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ULTRAVIOLET REFLECTANCE OF SPIDERS AND THEIR WEBS

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ABSTRACT. To determine the reflectance of spider webs and spiders under ultraviolet (UV) light, spiders and their webs were photographed under normal (white) light and under UV light. It was found that all silk in araneoid webs reflect slightly more UV light than white light; i.e., they had a positive UV-brightness. However, the often cited, particularly high UV-brightness of stabilimenta could not be confirmed. Spiders differed in their UV-brightness, with most spiders reflecting less UV light than white light. Based on the knowledge of the visual system of insects and invertebrates it is suggested that the main function of stabilimenta is predator defense. However, drawing a final conclusion requires more knowledge on the way potential predators and prey perceive spiders, spider webs and stabilimenta.

Keywords: Stabilimentum, camouflage, predator-prey, spider silk, visibility

The function of stabilimenta in orb-webs is the subject of an intense debate. Originally, it was suggested that stabilimenta serve to stabilize the web, hence the name stabilimentum (Simon 1893). More recent studies suggest that in most species, stabilimenta serve a visual function towards prey and/or predators of the spiders, also reflected in the fact that no spider species that removes the web during the day is known to build a stabilimentum (Herberstein et al. 2000). However, whether prey or predators are the intended viewers of stabilimenta remains hotly debated. Results of several studies that showed that stabilimenta attract prey could not be confirmed by others. The function of stabilimenta to deter or confuse predators is equally disputed, especially since it is not easily amenable to experiments (for a review see Herberstein et al. 2000). Predatory spiders that have recently been shown to use stabilimenta to find their prey spider (Seah & Li 2001) are quite certainly not the intended viewers of the stabilimenta.

Craig & Bernard (1990) assessed the reflectance of spider silk by measuring the reflectance of individual silk strands for wavelengths between 340 and 700 nm at 10 nm increments. They concluded that cribellate sticky silk and stabilimenta, but not other silk types of araneoid orb-webs, have a high reflectance in the ultraviolet (UV) spectrum. In a later study using the same method, Craig et al. (1994) argue that silk of primitive spiders and cribellate silk of uloborids have a high UV reflectance whereas derived (araneoid) aerial web spinners produce viscid silks that are spectrally flat or have a low UV reflectance. Watanabe (1999) measured the reflectance of the stabilimentum of a uloborid species and found that it was fairly flat, with a slightly higher reflectance in the UV range. The high UV reflectance of stabilimenta has been considered by several authors to be an attractor for prey (Craig & Bernard 1990; Tso 1998; Watanabe 1999), whereas other authors have questioned this function (Eisner & Nowicki 1983; Blackledge 1998b; Blackledge & Wenzel 1999, 2000).

Most, if not all, spiders that build a stabilimentum sit on the hub of the web (Scharff & Coddington 1997). However, the appearance under UV light of the web together with the spider has been documented only once with three pairs of photographs of a single species taken in the field (Craig & Bernard 1990). Taking comparative pictures in the field is problematic since lighting is neither constant nor controllable. The aim of the present study is to compare the appearance of spiders and their webs under UV light and white light under standardized lighting conditions. In particular I asked the following questions: 1. can the results of Craig & Bernard (1990) and Craig et al. (1994) be confirmed using an

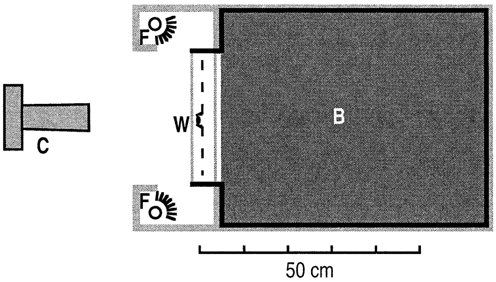


Figure 1.—Layout of the 'black box' (modified after Langer & Eberhard 1969) used to take the pictures, seen from above. B = box lined with black velvet, C = camera, F = fluorescent bulbs (vertical) and W = web with the spider. The bulbs used were either UV bulbs for the UV treatment or white bulbs for the white light treatment (cf. Fig. 2).

