

Reflections on the tapetum lucidum and eyeshine in lycosoid spiders

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Abstract. In the lycosoid spiders, the secondary eyes possess a grate-shaped tapetum lucidum that reflects light, causing eyeshine when these spiders are viewed with approximately coaxial illumination. This guanine-based reflective surface is thought to increase visual capabilities in low light. We explored the eyeshine of the posterior medial eye in eight taxa of pisaurid and lycosid spiders. The taxa included four pisaurids: *Dolomedes tenebrosus* Hentz 1844, *D. triton* (Walckenaer 1837), *D. scriptus* Hentz 1845 and *D. vittatus* Walckenaer 1837; and four lycosids: *Gladicosa pulchra* (Keyserling 1877), *Hogna* sp. (cf. *Lycosa lenta* (Hentz 1844) sensu Wallace 1942), *Rabidosa punctulata* (Hentz 1844) and *Varacosa avara* (Keyserling 1877). We found that there were significant family- and species-level differences in both the reflected spectra and the intensity of reflection. Although the peaks of the reflected spectra were in the green range for all spiders, the mean peak was further toward the blue end of the spectrum for the lycosids than for the pisaurids. Variation among species (about 54% of the total variation) was dominated by *G. pulchra* (Lycosidae) and *D. vittatus* (Pisauridae), both of whose spectra peaked near yellow, vs. *V. avara* (Lycosidae), whose spectra peaked to the blue side of green. The lycosid spiders showed overall brighter eyeshine. However, when corrected for their larger eyes, the lycosid spiders' reflections were dimmer for their eye size than were those of the pisaurid spiders. These results demonstrate that the reflective qualities of the tapeta, and perhaps the absorptive qualities of other tissues and media that the light must traverse, vary widely among lycosoid spiders. This variation may signal both functional differences in visual capabilities and interesting developmental or selective histories within this clade.

Keywords: Lycosidae, Pisauridae, posterior medial eye, vision

Eyes provide information to animals based on the reflection, refraction and emission of light in their environment (Ghering 2004). It is clear that varied evolutionary histories of eyed taxa have shaped the great diversity of eye morphologies (Goldsmith 1990; Land & Fernald 1992). For example, among invertebrates, spiders are unusual in that they possess eyes that function by corneal refraction (Land 1985; Land & Fernald 1992). Spiders are also unusual because they typically have eight eyes, where the primary eyes and the secondary eyes are specialized for different functions: the anterior medial pair of eyes (the primary eyes) are adapted for image formation (Land 1985), and the secondary pairs of eyes (anterior lateral, posterior medial and posterior lateral) are adapted for motion detection (Blest 1985; Land 1985; Land & Nilsson 2001; Neuhofer et al. 2009).

Across spider taxa, the relative importance and optimization of different aspects of vision are quite varied. Although orb-weavers are thought to have weak visual acuity (Land & Nilsson 2001), hunting spiders are reported to have image formation comparable (relative to body size) to human eyes (Land 1985). Even in the hunting spiders, however, eye use varies. For example, the ogre-faced spiders have posterior medial (PM) lenses that optimize light sensitivity (Blest & Land 1977), whereas in other hunting spiders image formation is optimized. In the salticids, the anterior medial pair of eyes is the largest and has the greatest resolution and sensitivity (Land 1969). However, the maximal resolution in lycosoids is in their largest eye pair, the posterior median eyes (PMEs; Homann 1931, as cited in Yamashita 1985; Williams 1979). The relative size and sensitivity of the eye pairs suggest that the PMEs are particularly important to the lycosoid spiders (Pirhofer-Walzl et al. 2007).

Probably because of the lycosoid spiders' crepuscular or nocturnal habits (Ortega-Escobar 2002), they possess several adaptations that enhance the function of the secondary eyes in low light conditions. The wide aperture of their lenses increases sensitivity in low light (Land & Nilsson 2001) and, as in many other families, these spiders adjust neural sensitivity on a diel basis to make use of available light by maximizing neural sensitivity in dark hours (Blest & Day 1978; Yamashita 1985). Also like many other spiders, lycosoids possess a tapetum lucidum ("silvery carpet"), a surface that reflects light back through the retina thereby increasing the likelihood that any photon will be captured by a photoreceptor (Schwab et al. 2002).

Spider tapeta fall roughly into three categories based on their morphology, but all of the lycosoids share the property of having a grate-shaped tapetum (Homann 1931, as cited in Land 1985; Land 1985). In this kind of tapetum, multilayers of guanine form strips of reflectors that underlie the rows of receptors (Land 1985; Oxford 1998), thus reflecting a "grate" pattern. These arrays often result in overlap of neural receptors, an overlap that reduces the resolving power of the eyes but maximizes their sensitivity to light (Blest & Day 1978). Grate-shaped tapeta can also facilitate navigation by detection of the polarization of light (Dacke et al. 2001; Warrant & Dacke 2010). Finally, it is the tapetum of a lycosoid that accounts for eyeshine, the bright pinpoints of glittering reflection experienced by a person wearing a headlamp that is pointed at the spider from a distance.

In the present study, we measured the intensity and spectral properties of eyeshine from the PMEs in lycosoid spiders in two families: Lycosidae (wolf spiders) and Pisauridae (nursery web spiders). Spiders in these families have much in common.

First, they share a common phylogeny, being on the same branch of the “higher lycosoids” with Miturgidae and Trechaleidae (Coddington 2005). In addition, and perhaps therefore, they also share many morphological (e.g., stance, shape), predatory (e.g., wander and pounce), circadian (crepuscular or nocturnal) and habitat characteristics. We might expect, then, that they would also share characters that enhance evening and night vision, and this expectation serves as our null hypothesis: because of their shared phylogeny, lycosids and pisaurids should vary little, either between families or within families, in the attributes of their eyeshine. On the other hand, a close look at each family reveals numerous differences (Ubick et al. 2005), both within and between the families, raising the possibility that eyeshine, too, would vary. Although lycosids are known to share grate-shaped tapeta, as do many other spider taxa, there are variations in the overall structure and function of the tapeta within this group (Land 1985). Certainly, many individual analyses of lycosoid eye structures have been conducted (Fenk & Schmid 2010; Jonasova & Kozmik 2008; Ortega-Escobar 2006; and see references therein), with a particular emphasis on *Cupiennius salei* (Strausfeld & Barth 1993). The degree and patterns of variations in eye morphology and function within and between the lycosoid spiders is not known. Variation, then, serves as our working hypothesis: because of divergent recent evolutionary histories, pisaurids and lycosids should be quite different in the attributes of their eyeshine, and those differences should be greater between the families than they are within the families.

