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Spider signals: are web decorations visible to birds and bees?

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We are becoming increasingly aware of animal communication outside the range of human sensitivity. Web decorations are silk structures used by orb-web spiders to deceive prey and predators. However, despite the level of interest in these structures, their visibility to prey and predators has never, to our knowledge, been objectively assessed. Here, we use spectrophotometric analyses to show that the decorations of all five tested spider species are visible to honey bees and birds over short and long distances. Furthermore, the discoid decorations of one species may provide some protection against arthropod predators. However, these decorations are inefficient at camouflaging the spider against birds, despite the overlap between the spider's body and web decoration.

Keywords: visual signals; chromatic contrast; achromatic contrast; stabilimenta; *Argiope*; *Zosis*

1. INTRODUCTION

The effect of signals on receivers is often difficult to interpret, especially if the signal is communicated outside human receptor sensitivities; for example, in ultraviolet channels (Bennett *et al.* 1994). Behavioural tests can infer that a receiver can detect a signal only if a response is measured. This can result in considerable controversy regarding whether a receiver detects a signal but ignores or simply cannot detect it. The century-old debate surrounding the visibility of web decorations (Herberstein *et al.* 2000) is a classic example of this. Here, for first time, to our knowledge, we unambiguously demonstrate the level of visibility of web decorations to different classes of receivers, using new technologies in measuring signals and by incorporating receiver physiology. Our data will focus and rejuvenate this field, influence future studies and possibly resolve some controversy.

Web decorations are silk structures included in the webs of many diurnal orb-web spiders. These structures have evolved nine times in three different families (Scharff & Coddington 1997) and occur in at least 78 species from 22 genera (Herberstein *et al.* 2000). Despite considerable interest and the frequency of decorating species, the function of these intriguing structures remains unresolved. While a visual function is most likely, studies on different species have generated contradictory results (Herberstein *et al.* 2000). Nevertheless, decorations are likely to be deceptive signals that either attract prey (e.g. Tso 1998; Bruce *et al.* 2001), provide protection through camouflage (e.g. Eberhard 2003) or act as a warning signal (e.g. Blackledge & Wenzel 1999). However, it is unclear if these signals are visible to potential prey and predators (Craig & Bernard 1990; Blackledge & Wenzel 2000).

We used spectrophotometric analyses to investigate the visibility of decorations from five spider species (figure 1) to both hymenopterans (*Apis mellifera*) and passerines (*Parus caeruleus*). These animals are potential prey (bees) and predators (birds) that have co-evolved with the cosmopolitan genus *Argiope*. The spider species chosen represent two families (Araneidae and Uloboridae), with separate evolutionary origins of decorations (Scharff & Coddington 1997). The four *Argiope* species construct three decoration patterns (cruciate, linear and discoid), allowing us to compare reflectance to decoration form. The uloborid, *Zosis geniculatus* constructs an irregular mat (figure 1*d*). We also measured the reflectance of a common green foliage background (*Lomandra longifolia*) to calculate both the chromatic (colour) and the achromatic contrast (brightness) between the decorations and the background. Generally, colour contrast is used for short-range detection, whereas brightness contrast is used for long-range detection (Giurfa *et al.* 1997). Furthermore, as decorations may camouflage the spider's body we measured the reflectance of the abdomen of *A. mascordi* (figure 1*c*) and calculated the chromatic and achromatic contrast between the spider and the decorations.

2. MATERIAL AND METHODS

(a) *Specimen collection and storage*

We collected four species of spider from the genus *Argiope* (Araneidae); *A. aetherea* and *A. picta* from the east coast of Queensland, *A. mascordi* from Cania Gorge, Queensland, and *A. keyserlingi* from Sydney and Brisbane. We also collected one uloborid species, *Z. geniculatus*, from Brisbane. The spiders were transported to the laboratory and housed in individual Perspex frames ($50\times50\times10$ cm^3), where they constructed orb-webs. The spiders were maintained on a diet of blowflies (*Lucilia cuprina*), crickets (*Acheta domestica*) and fruitflies (*Drosophila melanogaster*) and periodically sprayed with water. As *Argiope* are commonly found in *L. longifolia* plants we used this as the background for our measurements. *Lomandra longifolia* was collected from the grounds of Macquarie University, Sydney.

