

# Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage?

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## Summary

Many animals have conspicuous body colour that may serve physiological, camouflage or communicative functions. This study investigated the influence of bright coloration in orb-weaver spiders on the response of predator and prey using *Argiope keyserlingi*, the St Andrew's Cross spider. This species has three conspicuous yellow bands on its dorsal abdominal surface. These bands could act as camouflage devised through disruptive colouration or attract prey to the web by exploiting colour preferences in the insect visual system. In the field, naturally yellow spiders captured more prey than spiders where the yellow bands were coloured over with black marker. Similarly, some prey (Harlequin beetles: *Tectocoris diophthalmus*) moved towards yellow spiders and away from blackened spiders in Y-choice tests. However, native bees (*Trigona carbonaria*) did not seem to discriminate naturally coloured spiders at a distance when approaching a spider on a web or an empty web. Similarly, praying mantid predators (*Pseudomantis albofimbriata*) preferred blackened spiders over yellow spiders in a Y-maze, but they showed no preference when offered an empty web and a web occupied by a naturally coloured spider. Thus our data suggest that the main function of the conspicuous yellow bands is crypsis, perhaps via disruptive colouration that obscures the outline of the spider.

*Keywords:* *Argiope keyserlingi*, crypsis, aposematism, Araneidae, Mantidae.

## Introduction

Colouration and patterning in animals may have camouflage or communicative functions, which may not be mutually distinct or clearly distinguishable

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from one another (Ortolani, 1999). The colour of many species renders them invisible to potential predators and prey through background matching (crypsis). For example cuttlefish (Hanlon et al., 1999) and crab spiders (They & Casas, 2002) are able to change their body colour to match and blend with their immediate surrounds. This crypsis can be enhanced through a disruptive colouration, which breaks up an organism's body contours, making it less visible to predators or prey (Cuthill et al., 2005; Merilaita & Lind, 2005).

Colour schemes that do not match the background, such as disruptive colouration or deceptive resemblance can also achieve camouflage. In disruptive coloration patterns detract from the true outline of the body but do not necessarily match the background (Merilaita, 1998). For instance, the marine isopod *Idotea baltica* lives on algae and displays white spots on its body. The spots do not match the coloration patterns of the algae, but break up the contour of the animal (Merilaita, 1998). In deceptive resemblance, an organism resembles the colour and form of objects in the environment (Hanlon et al., 1999), such as the 'bird-dropping spider' *Phynarrachne rugosa*, which bears a remarkable morphological resemblance to bird dropping (Main, 1976).

Conspicuous body colour does not match background colour and can deter potential predators. Unpalatable species often display bright warning colours (aposematism) that a predator will recognise as unpalatable or noxious (e.g., Lindstrom, 1999; Endler & Mappes, 2004; Merilaita & Tullberg, 2005). Often similar colour patterns are used by several unrelated unpalatable species (Mullerian mimicry: Mallet & Joron, 1999). For example, the similar warning colours used by the unpalatable and aggressive tiger beetle (*Pseudoxycycheila tarsalis*) and equally unpalatable mutillid wasps (Hymenoptera: Mutileidae; Schultz, 2001). However, mimicry can also be exploited by species that dishonestly display aposematic warning colours (Batesian mimicry: Mallet & Joron, 1999). For example, the palatable grasshopper *Condylodera tricandyloides* mimics the colouration of tiger beetle species and thus avoids predation (Wickler, 1968).

Conspicuous colour may also be used to attract or deceive prey (aggressive mimicry). Many flying insects are attracted to vibrant colours, such as those displayed by flowers, and predators can display similar colours to attract such prey. For example, in Australian crab spiders, the body colour of the spider can form a strong contrast against the flower background. Insect prey, such as European honeybees and native Australian bees are attracted to

flowers occupied by the spider (Heiling et al., 2003; Heiling & Herberstein, 2004; Heiling et al., 2005b). In this system, the spiders reflect more UV light than the flowers resulting in a strong colour contrast (Heiling et al., 2005a). However, the conspicuous body colour of these crab spiders also makes them more visible to avian predators (Heiling et al., in prep). Distinctive and conspicuous colouration may therefore have many conflicting rewards: while it may be useful in attracting prey or mates, it may also aid detection by a predator.

Visibility and recognition by predators and prey is crucial in sit-and-wait predators that hunt in exposed sites. Diurnal orb-web spiders (Araneidae) mostly reside at the hub of their web throughout the day and are thus exposed to predators such as praying mantids and wasps (Cloudsley-Thompson, 1995). These spiders will often display cryptic body coloration, to conceal themselves from predators (Oxford & Gillespie, 1998). Camouflage from prey is also vital for the spider's foraging success. If prey can identify a spider on the web early enough they may be able to avert flying into the web (Craig, 1986). Nevertheless, many orb-web spiders display conspicuous colours such as the red, yellow, and white (Oxford & Gillespie, 1998), which are likely to influence the behaviour of insect predators and prey (Hauber, 2002). Yellow and white stripes, bands and dots on the abdomen are very common in females of the genus *Argiope* (Levi, 1983). Males are much smaller than (adult) females, and have relatively inconspicuous coloration, however, they do not regularly build webs as adults (Levi, 1983).