METHODS

Spiders.—We concentrated on four species of fishing spiders (Araneae: Pisauridae) and four species of wolf spiders (Araneae: Lycosidae). The pisaurids, *Dolomedes tenebrosus* Hentz 1844, *D. triton* (Walckenaer 1837), *D. scriptus* Hentz 1845, and *D. vittatus* Walckenaer 1837, were collected from two sites in Bedford County, Virginia, in September and October 2011. The lycosids, *Gladicosa pulchra* (Keyserling 1877), *Hogna* sp. (cf. *Lycosa lenta* (Hentz 1844) sensu Wallace 1942), *Rabidosa punctulata* (Hentz 1844), and *Varacosa avara* (Keyserling 1877), were collected in Lafayette County, Mississippi, in September 2011. In all taxa, our subjects included only mature or penultimate females.

Captured spiders were transported and maintained either on water with closed-cell foam floats in 710-ml plastic deli containers (pisaurids) or in 44–147-ml vials (lycosids). During their brief maintenance period, ending on the day of experimentation 2–7 days after capture, the spiders were provided with water but no food.

On the day of experimentation, we used a random number generator both to determine the order of spider testing by species and to determine the order of testing of individuals within each species, ensuring that any order or time-of-day effects would be randomly distributed among and within the eight taxa of spiders.

Specimen preparation, mounting, and positioning.—Spiders were anesthetized with CO₂ and killed by the rapid (<15 s, total) amputation of the abdomen at the pedicel and of all eight legs at the coxa-trochanter joints. The cephalothorax was then glued, sternum down, using quick-setting epoxy glue (Loctite® Weld™) to a small platform of card stock that was

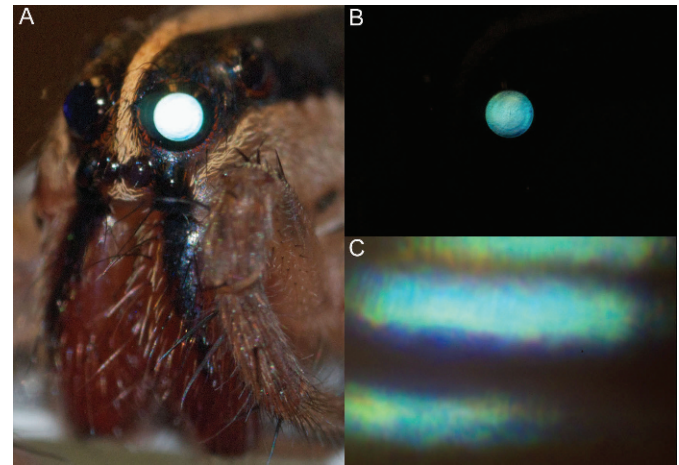


Figure 1.—Eyeshine of *Rabidosa punctulata*. A) Reflection from the tapetum of the posterior medial eye is visible because part of the lighting for the image was coaxial; i.e., in line with the lens-to-sensor axis of the camera. Indirect lighting was provided by an off-camera flash. B) In the absence of indirect lighting, and with a shorter exposure, only the tapetal reflection is visible and no other reflections (e.g., from other eyes or the spider's cuticle) can be seen. C) Under identical lighting conditions but with the lens removed from the camera and using a longer exposure, some of the structure of the tapetum itself is visible.

itself attached with glue or tape to the top of a 3-mm diameter steel flat-topped screw. This screw with its appended cephalothorax was then mounted at the top of a planetary gear assembly that was driven by a computer-controlled stepping motor (Fig. 2). The cephalothorax/card/screw combination made it possible to center the left posterior median eye (PME) approximately on the long axis of the screw, so that rotation of the screw would leave the PME at the same location (but with a different orientation). Our standardized position had the axis of rotation 21° from vertical, leaning toward the camera or the spectrometer probe (Fig. 2), with the specimen rotated 22.5° clockwise relative to the starting position at which both posterior median eyes were facing the camera or probe. The precision of this standardized 22.5° clockwise rotation was achieved using the computer-controlled planetary gear assembly. This put the camera or probe directly opposite and facing the left PME of each specimen. Representative resulting camera views are shown in Figs. 1A & B.

The assembly bearing the specimen and its positioning hardware was easily slid between two precisely marked locations on the laboratory bench. At one location, the specimen was directly in front of a camera (Nikon D200) attached to a photographic bellows (Nikon PB-4) that was equipped with an enlarging lens (50 mm f/3.5). Lighting to make eyeshine visible to the camera was provided by a high-output white LED (Radio Shack 276-0005) made coaxial with the camera-to-specimen axis by directing the light using a glass coverslip (thickness = 0.145 mm) as a partially silvered mirror (see Fig. 1 in Mueller & Labhart 2010). The photographic assembly, including the light source, was fixed in place so that when the specimen was in view, it was already in focus and coaxially illuminated.

