Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae)

Alex A. Bush^{1,*}, Douglas W. Yu¹ and Marie E. Herberstein²

¹School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, UK

²Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

There are two major competing explanations for the counter-intuitive presence of bright coloration in certain orb-web spiders. Bright coloration could lure insect prey to the web vicinity, increasing the spider's foraging success. Alternatively, the markings could function as disruptive camouflage, making it difficult for the insect prey to distinguish spiders from background colour variation. We measured the prey capture rates of wasp spiders, *Argiope bruennichi*, that were blacked out, shielded from view using a leaf fragment, or left naturally coloured. Naturally coloured spiders caught over twice the number of prey as did either blacked-out or leaf-shielded spiders, and almost three times as many orthopteran prey. Spectrophotometer measurements suggest that the bright yellow bands on the spider's abdomen are visible to insect prey, but not the banding on the legs, which could disguise the spider's outline. Thus, our results provide strong support for the hypothesis that bright coloration in the wasp spider acts as a visual lure for insect prey and weak support for the hypothesis that the arrangement of the banding pattern across the spider's body disguises the presence of the spider on the web.

Keywords: *Argiope bruennichi*; aggressive mimicry; sensory trap; foraging success; Orthoptera; silk decoration

1. INTRODUCTION

The avoidance of recognition by potential prey is vital to the hunting success of sit-and-wait predators such as orb-web spiders (Craig 1986). Nevertheless, many diurnal orb-web spiders not only rest at the web hub but also seem to advertise their presence with bright body coloration (Oxford & Gillespie 1998). For example, among females of the genus *Argiope*, yellow and white stripes, bands and spots are common (Levi 1983). Any potential benefit to females of using visual signals to attract males would appear to be outweighed by the cost of a lower prey capture rate, particularly as male *Argiope* locate females using long-range and contact pheromones (Gaskett 2007). There is also a potential cost to spiders of increased visibility to their own predators.

There are, however, two ways by which bright coloration could increase prey capture rate and therefore be selectively advantageous. The first is that conspicuous coloration might act as a sensory trap, mimicking signals that elicit out-of-context behaviours by exploiting the adaptive neural responses of signal receivers (Edwards & Yu 2007). Many flying insects are attracted to the vibrant colours of flowers, and predators could take advantage of this. For example, the Australian crab spider, *Thomisus spectabilis*, closely matches flower colour within the human visibility spectrum, but contrasts strongly under UV, which bees can also see. Studies have concluded that this UV colour contrast is a sensory trap that results in more frequent visits to flowers occupied by crab spiders (Chittka 2001; Heiling *et al.* 2003, 2005). Similarly, Tso *et al.* (2002) and Tso *et al.* (2004)

found that naturally occurring melanics of the wood spider *Nephila maculata*, on which UV-reflective markings are absent, have lower rates of insect interception and catch fewer insects than do brightly coloured morphs. Also, experimentally obscuring the yellow or silver banding of the orchid spider *Leucauge magnifica* reduces the prey capture rates by up to three times compared with naturally coloured controls (Tso *et al.* 2006).

However, an alternative explanation is that bright coloration is a form of disruptive camouflage. Bands and stripes extending to the edge of the abdomen could break up the outline of the spider when seen through the chromatic vision of insects and therefore contrast less with the vegetation background (Briscoe & Chittka 2001; Cuthill *et al.* 2005). Under this interpretation, obscuring bright colours would cause spiders to be more visible as spiders, and thus, should also reduce prey capture rates.

In this study, we use a British species of the otherwise largely tropical *Argiope* genus, *Argiope bruennichi*, commonly known as the wasp spider (Becker 1983; Levi 1983), to test both hypotheses. We black out the yellow and white bands on some spiders, other spiders are shielded with a leaf fragment and some spiders are left naturally coloured as controls. We predict that if body coloration serves as an attractant, naturally coloured spiders will capture more prey than will either leaf-shielded webs or blacked-out conspecifics. Alternatively, if bright coloration acts as a disruptive camouflage, leaf-shielded and naturally coloured spiders will have similar insect-capture rates, and both rates will be higher than with blacked-out spiders. Previous investigations have not used a leaf-shield treatment and therefore have not been able to distinguish sharply between the prey-attraction and camouflage hypotheses (Craig & Bernard 1990; Craig & Ebert 1994; Hauber 2002).