The St Andrew's cross spider *Argiope keyserlingi* has three conspicuous bands of yellow and five yellow spots on the dorsal abdomen. The rest of the spider body may be coloured a pale brown to a black colour. The yellow, which is formed by ommochromes (derivatives of the amino acid tryptophan), is deposited in the cells of the hypodermis over a background of white formed by guanine crystals in the digestive diverticula (Oxford & Gillespie, 1998). Previous experiments suggest that the yellow colouration is important for prey attraction. *Argiope argentata*, which has similar coloration to *A. keyserlingi*, was more successful at catching prey when its yellow colour was visible, compared to when they were covered with grass 'shields' whilst on their webs (Craig & Ebert, 1994). Recent experimental field studies have found that the yellow body coloration of other orb-web spiders also increases their foraging success (Hauber, 2002; Tso et al., 2002; Tso et al., 2004).

**Table 1.** Specific hypotheses that predict prey and predator response to yellow bands on the abdomen of *A. keyserlingi* under the prey attraction, warning colour and camouflage mechanisms. A neutral response refers to a by chance encounter rate.

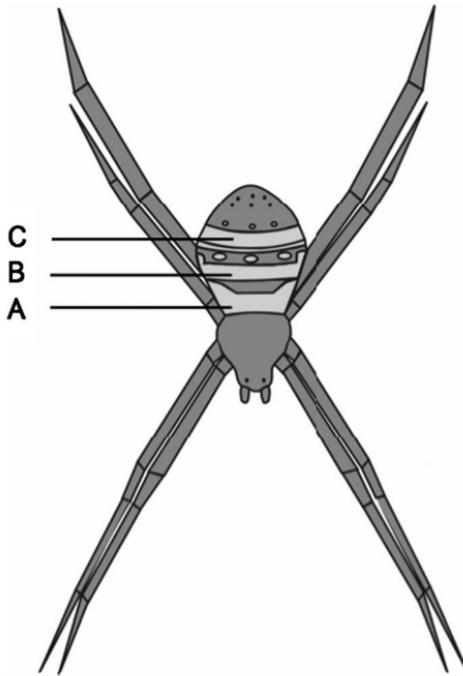
Hypothesis	Prey response	Predator response
Prey attraction	Attracted to yellow spiders, neutral or repulsed by blackened spiders	Attracted to yellow spiders
Camouflage	Neutral response to yellow spiders, repulsed by blackened spiders	Neutral to yellow spiders, attracted to blackened spiders
Warning colour	Repulsed by yellow spiders, neutral towards blackened spiders	Repulsed by yellow spiders, neutral or attracted to blackened spiders

However, it is not clear whether this increase in foraging success is a result of prey attraction, or from camouflage due to the disruptive colour pattern. Some predators of *A. keyserlingi* are also insects. To date the only predatory attacks we have witnessed are those by the praying mantids *Pseudomantis albofimbriata* and *Archimantis latistylus* (Bruce et al., 2001). These predators potentially have some overlap in the spectral sensitivities of the prey, with sensitivity peaks in the UV (370 nm) and the blue (510-520 nm; Sonntag, 1971) although it is not known if praying mantids use colour vision to detect prey. Thus, the yellow coloration may also be visible to predators, advertising the presence of the spider. Alternatively, the yellow abdominal bands may deter potential predators by acting as a warning or mimicry of aposematism, or they may camouflage the spiders against their predators. If these conspicuous colour patterns function to camouflage the spider we predict that both prey and predators would not distinguish between an empty web and a web occupied by a spider. Manipulation of the abdominal stripes, on the other hand would increase the visibility of spiders thereby deterring prey and alerting predators to their presence (see Table 1 for a summary of hypotheses).