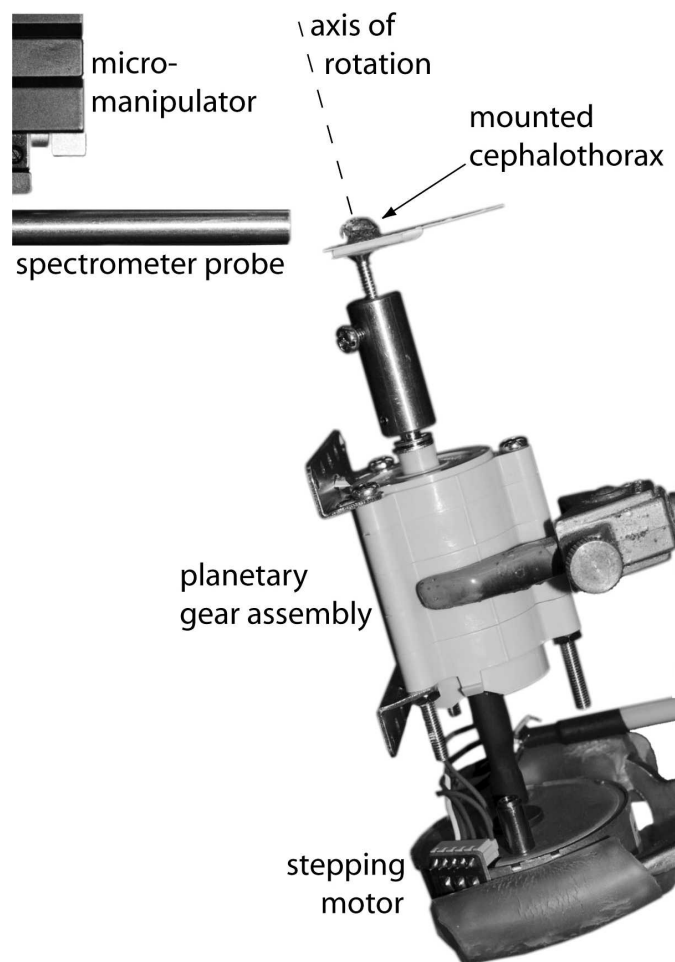


Figure 2.—Details of positioning of a spider's cephalothorax. The stepping motor drove a planetary gear assembly resulting in rotation of the specimen in increments of 0.09° . The angle of the axis of rotation was fixed at approximately 21° from vertical. The spectrometer probe was horizontal. It bore six optical fibers for illumination surrounding a single read fiber with a diameter of $400\ \mu\text{m}$ and an acceptance angle of 24.8° .

When placed at the second location, the specimen was about 0.5 cm from the front face of the micromanipulator-mounted fiber optic probe used both to illuminate the left PME and to collect the reflected light for spectral analysis. The core of the probe (Ocean Optics QR400-7-UV-VIS) consisted of six illuminating optical fibers surrounding a single read optical fiber so that, as was the case with the camera's illumination, the illumination used for spectral collection was coaxial with the sensor-to-specimen axis. Each of the seven fibers in the probe had a diameter of $400\ \mu\text{m}$, and the read fiber had an acceptance angle of 24.8° . The measured intensity of light reflected by the spiders' tapeta varied with the distance between the face of the probe and the left PME. To normalize intensity so that comparable spectra could be collected, we used the micromanipulator to adjust the probe-to-PME distance so that the peak intensity recorded by the spectrometer was close to 10,000 counts (measured mean $\pm$ SE: $9,785 \pm 116$). We then measured the probe-to-PME distance as a direct index of reflection intensity—the closer the probe had to be to achieve 10,000 counts, the dimmer the reflection was.

Experimental procedures.—We used two procedures in this study, one to collect standardized data from female representatives of each of the eight species of spiders and the other to collect longitudinal post-mortem data from one spider. For both procedures, the preparatory stages were identical (above).

Our standardized data collection procedure involved making three photographic exposures, shifting the specimen-positioning assembly 25 cm to the location of the spectrometer probe, and collecting one spectrum. The three photographs, in order, were 1) an image of the spider illuminated both by the coaxial LED light and an overhead flash (exposure: $1/16$ of maximum flash intensity, $f/8$, $1/10$ s, with sensor set at ISO 400); 2) an image of the spider illuminated only by the coaxial LED light (exposure: $1/100$ s exposure $f/8$ with sensor set at ISO 400); and 3) an image from exactly the same position but with the enlarging lens removed so that no optics intruded between the spider's eye and the camera's sensor (exposure: 1 s with sensor set at ISO 400). In the lens-on conditions (1 & 2), the enlarging lens's surface was 61 mm from the spider's PME; in the lens-off condition (3), the sensor was 214 mm from the PME.

We collected the single spectrum after adjusting the probe-to-eye distance, as described above. Spectra were automatically time-stamped, making it possible to determine how long it took to run a specimen through the standardized procedure. It took 7.0 ± 0.3 min (mean $\pm$ SE) for two of us to position, photograph and collect a spectrum from one spider. We anaesthetized, killed, and mounted the spiders one at a time, in the same order in which they were to be tested; we estimate that each took about four min to prepare once anesthesia was achieved. As a result, a spider's maximum time from death to the end of the measurement procedure was about 11 min.

We undertook the collection of longitudinal data, spectra only, on a single female *Hogna* sp. The purpose of this procedure was to get an estimate the rate at which tapetal reflection decayed after death, our concern being to avoid tapetal degradation as a confounding variable. In this procedure, we anesthetized, killed, mounted, and positioned the spider in our standardized way, skipped the photography, and collected 22 spectra over the subsequent five h.

Spectral measurement and analysis.—Light produced by a tungsten halogen light source (Ocean Optics HL-2000; color temperature = 2,960 K) was delivered to the specimen via optical fiber, and the part of it reflected by the left PME was transmitted via optical fiber to a high-resolution spectrometer (Ocean Optics 4000). Output from the spectrometer was collected by software (SpectraSuite by Ocean Optics) and exported as text (3,648 wavelength-intensity pairs; wavelength range = 357.9–819.5 nm). When spectra were collected, the only other light sources in the laboratory were the fluorescent fixtures providing general room illumination. A light meter, with its sensor positioned at the location and orientation of a spider's left PME during testing, revealed that the fiber optic illumination was 225–5892 times as intense (varying inversely with the distance between the fiber optic source and the light sensor) as the general room illumination at that same location. This, as well as inspection of spectra when the room lights were on and when they were off, persuaded us that making our

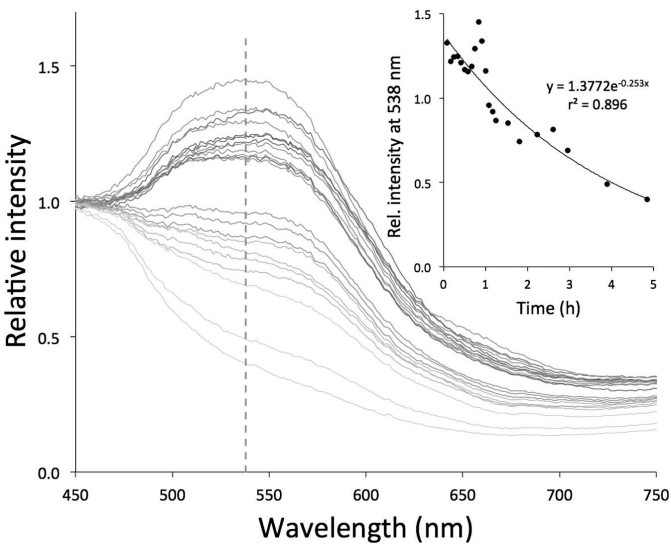


Figure 3.—Reflectance spectra showing the decline in eyeshine intensity with time after the death of a single *Hogna* sp. Spectra taken earlier in the post-mortem period are rendered with darker lines. The vertical dashed line is set at 538 nm. Inset: the intensity of eyeshine at 538 nm as a function of time after death; the line shows exponential decay of intensity.

spectral measurements under general room illumination would not influence our results.