* Author for correspondence (alex.a.bush@hotmail.co.uk).

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A closely related problem in the understanding of spider prey-capture strategies is to explain the function of the silk web decorations (historically known as stabilimenta) that are typically built by spiders in the genus *Argiope*. The most commonly tested explanations for silk decoration function are prey attraction (through signals communicated in the UV spectrum), predator avoidance or ‘advertising’ the web to warn away large vertebrates from accidentally damaging the web (Herberstein *et al.* 2000; Li 2005; Bruce 2006). Conflicting results (Tso 1998; Blackledge & Wenzel 1999) have meant that no clear consensus exists yet. Therefore, our study also considers the possible effects of silk decoration on prey capture in *A. bruennichi*.

2. MATERIAL AND METHODS

(a) Sampling

Fieldwork was conducted in southern Dorset, England (UK Grid Ref. SY967840), in a 30 × 30 m² area of 1–1.5 m high vegetation dominated by soft rush (*Juncus effusus*), gorse (*Ulex europaeus*) and bramble (*Rubus fruticosus* agg.) to which *A. bruennichi* most often attached its webs. Recording took place between 10.00 and 17.00 hours on sunny days when the ambient temperature was between 23 and 27°C.

Argiope bruennichi (Scopoli 1772) is a generalist predator, although studies suggest that Orthoptera are its main prey (Pasquet 1984; Barabasz & Górz 1998) with behavioural adaptations specific to them (Pasquet & Leborgne 1998). Males are inconspicuous with the cephalothorax and abdomen just 4–5 mm long compared with females that are 11–15 mm and larger when full of eggs (Roberts 1995). Orb webs are built close to ground level and often contain linear silk decorations, zigzagging vertically from the web hub. Our study includes only females, as males do not build webs and are dull in colour in contrast to the brightly coloured females.

The possibility of prey attraction by silk decoration in *A. bruennichi* has been tested before, but no relationship has been found (Prokop & Grygláková 2006), in part because orthopterans (over 40% of prey) do not seem to exhibit the same orientation response to silk decorations as do other insects (Tso 1998). Consequently, in those webs where silk decorations occurred (44% of all webs), they were not removed but were roughly equally distributed among the three treatments (table 1).

We applied two experimental treatments. In treatment 1 (‘leaf shielded’, figure 1a), spiders were left on their webs but hidden behind small leaf shields approximately 5 cm in diameter on dark green wire stands, placed 3–4 cm in front of and parallel to the web hub, where the spider resides (Craig & Ebert 1994). In treatment 2 (‘blacked out’, figure 1b), the yellow/white bands on the dorsal surface of the spiders’ abdomens were painted black using a xylene-free marker pen. Finally, for treatment 3 (control) spiders (‘naturally coloured’, figure 1c), leaf shields were not used and the yellow/white bands were not blacked out. However, to control for any potential odour effects of the marker pen on treatment 2 spiders, the (otherwise) naturally coloured spiders (treatment 3) were marked on the dark ventral surfaces of the legs, and the leaf shields used in treatment 1 were also marked with the pen on the side facing the spider. The ventral surface of *A. bruennichi*’s abdomen displays some yellow coloration that was left untouched in all three treatments.

Table 1. Mean and s.e. of web and spider characteristics in each of the three treatments. (Treatment 1, leaf-shielded spiders; treatment 2, blacked-out spiders and treatment 3, naturally coloured spiders. The *p* values refer to the significance of treatment level in explaining variance in each row value (ANOVA, d.f. = 2).)

	treatment 1 (<i>N</i> = 45)	treatment 2 (<i>N</i> = 45)	treatment 3 (<i>N</i> = 70)	<i>p</i>
web area (cm ²)	387 ± 37	365 ± 34	386 ± 30	0.886
hub height (cm)	29.5 ± 1.7	32.8 ± 1.9	31.7 ± 1.7	0.503
spider body length (mm)	13.0 ± 0.3	12.5 ± 0.3	13.2 ± 0.3	0.069
presence of silk decoration (%)	44	46	43	—
decoration length (mm) ^a	23.9 ± 1.9	29.1 ± 2.7	23.9 ± 2.0	0.571

^a Length square root transformed.