## Methods

### *Field observations and experiments*

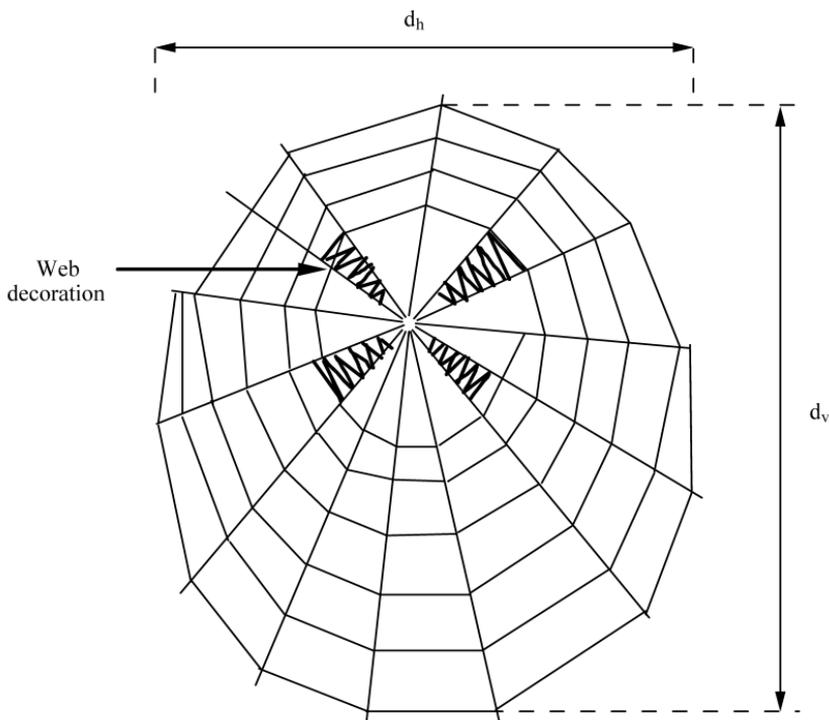
All field observations and experiments were carried out at Bicentennial Park West Pymble, Sydney, NSW, where most spiders were found on *Loman-*



**Figure 1.** Schematic representation of *A. keyserlingi* showing the three yellow bands on the dorsal abdomen (Band A, B and C).

*dra* spp. plants. Field observations to identify the prey spectrum of *Argiope keyserlingi* were carried out over 10 days during January 2002. Each day around 30 randomly selected spider web sites were tagged and monitored every 45 mins for 8 hours between 8 am and 7 pm. Prey caught by each spider was removed from the webs and stored in 70% ethanol and identified to order in the laboratory. A total of 300 spiders were observed and care was taken to observe each spider only once. However, some individuals may have been observed more than once, as they occasionally move web site and we did not tag the spiders themselves to minimise disturbance.

Field experiments were carried out in February 2002 to determine the effect of the yellow markings upon prey capture by *A. keyserlingi* under natural conditions. Spiders were collected from the field and taken to the laboratory at Macquarie University. There the spiders were paired based on similarities in size. They were randomly assigned to one of two treatments. Spiders were anaesthetised with CO<sub>2</sub> and individuals in the experimental treatment (blackened) had their yellow markings coloured over with waterproof, xylene free,



**Figure 2.** Schematic representation of an *A. keyserlingi* web showing four web decorations and web parameters recorded in the field:  $d_v$  is the vertical diameter and  $d_h$  the horizontal diameter. Modified from Herberstein, 2000.

black Artline<sup>®</sup> permanent marker (Figure 1). Spiders in the control groups (yellow), where coloured on their tibia with the same marker to control for the effect of odour on potential prey and painting on the behaviour of spiders. We attempted to colour a similar area of legs in control spiders as the areas coloured in the experimental spiders.

Spiders were returned to the field and released onto existing webs from which the occupant was removed. As web area can affect prey capture success but also varies greatly between individuals, we recorded web area. Web area was calculated from the web diameters (Web area =  $(d_v/2)(d_h/2)\pi$ , where  $d_v$  is the vertical diameter and  $d_h$  the horizontal diameter (Figure 2; Herberstein & Tso, 2000). In addition, *A. keyserlingi* decorate their webs with up to 4 bands of thin silk (Figure 2) that can also affect prey capture (Bruce et al., 2001). Thus we measured the length of the silk decorations (see Figure 2) and the number of days the spiders were observed. Spiders that settled at the hub of their adopted web were visited every 45 minutes for