(b) *Measurement of reflectance*

Freshly constructed web decorations were collected from 6 to 11 different adult female spiders per species. We measured each decoration six times against a black felt background. Webs were collected once only from each individual spider. Measurements were taken from 10 individual *L. longifolia* plants immediately after collection, and each sample was measured five times. The abdomen of *A. mascordi* was measured for nine different individuals. Each individual was measured six times, sampling the diversity of colour patterns on the abdomen. The reflectance was measured using an Ocean Optics USB2000 spectrophotometer (Ocean Optics Incorporated, Dunedin, Florida, USA) equipped with a PX-2 pulsed xenon light source. Measurements were taken at an angle of 45°. The spectrophotometer was connected to a PC running Ocean Optics ODIBase 32 v. 1.0.2.0 software with the integration time set at 7 msec and each measurement was averaged 10 times by the software. This configuration was chosen because it is sensitive in the biologically relevant range of 300–700 nm.

(c) *Data analyses*

An average proportion of light reflected at each 5 nm interval was calculated for each individual web, foliage or body measurement.

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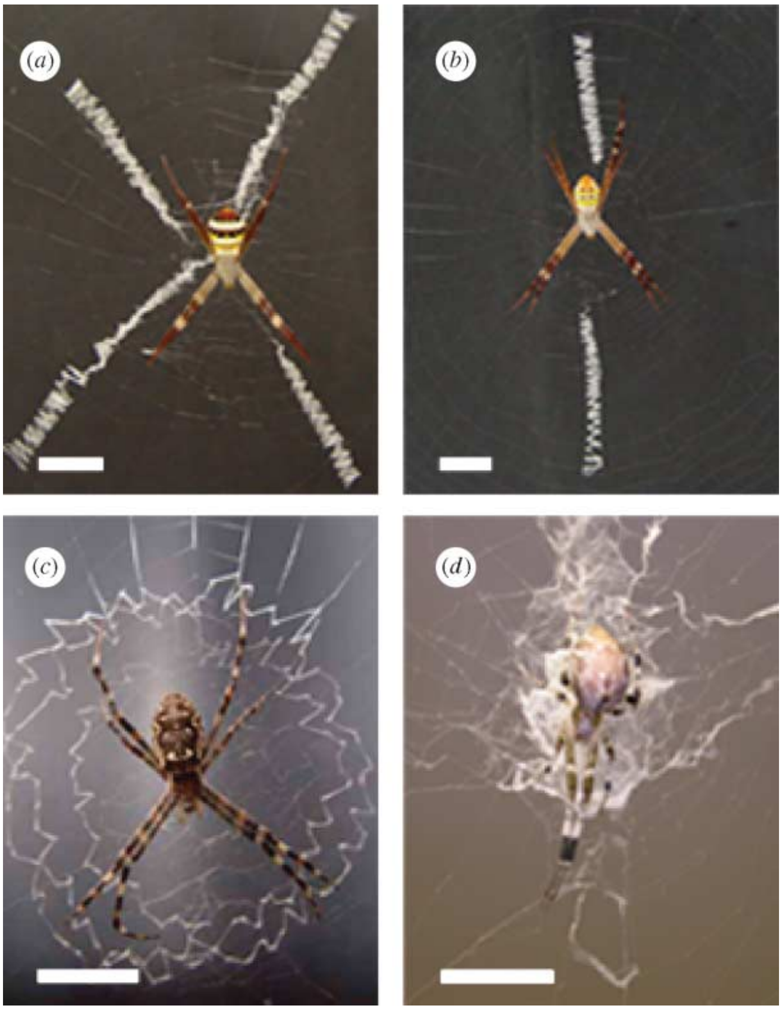

Figure 1. (*a*) *A. aetherea* with cruciate decoration (also built by *A. keyserlingi*). (*b*) *A. picta* with linear decoration. (*c*) *A. mascordi* with discoid decoration. (*d*) *Zosis geniculatus* with irregular mat decoration. The scale bars are 1 cm.