Treatments were assigned by rotating the treatment as each new individual’s web was located. A total of 160 spiders were observed, 45 each in treatments 1 (leaf shield) and 2 (blacked out) and 70 naturally coloured controls. After each spider was treated, it was allowed 15 min to recover its original position and then scored every 20 min for prey capture for 7 hours per day over six non-consecutive days, between 12 August and 3 September 2006. Orthopteran prey were distinguished as these are the largest prey items. We counted only prey capture by the spiders and not web interceptions that did not result in capture. As all three treatments contained a spider, we assume that there was no systematic bias in the spider’s ability to capture a prey item that contacted the web. Importantly, the removal of prey by *A. bruennichi* from the web for consumption at the hub ensures that the web remains empty, thus maintaining low web visibility for other potential prey.

Spider body length was recorded to the nearest mm, as was the length in mm of the silk decoration if present. Maximum web width and height were recorded to the nearest cm and converted to a rough web area that equals $\pi(\text{width}/2)(\text{height}/2)$. Hub height from the centre of the web vertically to the ground was recorded to the nearest cm.

Owing to the high frequency of zeros in the dataset, indicating that prey capture can be thought of as a Poisson process, we used a generalized linear model (Poisson error and log link) to identify which of the predictors (treatment, spider length, web area, hub height and stabilimentum length) significantly explain variance in the total prey and in the Orthoptera captured. Because all but treatment effects reflect natural variation, we do not test for two-way interactions (Crawley 1993). We used three response variables: total prey; orthopteran prey only; and non-orthopteran prey only. The sum of the latter two categories equals total prey. All data are expressed as mean ± s.e. unless stated otherwise. Finally, any significant (or non-significant) effect of the variables’ web area, hub height, spider size and silk decoration length must be taken with some caution, as they were not experimentally manipulated and because some exhibit significant correlations, producing multicollinearity (data not shown). Larger spiders produce webs that are bigger and higher from the ground. Larger webs also have longer stabilimenta, but there is no direct correlation of spider size with stabilimenta length. Analyses were conducted with GLMSTAT v. 6.0.0 (Beath 1997).

Figure 1. (a) Leaf-shielded, (b) blacked-out and (c) naturally coloured individuals. Web decoration is visible in the lower part of (b).

Figure 2. Reflectance data were collected from eight points. (a) The upper thorax (T), the dorsal light yellow (YL), dark yellow (YD) and black abdomen stripes (BD), and the light (LL) and dark leg stripes (DL). (b) The ventral yellow (YV) and black stripes (BV). (For colour version see electronic supplementary material.)

(b) Reflectance analysis

Following the field study, the spectral reflectance function of spider body parts was measured with a spectrophotometer (AvaSpec-2048, Avantes, The Netherlands) relative to a white reflection standard, using a deuterium–halogen light source (DH 2000; Ocean Optics, Dunedin, FL, USA). Reflectance spectra were measured from 300 to 700 nm (resolution 0.01 nm). Three repeat measurements were taken from an individual recently euthanized by freezing from eight different areas outlined in figure 2.

Colour sensitivity was based on the perception of bees, as their visual ecology has been studied most conclusively. The relative amount of light absorbed by each photoreceptor class is given by P

$$P = R \int_{300}^{700} IS(\lambda) \cdot S(\lambda) \cdot D(\lambda) d\lambda,$$

where $IS(\lambda)$ is the spectral reflectance function of the spider coloration; $S(\lambda)$ is the spectral sensitivity function of the bee photoreceptors; and $D(\lambda)$ is the daylight illuminating spectrum. The sensitivity factor, R , is determined by

$$R = \left(\int_{300}^{700} I_B(\lambda) \cdot S(\lambda) \cdot D(\lambda) d\lambda \right)^{-1},$$

where $I_B(\lambda)$ is the spectral reflection function of the background. The nonlinear transfer function relating the receptor excitation, E , to photoreceptor absorption, P , is given as

$$E = \frac{P}{1 + P}.$$

Coding is performed using individual colour opponent mechanisms for each of the bee's three excitation values based on UV, blue and green photoreceptors (Dyer & Chittka 2004). This three-dimensional space can then be plotted in a colour hexagon allowing us to visualize a bee's subjective coloured view of the world (Chittka 1992). Euclidean distances (D_{St}) between plotted stimuli are calculated as (Tso *et al.* 2004)

$$D_{St} = \sqrt{D_x^2 + D_y^2}.$$

The distances between colour loci are correlated with a bee's ability to discriminate between those colours. The minimum significant distance used was 0.1 units and higher values denote greater distinction between colours (Dyer & Chittka 2004; Raine & Chittka 2007).