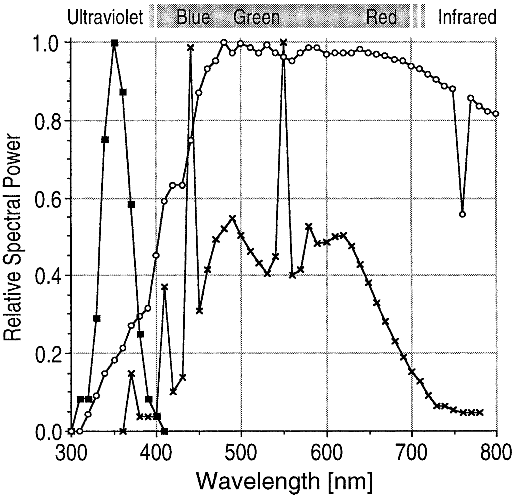


Figure 2.—Relative spectral irradiances of sunlight (open circles), and of the artificial lights used (black squares: UV fluorescent bulbs Sylvania black light 'F15W/BLB -T8', crosses: Osram 'L 15W/12–950—Daylight'). Curves were normalized to have their maximum at 1.0. The gray bar at the top indicates the range of wavelengths visible to humans.

alternative technique and 2. what is the appearance of web building spiders under UV light.

METHODS

Spiders were collected in the wild and acclimatized to laboratory conditions where they built webs in acrylic plastic frames (30 x 30 x 5 cm). The frames with the spiders were placed at the front of a 'black box' (Fig. 1) and photographed there. Each spider in its web was photographed under UV light and under white light (Fig. 2). Unless indicated otherwise, whenever 'white' is used in the present paper, it implies white to the human eye. Light was switched between UV and white by exchanging the fluorescent bulbs, thus ensuring that, apart from the spectral distribution, lighting was identical in both treatments. Pictures were taken with a Nikon F camera with a 105 mm UV lens and, where necessary, a Nikon M2 macro adapter on Kodak Tri-X Pan 400 ASA B/W film (this film has a high sensitivity down to 300nm; Kodak, pers. comm). For pictures taken under UV light, a UV transmitting 'black' filter was placed in front of the lens. Pictures under UV light were exposed for 3 sec and those under white light for 1 sec. These exposure times resulted in the same shade of gray when taking a picture of a standardized Kodak gray card, which reflects 18% of the incident light across all wavelengths. The gray card was photographed together with the spider at the edge of all pictures (visible at lower edge of Figs. 9, 10, 13, 14). For all spider pictures, an aperture of f = 16 was used. Negatives were developed commercially, which resulted in slight differences in development between films. However, both pictures of one object were always on the same film and therefore underwent identical development.

Negatives were scanned with a Polaroid 'SprintScan35' slide scanner. After scanning, contrast was enhanced by 20 steps with Adobe Photoshop. To allow exact comparison, brightness and contrast of the picture were further adjusted in such a way that the brightness value of the gray card and the brightness value of the dark background were the same in both pictures of each pair.

The reflectance of spider, silk and stabilimenta was estimated by measuring their brightness value (in percent, ranging from 0 = black to 100 = white) at the same position in the two pictures using the utility Apple DigitalColour Meter on pictures that were suitably enlarged or reduced with Photoshop. For the measurements of the brightness values of the different kinds of silk, four pairs of measurements were taken for each picture and silk type. The brightness of each spider was measured three times, once on the cephalothorax and twice on the abdomen. A measurement of the absolute brightness of the silk or

Table 1.—Reflectance of spiders under UV light and under white light. Values for debris and egg sac stabilimenta are given in the text. Abbreviations: CH = Switzerland; KE = Kenya, LK = Sri Lanka; MX = Mexico; SG = Singapore; ZA = South Africa.

