Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web

SEAN J. BLAMIRES*, DIETER F. HOCHULI and MICHAEL B. THOMPSON

Heydon-Laurence Building A08, School of Biological Science and Institute of Wildlife Research, University of Sydney, NSW 2006, Australia

An effective visual signal elicits a strong receiver response. The visual receptors of most insects are sensitive to ultraviolet (UV), blue and green light. The decorations of certain orb web spiders may be described as a type of visual signal, a sensory trap, as they exploit visual biases in insects. We filtered UV and blue light from the decorations of *Argiope keyserlingi*, under field conditions, using plastic sheets to test if the UV and blue light reflected affects the type of prey caught. We found that houseflies, blowflies, stingless bees, honeybees and vespid wasps were caught more frequently in webs with decorations than webs without, while ichneumonid wasps were caught less frequently. Blowflies, stingless bees, honeybees and vespid wasps were caught more often in unfiltered decorated webs. These insects also have receptor sensitivities in the blue and UV. We showed that exploiting visual sensory biases plays an integral role in attracting insects to orb web decorations. Whether UV light, blue light, or both, are the most important cue, however, requires further study. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **94**, 221–229.

ADDITIONAL KEYWORDS: animal signals – blue light – decorations – insect vision – orb web spider – prey capture success – sensory trap – ultraviolet light.

INTRODUCTION

To be effective, a signal must elicit an appropriate response by the receiver. A signal therefore must: (1) stimulate the receiver's sensory detectors (Endler, 1990; Rowe, 1999); (2) offer, or appear to offer, something meaningful, for example food, to the receiver (Guilford & Dawkins, 1991); and (3) be distinguishable from background noise (Endler, 1992; Vorobyev & Osorio, 1998; Rowe, 1999). Sensory exploitation is when a signaller exploits some pre-existing sensory response in the receiver to achieve its own ends (Sakaluk, 2000; Maynard Smith & Harper, 2003). A sensory trap is a deceitful form of sensory exploitation (Christy, 1995). A deceptive signal is costly to use

frequently, as selection pressure on signal identification by the receiver is strong (Wiley, 1994; Viljugrein, 1997). Effective sensory traps therefore exploit sensory cues that the receiver is highly sensitive to, or reliant upon.

Visual signals must contrast with the background and be attuned to the visual acuity of the intended receiver (Endler, 1992). Flowers attract honeybees, for example, by reflecting light most strongly in the ultraviolet (UV; ~340 nm), blue (~430 nm) or green (~540 nm) – the wavelengths at which honeybee visual receptors are maximally sensitive (Briscoe & Chittka, 2001) against a grey background (Backhaus, Werner & Menzel, 1987; Chittka *et al.*, 1994; Spaethe, Tautz & Chittka, 2001). Merely contrasting against the background is not enough to provoke the receiver to respond. The signal must be identified by the receiver as an object to which a response is desirable (Goldsmith & Bernard, 1974;

*Corresponding author. E-mail: sbla3978@mail.usyd.edu.au

Endler, 1990). The signal reflectance function provides information about the amount of light reflected from a signal over the visible spectrum (Chittka *et al.*, 1994; Heiling, Cheng & Herberstein, 2004; Heiling *et al.* 2005). How a signal is interpreted by the receiver may be determined from receptor excitation (*E*) values, which can be calculated upon determining the background reflectance, the sensitivity function of the receptor(s) under investigation, the standard daylight reflectance and the signal reflectance (Chittka *et al.*, 1994; Thery *et al.*, 2005). Maximum sensitivity (λ_{max}) values of many insects have been calculated (Briscoe & Chittka, 2001), but, at present, the only insect group for which there are sufficient data across the visible spectrum to confidently calculate *E*-values for is the bees (Apidae). However, bee visual sensitivity curves are considered typical of insects with trichromatic vision, so may be reliably assumed to represent other insect groups (Menzel *et al.*, 1986; Peitsch *et al.*, 1992).