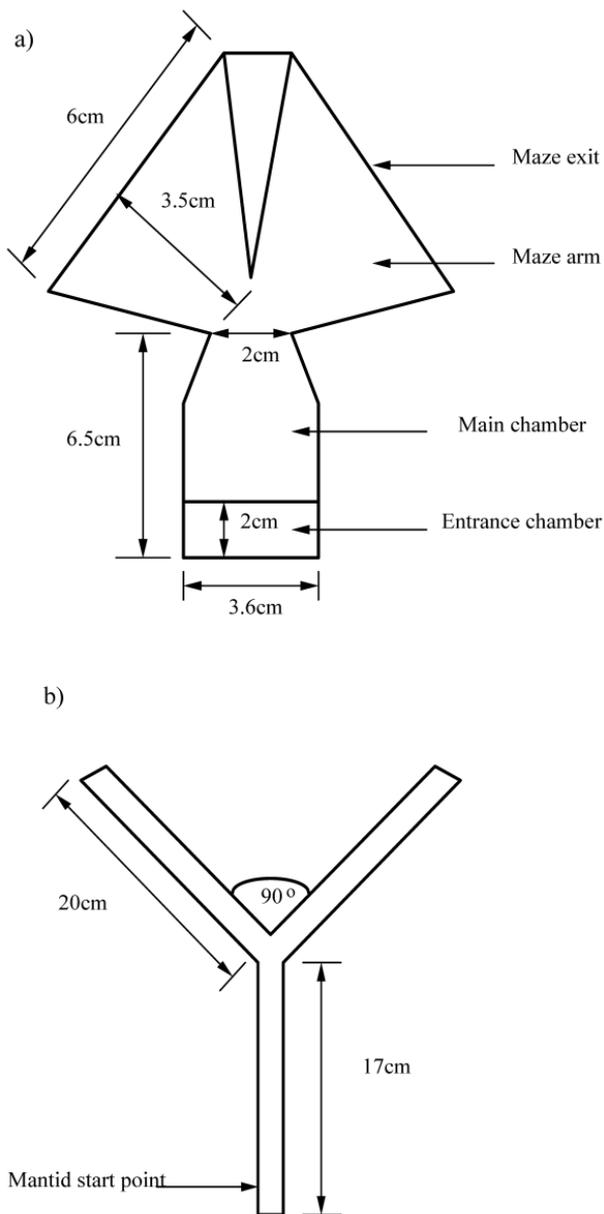
8 hours from 8 am to 4 pm and every item captured in the web or fed upon by the spider was recorded. Prey was not collected from the web to minimise disturbance. Prey capture rates were calculated as the number of prey captured per hour over the observation period. We only included spiders in the analysis that were observed for more than two days.

#### *Animal collection and maintenance*

Spiders used in laboratory experiments were collected from the field site in the summer of 2001/2002 and 2004/2005, and also from Brisbane, Queensland in 2001/2002. Spiders were housed in square Perspex frames (50 × 50 × 15 cm) in upturned plastic cups that had the bottom replaced by gauze (12.5 × 9 × 9 cm). Spiders were fed blowflies (Diptera: *Lucilia cuprina*) or crickets (Saltatoria: *Achaeta domestica*) twice a week whilst in the lab and sprayed daily with water. Prior to experiments, all spiders were weighted on an electronic balance.

Praying mantids (Mantodea: *Pseudomantis albofimbriata*) used in laboratory experiments were collected from the field site or reared from cocoons in the laboratory. We used adult female mantids for the predator experiments as they had been observed stalking and eating *A. keyserlingi* at the field site and they are more responsive to Y-maze experiments than males (Bruce et al., 2001). In the laboratory they were housed in enclosures constructed from fly wire (25 × 21 × 21 cm) or plastic cups (12.5 × 9 × 9 cm). Mantids were fed blowflies or crickets each week and were sprayed with water once a day. Prior to experiments, all mantids were weighted on an electronic balance.

We selected two types of potential prey for laboratory experiments. Harlequin bugs (Hemiptera: *Tectocoris diophthalmus*) were used as a prey in 2001/2002 because hemipterans were captured at high frequencies by *A. keyserlingi* in the field and the Harlequin bugs were available on campus. *T. diophthalmus* were collected on the day of experiments and each bug was only used once. A cold spell in 2002 coincided with the disappearance of the harlequin bug population on campus, with only one of two choice experiments completed. Subsequently, in 2004/2005, stingless Australian native bees (Hymenoptera: *Trigona carbonaria*) collected from an artificial hive on Macquarie University campus were used for both choice experiments. The distribution of these native bees overlaps with that of *A. keyserlingi* and they are thus potential prey. *Trigona carbonaria* is a small black bee without obvious stripes.



**Figure 3.** Schematic representation of the Y-maze apparatuses used in the prey and predator choice experiments. (a) Enclosed Y-maze used in prey response experiment. (b) Open Y-maze used in predator response experiments.

*Predator and prey response to yellow colouration*

Laboratory experiments were carried out to determine the influence of the yellow coloured bands on the response of prey and predators under controlled conditions using Y-mazes. Prey or predators were introduced to the entry of the Y-maze (Figure 3a, b) and allowed to approach one of two stimuli placed at the exits of the maze. A choice was recorded when the prey or predator arrived at one of the exits of the Y-maze. We conducted two choice experiments. The first experiment tested the visibility of naturally coloured spiders by offering prey and predators a spider on a web versus an empty web. In the second experiment we tested how the yellow bands affected spider visibility by offering prey and predators spiders with natural yellow bands versus spiders with blackened bands (Figure 1). We covered the dorsal yellow bands with waterproof black Artline<sup>®</sup> permanent and xylene free marker, and to control for olfactory cues, we applied the marker to the ventral areas and legs of the control spiders. The area blackened by the marker did not reflect any light from 300 to 750 nm. Spiders were randomly assigned to each side of the maze. Each spider and web were used only once in the experiments.