We used a Mathematica 8 (Wolfram Research, Inc.) procedure to make a derivative spectrum composed of the 364 blocks of 10 intensity measures (averaged) in the original spectrum. We repeated this data reduction and smoothing step for all PME reflection spectra and for a spectrum that measured the tungsten halogen light source itself. In Excel (Microsoft Excel for Mac 2011), we divided each PME spectrum intensity value by the intensity value of the illuminating light source at the corresponding wavelength, resulting in the relative intensity spectra that we subsequently used in all of our analyses.

We adopted peak wavelength (the wavelength at which a spectrum had the highest relative intensity) as our metric of the characteristic shape of a spectrum, comparing peak wavelengths among species via ANOVA and Tukey’s multiple comparison tests, and between families using Student’s t-test. But characterizing a spectrum with one number could be so crude an abstraction that other salient characteristics could be missed. Therefore, to explore other kinds of differences in the spectra at the species and family level, we looked at the slopes of 15 30-nm segments of the spectra (sensu Thorpe 2002) using R (<http://www.R-project.org>). These segments included each 30-nm segment from 360–810 nm. These 15 data points for each spider were analyzed using principal components analysis (PCA), where PCA then generates 15 independent components, each a linear combination of the 15 slope values. The first of these components was then analyzed by ANOVA, just as we had analyzed peak wavelengths. We calculated the linear correlation between peak wavelengths and the corresponding first components derived from the PCA procedure to determine whether the PCA was revealing salient features of the spectra that had been overlooked because of our reliance on peak wavelengths.

Table 1.—ANOVA of the peak eyeshine wavelengths (Fig. 4A) of the eight species of lycosoids. Overall, the variation was highly significant ($F_{7,53} = 8.897$, $P < 0.0001$). When the data were pooled by family (Fig. 4A), the mean wavelength of the pisaurids was significantly longer by 20 nm (one-tailed $t_{59} = 2.87$, $P = 0.0033$). Only the significant comparisons ($P < 0.05$) are shown for the ANOVA post hoc tests.

Variance	Sum of squares	df	Proportion of variance
Between species	27670	7	0.54
Within species	23540	53	0.46
Tukey’s Multiple Comparison Test	Mean difference (nm)	<i>q</i>	<i>P</i>
<i>D. triton</i> vs. <i>V. avara</i>	36	4.69	< 0.05
<i>D. vittatus</i> vs. <i>Hogna</i> sp.	38	5.67	< 0.01
<i>D. vittatus</i> vs. <i>R. punctulata</i>	40	5.93	< 0.01
<i>D. vittatus</i> vs. <i>V. avara</i>	51	7.37	< 0.001
<i>G. pulchra</i> vs. <i>Hogna</i> sp.	54	7.14	< 0.001
<i>G. pulchra</i> vs. <i>R. punctulata</i>	55	7.37	< 0.001
<i>G. pulchra</i> vs. <i>V. avara</i>	67	8.65	< 0.001

Morphological measurements.—After testing, specimens were preserved in 95% ethanol. We measured left PME diameters using ImageJ (freeware from the National Institutes of Health) to analyze the photographs of eyeshine in which illumination came both from an overhead flash and from the coaxial LED light source (e.g., Fig. 1A). We measured prosoma width, a commonly-used index of overall spider size (Hagstrum 1971; cf. Suter & Stratton 2011), with an ocular micrometer while viewing each ethanol-preserved specimen under a dissecting microscope.

RESULTS

Post mortem, the eyeshine in *Hogna* sp. decayed exponentially over the course of five h (Fig. 3), as measured by the intensity of reflected light at 538 nm. The regression equation in Fig. 3 allowed us to calculate the expected change in eyeshine intensity at 11 min, the maximum time between death and our collection of the reflectance spectrum and the peak intensity measurement for any spider we tested. At 11 min post mortem, the eyeshine would have decayed by 4.1%. For our purposes, this indicates that collecting data within the first 11 min post mortem confined the temporal component of intensity and spectrum variation to less than 5%. In addition it is worth noting that Fig. 3 shows hints of complexity in the decay of eyeshine (the rise above baseline values as the 1-h mark approached).

Spectral characteristics.—Peak eyeshine wavelengths varied significantly (Table 1, Fig. 4A) both among the eight species tested ($F_{7,53} = 8.897$, $P < 0.0001$) and between Pisauridae and Lycosidae (one-tailed $t_{59} = 2.87$, $P = 0.0033$). On average, the pisaurid spectra peaked within the green part of the spectrum, but about 20 nm more toward yellow than did the lycosid spectra. The variation among species (about 54% of the total variation in peak wavelength) was attributable especially to *G. pulchra* (Lycosidae) and *D. vittatus* (Pisauridae), both of whose spectra peaked in or near yellow, vs. *V. avara* (Lycosidae), whose spectra peaked to the blue side of green. The mean peak