Figure 3. Mean non-orthopteran (dark grey bars) and orthopteran (light grey bars) prey per day caught by spiders in each treatment (1, leaf-shielded individuals; 2, blacked-out individuals; and 3, naturally coloured individuals). Error bars, 95% CI.

3. RESULTS

(a) Prey capture

The overall average web area was 380 ± 19 cm² and hub height 31 ± 1.1 cm. Mean adult-female body length was 12.9 ± 0.2 mm. Across treatments, there was no significant difference in web area, hub height, spider size or silk decoration length (table 1).

Spiders in treatment 3 (naturally coloured) captured on average more than twice as many total prey, and approximately three times as many orthopterans, as did spiders in the other two treatments (figure 3). Only the treatment predictor remained in the minimal significant model in which either total prey (generalized linear model, Poisson error, log link; total prey, $\chi^2_2 = 22.97$, $p < 0.0001$, variance explained = 15.9%) or orthopterans only ($\chi^2_2 = 15.57$, $p = 0.004$, 15.9%) was used as the response variable. Pooling treatments 1 (leaf shield) and 2 (blacked out) did not increase residual deviance by a significant amount (total prey: +0.02 scaled deviance; orthopterans only: +0.2, +1 residual d.f.). Thus, the higher level of prey capture observed in naturally coloured spiders is statistically significant, and the blacked-out and leaf-shielded spiders were not significantly different in prey capture success (figure 3).

If we limit the response variable to non-orthopteran prey, we detect significant effects of treatment, spider size and hub height on prey capture (total model $\chi^2_4 = 18.6$, $p = 0.001$, variance explained = 12.0%; $Ln(\text{non-orthopteran prey}) = -3.0 + 0.18(\text{spider size}) - 2.0(\text{hub height}) + 0.37$ (if blacked out) + 0.78 (if naturally coloured)). Pooling treatments 1 and 2 again did not increase residual deviance by a significant amount (+1.04) but did cause hub height to become marginally non-significant ($p = 0.053$), so the minimal model after pooling includes only pooled treatment and spider size (total model $\chi^2_2 = 13.77$, $p = 0.001$, variance explained = 8.9%; $Ln(\text{non-orthopteran prey}) = -2.0 + 0.12(\text{spider size}) - 0.60$ (if treatment 1 or 2)).

(b) Reflectance data

Differences between hexagon coordinates represent a sliding scale of distinction and although no statistical test can be used to test the significance of any observed difference in this case, the current opinion is that values over 0.1 units indicate distinct colours and higher values convey greater differences (Dyer & Chittka 2004). The majority of colours on a wasp spider immediately obvious to human eyes appear to register as distinct to a bee's vision as well (table 2, figure 2 and the electronic supplementary material, appendix A). Notable exceptions, though close, are the dark and light leg stripes that were not different enough from each other to be classed as distinguishable.

4. DISCUSSION

This study has shown that naturally coloured wasp spiders, *A. bruennichi*, captured significantly more prey than did either blacked-out or leaf-shielded conspecifics (figure 3). This result supports the hypothesis that bright coloration in wasp spiders attracts insect prey. This hypothesis is consistent with the general expectation that the colour yellow is perceived by prey insects as similar to certain food resources such as flowers, new leaves or plant growth (Prokopy & Owens 1983; Tso *et al.* 2006). A previous study of *Argiope argentata* also found a significant attractive function of the ventral, as well as the dorsal, surface of the abdomen (Craig & Ebert 1994), so it is possible that if the ventral surface had also been blacked out in this study, the difference in prey capture could have been even greater (Tso *et al.* 2006).

These results do not support the disruptive-camouflage hypothesis because leaf-shielded (and thus, apparently empty) webs should have captured as much prey as did naturally coloured spiders, but did not. By contrast, another investigation concluded that coloration in *A. bruennichi* does serve as camouflage. Václav & Prokop (2006) compared the dark, dull nocturnal orb-web spider *Larinioides cornutus* to *A. bruennichi* by placing anaesthetized spiders of both species on artificial webs. *Argiope bruennichi* webs caught more prey than did *L. cornutus* webs, but *A. bruennichi* webs did not catch significantly more prey than did empty webs. Václav & Prokop's results are consistent with the disruptive-camouflage hypothesis and contradict the results and interpretation from this study. However, there were also striking differences in prey composition; Orthoptera were minimally represented in the intercepted species to the extent that they were excluded from the analysis because they were not typical prey species. By contrast, Orthoptera represented 43% of all prey caught in this study, and this, combined with other differences in methodology such as artificial webs and anaesthetized spiders that did not clear webs of prey, could explain our different results.