		UV-brightness			
Species	Origin	spider	dry silk	sticky silk	silk stabilimentum
Achaeraranea lunata (Clerck, 1757)	CH	−15	15		
Agelenatea redii (Scopoli, 1763)	CH	−2	12	10	11
Arachnura sp.	LK	−14	12		
Araneus diadematus Clerck, 1757	CH	−14	14	11	
Araneus quadratus Clerck, 1757	CH	−8	10	2	
Argiope argentata (Fabricius, 1775)	MX	−2	8	6	6
Argiope bruennichi (Scopoli, 1772)	CH	−5	6	3	8
Argiope versicolor (Doleschall, 1859)	SG	−18	7	8	
Cyclosa conica (Pallas, 1772)	CH	−1	6	12	9
Cyclosa insulana (Costa, 1834)	ZA	−3	14	12	8
Cyclosa turbinata (Walckenaer, 1842)	MX		15	11	
Cyclosa walckenaeri (O.P.-Cambridge, 1889)	MX	−11	9	12	11
Cyrtophora citricola (Forskål, 1775)	ZA	−5	8		
Micranthena gracilis (Walckenaer, 1805)	MX	−14	12		
Nephila senegalensis (Walckenaer, 1842)	KE	−2	5	−1	
Nephila sp.	ZA	−2	23	15	
Steatoda triangulosa (Walckenaer, 1802)	CH	−18	7		
Uloborus sp.	ZA	−23	16	25	11
Verrucosa arenata (Walckenaer, 1842)	MX	2	7	9	
Zilla diodia (Walckenaer, 1802)	CH	−1	16	15	
Zosis geniculatus (Olivier, 1789)	LK	4	18	26	16

the spider in comparison with the gray card was not possible because the brightness of the silk largely depends on its position relative to the light source (cf. brightness of radii within Figs. 11, 12) and because the position of the gray card differed from one pair of pictures to the next.

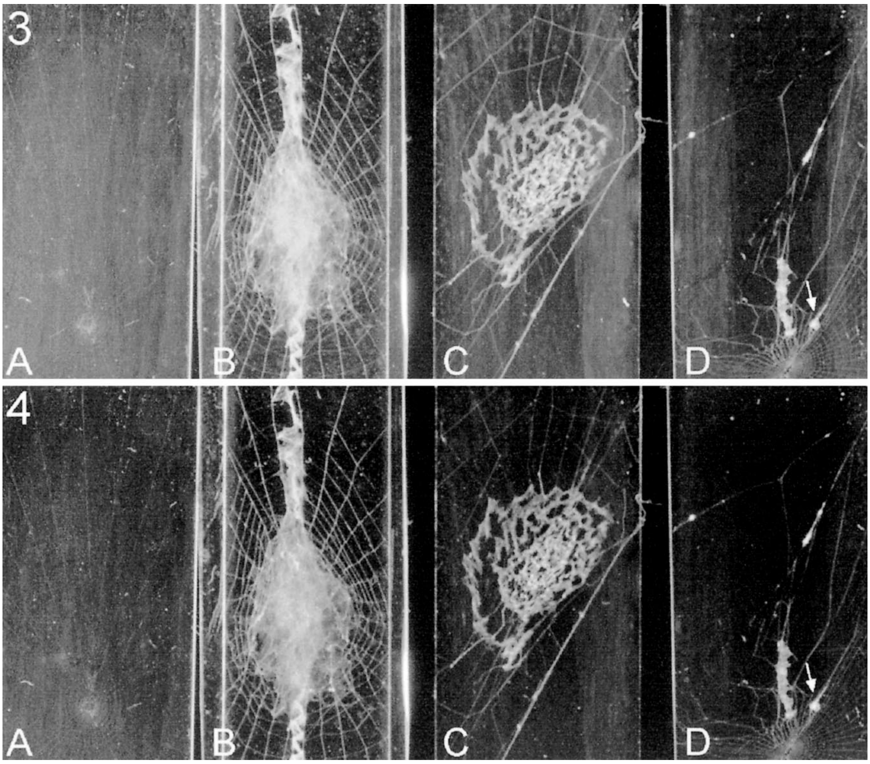
The relative reflectance of the silk and the spiders was then assessed by subtracting the brightness value under white light from the brightness value under UV light. I will use the term UV-brightness for this difference. Positive UV-brightness values indicate higher brightness under UV than under white light. Nomenclature of orb-web elements follows Zschokke (1999).

RESULTS

Reflectance of silk.—I found that all silks (dry silk, cribellate and ecribellate sticky silks, stabilimenta) reflected UV light better than white light, i.e., had a positive UV-brightness (Table 1; Figs. 3, 4).

