Signal conflict in spider webs driven by predators and prey

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Variation in the sensory physiologies of organisms can bias the receptions of signals, driving the direction of signal evolution. Sensory drive in the evolution of signals may be particularly important for organisms that confront trade-offs in signal design between the need for conspicuousness to allow effective transfer of information and the need for crypsis of the signal to unintended receivers. Several genera of orb-weaving spiders include conspicuous silk designs, stabilimenta, in the centre of their webs. Stabilimenta can be highly visible signals to predators, warning them of the presence of a noxious, sticky silk web. However, stabilimenta can also be used by prey as a signal in avoidance of webs, creating a trade-off in signal visibility. I argue that the derived spectral properties of stabilimentum silk have resulted in part from this conflict. The innate colour preferences of insects, their ability to learn colours, and the spectral properties of flowers all suggest that the reflectance spectra of stabilimenta renders them relatively cryptic to many insect prey, while maintaining their visibility to vertebrate predators.

Keywords: aposematic; *Argiope*; silk; sensory drive; ultraviolet; stabilimenta

1. INTRODUCTION

Sensory biases in reception of signals are caused by variation in the sensory physiologies of receivers and can affect the evolution of signal design in a process termed sensory drive (Endler 1978, 1992, 1993a; Guilford 1990; Guilford & Dawkins 1991; Fleishman 1992; Ryan & Rand 1993). Sensory drive has been used to account for the diversification of a variety of visual and vocal signals in vertebrates (Basolo 1990; Endler 1991, 1992; Fleishman 1992; Ryan & Keddy-Hector 1992; Ryan & Rand 1993) and arachnids (Clark & Uetz 1992, 1993; Proctor 1992; McClintock & Uetz 1996). However, most of these studies involved sexual signalling, leaving the role of sensory drive in the evolution of interspecific signals unexplored. Furthermore, the physiological bases of sensory biases have rarely been well documented. Although such study typically demands elaborate experiments to demonstrate sensory biases and to determine the ancestral state of signal features, we already have the relevant data to examine the possible role of sensory biases in the form and function of stabilimenta in the webs of spiders. Stabilimenta are conspicuous silk designs that many diurnal orb-weaving spiders include at the centre of their webs (see figure 1). Stabilimenta can function as visual warnings to predators for the presence of noxious, sticky silk in orb webs (Horton 1980; Eisner & Nowicki 1983; see table 1), but they also provide visual signals that prey can use to avoid webs (see table 1). This creates a conflict in the selection for visibility of stabilimenta to different receivers. I suggest that the design of stabilimenta reflects this conflict between visibility to predators and prey of spiders, and is such that stabilimenta are obvious signals to predators while remaining relatively cryptic to insect prey.

2. THE ORB WEB AS A VISUAL SIGNAL TO PREDATORS

The primary function of orb webs is prey capture (Eberhard 1990), but webs can also be a valuable defence (Edmunds & Edmunds 1986; Jackson *et al.* 1993; Cloudsley-Thompson 1995). The sticky capture silk of webs is capable of entangling predators such as jumping spiders (Salticidae) and wasps (Sphecidae and Pompilidae) (Edmunds & Edmunds 1986; Cloudsley-Thompson 1995), and it is a noxious stimulus avoided by vertebrate predators such as birds (Horton 1980; Eisner & Nowicki 1983; Blackledge & Wenzel 1998; see table 1). Yet, there is little advertisement of these noxious and sometimes lethal aspects of webs to the predators of spiders. Instead, orb webs are usually quite cryptic, indicating the great importance of low visibility of webs for effective prey capture (Rypstra 1982; Craig 1986, 1988; Uetz 1990; Craig & Freeman 1991).

Unlike the web itself, stabilimenta can be highly conspicuous signals to predators. The designs include broad bands of bright white silk that form vertical lines or crosses at the centre of the webs of *Argiope* spp. and several other genera of orb-weaving spiders in the Orbiculariae (reviewed in Nentwig & Heimer 1987; Eberhard 1990). Although once thought to stabilize webs (e.g. Robinson & Robinson 1970a, 1973), there is little evidence to support such a hypothesis, as stabilimenta are the last structure added to webs and they are only loosely attached to the webs (Eberhard 1973; Edmunds 1986). Furthermore, webs with stabilimenta removed are able to function better at catching prey (table 1). Although other functions have been proposed (reviewed in Eberhard 1990), there is substantial evidence that such linear stabilimenta are defensive signals that may be aposematic,

Figure 1. Female *Argiope aurantia* in a web containing a stabilimentum. The web itself has been coated with corn starch to enhance its visibility. Scale bar *ca.* 3 cm.