The spiders were placed onto webs without silk decorations attached to 15 cm diameter wire rings. Spiders on webs were suspended approximately 5 cm from the exits of the Y-maze, at an equal height. The web background consisted of a pair of 1:1 (mirror imaged) photographs depicting *Lomandra* spp., a common substrate for *A. keyserlingi*. We ensured the reflectance properties of the photographs were similar to real plants by inspecting the reflectance curves of photographs and plants generated by the spectrophotometer. Using photographs rather than real plants provided us further experimental control as it reduced natural variation in plant colour. In 2001/2002 the experiments were performed in a laboratory, with the webs and spiders being lit from the front with 60 W Philips Practitione<sup>®</sup> (daylight) light globes. In 2004/2005, we conducted the choice experiments under natural light.

Prey (Harlequin bugs and native bees) responses to *A. keyserlingi*'s yellow coloration were carried out using a small, enclosed Perspex Y-maze (Figure 3a). The two openings of the maze were covered using cling wrap to eliminate olfactory cues and the prey was released at the entry. We measured the time it took the prey to arrive at one of the two exits. No prey was used twice. Between each trial the maze was cleaned with 70% ethanol and openings were covered using new cling wrap.

In a more natural field study, using native bees from a hive on the Macquarie University campus, we observed the flight patterns of native bees as they approached an empty web or a web occupied by *A. keyserlingi*. Since these bees tend to fly in a straight line on their return flight to the hive, we placed the hoop 5 cm from the hive entrance. In order to provide a naturalistic background the hive box was covered with a photograph of *Lomandra* spp., the common vegetation substrate for *A. keyserlingi* webs. The three treatments were (1) an empty hoop, (2) a hoop with web and (3) a hoop with a spider on the web. The order of these three treatments was randomised. For this experiment, we used webs from sub-adult female *A. keyserlingi*. Approaching native bees were monitored in 1 minute trials ( $N = 50$  trials) and all native bees that flew through the hoop were counted. In addition we also noted if the native bees contacted the web as they went through the hoop, or if they avoided the web. The number of bees that flew through the empty hoop gave us an estimate of bee abundance, which varied between days.

To test the response of predatory mantids (*Pseudomantis albofimbriata*), we used an open Y-maze (Figure 3b), as the mantids did not respond in an enclosed maze. The maze was surrounded by an arena of black cardboard to prevent distraction of the mantid by the observer. Mantids were placed onto the maze entry by hand. We measured how long it took the mantid to approach one of the two exits.

### *Spectrophotometry*

We collected spectrometric data to visualise the yellow colour of the spiders and to ensure that covering the yellow bands with black marker efficiently reduced light reflectance. The reflectance spectrum of the yellow bands (Figure 1) was measured for the dorsal body surface. The Ocean Optics spectrophotometer with a PX-2 pulsed light source was calibrated using a WS-1 reflectance standard (Ocean Optics Inc., Dunedin, Florida) and black felt as the dark standard. Measurements were taken with a 400  $\mu\text{m}$  probe, mounted at a 45-degree angle with integration time of 7 milliseconds averaging 10 spectra from 300 to 750 nm. A total of five spiders were measured with 10 measurements taken from each of the three dorsal bands as these showed more variation. The reflectivity measurements of the three dorsal bands were averaged across all individuals. The normalized reflectance was then obtained by dividing the averaged values across 10 nm bins (e.g., 340-349 nm) by the highest mean.

**Table 2.** Web area, web decoration length, prey capture rates and number of days observed for blackened and yellow striped spiders in the field. All data are mean  $\pm$  SE.

Parameter	Blackened	Yellow
Web area (cm <sup>2</sup> )	762.13 $\pm$ 105.32	648.25 $\pm$ 62.31
Length of silk decorations (mm)	3.57 $\pm$ 0.76	2.67 $\pm$ 0.72
Number of days observed	2.79 $\pm$ 0.27	3.26 $\pm$ 0.33
Prey capture rate (item/hour)	0.365 $\pm$ 0.082	0.829 $\pm$ 0.22

### *Data analysis*

All data were tested for normality using Kolmogorov-Smirnov test. Data that were not normally distributed were log transformed. Prey capture rates were calculated as number of items per hour of observation. As web area and the length of silk decorations can influence prey capture rates in spiders (e.g., Herberstein, 2000), we used these variables as covariance when comparing prey capture rates between yellow and blackened spiders in the field. The number of days spiders were observed in the field were analysed using two-sample *t*-tests. Spider weights for the laboratory experiments were analysed using paired *t*-tests. Treatment and directional preferences in the Y-choice experiments were analysed using binomial probability. For the native bee response in the field, we used ANCOVA using the number of native bees flying through the empty hoop as covariance, as this estimates overall bee activity during any trial. We compared two measurements of bee behaviour between webs with and webs without a spider: the total number of native bees going through the hoop and the number of native bees avoiding contact with the web.