Most kinds of silk had an intermediate, positive UV-brightness (ecribellate sticky silk: +9, araneid and nephiline dry silk: +11; theridiid dry silk: +11; uloborid stabilimentum: +13; araneid silk stabilimentum: +9), cribellate sticky silk had the highest UV-brightness (+25), dry silk of uloborid webs also had a high UV-brightness (+17), whereas detritus stabilimenta (wrapped prey remains and shed skins) of *Cyclosa conica* and *C. insulana* both showed a neutral UV-brightness (+1 & 0), and the egg sac 'stabilimentum' (Levi 1977) of *C. turbinata* even had a negative UV-brightness (-6). Similarly, the cocoon of *A. versicolor* was also found to have a negative UV-brightness (-9).

Reflectance of spider.—Most spiders appeared darker under UV light than under white light, i.e., had a negative UV-brightness. However, there was some variation between species, ranging from fairly low UV-brightness to neutral UV-brightness (Figs. 5–12, Table 1). Only a few of the species analyzed showed different patterns under UV light compared to white light: the bright yellow ab-



Figures 3–4.—Stabilimenta and hub decorations of *Zilla diodia* (A), *Argiope bruennichi* (B), *Zosis geniculatus* (C) and *Cyclosa conica* (D) mounted on microscope slides photographed under UV light (3) and white light (4). The stabilimentum of *C. conica* is a pure silk stabilimentum. The small bright spot to the right of the stabilimentum (arrow) is the wrapped remains of a fruit fly *Drosophila* sp., as it is sometimes incorporated into the stabilimentum.

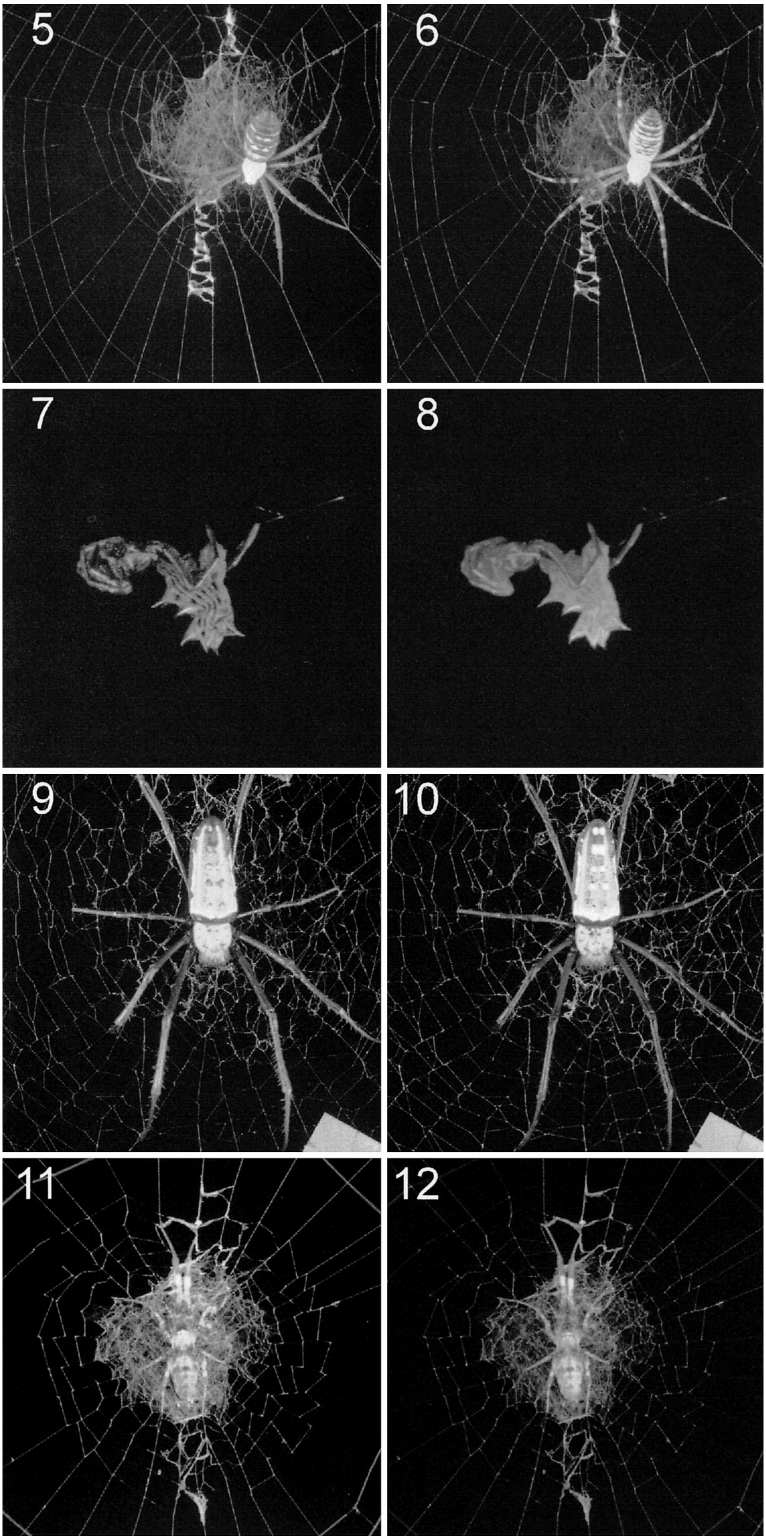
dominal spots of *Nephila senegalensis* disappeared under UV light (Figs. 9, 10) and juvenile *Micrathena gracilis* showed dark spots under UV light that were not visible under white light (Figs. 7, 8). On average, the abdomen of spiders had a lower UV-brightness (-8) than the cephalothorax (-4).