Many orb web spiders, particularly those of the genus *Argiope*, add conspicuous silk decorations, sometimes called stabilimenta, to their webs (Herberstein *et al.*, 2000a; Bruce, 2006). Decoration silks differ spectrally from other orb web silks, apart from the capture silks of Uloborids (Kohler & Vollrath, 1995), by reflecting light in the UV (300–400 nm) (Craig, Bernard & Coddington, 1994; Herberstein *et al.*, 2000a; Bruce, Heiling & Herberstein, 2005). The functional significance of the decorations has been a contentious issue for some time (Herberstein *et al.*, 2000a; Bruce, 2006). Initial experiments relied on observations in the field and an array of possible functions; for example, advertising the web to birds, web stabilization, camouflage and prey attraction (i.e. acting as a sensory trap) were implied (Eisner & Nowicki, 1983; Craig & Bernard, 1990; Schoener & Spiller, 1992; Tso, 1996; Blackledge, 1998; Tso, 1998). There is much experimental evidence supporting a prey attraction function (Herberstein *et al.*, 2000a; Bruce, 2006); for example, removing decorations from orb webs reduces prey capture success, while transplanting decorations onto spectrally neutral insect traps increases prey capture success (Craig & Bernard, 1990; Tso, 1998; Bruce, Herberstein & Elgar, 2001). Laboratory studies assessing the influence of decorations on fitness attributes of individual spiders have strongly supported the prey attraction hypothesis (Herberstein, Craig & Elgar, 2000b; Craig *et al.*, 2001; Li, 2005). Studies exposing prey, usually *Drosophila* spp., to decorations with and without UV filtered from an artificial light source (Watanabe, 1999; Li *et al.*, 2004), and models of decoration visibility (Bruce *et al.*, 2005), have implicated UV reflection as a mechanism for attracting insects. However, because of the difficulty involved in manipulating light in the field, verification using field studies that examine the influence of the decorations on a wide range of prey are lacking, (Young, David & Gibson, 1987; Church *et al.*, 1998; Heiling *et al.*, 2005).

We performed a series of field experiments in which we removed decorations and altered the light being reflected from decorations of the orb spider *Argiope keyserlingi*, to assess which taxa of insects are influenced (i.e. caught either more or less often) by the addition of decorations in webs. We then assessed how the natural light reflected by the decorations serves as a signal to attract, or deter, these insects. We predicted that insects with UV sensitivities would be caught less frequently when webs had UV filtered from their decorations, which would support the hypothesis that decorations attract certain prey via UV reflectance.

MATERIAL AND METHODS
DECORATION REMOVAL EXPERIMENT

We collected approximately 200 spiders from the gardens of the University of Sydney and placed them in perspex enclosures ($0.5 \times 0.5 \times 0.15$ m) with front and back removable lids. We placed two blowflies (*Musca domestica*) in each enclosure and gave the spiders 5 days to build an orb web. Twelve spiders with webs containing no decorations and 24 with fully cruciform decorations (i.e. containing four arms) were removed from their webs. When too few webs with cruciform decorations were encountered after 5 days, the spiders were changed. The new spiders were fed and given 3 days to build a web. In half of the webs with decorations, the decorations were removed using forceps. Because some damage occurred to the spiral threads onto which the decorations were attached during their removal, all spiral threads within 3 mm of the hub were plucked to control for damage, taking caution not to damage any radial threads, in both webs with decorations intact and webs without decorations. We calculated web capture area of each web using the formula of Blackledge & Gillespie (2002):

$$\text{Area} = (d_v/2)(d_h/2)\pi - (H/2)^2\pi \quad (1)$$

where d_v equals the height of the capture area, d_h equals the diameter of the capture area and H equals the vertical diameter of the web. We ensured that average spiral distances (measured according to Kohler & Vollrath, 1995) did not vary significantly between treatments by using a Wilcoxon two-sample *T*-test ($T = 159.0$, $P = 0.70$).

Enclosures containing webs ($N = 36$; 12 with decorations, 12 without decorations and 12 with decora-

tions removed) had their lids removed and were placed on 60-mm wooden blocks within sedge (a preferred habitat of *A. keyserlingi*; Blamires, Hochuli & Thompson, 2007) in the University of Sydney gardens at approximately 09.30 h. To account for possible local differences in insect abundance, influences of wind and angle of incident solar radiation on the ability of orb webs to catch insects (Nentwig & Heimer, 1987), two randomly chosen locations ($N = 6$; three facing east–west and six north–south, per treatment per location) were used. Webs were checked hourly and all prey entangled were removed. The few ($N = 3$) webs that sustained wind-induced damage were removed from the area and not used in subsequent analyses. After 6 h, all webs were returned to the laboratory. We did not leave the webs out at night, as *A. keyserlingi* is diurnal and dismantles its web at sunset, thus any insects caught at night are not likely to represent potential prey. Insects caught in each web were counted, identified to the lowest possible comparable taxonomic rank (family in this instance) using appropriate keys (Naumann, 1994) and had their body length (head and cephalothorax) measured to the nearest millimetre. The experiment was repeated four times, each time using different spiders ($N = 144$ spiders in total).
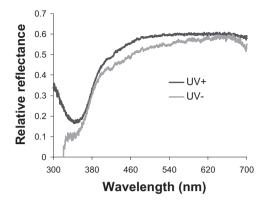
UV FILTRATION EXPERIMENT