Our results also revealed a significant, though weakly negative effect of hub height, as well as a stronger positive effect of spider size on the capture of non-orthopteran prey. Hub height affects web design, and greater web area has previously been shown to increase prey capture in *A. bruennichi* (Szymkowiak *et al.* 2005; Prokop & Grygláková 2006). However, since hub height and web area are significantly correlated with each other in our study and

Table 2. Distances between colour coordinates produced from reflectance data of separate areas of *A. bruennichi*. (Colour differences greater than 0.1 units (asterisks) are considered distinguishable by bees (Raine & Chittka 2007).)

spider feature	T	YL	YD	BD	YV	BV	LL	DL
thorax (T)		0.094	0.176*	0.119*	0.296*	0.198*	0.140*	0.205*
light yellow (dorsal) (YL)			0.186*	0.157*	0.235*	0.239*	0.239*	0.253*
dark yellow (dorsal) (YD)				0.209*	0.108*	0.299*	0.231*	0.302*
black stripe (dorsal) (BD)					0.353*	0.097	0.106*	0.187*
ventral yellow (YV)						0.445*	0.383*	0.449*
black stripe (ventral) (BV)							0.077	0.093
light leg stripe (LL)								0.082
dark leg stripe (DL)								

spider size is correlated with both of those, any or all could be the causal variable making biological interpretation difficult.

The length or occurrence of silk decorations did not explain variance in prey capture in any of the treatments, contrary to the expectations given that silk decorations increase web visibility and represent an energetic investment by the spider (Herberstein *et al.* 2000). So why do almost half of webs contain them? Conflicting results in the literature have so far meant that no clear conclusion has yet been reached. For instance, two studies using *Argiope aurantia* found that the presence of web decoration could either increase prey capture by more than 40% (Tso 1998) or decrease it by 34% (Blackledge & Wenzel 1999). It seems probable that decoration has evolved to serve many purposes among different lineages of spiders (Herberstein *et al.* 2000).

Insect vision has been best studied in the case of pollinators such as bees (Chittka & Raine 2006) and, therefore, we used a bee-response model to understand how insects in general might perceive *A. bruennichi*. Our spectrophotometer results confirm that *A. bruennichi*'s contrasting coloration should be detectable by insects. Specifically, the dark and light yellow stripes on the dorsal abdomen were distinct from all other areas, and the thorax was also divergent from most other areas (table 2).

However, the leg stripes are duller (table 2) and therefore less perceptible by insects, which could help to disguise the spider's outline. Thus, although the prey capture results (figure 3) do not suggest a role for disruptive camouflage, the apparent low visibility of some body parts (table 2) does suggest a small role for camouflage (Spaethe & Chittka 2003; Tso *et al.* 2006) and would help reconcile our results with those of Václav & Prokop (2006).

Finally, a possibility not directly tested in this study is that the yellow and black patterning of *A. bruennichi* has additionally evolved an aposematic pattern in order to mimic wasps and deter vertebrate predators (Merilaita & Tullberg 2005) and/or avoid recognition by invertebrate predators, particularly predatory wasps (Blackledge & Pickett 2000; Blackledge & Wenzel 2001). However, during fieldwork, not one blacked-out spider disappeared from its web, and although this is far from conclusive evidence that aposematism does not exist in *A. bruennichi*, it suggests low importance. *Argiope bruennichi* webs are low to the ground and sheltered between high stems of reed, gorse and/or bramble, which place them at a lower risk of predation compared with other more prominently displayed spiders nearby, such as *Araneus diadematus*, which are drably coloured.

In summary, our study showed that diurnal orb-web spiders are not simply sit-and-wait predators passively filtering prey from the air. *Argiope bruennichi* appears to have evolved bright coloration to create a sensory trap that improves foraging success. Lower visibility of the legs might also help to disguise the outline of the spider from its prey and from predators of spiders.

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