## **Results**

### *Field observations and experiments*

A total of 92 prey items were collected from 300 field webs. The major (>10%) prey types were Hymenoptera (38%), Coleoptera (23%) and Hemiptera (15%). The minor taxa (<10%) included Araneae, Lepidoptera, Odonata and Orthoptera. Eight percent of the prey was unidentifiable.

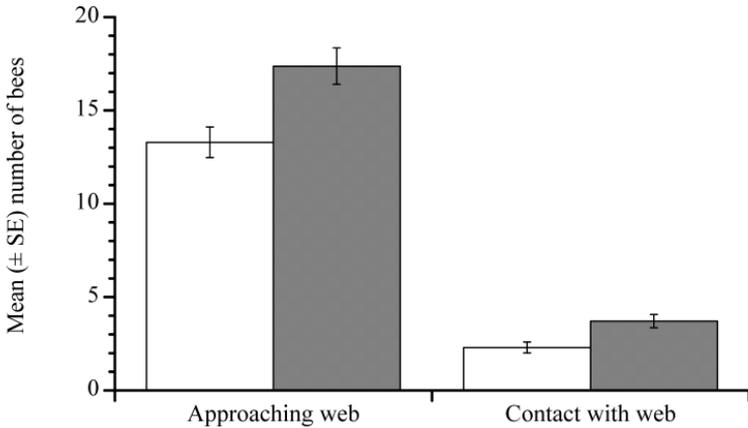
Of the 90 spiders that were released in the field experiments, 38 (19 experimental and 19 controls) were observed for more than one day (multiple observations were averaged per individual). The presence of the yellow coloration significantly affected spider foraging performance ( $F_{1,37} = 4.34$ ,  $p = 0.044$ ). As predicted, the yellow spiders captured more prey than blackened spiders (Table 2). However, the two covariates, web area ( $F_{1,37} = 0.03$ ,  $p = 0.96$ ) and the length of silk decorations ( $F_{1,37} = 0.696$ ,  $p = 0.41$ ) did not significantly affect prey capture rates between the two treatments. Both treatment groups were observed for a similar number of days ( $t_{36} = -1.11$ ,  $p = 0.28$ ; Table 1).

### *Prey response to yellow coloration*

The Harlequin bugs used as potential prey took around 5 minutes to complete a trial (mean  $\pm$  SE =  $321.8 \pm 61.5$  sec) and showed no directional preferences for the left or right hand side of the maze (binomial probability:  $p = 0.59$ ,  $N = 20$ ). There were no differences in the weight of the yellow striped (mean  $\pm$  SE =  $0.20 \pm 0.074$  g) and blackened spiders (mean  $\pm$  SE =  $0.21 \pm 0.076$  g; paired  $t$ -test:  $t_{19} = 0.037$ ,  $p = 0.971$ ). Eighty percent of Harlequin bugs chose the yellow striped spiders (binomial probability:  $p = 0.012$ ,  $N = 20$ ).

The native bees (*Trigona carbonaria*), however behaved differently to the Harlequin bugs in Y-maze experiments. Native bees completed the trials much quicker (mean  $\pm$  SE =  $8.5 \pm 1.2$  sec for the yellow vs black spider choice; mean  $\pm$  SE =  $16.98 \pm 5.6$  sec for the spider vs empty web choice) than the bugs. Native bees had no directional preference in the Y-maze, 12 of the 19 native bees chose the left exit (binomial  $p = 0.36$ ). We found no preference for either yellow striped or black spiders on a web: 47% (9/19) of native bees approached the yellow spiders (binomial  $p = 1.0$ ). There were no differences in the weight of the yellow striped (mean  $\pm$  SE =  $0.25 \pm 0.022$  g) and blackened spiders (mean  $\pm$  SE =  $0.24 \pm 0.021$  g; paired  $t$ -test:  $t_{18} = 1.13$ ,  $p = 0.27$ ). When we offered the native bees a choice between a yellow spider on a web and an empty web, they showed no directional preference (8/18 bees chose the left exit; binomial  $p = 0.81$ ) and showed no preference for the yellow striped spider (11/18 bees approached the spider; binomial  $p = 0.48$ ).

In the field choice experiment, it appears (Figure 4) that fewer bees approached webs with a resident spider, but this was not significant ( $F_{1,99} =$