Reflectance of background vegetation.—As a control of my approach and to compare reflectance patterns and UV-brightness of flowers with that of spiders and their webs, I photographed nine different flowers and a variety of plants using the same method as I used for spider pictures, albeit with a smaller aperture (f = 32).

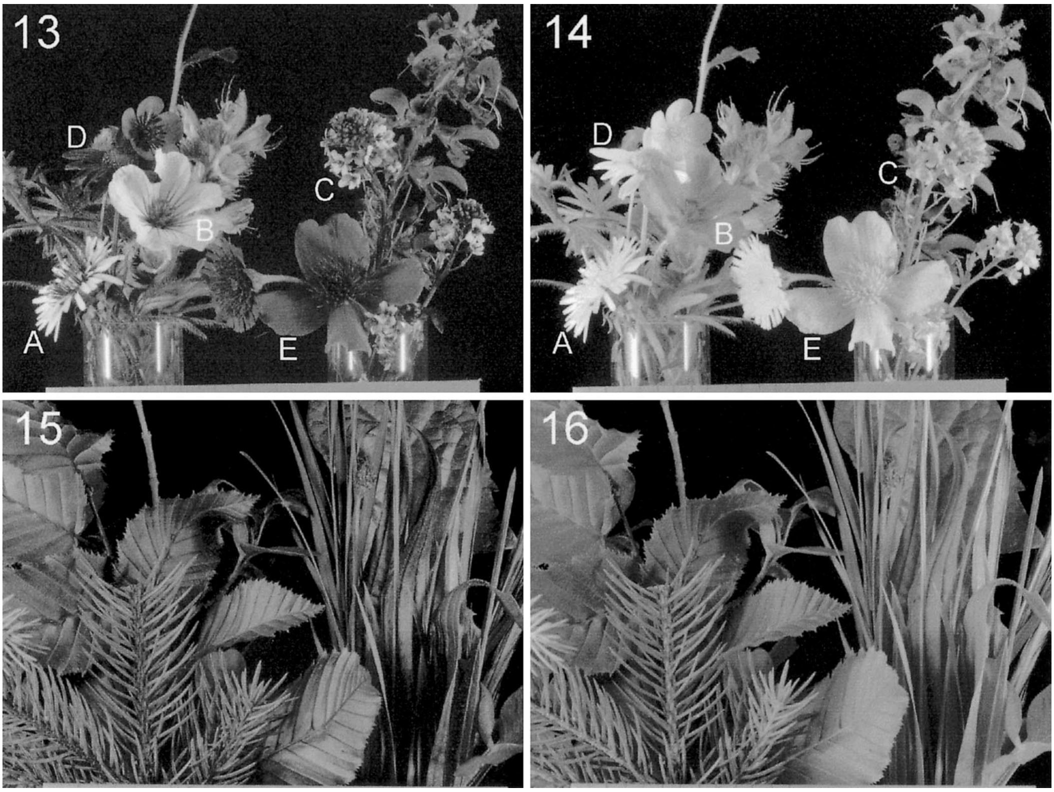
Stems and leaves generally appeared somewhat darker under UV light than under white light (UV-brightness = −5, Figs. 13–16). The UV-brightness of the flowers varied considerably (Figs. 13, 14). Two flowers (*Geranium sanguineum* and *Echium vulgare*) had a positive UV-brightness of 20 and 4 respectively, whereas the other seven flowers had a negative UV-brightness ranging from almost neutral (-2, *Barbarea vulgaris*) to −70 (*Leucanthemum vulgare*). Some of the UV-bright to UV-neutral flowers showed dark, distinct patterns under UV light, which are thought to serve as guiding lines for visiting pollinating insects (Figs. 13, 14; Jones & Buchmann 1974).