Another ~200 spiders were collected and induced to build orb webs as described above. Spiders were removed from 24 webs containing no decoration and 24 with fully cruciform decorations. Twelve webs with and without decorations were placed between two 0.3×0.21-m transparent plastic sheets, which acted as an absorption filter (Wyszecki & Stiles, 1982), the other 12 decorated and undecorated webs were left in their perspex frames. All plastic sheets were covered, except for a 5-mm radius about the hub (to ensure no interference with light illuminating from decorations) with a sticky, transparent resin (Tanglefoot; Tanglefoot Co., Grand Rapids, MI, USA) using a paint brush. Comparable studies (e.g. Tso, 1998) have used transparent Tanglefoot traps as a web surrogate for sampling the naturally occurring prey of orb web spiders. Additionally, we found that sampling prey by this means is useful for predicting orb web architecture (Blamires *et al.*, 2007). The traps however, have different spectral, mechanical and adhesive properties than spider webs (Shelley, 1984). We thus controlled for this by first comparing the insects captured in normal webs (hereon called unfiltered webs) and webs enclosed within a filter (hereon called filtered webs) that were undecorated. Any insect groups caught in different amounts were assumed to be sensitive to the spectral, mechanical and/or adhesive differences

between the unfiltered and filtered webs without decorations and, thus, were not used for comparisons between decorated 'webs'. This procedure also accounted for any insects that may be in different abundance during each experiment.

All 'webs' were placed in exposed (i.e. unshaded) locations, among sedge in either of two sites ($n = 6$ of each treatment at each site) within the University of Sydney gardens. Each sheet was attached from above and below (to keep them taught) to string, which was tied to wooden stakes so as to face either east–west or north–south ($n = 3$ per treatment per site in each direction), using Bulldog clips, which also acted to keep the webs enclosed between the sheets. At the same time, six unfiltered webs; three facing either east–west or north–south, were placed at each site. Both the unfiltered and filtered webs were put out at ~09.00–09.30 h and collected at ~15.00–15.30 h. Insects caught in both the unfiltered and filtered webs were removed using forceps. Those found on filtered webs were soaked in turpentine overnight to dissolve the Tanglefoot. All insects were counted, identified to the lowest possible taxonomic rank and measured to the nearest millimetre. The experiment was repeated four times. All experiments were conducted successively in October–November 2004.

STATISTICAL ANALYSES

The influence of the presence or absence of web decorations on the number of individuals captured in the decoration removal experiment was determined across the identifiable insect groups by a one-factor (decorations: present, absent or removed) multiple analysis of variance (MANCOVA; web area the covariate). We used a one-factor (webs: unfiltered vs. filtered) MANCOVA to compare the capture rates of all identifiable insects in undecorated webs in the UV filtration experiment. Two-factor (decorations: present/absent and webs: unfiltered/filtered) MANCOVAs were carried out to compare the capture rates of the insect groups – excluding any groups that were caught in different frequencies in the unfiltered and filtered undecorated webs. Bartlett's tests and Kolmogorov–Smirnov tests were used to test for homogeneity of variances and normality of distributions, respectively. Logarithmic data transformations were performed, as means and variances were positively correlated (Green, 1979), where the data failed either test. Parallelism tests were carried out to check the homogeneity of slopes. Tukey's Honestly Significant Difference (HSD) analyses were used to determine the influential factors when significant differences were found.

