor these webs either by holding one end of the resting thread or by holding one or two capture threads at the point where they diverged from the resting thread. The former position brings a spider close to the twig or moss to which its web is anchored and permits it to extend its long first pair of legs forward allowing it to be as cryptic as possible. This position is often assumed after its web is disturbed. It places the spider in a better position to adjust the tension of a capture thread or to jerk a thread that had snared a prey. However, it also requires the spider to run onto its web and flex at least one of its legs, probably rendering it more vulnerable to predation. In both monitoring positions vision could warn a spider of potential predators, thereby enabling it to remain motionless even if web vibrations are detected. Although spiders monitoring their webs from the resting thread's attachment point are more cryptic, they are probably less able to adjust web tension if a prey is detected. Elasticity of the resting thread and the oblique angles of capture threads would make such quick alterations difficult. Thus, the importance of vision may change with web monitoring behavior and, perhaps, even with time of day.

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