DISCUSSION

Reflectance of silk.—It is striking, that most silk types showed a very similar UV-brightness of around +10, the only exceptions being sticky (cribellate) and dry silk in uloborid webs, and detritus and egg sac stabilimenta of *Cyclosa* spp. My study thus could confirm that cribellate sticky silk has a higher UV-brightness than ecribellate sticky silk (Craig & Bernard 1990; Craig et al. 1994).



Figures 5–12.—Spiders and central part of their webs photographed under UV light (left) and white light (right): 5, 6. *Argiope bruennichi*; 7, 8. juvenile *Micrathena gracilis*; 9, 10. *Nephila senegalensis*; 11, 12. *Zosis geniculatus*.



Figures 13–16.—Plants under UV light (left) and white light (right). Stems leaves, and many flowers appear darker under UV light than under white light. The flowers of the dandelion (*Taraxacum officinale*, yellow colored, A) the bloodred cranesbill (*Geranium sanguineum*, purple colored, B) and the winter cress (*Barbarea vulgaris*, yellow colored, C) show distinct, contrasting patterns under UV light, which are thought to serve as guiding lines for visiting pollinating insects. Note that the two flowers that appear white (Oxeye daisy, *Leucanthemum vulgare*, D) or whitish (Clematis, *Clematis* sp., E) to us are among the darkest under UV light. Pictures taken with a smaller aperture than, but otherwise identical set-up as the spider pictures. A colored version of Fig. 14 can be found at http://faculty.vassar.edu/suter/joaserver/.

However, my study could not confirm that stabilimenta have a higher UV-brightness compared to other silks in orb-webs (Craig & Bernard 1990). It is not clear why my results differ from those of earlier studies. There are several possible explanations: 1. The difference in UV-brightness between the stabilimenta and other silk types is too small to be detected using photographs. 2. The measurements of Craig & Bernard (1990) and Craig et al. (1994) considered each wavelength separately, whereas the measurements in the present study are integrations over a range of wavelengths. 3. Craig & Bernard 1990 did not consider wavelengths shorter than 340 nm and their measurements suggest that UV reflectance of stabilimenta drops off below 360 nm; whereas measurements in my study considered wavelengths down to 300 nm (wavelengths < 340 nm may not be very relevant biologically, since few insects are sensitive to wavelengths < 340 nm; Briscoe & Chittka 2001). 4. The reflectance measurements of Craig & Bernard (1990) may have been biased since the diameter of some of the spider's silks (0.4–4 μm; Craig 1986; Vollrath & Köhler 1996; Zschokke 2000) lies in the range of the wavelengths of visible light (0.4–0.7 μm), and the interactions between light and such thin objects are rather complex (Craig 1988; Nishiyama et al. 2001). 5. Since the reflectance of silk depends on the incident angle of the light (cf. radii in Figs. 11, 12), Craig & Bernard's measurements, which used the same incident angle of light for all measurements, may not be representative, especially if there is an interaction between the incident angle of light and wavelength. 6. If some silk types are fluorescent, this could result in an over-estimation of their UV reflectance using the method of Craig & Bernard.

Whichever method is used to measure silk reflectance, one conclusion remains the same: all silks in orb-webs (including stabilimenta) reflect more UV light than the background vegetation, which reflects little UV light, and therefore appears darker under UV light (Frolich 1976; Chittka et al. 1994; Figs. 15, 16). However, the analysis presented in this paper shows that the UV-brightness of silk stabilimenta is much smaller than that of some flowers, and it is therefore questionable whether stabilimenta can attract pollinating insects through their UV reflectance.