To determine if the insects were likely to perceive a colour difference between unfiltered and filtered webs,

Figure 1. Reflectance functions for filtered and unfiltered decorations. The mean ($N = 10$) relative reflectance was calculated every 5 nm, over the 300 nm to 700 nm spectra.

we calculated *E*-values for bee UV, blue and green photoreceptors when exposed to either unfiltered or filtered decorations from the equations (Chittka *et al.*, 1994):

$$R = 1 \Big/ \int_{300}^{700} I_B(\lambda) S(\lambda) D(\lambda) \, d\lambda \qquad (2)$$

$$P = R \int_{300}^{700} I_S(\lambda) S(\lambda) D(\lambda) \, d\lambda \qquad (3)$$

and

$$E = P/(P + 1) \qquad (4)$$

where R is an arbitrary measure called the 'sensitivity factor' of the receptor under investigation, P is an arbitrary measure called the 'quantum flux' of the receptor, $I_B(\lambda)$ is the reflectance function of the background, $S(\lambda)$ is the sensitivity function of the receptor under investigation, $D(\lambda)$ is the daylight standard (CIE illumination function D65) irradiance function and $I_S(\lambda)$ is the signal reflectance function. We assumed that (1) the areas that the webs were placed in were permanently devoid of shade, (2) only green light is emitted from the background (Bruce *et al.*, 2005) and (3) the reflectance function of all insect receptors in UV, blue and green, is approximately represented by the receptor sensitivity function of bee UV, blue and green receptors (Peitsch *et al.*, 1992). We calculated quantum flux upon spectroradiometric analyses (using a USB 2000 spectroradiometer; Ocean Optics Inc., Dunedin, FL, USA) of 10 unfiltered and 10 filtered decorations. We calculated mean relative reflectance (a measure where 1.0 = maximum reflectance) every 5 nm across the 300–700 nm spectra to create reflectance functions for filtered and unfiltered decorations (Fig. 1), using OODBase 32 software (Oceans Optics Inc.) (Heiling *et al.*, 2004, 2005). We used a series of paired *t*-tests to test the

influence of unfiltered and filtered decorations on the excitation values of the bee UV, blue and green receptors.

RESULTS

DECORATION REMOVAL EXPERIMENT

The principal insect groups captured were dipterans (flies) and hymenopterans (bees and wasps). No beetle, bug, cricket or cockroach group was captured in adequate numbers for inclusion in analyses. The mean number of individuals of each insect group caught in each trap differed between treatments (one-factor MANCOVA, Wilk's $\lambda = 0.88$; d.f. = 2.23; $P < 0.001$), with decorated webs catching significantly more houseflies, blowflies, honeybees, stingless bees and vespid wasps, but fewer ichneumonid wasps. Webs with no decorations caught significantly more honeybees than webs that had decorations removed. The mean number of mosquitoes, dance flies, moth flies, small parasitic wasps and mud-dauber wasps caught per trap was not affected by decoration removal (Table 1).

UV FILTRATION EXPERIMENT

More mosquitoes, dance flies, moth flies, houseflies and small parasitic wasps and ichneumonid wasps were caught in unfiltered (i.e. webs alone) than filtered (i.e. webs within plastic sheets) webs without decorations. Accordingly, we did not compare their numbers caught in unfiltered and filtered webs when decorations were present, as characteristics of the treatments may be attributable to differences in capture rate. The filters had a significant effect on the mean number of blowflies, stingless bees, honeybees and vespid wasps caught (two-factor MANCOVA, Wilk's $\lambda = 0.09$; d.f. = 1,23; $P < 0.0001$); all were caught in fewer numbers when decorations had light reflected from them filtered (Table 2).

We found a significant difference in the bee UV and blue receptor excitation values. The green receptor excitation values differed, but to an insignificant extent (Table 3). Thus, the filtered and unfiltered webs were likely to be interpreted differently by insects with UV- and blue-sensitive receptors.

DISCUSSION

We found that removing decorations reduced the number of dipterans and hymenopterans caught in webs of the orb spider *A. keyserlingi*. When we added a filter, thus altering the visibility of the decorations by reducing the UV and blue receptor responses of the insects, fewer blowflies, honeybees, stingless bees and

Table 1. Mean number of positively identified insects caught per web per day in webs without decorations (No decorations), with decorations (Decorations) and with the decorations removed ($N = 12$ for each treatment) and the results of a MANCOVA (d.f. = 1,23) and Tukey's HSD test