Table 1. *Comparison of a decrease in bird damage and an associated foraging cost from including stabilimenta in the webs of* A. aurantia

(Data are from paired comparisons of webs, with and without stabilimenta, under field conditions. The χ^2 test compared the number of damaged webs that contained stabilimenta with the number of damaged webs that did not contain stabilimenta. The *G*-test examined the probability that, from a total of 55 trials at eight sites, seven sites would have webs without stabilimenta, which would catch the most prey. Adapted from Blackledge & Wenzel (1998).)

	% webs damaged by birds	mean prey capture rate
webs containing stabilimenta	39	2.0 ± 0.3 prey per 3 h
webs without stabilimenta	71	2.9 ± 0.3 prey per 3 h
	$\chi^2 = 17.2$, d.f. $= 1$, $p < 0.005$ ($n = 41$)	$G = 5.603$, d.f. $= 1$, $p < 0.025$ ($n = 55$)

obfuscate the outline of spiders, or startle predators (Hingston 1927; Marson 1947; Marples 1969; Ewer 1972; Eberhard 1973; Lubin 1975; Tolbert 1975; Edmunds 1986; Neet 1990; Schoener & Spiller 1992; Kerr 1993; Blackledge 1998). In particular, experiments have demonstrated the effectiveness of stabilimenta as a highly visible aposematic signal, which can warn birds away from webs (Horton 1980; Eisner & Nowicki 1983; see table 1).

Linear stabilimenta consist of broad bands (see figure 1) of thin silk fibres, which greatly enhances the visibility of stabilimenta compared with that of the individual fibres that constitute them. Stabilimentum silk is bright white (Eberhard 1973; Craig & Bernard 1990), and this maximizes photic stimulation of vertebrate eyes and differentiates the silk from a background of soil and foliage, which weakly reflects most wavelengths of light (Endler 1993b; Chittka et al. 1994). Unlike the sticky silk of many orb webs, the reflectance spectrum of stabilimentum silk includes a strong ultraviolet (UV) component, similar in magnitude to other reflected wavelengths (Craig & Bernard 1990). The possibility that this may further enhance visibility of stabilimenta to vertebrates needs to be investigated, as UV has been implicated as an important additional wavelength of light in the vision of a wide variety of birds (Goldsmith 1980; Burkhardt 1982, 1996; Bennett & Cuthill 1994; Maier 1994; Viitala et al. 1995) and many other potential vertebrate predators, including lizards (Fleishman et al. 1993; Loew 1994; Ellingson et al. 1995) and rodents (Jacobs et al. 1991; Jacobs 1992). Whereas the capture silks of webs are inconspicuous, the shape and reflectance of stabilimenta seem to maximize the potential for vertebrate predators to differentiate stabilimenta from environmental noise such as soil and foliage, as supported by use of stabilimenta in web avoidance by birds (Horton 1980; see table 1).

3. STABILIMENTA ARE INCONSPICUOUS TO PREY

Although a consideration of the entire reflectance spectra of stabilimenta suggests otherwise (see below), the reflectance of UV light by stabilimenta has been used to argue that the designs attract insect prey, particularly foraging bees, to webs (Craig & Bernard 1990; Craig 1991, 1994a; Elgar et al. 1996; Tso 1996). The prey-attraction hypothesis has been supported by correlations between the presence of stabilimenta in webs and high prey-capture success in both *Argiope argentata* and *A. trifasciata* (Craig & Bernard 1990; Tso 1996). However, Blackledge (1998) found that increased feeding success increased the probability that *A. trifasciata* would include stabilimenta in webs, causing the same pattern. Thus, correlations between prey capture and stabilimentum presence could result from the influence of high prey-capture success increasing the frequency of building stabilimenta, rather than from stabilimenta increasing prey capture. Furthermore, Blackledge & Wenzel (1998; see table 1) demonstrated that stabilimenta caused a reduction, not an increase, in the prey capture success of *A. aurantia* when webs with and without stabilimenta were paired in the field. Thus, the ability of prey to use stabilimenta as a visual signal in web avoidance is likely to have been a serious selective constraint on the evolution of the design of stabilimenta, just as it has been on the capture silks of orb webs.