Reflectance of spiders.—Spiders varied in the way they reflect UV light compared to white light. There seems to be a trend for the more colorful species (e.g., *A. bruennichi*, *A. argentata*, *N. senegalensis*, *V. arenata*) to show a neutral UV brightness, whereas the more cryptic species (e.g., *Arachnura* sp., which tries to mimic a dead leaf, *Micrathena gracilis*, which resembles a ball of dirt) seem to have a lower UV-brightness. One can speculate that the reduced reflectance under UV light, which is comparable to that of the background vegetation, is part of the camouflage of this spider. Due to the simultaneous positive UV-brightness of silk, and the negative or neutral UV-brightness of the spiders, the spiders with a hub stabilimentum appear more cryptic under UV light than under white light (Figs. 5, 11).

Visibility of webs.—The visibility of the web is crucial for the spider: the web should be simultaneously invisible or attractive to the spider's prey and invisible or deterring to the spider's potential predators (Blackledge 1998a). Many of these potential prey or predator species (e.g., insects and birds) are known to have UV receptors (Menzel & Backhaus 1991; Finger & Burkhardt 1994), and consequently, the UV reflectance of spiders and their webs must be considered. At the same time, color perception and spatial resolution of the visual systems of potential prey or predator species must be taken into account.

Insect vision differs fundamentally from that of humans and other vertebrates. First, many insects can detect UV light but few are sensitive to red (Briscoe & Chittka 2001). Second, insects differentiate colors primarily through their color contrast and not through brightness (Fukushi 1990; Backhaus 1991; Chittka et al. 1992; Chittka et al. 1994). To insects, objects that we perceive as white and that also reflect UV light (i.e., have a flat spectrum), have the same color as the background (e.g., leaves, bark, soil), all appearing achromatic at the center of the insect color space, since insects are not able to detect red light, which we use to distinguish white objects from leaves or soil. As a consequence, there are very few white (i.e., white for humans), insect pollinated flowers that also reflect in the UV wavelengths (Kevan et al. 1996; see also Figs. 13, 14). Silk stabilimenta probably also fall into this category: to humans they appear white and they reflect UV light. We may therefore conclude that stabilimenta, being achromatic, are not very conspicuous to insects (Blackledge 1998a).

Our eyes have a maximum resolution of 0.3 min of arc. To be able to see a typical spider thread with a diameter of two μm with the naked eye would require us to approach it to a distance of less than two cm, at which distance we are not able to focus on it. We can therefore perceive spider threads only if there is a large contrast between the thread and the background compensating for the lack of spatial resolution of our eyes. In a similar way, the apparent size of all fixed stars in the sky at night falls below our eye's resolution, but we can nevertheless perceive many of them, thanks to their great contrast to the dark sky. Since spider silk is white, the best way for us to achieve the necessary high contrast to see single threads, is to view them brightly illuminated against a dark background. The spatial resolution of insect's eyes is roughly 100 times poorer than our own (Wehner 1981), which would require the insects to approach the web to less than a mm to be able to see it. It is not known, how and under what circumstances the insect eyes can make up for the lack of resolution to see spider threads. However, Rypstra (1982) and Craig (1986) have reported that *Drosophila* sometimes change their flight path as they approach silk strands, suggesting that they are able to detect them.

It is not quite certain how insects perceive stabilimenta, which have a fairly flat spectrum and which could therefore be expected to appear rather dull and colorless to them. In one experiment, Blackledge & Wenzel (2000) found that they could not train bees to associate a reward with stabilimentum silk, whereas they could train bees to associate a reward with silks that have UV reflective peaks. On the other hand, Blackledge & Wenzel (2001) also showed that spiders in stabilimenta decorated webs were more likely to survive attacks of mud-dauber wasps, suggesting that the wasps were able to perceive the stabilimentum.

Bird vision is more similar to that of humans, but it often—like that of insects—extends into the UV (Finger & Burkhardt 1994). Consequently, stabilimenta are probably quite conspicuous to birds. Since birds are only rarely the prey of spiders, it may be concluded that the main function of stabilimentum is probably deterrence against birds, rather than attraction of prey; thus confirming the studies of e.g., Lubin (1975), Horton (1980), Eisner & Nowicki (1983), Schoener & Spiller (1992) and Blackledge & Wenzel (1999). However, before any final conclusions can be drawn, much more must be learned about the way different potential prey and predators perceive spiders and their webs.

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