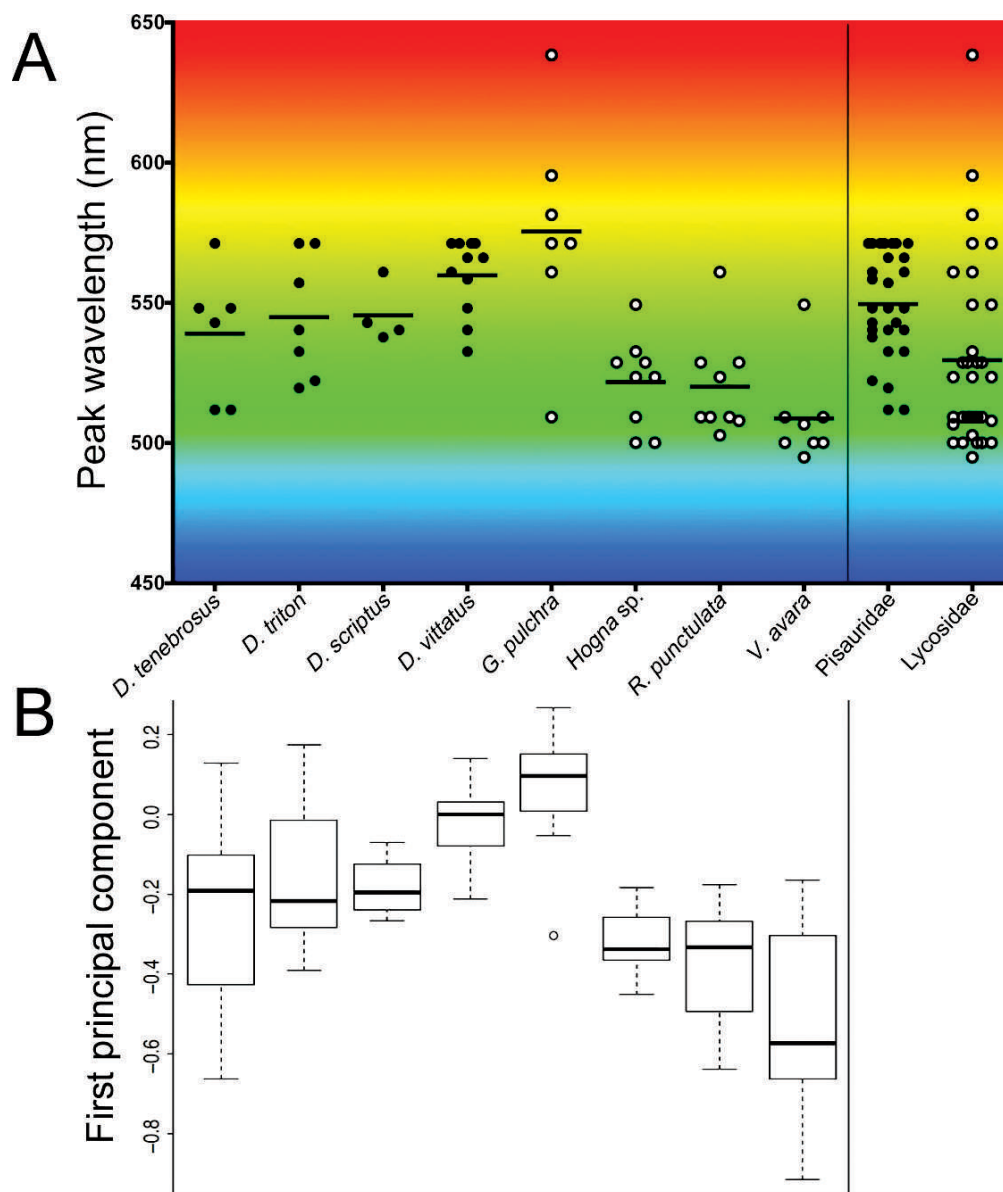


Figure 4.—A) Mean peak eyeshine wavelengths varied from yellow (e.g., *Gladicosa*) to blue-green (e.g., *Varacosa*). The mean wavelength of the eyeshine of the pooled pisaurids was more toward the red than was the mean of the pooled lycosids. Analyses of these differences are shown in Table 1. B) Principal component analysis yielded a first component that closely matched the peak wavelengths data, indicating that most of the variation in spectral properties was captured by our analysis of the peak wavelengths. In this plot, heavy horizontal lines represent means, the boxes show 95% confidence intervals, and the whiskers indicate ranges; the single open circle for *Gladicosa* designates an outlier.

wavelength of *G. pulchra* (yellow) and that of *V. avara* (blue-green) were separated by 67 nm.

Our principal components analysis of the spectra, designed to reveal differences that were not captured by our use of peak wavelength as an index of overall spectral shape, failed to elucidate any additional salient spectral characteristics. The first principal components closely matched the peak wavelengths (Fig. 4B; $r = 0.969$, $P < 0.0001$). For this reason, we adopted peak wavelength as our sole index of the spectral quality of tapetum reflectance.

Eyeshine intensity.—The intensity of a spider's eyeshine depends not only on how much of the light entering the eye leaves the eye again as reflected light but also, presumably, on the size of the eye itself. Our interest was in the former,

so we had to eliminate eye size as a confounding variable. PME diameter varied linearly with prosoma width (our proxy for spider size) in both lycosids and pisaurids (Fig. 5), with lycosid eye diameters exceeding pisaurid eye diameters by 65–85% in the range of overlap of prosoma widths. PME diameter also varied significantly (Fig. 6, Table 2) among the eight species studied ($F_{7,62} = 27.02$, $P < 0.0001$) and between the pooled Pisauridae and the pooled Lycosidae (two-tailed $t_{68} = 4.75$, $P < 0.0001$). Our solution was to regress measured eyeshine intensity, as measured by the distance between the spectrometer probe and the spider's PME, on PME diameter—eyeshine intensities above the regression line would then represent brighter eyeshine than would be expected relative to eye diameter, and intensities

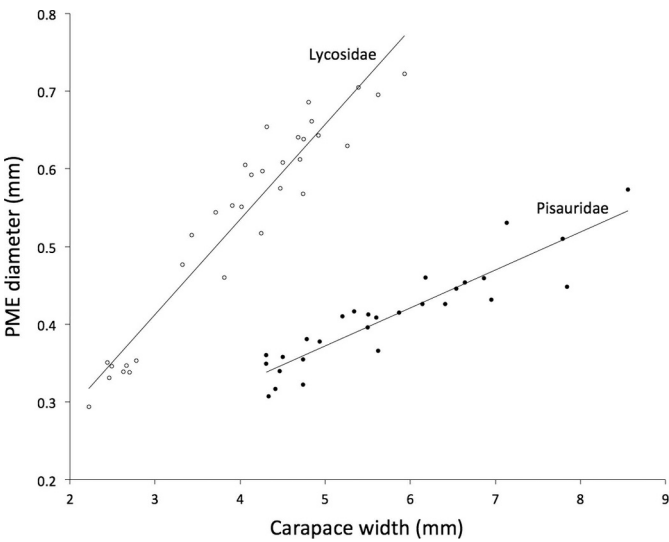


Figure 5.—In both Lycosidae and Pisauridae, PME diameter varied linearly with carapace width (Lycosidae: $r^2 = 0.918$, $P < 0.0001$; Pisauridae: $r^2 = 0.839$, $P < 0.0001$). The slopes of the lines were significantly different ($F_{1,56} = 87.28$, $P < 0.0001$). In the range of overlap of carapace widths, lycosid PME diameters are 65–85% larger than pisaurid PME diameters.

below the regression line would represent relatively dim eyeshine.