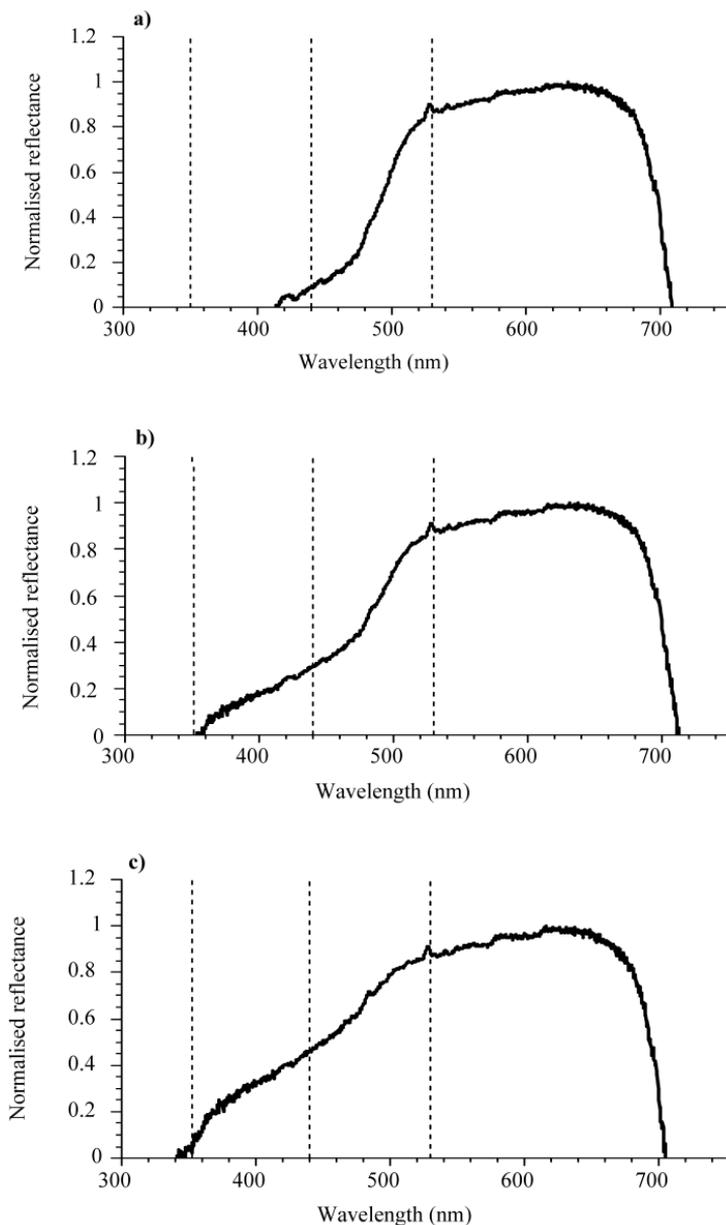
**Figure 4.** The number (mean  $\pm$  SE) of native bees approaching and contacting an empty web (dark bars) or a spider occupied web (white bars).

2.4,  $p = 0.13$ ) while overall bee abundance (covariate) had a significant influence on the number of bees approaching the webs ( $F_{1,99} = 50.9$ ,  $p < 0.001$ ). However, of those bees that approached the webs, more were entangled in the web, making contact with the sticky spirals when a spider was present (Figure 4;  $F_{1,99} = 4.9$ ,  $p = 0.029$ ). However, this was prior to any attack behaviour of the spider. Overall bee abundance (covariate) had a significant influence on the number of bees entangled ( $F_{1,99} = 6.4$ ,  $p = 0.013$ ).

#### *Predator response to yellow coloration*

When we offered a known mantid predator (*Pseudomantis albofimbriata*) a choice between a yellow and a blackened spider on a web, 90% percent of the mantids chose blackened spiders (binomial probability:  $p = 0.021$ ,  $N = 10$ ). The mantids showed no directional bias for the left or right sides of the maze (binomial probability:  $p = 0.117$ ,  $N = 10$ ) and spider weights of the yellow striped (mean  $\pm$  SE =  $0.272 \pm 0.056$  g) and blackened spiders (mean  $\pm$  SE =  $0.265 \pm 0.058$  g) were not significantly different (paired  $t$ -test:  $t_9 = 0.540$ ,  $p = 0.602$ ).

When we offered a different set of mantids the choice between a yellow striped spider on a web and an empty web, there was no directional preference (8/19 mantids chose the left exit; binomial  $p = 0.144$ ). While 68% of mantids approached the yellow spiders, this was not significant (binomial  $p = 0.167$ ,  $N = 19$ ).



**Figure 5.** Reflectance spectra of the dorsal abdominal yellow bands (A, B and C) of *A. keyserlingi* (see Figure 1 for an indication of band location). Hatched lines indicate the maximal sensitivities of the three receptor types in the insect trichromatic vision (UV = ~350 nm, blue = ~440 nm and green = ~530 nm). Normalised reflectance was calculated from 5 spiders with 10 measurements per spider per band.

### *Yellow coloration reflectance*

The first dorsal band (Figure 1, Band A and Figure 5a) starts to reflect light in the visible spectrum between 410 and 420 nm. At approximately 480 nm the reflectance increases quite rapidly until it levels off at  $\sim 510$  until  $\sim 660$  nm and drops off at 710 nm. The second (Band B) and third (Band C; Figure 5) dorsal bands are different because they reflect in the UV range from 360 and 340 nm respectively. Their reflectance levels off at around 500 until 680 nm. By contrast, when the bands were covered by black marker, no light was reflected from 300 to 750 nm.