The innate colour preferences of insects, their ability to learn colours, and the design of floral signals all suggest that the visibility of stabilimenta to insects is greatly reduced by the spectral properties of stabilimentum silk. Hymenoptera, particularly bees, are one of the most common prey items of *Argiope* spp. (Robinson & Robinson 1970b; Brown 1981; Murakami 1983; Howell & Ellender 1984; McReynolds & Polis 1987; Nyffeler & Breene 1991; Bradley 1993; Craig & Ebert 1994) and are also among the most manoeuvrable and visual flying insects. Bees and many other insects possess trichromatic vision, similar to that of humans but shifted *ca.* 100 nm shorter, with photopigments sensitive to three broad categories of

light: long UV (*ca.* 350 nm), blue (*ca.* 440 nm) and green (*ca.* 530 nm) (Goldsmith & Bernard 1974; Peitsch *et al.* 1992; Troje 1993; Chittka 1996). Additional red photoreceptors or red-shifted green photoreceptors can be found in some insects but do not appear to be the norm, particularly for pollinating Hymenoptera (Bernard & Remington 1991; Peitsch *et al.* 1992). Colour is the primary cue used in floral discrimination by many pollinating insects, even when other cues such as intensity or pattern differences are available (Giurfa *et al.* 1995*a,b*; Giurfa & Vorobyev 1997; Kelber & Pfaff 1997; Menzel *et al.* 1997; Orth & Waddington 1997). However, few pollinating insects are attracted to stimuli with achromatic reflectances, such as stabilimenta. Naive honeybees show an innate preference for bee-green and bee-UV-blue colours (Giurfa *et al.* 1995*b*), whereas bumblebees (*Bombus terrestris*) have innate preferences for any spectrally pure colour that stimulates only one or two classes of their photoreceptors (Lunau & Maier 1995; Keasar *et al.* 1997), and the hover fly (*Eristalis tenax*) is attracted to only human yellow (Lunau 1988). For each of these species, spectrally impure (white+UV) objects that stimulated all three classes of photoreceptors were the least attractive to naive insects, regardless of their intensity (Lunau *et al.* 1996). Even with previous foraging experience, many insects are still not attracted to white+UV objects (Allan & Stoffolano 1986; Scherer & Kolb 1987; White *et al.* 1994).

Insects can also be easily trained to distinguish and associate colours, including human white, with a foraging reward (Goldsmith 1961; von Frisch 1967). Again, any chromatic stimulus is easily associated with food, whereas an achromatic (white+UV) signal is poorly learned by many Hymenoptera, Diptera, and Lepidoptera (Hertz 1939; von Frisch 1950; Daumer 1963; Troje 1993; White *et al.* 1994; Giurfa & Vorobyev 1997). Hertz was the first to demonstrate this phenomenon in honey bees (*Apis mellifera*) and her findings are summarized in von Frisch (1950):

> 'It is always very easy to train them to a true color, but training to a *white* paper or cardboard is sometimes easy and sometimes quite difficult. She tested various white papers and found that some of them absorbed ultraviolet rays. To these papers the bees could be trained very easily. But other white papers reflected the ultraviolet, just as they did the rays visible to us. This white the bees could not remember, and they could not learn to seek it out with certainty…'

It has already been shown that the colour of spider silks can be an important cue in avoidance of webs by insects (Craig 1994*b*). The unattractiveness of white+UV signals to naive pollinating insects, and their difficulty in learning white+UV, indicates that such signals are poorly perceived by some of the most common prey of *Argiope*.

Why are achromatic (white+UV) objects treated so differently by insects that are otherwise quite adept at using colours in foraging tasks? Simply put, white+UV objects have a poor colour contrast with typical backgrounds of soil and foliage when viewed by insects. Both soil and foliage weakly reflect all wavelengths of light perceived by bees and other trichromatic insects, thus appearing achromatic at the centre of insect colour space

(von Frisch 1967; Kevan 1972; Chittka *et al.* 1994; Lunau 1996). They are used as a neutral grey standard for comparison to other objects (von Frisch 1967; Kevan 1972; Chittka *et al.* 1994; Kevan *et al.* 1996). Humans differentiate soil and foliage largely on the basis of the strong absorption of red light by the latter, thus perceiving them as having different colours (Chittka *et al.* 1994; Kevan *et al.* 1996). Unlike white−UV objects, the presence of a UV component in white coloration also causes an equal stimulation of the three photoreceptor classes of insects. Thus, white+UV objects will appear achromatic, again near the centre of the colour space of bees (Chittka *et al.* 1994; Kevan *et al.* 1996). Because honeybees and many other insects do not use brightness cues when discriminating colours (von Frisch 1950; Backhaus *et al.* 1987; Fukushi 1990; Backhaus 1991; Chittka *et al.* 1992; Troje 1993; Giurfa *et al.* 1995*a*), the difference between the brightness of stabilimenta and soil or foliage also does not help differentiate them through colour. Therefore, stabilimenta, soil and foliage all appear as non-descript greys at the centre of honeybee colour space, and stabilimenta thus provide a signal of poor colour contrast with environmental noise to insect prey.