Order	No decorations	Decorations	Decorations removed	Statistics	
				F	*P*
Diptera					
Mosquitoes (Culicidae)	0.57 (0.07)	0.63 (0.03)	0.58 (0.07)	0.94	0.29
Dance flies (Empididae)	0.49 (0.07)	0.41 (0.07)	0.52 (0.06)	0.43	0.50
Moth flies (Psychodidae)	0.43 (0.12)	0.44 (0.05)	0.59 (0.18)	1.56	0.09
Houseflies (Muscidae)	0.78 (0.12)	1.43 (0.09)*	0.79 (0.09)	11.35	< 0.001
Blowflies (Calliphoridae)	0.88 (0.14)	1.44 (0.08)*	0.83 (0.09)	20.03	< 0.0001
Hymenoptera					
Small parasitic wasps	0.69 (0.03)	0.53 (0.02)	0.59 (0.04)	1.20	0.27
Honeybees	1.03 (0.05)*	1.37 (0.09)*	0.79 (0.09)*	23.34	< 0.0001
Stingless bees	1.07 (0.13)	2.11 (0.22)*	0.93 (0.17)	35.19	< 0.0001
Ichneumonid wasps	1.25 (0.03)	0.39 (0.01)*	1.20 (0.11)	100.09	< 0.0001
Vespid wasps	0.24 (0.01)	0.54 (0.02)	0.22 (0.04)	11.61	< 0.0001
Mud-dauber wasps (Sphecidae)	0.44 (0.04)	0.34 (0.13)	0.49 (0.08)	1.08	0.19

Standard errors (SE) shown in parenthesis.

*Indicates the treatment that significantly differed ($P < 0.05$).

vespid wasps were caught, demonstrating that the insects caught in webs with decorations depends largely on the spectral properties of the decorations.

As honeybees, stingless bees, vespid wasps and blowflies have visual receptors with peak sensitivities in the UV and show phototaxis and/or negative geotaxis toward UV light (Rudiger, Steiner & Gemperlein, 1986; Briscoe & Chittka, 2001), UV reflecting *A. keyserlingi* decorations may be exploiting a pre-existing visual bias in these insects and, hence, may be regarded a sensory trap. Similar responses to web decorations may be expected in other insects, e.g. dragonflies, beetles (e.g. *Carabus* spp.), some other dipterans (e.g. *Bibius* spp.) and most Hymenoptera, which have similar peak sensitivities in the UV or are attracted to, or naturally move toward, UV light (Briscoe & Chittka, 2001).

Despite small parasitic wasps and sphecid wasps having sensitivities to UV light (Briscoe & Chittka, 2001), the presence of web decorations had no effect on their capture rates. Some sphecid flies lack UV receptors (Briscoe & Chittka, 2001), so it may be possible that sphecid wasps also lack UV receptors, explaining why the presence of UV reflecting decorations had no affect on their capture rate. Intracellular recordings have, however, failed to find UV and blue receptors in ichneumonid wasps (Briscoe & Chittka, 2001). We found that the capture rates of ichneumonid wasps were negatively affected by filtering UV and blue light from the decorations, alluding to the possibility that certain insects may be attracted to orb

web decorations using cues other than UV or blue light (Chittka, 1996). Even though ichneumonid wasps have green sensitive receptors (Briscoe & Chittka, 2001), it is unlikely that green light is an attractant in *A. keyserlingi* web decorations as green light contrasts poorly with the predominantly green background (see Bruce *et al.*, 2005). Because the differences in the calculated receptor excitation values in the green for filtered and unfiltered webs neared significance ($P = 0.052$), it is possible that the intensity of the green light reflected from the decorations with and without filters was perceived differently by green-sensitive insects. Ichneumonids, alternatively, may detect visual signals by different means, perhaps based on prior experiences (Chittka, Ing & Raine, 2004), than bees.

Most insect receptors are sensitive to both blue and UV light (Menzel, 1979; Menzel *et al.*, 1986; Briscoe & Chittka, 2001). While the influence of UV over insect behaviour has received a lot of attention, many insects show marked behavioural responses to blue stimuli (Backhaus *et al.*, 1987; Fukushi, 1989). Blue light, thus, may be a prey-attracting stimulus in web decorations that has gone largely ignored. The reflectance functions (Fig. 1) show that the unfiltered decorations are brighter in the blue than the filtered decorations and we, additionally, found that the insect blue receptors received greater stimulation (Table 3) from unfiltered decorations. Blue light illuminating from the decorations of filtered webs was, thus, less visible to dipteran and hymenopteran insects than