Table 1. Summary of one-sample *t*-tests of chromatic and achromatic contrasts of web decorations against *L. longifolia* and the abdomen of *A. mascordi* against its decorations.
(*Indicates the contrast was significantly above (contrast) the detection threshold ($p<0.001$). **Indicates the contrast was marginally significantly ($p=0.01$–0.05) above the detection threshold.)

comparison	honey bee		blue tit	
	chromatic contrast	achromatic contrast	chromatic contrast	achromatic contrast
Argiope versus *L. longifolia*	$t_{36}=29.1^{*}$	$t_{36}=21.2^{*}$	$t_{36}=18.6^{*}$	$t_{36}=21.7^{*}$
Z. geniculatus versus *L. longifolia*	$t_{9}=30.3^{*}$	$t_{9}=13.1^{*}$	$t_{9}=14.2^{*}$	$t_{9}=13.6^{*}$
A. mascordi body versus decoration	$t_{9}=2.31^{**}$	$t_{9}=3.03^{**}$	$t_{9}=7.53^{*}$	$t_{9}=5.68^{*}$

The mean of these measurements was calculated across all measurements for that individual to obtain an average. We used these average proportions to calculate the receptor excitation values for the three (UV, blue and green) *A. mellifera* (Chittka 1996) receptors and the four (UV, blue, green and red) *P. caeruleus* (Hart *et al.* 2000) receptors for the web decorations, green foliage and spider abdomen (*A. mascordi*). The equations incorporate the specific receptor sensitivities and the D65 daylight standard along with the measured reflectance proportions for each sample. These calculations generate the potential proportion of maximum excitation for each of the receptors. From this, the chromatic colour contrast and achromatic contrast were calculated using the equations described in Théry *et al.* (2005). Chromatic contrast is the sensitivity of all receptor types of the background (*L. longifolia* or web decorations) subtracted from the sample (web decorations or spider abdomen). The achromatic contrast is calculated by dividing the excitation value of the green receptor (bees) or the double cone receptor (birds) of the sample with that of the background. In this case, a value of one would represent no achromatic contrast.

We used the statistics software SPSS v. 11.0 for data analyses. The chromatic contrasts were compared with the detection thresholds for both *A. mellifera* (0.05; Théry *et al.* 2005) and *P. caeruleus* (0.06; Théry *et al.* 2005) using one-sample *t*-tests ($\alpha=0.05$). Achromatic contrasts were compared with unity (no contrast) via the same statistical procedure.

3. RESULTS

The visible contrast (chromatic and achromatic) created by decorations against their background was similar between the four *Argiope* species measured. Therefore, we pooled the values for *Argiope* in subsequent analyses. Our data suggest that honeybees and birds are able to see decorations of both spider families over short distances as the chromatic contrast was significantly greater than the threshold values of 0.05 and 0.06, respectively (Théry *et al.* 2005; figure 2*a*; table 1). Furthermore, decorations built by *Argiope* and *Zosis* are detectably brighter than the *L. longifolia* background for both honeybees and blue tits, suggesting that honeybees and birds can see them over long distances (figure 2*b*; table 1).

We also investigated whether discoid decorations camouflage spiders as, in this type of decoration, almost the entire spider overlaps with the decoration (figure 1*c*). The chromatic contrast of the body of *A. mascordi* against its decorations was marginally significantly above ($p=0.046$) the detection threshold of honeybees, suggesting that they may obscure the spider over short distances (figure 2*a*; table 1). However, the chromatic contrast was highly significantly above the detection threshold for blue tits, suggesting inefficient camouflage of the spider at short distances (figure 2*a*; table 1). Furthermore, the body of *A. mascordi* was significantly brighter than their decorations for honeybees and blue tits (figure 2*b*; table 1), implying inefficient camouflage over long distances.

4. DISCUSSION

Web decorations form a strong chromatic and achromatic contrast against their natural background, which makes them detectable over short and long distances to both honeybees and birds. Interestingly, these patterns are consistent even though we sampled web decorations from two different families with independent points of evolution (Scharff & Coddington 1997).

Even though our data unambiguously demonstrate the visibility of web decorations to invertebrate and vertebrate models, the responses of receivers may be variable. For example, insect prey may be attracted to the chromatic contrast of the signal, especially its UV component (Craig & Bernard 1990). Alternatively, prey may detect the presence of the web via the visible web decorations and avoid capture (Blackledge & Wenzel 1999). Moreover, birds may detect and avoid webs that contain web decorations, reducing web damage to the spider, while birds that feed on spiders may actually locate their prey via web decorations. Indeed, arthropod predators of *Argiope*, such as praying mantids and jumping spiders, approach decorated webs more frequently than undecorated webs (Bruce *et al.* 2001; Seah & Li 2001).