As expected, eyeshine intensity did vary directly with PME diameter (Fig. 7), and variation in eye size accounted for about 42% of the variation in eyeshine intensity ($r^2 = 0.4193$, $F_{1,45} = 32.49$, $P < 0.0001$). Residuals from this regression relationship (Fig. 8, Table 3) showed significant variation overall (ANOVA, $F_{7,39} = 4.661$, $P = 0.0007$), and pisaurid eyeshine was significantly brighter, relative to eye size, than lycosid eyeshine (two-tailed $t_{45} = 3.64$, $P = 0.0007$). *V. avara*, the lycosid spider with the smallest eyes of all the species (Fig. 6), also had the dimmest eyes relative to eye diameter (Fig. 8) and accounted for most of the between-species variation in relative brightness of eyeshine (Table 3).

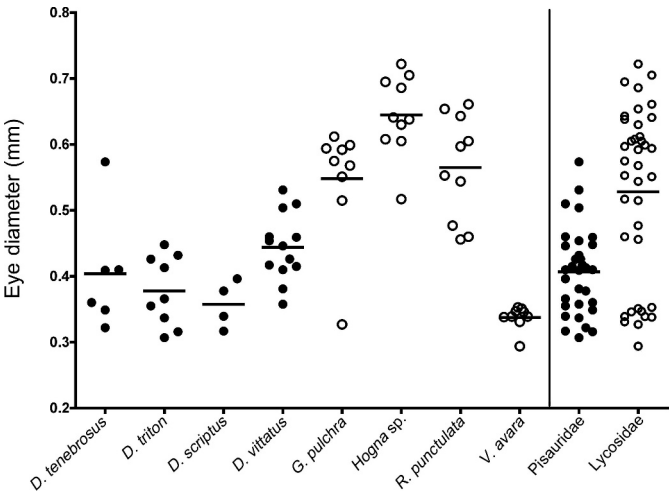


Figure 6.—PME diameter varied strongly among the eight species of spiders and between the two families. Lycosids had larger PMEs than did pisaurids, and lycosid eyes were also more variable (Table 2).

Table 2.—ANOVA of posterior median eye diameters (Fig. 6) of the eight species in the study. Overall, the variation was highly significant ($F_{7,62} = 27.02$, $P < 0.0001$). When the data were pooled by family (Fig. 6), the eyes of the lycosids were significantly larger by 0.13 mm (two-tailed $t_{68} = 4.75$, $P < 0.0001$). Only the significant comparisons ($P < 0.05$) are shown for the ANOVA post hoc tests.

Variance	Sum of squares	df	Proportion of variance
Between species	0.7698	7	0.75
Within species	0.2523	62	0.25
Tukey's Multiple Comparison Test	Mean difference (mm)	q	P
<i>D. tenebrosus</i> vs. <i>G. pulchra</i>	−0.14	6.06	< 0.01
<i>D. tenebrosus</i> vs. <i>Hogna sp.</i>	−0.24	10.33	< 0.001
<i>D. tenebrosus</i> vs. <i>R. punctulata</i>	−0.16	6.91	< 0.001
<i>D. triton</i> vs. <i>G. pulchra</i>	−0.17	8.01	< 0.001
<i>D. triton</i> vs. <i>Hogna sp.</i>	−0.27	12.88	< 0.001
<i>D. triton</i> vs. <i>R. punctulata</i>	−0.19	9.03	< 0.001
<i>D. vittatus</i> vs. <i>G. pulchra</i>	−0.10	5.33	< 0.01
<i>D. vittatus</i> vs. <i>Hogna sp.</i>	−0.20	10.58	< 0.001
<i>D. vittatus</i> vs. <i>R. punctulata</i>	−0.12	6.38	< 0.001
<i>D. vittatus</i> vs. <i>V. avara</i>	0.11	5.44	< 0.01
<i>D. scriptus</i> vs. <i>G. pulchra</i>	−0.19	7.03	< 0.001
<i>D. scriptus</i> vs. <i>Hogna sp.</i>	−0.29	10.76	< 0.001
<i>D. scriptus</i> vs. <i>R. punctulata</i>	−0.21	7.77	< 0.001
<i>G. pulchra</i> vs. <i>Hogna sp.</i>	−0.10	4.66	< 0.05
<i>G. pulchra</i> vs. <i>V. avara</i>	0.21	9.90	< 0.001
<i>Hogna sp.</i> vs. <i>V. avara</i>	0.31	14.82	< 0.001
<i>R. punctulata</i> vs. <i>V. avara</i>	0.23	10.97	< 0.001

The differences in eyeshine we have reported here require that we reject our null hypothesis that, because of their shared phylogeny, lycosids and pisaurids should vary little, either between families or within families, in the attributes of their eyeshine. Instead, we accept the general assertion that, because of divergent recent evolutionary histories, pisaurids and lycosids and their constituent species show considerable variation in the attributes of their eyeshine.

DISCUSSION

Our sampling of eyeshine from eight species in two families of lycosoid spiders revealed a surprising and complex array of differences. The two families, Pisauridae and Lycosidae, had mean peak reflectances that differed significantly (Fig. 4). The intensity of eyeshine was strongly influenced by eye diameter (Fig. 7), and lycosids had larger eyes relative to body size than did pisaurids. However, residuals from the regression of reflection intensity on eye diameter showed that pisaurid eyeshine was significantly brighter (relative to eye size) than lycosid eyeshine (Fig. 8). In addition to those strong family differences, we also detected interesting species-level variation in peak reflectance and eyeshine intensity. Peak reflectance was relatively uniform among the pisaurids but among the

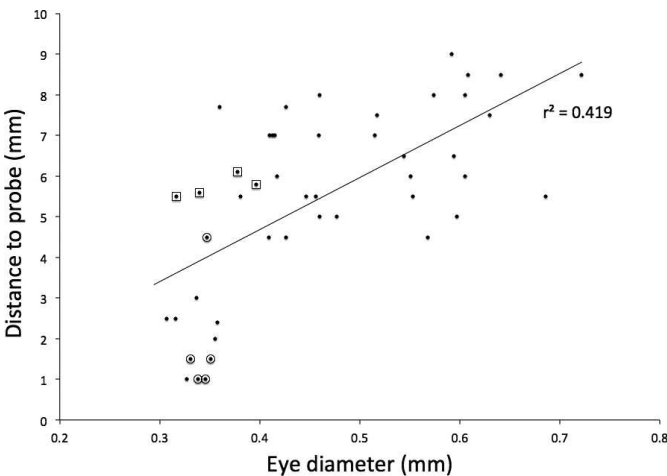


Figure 7.—Eye diameter appears to drive the intensity of eyeshine, accounting for about 42% of the variation in intensity. The most conspicuous variant was *V. avara* (circled data) with eyeshine that was significantly dimmer than expected relative to eye diameter. In contrast, *D. scriptus* (data surrounded by squares), a spider with eyes of about the same size, had eyeshine that was much brighter relative to eye diameter (Fig. 8).

lycosids, *Gladicosa pulchra* was significantly red-shifted relative to the other three species (Fig. 4). And with respect to intensity, *D. scriptus*, *D. tenebrosus*, and *D. vittatus* were brighter (relative to eye size) than expected and *V. avara* was dimmer (Fig. 8).