Table 2. Mean number of positively identified dipteran (Diptera) and hymenopteran (Hymenoptera) insects caught per web per day for: (1) unfiltered webs (webs themselves) and filtered (webs placed between plastic sheets and coated, except around the hub, with Tanglefoot) and without decorations (No decorations) and (2) unfiltered and filtered webs with decorations (Decorations)

	No decorations				Decorations			
	Unfiltered webs	Filtered webs	F	P	Unfiltered webs	Filtered webs	$F_{2,22}$	P
Diptera								
Mosquitoes (Culicidae)	0.27 (0.02)	0.52 (0.07)	6.89	0.02	–	–	–	–
Dance flies (Empipidae)	0.18 (0.06)	0.47 (0.06)	9.34	<0.001	–	–	–	–
Moth flies (Psychodidae)	0.19 (0.04)	0.53 (0.08)	9.98	<0.001	–	–	–	–
Houseflies (Muscidae)	0.34 (0.04)	0.78 (0.11)	8.23	0.004	–	–	–	–
Blowflies (2Calliphoridae)	0.50 (0.01)	0.50 (0.01)	0.12	>0.05	0.75 (0.10)	0.15 (0.01)	45.33	<0.0001 (S)
Hymenoptera								
Small parasitic wasps	0.17 (0.01)	0.69 (0.02)	21.20	<0.0001	–	–	–	–
Honeybees	0.77 (0.13)	0.67 (0.08)	0.12	>0.05	1.20 (0.08)	0.51 (0.01)	64.76	<0.0001 (S)
Stingless bees	1.01 (0.04)	0.89 (0.04)	0.59	>0.05	0.88 (0.04)	0.26 (0.12)	99.15	<0.0001 (S)
Ichneumonid wasps	1.03 (0.04)	0.75 (0.01)	13.76	<0.0001	–	–	–	–
Vespid wasps	0.14 (0.01)	0.20 (0.09)	1.41	>0.05	0.42 (0.03)	0.06 (0.01)	105.30	<0.0001
Mud-dauber wasps (Sphecidae)	0.35 (0.03)	0.62 (0.01)	6.08	0.01	–	–	–	–

Standard errors (SE) shown in parenthesis.

$N = 12$ for each treatment, found using MANCOVA ($P < 0.05$; d.f. = 1,23) and Tukey's HSD tests. To eliminate the possibility that differences in the physical or spectral properties of the two trap types caused the differences in insects caught, no analyses were carried out (indicated by –) between unfiltered and filtered decorated webs when a significant difference was found between unfiltered and filtered undecorated webs.

Table 3. A comparison of bee visual receptor excitation values (E-values) for *Argiope keyserlingi* unfiltered and filtered decorations, where E_{UV} equals receptor excitation values of bee UV receptors, E_{BLUE} equals receptor excitation values of bee blue receptors and E_{GREEN} equals receptor excitation values of bee green receptors

	Unfiltered webs	Filtered webs	T_{56}	P
E_{UV}	0.808 ± 0.017	0.682 ± 0.005	28.12	< 0.0001
E_{BLUE}	0.528 ± 0.008	0.498 ± 0.010	20.34	< 0.001
E_{GREEN}	0.591 ± 0.001	0.576 ± 0.010	1.61	0.052

The results show that bee UV and blue receptors are more excited by unfiltered decorations than filtered decorations and that bee green receptors are not excited significantly differently when exposed to either unfiltered or filtered decorations.

that illuminating from the decorations of unfiltered webs. Although it undoubtedly plays a role, we propose that the reflection of blue light from orb web decorations is less marked than UV as an insect attractant because (1) blue light reflected from decorations would be poorly contrasted against a green background, the background colour that *A. keyserlingi* decorations are generally contrasted against (Bruce *et al*., 2005) and (2) when sensitive to both UV and blue light, many insect receptors are more sensitive (up to 16 times; Srinivasan & Lehrer, 1985) to UV than blue. The shape of the decorations is probably not a cue that attracts insects, as when orb spiders build decorations of different shape insects are attracted similarly (Craig & Bernard, 1990; Tso, 1996, 1998; Seah & Li, 2002). The cues deterring ichneumonid wasps or why sphecid and small parasitic wasps are unresponsive to *A. keyserlingi* decorations remains unresolved, but it indicates that they are likely to have different spectral sensitivities than bees (Briscoe & Chittka, 2001). Their responses to decorations, however, are not likely to be influential on prey capture success in *A. keyserlingi*, because they are either too small to be a major component of the diet or are avoided because they are potential predators.