The camouflaging properties of web decorations against the colour of the spider have long been speculated on (Eberhard 1973, 2003), and this is the first study, to our knowledge, to assess this spectrally. We found that decorations would provide inefficient camouflage for spiders against birds over both short and long distances. However, there was only a marginal chromatic contrast between *A. mascordi* and its decorations for honeybees. It is possible that the discoid decorations of this species provide some protection against arthropod predators with similar visual systems to honeybees. Furthermore, it is still unclear how cruciate or linear decorations could function to obscure the spider, as there is only minimal overlap between decoration and spider body (figure 1*a*,*b*).

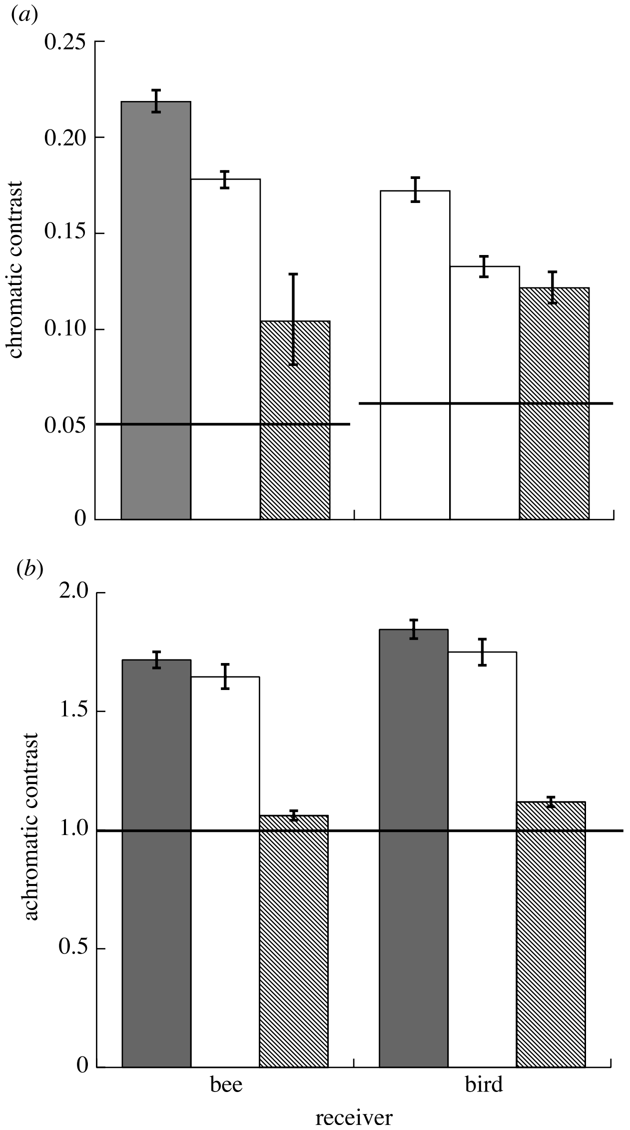

Figure 2. (*a*) The mean (± s.e.) chromatic contrast of *Argiope* (grey bars; $n=37$) and *Z. geniculatus* (white bars; $n=10$) decorations against a green foliage background ($n=10$) and the chromatic contrast of the body of *A. mascordi* (hatched bars; $n=10$) against its discoid decorations ($n=6$). The black lines represent the minimum detection threshold for honeybees (0.05) and blue tits (0.06). (*b*) The mean (± s.e.) achromatic contrast *of Argiope* (grey bars) and *Z. geniculatus* (white bars) decorations against a green foliage background and the achromatic contrast of the body of *A. mascordi* (hatched bars) against its discoid decorations. The black line represents the point of equal brightness (1.00).

The contrast of web decorations is consistent between families and different decoration patterns, raising the exciting possibility that their shape rather than spectral properties might explain variation in receiver response. From an evolutionary perspective it may be easier for spiders to change behaviour (how silk is laid on the web) rather than the physical properties of silk, which serves multiple functions (Vollrath 1999), to adapt to different prey and predator assemblages and environmental conditions.

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