Spectral composition of eyeshine.—As expected (Schwab 2002), the peak reflectivity of the eyeshine of both pisaurids and lycosids was in the green range, but the average peak lycosid eyeshine was significantly more toward blue-green than was the peak for pisaurids. However, family of origin accounted for less spectral peak variation than did species identity (Table 1), and the primary source of species variation

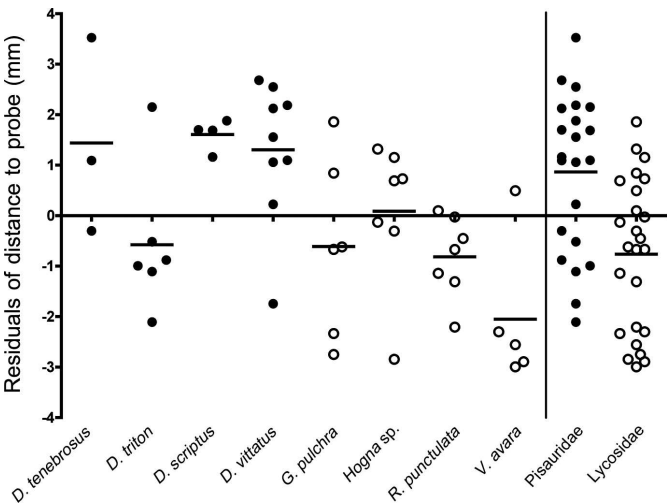


Figure 8.—Residuals from the regression of eyeshine intensity on PME diameter (Fig. 7) show that pisaurids' eyes, though smaller, are brighter relative to their size than are the larger eyes of lycosids (Table 3). *Varacosa avara*, a wolf spider, had the dimmest eyeshine relative to PME diameter, while *D. scriptus*, a fishing spider, had the brightest.

Table 3.—ANOVA of the residuals of the regression of eyeshine intensity on PME diameters (Fig. 8) for the eight species studied. Overall, the variation was highly significant ($F_{7,39} = 4.661$, $P = 0.0007$). When the data were pooled by family (Fig. 8), the residuals of the pisaurids were significantly higher by 1.63 mm (two-tailed $t_{45} = 3.64$, $P = 0.0007$), indicating that the pisaurids' eyeshine was significantly more intense relative to the spider's eye diameters. Only the significant comparisons ($P < 0.05$) are shown for the ANOVA post hoc tests.

Variance	Sum of squares	df	Proportion of variance
Between species	61.81	7	0.46
Within species	73.89	39	0.54
Tukey's Multiple Comparison Test	Mean difference (mm)	q	P
<i>D. tenebrosus</i> vs. <i>V. avara</i>	3.489	4.91	< 0.05
<i>D. vittatus</i> vs. <i>V. avara</i>	3.353	6.18	< 0.01
<i>D. scriptus</i> vs. <i>V. avara</i>	3.658	5.60	< 0.01

was the significantly red-shifted reflectance spectrum of the lycosid, *G. pulchra* (Fig. 4). Less conspicuous as sources of variation were the spectra of two of the pisaurids, *D. vittatus* and *D. triton*, that showed peaks at significantly longer wavelengths than did some of the lycosids. Selection or phenotypic plasticity related to behavioral and sensory attributes at the species level may account for these differences.

Outside of arachnids, closely related organisms in several taxa have been found to show differences in peak reception. These differences may correspond to the spectral properties of the environment. In several aquatic taxa, where the spectral environment varies strongly with depth, reception has been shown to be tuned to habitat. For example, moray eels' retinal structures, pigments, and spectral responses were consistent with the spectra available at the native depths of particular species (Wang et al. 2011). Seabream visual pigments vary such that the neural response is tuned to the environment (Wang et al. 2009). In stomatopods, midband receptors were tuned to the spectral environment (Cronin et al. 2000). These differences can be plastic. Differences in the spectral environment can result in developmental shifts in photoreceptor pigments, receptor morphology, and/or filtering pigments (guinea pigs, Hu et al. 2011; stomatopods, Marshall et al. 2007; and cichlid fish, Wagner & Kröger 2005). Evolutionarily, Fleishman (1992) reports feedback between sensory systems and signaling in lizards, suggesting coevolution. Similarly, despite likely costs due to avian predation, male lepidoptera produce colors that link closely with peak color reception in females (Stavenga & Arikawa 2006). Spiders face similar constraints; salticid males lacking critical wavelengths of colors failed to elicit courtship from otherwise receptive females (Lim et al. 2008).

We measured reflectance rather than reception, but a similar phenomenon has been reported in deep-sea fishes (Douglas et al. 1998). Like spiders, these deep-sea fishes possess guanine-based tapeta, and have lenses that differentially filter light. Although spider and fish eyes differ in many ways, Douglas et al. (1998) report that eyeshine is tuned to the spectral

environment of the fishes, is influenced both by tapetal reflection and ocular media, and is a relevant measure of sensitivity in fishes. Similarly, peak reflectance may relate to differences in the perceptive frequencies between the different spiders (Yamashita 1985). Although diel variation in the structure and sensitivity of the photoreceptors is known in spiders (Blest & Day 1978), the tapetum is not variable on a diel basis (Grusch et al. 1997). Differences in microhabitat use, positioning, or diel patterns of behavior could influence the quality of light experienced and thus optimal reception or reflection spectra. Considering the species in this study: the pisaurids are semi-aquatic (Carico 1973), *G. pulchra* is often arboreal (Eubanks & Miller 1992), and the other lycosids are typically found in disturbed soil, particularly in riparian zones (*Hogna* sp.: Walker et al. 1999), on leaf litter (*Varacosa* sp.: Brushwein et al. 1992), or in grasses (*Rabidosa* sp.: Reed et al. 2008).