Our study verified, under natural conditions, laboratory studies (Watanabe, 1999; Li *et al*., 2004) showing that orb web spider decorations function as a prey attractant, most likely by reflecting UV light. We manipulated the light reflected from webs in both the UV and blue and it remains unresolved which colour is more influential in acting as a cue for insects. We suspect that UV is more important, but further experimentation, perhaps using a non-toxic method of selectively filtering UV or blue light without emitting undue odour (Heiling *et al*., 2004, 2005) or altering the physical or chemical properties of the web, is required for confirmation. Nonetheless, our experiments suggest orb web decorations exploit a highly sensitive pre-existing visual bias in insects and, accordingly, orb web decorations may be regarded as

an effective, evolutionarily stable, deceptive signal (Viljugrein, 1997), or sensory trap.

REFERENCES

Backhaus W, Werner A, Menzel R. 1987. Color vision in honeybees: metric dimensions, constancy and ecological aspects. In: Menzel R, Mercer A, eds. *Neurobiology and behavior of honeybees*. Berlin: Springer-Verlag, 172–190.

Blackledge TA. 1998. Signal conflict in spider webs driven by predators and prey. *Proceedings of the Royal Society of London B* **265:** 1991–1996.

Blackledge TA, Gillespie RG. 2002. Estimation of capture areas of spider orb webs in relation to asymmetry. *Journal of Arachnology* **30:** 70–77.

Blamires SJ, Hochuli DF, Thompson MB. 2007. Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecology* **32:** 551–563.

Briscoe AD, Chittka L. 2001. The evolution of color vision in insects. *Annual Review of Entomology* **46:** 471–510.

Bruce MJ. 2006. Silk decorations: controversy and consensus. *Journal of Zoology* **269:** 89–97.

Bruce MJ, Heiling AM, Herberstein ME. 2005. Spider signals: are web decorations visible to birds and bees? *Biology Letters* **1:** 299–302.

Bruce MJ, Herberstein ME, Elgar MA. 2001. Signal conflict between prey and predator attraction. *Journal of Evolutionary Biology* **14:** 786–794.

Chittka L. 1996. Optimal sets of color receptors and color opponent systems for coding of natural objects in insect vision. *Journal of Theoretical Biology* **181:** 179–196.

Chittka L, Ing TC, Raine NE. 2004. Chance and adaptation in the evolution of island bumblebee behaviour. *Population Ecology* **46:** 243–251.

Chittka L, Shmida A, Troje N, Menzel R. 1994. Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Research* **34:** 1489–1508.

Christy JH. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist* **146:** 171–181.

Church SC, Bennett ATD, Cuthill IC, Partridge JC. 1998. Ultraviolet cues affect the foraging behaviour of blue tits. *Proceedings of the Royal Society of London B* **265:** 1509–1514.

Craig CL, Bernard GD. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71:** 616–623.

Craig CL, Bernard GD, Coddington JA. 1994. Evolutionary shifts in the spectral properties of spider silks. *Evolution* **48:** 287–296.

Craig CL, Wolf SG, Davis LD, Hauber ME, Maas JL. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. *Evolution* **55:** 986–993.

Eisner T, Nowicki S. 1983. Spider web protection through visual advertisement: role of the stabilimentum. *Science* **219:** 185–187.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* **41:** 315–352.

Endler JA. 1992. Signals, signal conditions and the direction of evolution. *American Naturalist* **139:** S125–S153.

Fukushi T. 1989. Learning and discrimination of coloured papers in the walking blowfly, *Lucilia cuprina. Journal of Comparative Physiology A* **166:** 57–64.

Goldsmith TH, Bernard GD. 1974. The visual system of insects. In: Rockstein M, ed. *The physiology of insecta*, Vol. II. New York: Academic Press, 165–272.

Green RH. 1979. *Sampling design and statistical methods for environmental biologists*. New York: John Wiley and Sons.

Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* **42:** 1–14.

Heiling AM, Cheng K, Chittka L, Herberstein ME. 2005. The role of UV in crab spider signals: effects of perception by prey and predators. *Journal of Experimental Biology* **208:** 3925–3931.