These results are also supported by, and may account for, the difficulty that the stingless bee, *Trigona fuscipennis*, has in learning to associate stabilimenta with the webs of *A. argentata* (Craig 1994*a*). The bees have particular difficulty associating stabilimenta with webs when the stabilimenta vary in shape, suggesting that colour is not the only cue that insects can use to avoid webs. If the bees had been able to use colour as a signal in avoidance of stabilimenta, they should have generalized their avoidance response to all shapes of stabilimenta in the experiment, as they do with chromatic colours when foraging (Backhaus *et al.* 1987; Chittka *et al.* 1992; Giurfa *et al.* 1995*a*). Stabilimenta can still be differentiated from the background on the basis of their shape, and any non-target object, such as leaves, will still be avoided when in the direct flight path of an insect. However, such motion- and form-sensitive responses are colour blind in insects and mediated only by green photoreceptors (Wehner 1981; Lehrer *et al.* 1985, 1988; Lehrer 1994). Detection of stabilimenta through green-contrast visual pathways is likely the most important factor accounting for the avoidance of stabilimenta found by Blackledge & Wenzel (1998). Despite this, the white+UV reflectance of stabilimenta causes the designs to be cryptically coloured to insects. This eliminates one of the most important visual cues for pollinating insects, making it difficult for them to associate stabilimenta with dangerous spider webs.

The poor ability of white+UV surfaces to function as obvious signals to pollinating insects is further supported by the scarcity of white+UV reflective flowers. The reflectance spectra of flowers appear to be designed to maximize the potential of the visual systems of pollinating Hymenoptera and Diptera to differentiate flowers from the background and to discriminate between species of flowers (Chittka & Menzel 1992; Troje 1993; Chittka *et al.* 1994; Lunau 1996). Whereas blue, red, and yellow flowers often include UV in their reflectance spectra, white flowers rarely reflect UV light (Daumer, in von Frisch 1967; Kevan 1983; Menzel & Shmida 1993; White *et al.* 1994). In one survey, only 4% of 219 species

of plants with white flowers included a substantial UV component in their reflectance (Chittka *et al.* 1994). The scarcity of white+UV flowers is again thought to be due to the poor contrast of such signals with soil and foliage backgrounds (Chittka *et al.* 1994; Kevan *et al.* 1996). Craig (1994*a*) suggested that there could be little selection for insects to associate stabilimenta with webs because insects had to use those same colour cues in discriminating flowers while foraging. However, it is clear that the achromatic spectra of stabilimenta are not similar to the spectra of flowers and that the ability of pollinating insects to learn to associate stabilimenta with spider webs will not be inhibited by counter-selection from the necessity of using colour cues in floral recognition. Instead, such learning in insects will be inhibited by the poor colour contrast of stabilimenta with the background, simply making the designs difficult for insects to detect.

4. CONCLUSION

Stabilimenta represent a compromise in visual signalling between advertising spider webs to predators and keeping webs cryptic to prey. The presence of stabilimenta in webs reduces the prey capture of *A. aurantia* (see table 1) and both *A. aurantia* and *A. trifasciata* reduce their investment in stabilimenta when starved (Blackledge 1998). Yet, stabilimenta also reduce the frequency of web destruction and predation by birds (Horton 1980; Eisner & Nowicki 1983; see table 1). Variation in the frequency with which stabilimenta are built by spiders results, in part, from trade-offs made between protection and foraging (Blackledge & Wenzel 1998). This conflict in signalling is greatly ameliorated by the spectral properties of stabilimentum silk. The white+UV reflectance spectrum of stabilimentum silk appears to be derived from bluer ancestral silks with a strong UV reflective peak (Craig *et al.* 1994). Although either spectrum would make stabilimenta contrast against environmental noise (soil and foliage) to vertebrate predators, only the relatively flattened spectrum of stabilimentum silk also results in a signal that is achromatic to insects and thus cryptic to the main prey of spiders. These observations suggest that conflicts in signal visibility and function between predators and prey of spiders have been important influences in the evolution of stabilimenta. They also demonstrate the importance that sensory drive can have in the evolution of defensive signals.

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