### **Discussion**

Our field experiment showed that the yellow stripes on *Argiope keyserlingi* are important for prey capture. In the field, under natural conditions, yellow-banded spiders captured more prey than spiders with blackened bands. These results are in accordance with previous studies on colouration in orb-web spiders. Craig & Ebert (1994), Tso et al. (2002) and Hauber (2002) all found that spiders with yellow body colour captured more prey than spiders without yellow body colour.

Our laboratory choice experiments using two different potential prey species however provide ambiguous results. Harlequin bugs moved towards yellow spiders and away from blackened spiders, while native bees showed no preference and approached blackened and yellow spiders at similar rates. This difference is likely due to the response of the prey animals to the Y-maze apparatus, rather than reflect any relevant biological differences. The native bees made their decisions within seconds, rather than the minutes that the Harlequin bugs took. Instead, open choice experiments such as those used by Heiling and colleagues (Heiling et al., 2003; Heiling & Herberstein, 2004) are more appropriate. Consequently, the results of our field experiments, observing native bees approach occupied and unoccupied webs, are more informative. These results indicate that overall, native bees did not detect the spiders in the web from a distance. Yet when it came to negotiating the web, they were more likely to be entangled or making contact with the web when a spider was present, even though the spider did not intervene.

Hymenopteran insects use different colour receptors to detect signals at different distances. Many insects have three colour receptors with peak sensitivities in the UV blue and green (Briscoe & Chittka, 2001). At greater

distances hymenopterans utilise their green receptor to detect a signal, yet at closer distances they use all three colour receptors (UV, blue and green; Girufa & Lehrer, 2001; Spaethe et al., 2001). Thus, it may be that as the native bees in our experiment approached the webs from a distance, using their green receptor, the spider was camouflaged. However, at closer distance, using all three colour receptors, the colour signal created by the spider was attractive leading to higher rates of web contact by native bees.

Similar studies argue that the bright yellow body colour of orb-web spiders actively attract prey to the web rather than renders the spider cryptic (Craig & Ebert, 1994; Hauber, 2002; Tso et al., 2002). The mechanism of attraction could be high levels of UV reflection from the yellow bands and spots (Craig & Ebert, 1994; Tso et al., 2002). In honeybees, the UV receptor is almost 16 times more sensitive than the blue and green receptors (Helfersen, 1972). Thus less UV light is required to excite the receptor. The yellow bands of *A. keyserlingi* in our experiments also reflected high levels of UV light, especially bands B and C. This would suggest that an attractive effect is possible. However, UV light is not the only colour that insects detect and show preferences for (Briscoe & Chittka, 2001; Kevan et al., 2001). In fact, many flowers are 'bee white' only reflecting in the blue and green, but not in the UV (Kevan et al., 1996). Many insects, such as butterflies use the green colour to identify suitable oviposition sites (Kelber, 2001). Innate colour preferences have also been recorded in butterflies for the colours yellow and to some extent blue and purple (Weiss, 1997).

Disruptive colouration works best when the colour patterns extend to the edge of the body, rather than being located centrally on the body (Cuthill et al., 2005). The bands on the dorsum of *A. keyserlingi* are also extended to the edge of the spider body, making them suitable mechanisms for disruptive colouration. Our data clearly show that the yellow bands on the abdomen of *A. keyserlingi* are important in capturing prey. The main mechanism, especially at a distance, may be crypsis via disruptive colouration (Merilaita, 1998), however, we can not discount a degree of attraction at close proximity to the web.

Tso et al. (2002) suggest that the attractive yellow coloration in the golden orb-web spider (*Nephila maculata*) may also attract the attention of predators, such as wasps and birds see also (Craig et al., 2001). The cost of increased exposure to predators may explain why in *N. maculata* colouration is polymorphic with some individuals bearing yellow dots on the abdomen

while others are melanic with a dark green abdomen (Tso et al., 2002). Unlike other spiders (e.g., Tso et al., 2002; Heiling et al., 2003) the yellow stripes on the abdomen of *A. keyserlingi* are not polymorphic, although they may vary in size between individuals. In our study, predatory mantids preferred blackened spiders to yellow spiders, suggesting that the yellow stripes do not attract predators. As with the prey response experiment, the coloration of *A. keyserlingi* may achieve predator deterrence by two mechanisms. The coloration may be disruptive and thereby rendering the spider less visible to predators, or it may aposematic, advertising danger to predators (Lindstrom, 1999; Endler & Mappes, 2004; Merilaita & Tullberg, 2005). When we offered mantids the choice of a yellow spider versus an empty web, there was no preference for the spiders, suggesting the mantids were unable to detect them. This supports a crypsis function, perhaps via disruptive colouration that obscures the outline of the spiders, but there is no evidence for aposematism.

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