Heiling AM, Cheng K, Herberstein ME. 2004. Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behavioral Ecology* **15:** 321–326.

Herberstein ME, Craig CL, Coddington JA, Elgar MA. 2000a. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews* **75:** 649–669.

Herberstein ME, Craig CL, Elgar MA. 2000b. Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evolutionary Ecology Research* **2:** 69–80.

Kohler T, Vollrath F. 1995. Thread biomechanics in the two orb-weaving spiders *Araneus diadematus* (Araneae, Ara-neidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *Journal of Experimental Zoology* **271:** 1–17.

Li D. 2005. Spiders that decorate their webs at higher frequency intercept more prey and grow faster. *Proceeding of the Royal Society of London B* **272:** 1753–1757.

Li D, Lim MLM, Seah WK, Tay S. 2004. Prey attraction as a possible function of discoid stabilimenta of juvenile orb-spinning spiders. *Animal Behaviour* **68:** 629–635.

Maynard Smith J, Harper D. 2003. *Animal signals*. Oxford: Oxford University Press.

Menzel R. 1979. Spectral sensitivity and colour vision in invertebrates. In: Autrum H, ed. *Handbook of sensory physiology,* Vol. VII/6A. *Comparative physiology and evolution of vision in invertebrates a: invertebrate photoreceptors*. Berlin: Springer-Verlag, 504–580.

Menzel RD, Ventura F, Hertel H, de Souza JM. 1986. Spectral sensitivity of photoreceptors in insect compound eyes: comparison of species and methods. *Journal of Comparative Physiology A* **158:** 165–177.

Naumann ID. 1994. *Systematic and applied entomology: an introduction*. Melbourne: Melbourne University Press.

Nentwig W, Heimer S. 1987. Ecological aspects of spider webs. In: Nentwig W, ed. *Ecophysiology of spiders*. Berlin: Springer-Verlag, 211–215.

Peitsch DA, Fietz H, Hertel J, de Souza D, Ventura F, Menzel R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A* **170:** 23–40.

Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* **58:** 921–931.

Rudiger P, Steiner A, Gemperlein R. 1986. Spectral sensitivity of *Calliphora erythrocephala and* other insect species studies with Fourier Interferometric Stimulation (FIS). *Journal of Comparative Physiology A* **158:** 669–680.

Sakaluk SK. 2000. Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. *Proceedings of the Royal Society of London B* **267:** 339–343.

Schoener TW, Spiller DA. 1992. Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support for the predator-defense hypothesis. *Behavioral Ecology and Sociobiology* **31:** 309–318.

Seah WK, Li D. 2002. Stabilimentum variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. *Journal of Zoology (London)* **258:** 531–540.

Shelley TE. 1984. Prey selection by the neotropical spider *Micrathena schriebersi* with notes on web site tenacity. *Proceedings of the Entomological Society of Washington* **86:** 493–502.

Spaethe J, Tautz J, Chittka L. 2001. Visual constraints in foraging bumblebees: flower size and color affects search time and flight behavior. *Proceedings of the National Academy of Sciences of the USA* **98:** 3898–3903.

Srinivasan M, Lehrer M. 1985. Temporal resolution of colour vision in the honeybee. *Journal of Comparative Physiology A* **157:** 579–586.

Thery M, Debut M, Gomez D, Casas J. 2005. Specific color sensitivities of prey and predator explains camouflage in different visual systems. *Behavioral Ecology* **16:** 25–29.

Tso IM. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Animal Behaviour* **52:** 183–191.

Tso IM. 1998. Isolated spider web stabilimentum attracts insects. *Behaviour* **135:** 311–319.

Viljugrein H. 1997. The cost of dishonesty. *Proceedings of the Royal Society of London B* **264:** 815–821.

Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proceeding of the Royal Society of London B* **265:** 351–358.

Watanabe T. 1999. Prey attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. *Behavioural Ecology* **10:** 607–611.

Wiley RH. 1994. Errors, exaggeration and deception in animal communication. In: Real RA, ed. *Behavioural mechanisms in evolutionary ecology*. Chicago, IL: University of Chicago Press, 157–189.

Wyszecki G, Stiles WS. 1982. *Color science: concepts and methods, quantitative data and formulas*. New York: John Wiley and Sons.

Young S, David CT, Gibson G. 1987. Light measurement for entomology in the field and laboratory. *Physiological Entomology* **12:** 373–380.