Habitat preferences have further behavioral and functional correlates that may also have influenced eye function and morphology. For example, there are notable differences in the typical posture and position of the spiders: *G. pulchra* orient vertically (downward) on trees (Eubanks & Miller 1992), the other lycosids are typically found in grasses or on leaf litter and may be best characterized as indifferent with respect to the direction of gravity, and the pisaurids orient at a downward angle, but not vertical, relative to the water surface (Carico 1973).

Relative intensity of the eyeshine.—Raw variation between species with respect to the intensity of reflection is partly a consequence of eye size. In our study, intensity varied linearly with eye diameter, and eye size accounted for about 42% of the variation in intensity (Fig. 7). At the same time, PME size in the spiders we studied varied substantially, with the lycosids, as expected, having larger eye diameters than did the pisaurids (Fig. 6, Table 2). Note that one of our initial observations had been that lycosid PME eyeshine was brighter than pisaurid PME eyeshine. This is strictly true, but only because, relative to spider size, lycosid PMEs are much larger (Fig. 5). Our analysis of the residuals from the regression of intensity on eye diameter provided a means whereby we could normalize intensity relative to eye diameter (Fig. 8, Table 3). Relative intensity of the eyeshine was quite variable, with the pooled pisaurids having brighter eyes relative to their eye diameters than the eyes of lycosids. The most conspicuous variants were the lycosid, *V. avara*, with eyeshine that was conspicuously dim relative to similarly sized PMEs to *D. scriptus*, which showed conspicuously bright eyeshine (Figs. 7 & 8). This is consistent with the overall trend of lycosid eyes reflecting less light relative to eye-size than the pisaurids.

At the family level, there was a strong and consistent difference in eye size and, correspondingly, overall intensity of reflection. In other taxa, Leuckart's Law suggests that faster moving animals would have larger eyes to maximize acuity, and such a correlation has recently been reported in mammals (Heard-Booth & Kirk 2012). In spiders, eye size is thought to correlate to visual acuity and, in general, eye size has been used as a proxy for the importance of visual stimuli (Pirhofer-Walzl et al. 2007). Further, in the pisaurids, visual acuity has been shown to be useful in predator detection (Williams 1979), but predator and prey detection using other sensory modes has

been demonstrated (Bleckmann & Rovner 1984; Bleckmann & Lotz 1987; Suter & Gruenwald 2000; Suter 2003). Similarly, other modes of communication are thought to be of primary importance for courtship and mating in pisaurid spiders (Roland & Rovner 1983; Arnqvist 1992). In the lycosids, larger eyes with greater light sensitivity would facilitate visual detection of predators and prey, and visual detection has been reported (Lohrey et al. 2009; Clemente et al. 2010). Substantial literature supports the importance of multi-modal communication for sexual selection in lycosids, particularly including visual stimuli (Hebets 2005; Rypstra et al. 2009). Rovner (1996) reported that although vibrations enhanced mate-searching, visual signals were important courtship cues. One model suggests that the sensory apparatus of female lycosids coevolved with the elaborate signals (Hebets & Uetz 1999), and this model is supported by data suggesting that the vibratory component of courtship is ancestral and the visual component derived within the family (Stratton 2005; Taylor et al. 2007).

It is plausible that these size and reflective intensity differences are functionally linked to vision capabilities. All of the taxa examined are considered to be primarily nocturnal or crepuscular with activity patterns consistent with those measured in *Cupiennius* sp. (Schmitt et al. 1990; Pirhofer-Walzl et al. 2007). Increased reflection may increase visual responsiveness in low light situations, but likely at the cost of some visual acuity (Land & Nilsson 2001). Thus, we might find that the increased reliance on visual signaling is associated with reductions of reflectance in lycosid eyes (relative to the pisaurids) to afford increased acuity to the lycosids. The conspicuously dim reflectance of the PM eyes in the small lycosid, *V. avara*, is consistent with such a trade-off. *Varacosa avara* has eyes similar in size to those of the much larger pisaurid spiders, but *V. avara*'s eyeshine is much less intense than that of the pisaurids. Their relatively small size may limit eye size, and thus acuity, perhaps requiring reduced tapetal reflections to achieve sufficient acuity. Trade-offs between visual abilities and tapetal reflection have been shown elsewhere. For example, in a study of lampreys, only the burrowing species show increased tapetal reflection. In that situation, the tapetal reflection correlated to a loss of cones and, hence, color vision (Collin & Potter 2000). Similarly, in decapod shrimp, larger shrimp had tapeta producing more intense reflection; and these increases were correlated to increased depth (and darker habitats) for these shrimp (Johnson et al. 2000). Selection favoring increased reflection at the cost of acuity in the *Dolomedes* species could be linked to these spiders' preferred microhabitat in riparian zones where light is often limited (Carico 1973), or may simply be consistent with less reliance on visual signaling.

It is important not to exaggerate the functional significance of our results. The reflectance that we have measured as eyeshine has both spectral and intensity properties, but we are still ignorant about the functional meanings of those properties. It is not clear, for example, whether a shift in peak wavelength of 55–60 nanometers toward the orange part of the reflected spectrum confers on *Gladicosa pulchra* a functionally different capacity to detect certain colors. The light reflected from the secondary eyes has traversed several layers of tissue, each of which must modify parts of the spectra to some degree. For

example, in *Cupiennius salei*, the light passes the lens, the vitreous body, the hypodermis layer, and the sensory cells before the tapetum reflects some of the light back through the same materials. Because the reflected light we collected and analyzed had been filtered by several additional layers of tissue after its second pass through the sensory cells, it is not clear exactly what wavelengths were available to the sensory cells (from Fig. 1B in Grusch et al. 1997). With respect to intensity, we cannot yet know whether eyeshine that is brighter relative to eye diameter means that the eye is more efficient at collecting photons (because the tapetum is a more efficient reflector) or is less efficient (because a greater proportion of the light is reflected back into the environment). Further exploration on lycosoid tapetal structures may reveal patterns in the observed tapetal variation. Tapeta vary even within the Lycosidae, such that the grate structure that is apparent in the taxa included in this analysis is not apparent in all lycosids. In the diurnal *Pirata*, for example, we found a punctuated sheet (isolated reflective segments) similar to those that Land reports in the thomisid *Tharpyra* sp. (Land 1985). We look forward to further explorations of eyeshine in lycosoid spiders that may reveal not only evolutionary and developmental constraints on visual reception in low-light situations, but also the functional consequences of differences in tapetal reflection.

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