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## Ultraviolet is a more important cue than reflection in other wavelengths for a jumping spider to locate its spider prey

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Keywords: Argiope versicolor orb-web spider Portia labiata short-wavelength ultraviolet web decoration Many orb-web spiders put silken decorations that reflect ultraviolet (UV: <400 nm) light in their web. The function of web decorations has been extensively studied: they may increase foraging success or reduce predation risk, but can also be a liability for the web-building spiders. Earlier studies have shown that the reflectance of silken decorations in UV helps an araneophagic jumping spider, *Portia labiata*, locate and prey on a web-decorating spider, *Argiope versicolor*. However, it is unclear whether the reflectance of silken decorations in UV is more important as a cue than reflectance in other wavelengths (400–700 nm) for *P. labiata* to locate the web-building spiders. We investigated the relative importance of reflection of web decorations at different wavelengths in assisting *P. labiata* in locating its prey, *A. versicolor*. Portia labiata was given a choice of four webs with cruciform silk decorations built by *A. versicolor*, the appearance of which was manipulated using coloured filters that selectively blocked UV, short-wavelength (SW: 400–500 nm), medium-wavelength (MW: 500–600 nm) and long-wavelength light (LW: 600–700 nm). Significantly fewer *P. labiata* preferentially approached the decorated webs from which the reflectance in UV was blocked than webs from which the reflectance in SW, MW and LW was blocked. These results suggest that the reflectance of decorations in UV is a more important visual cue than short, medium and long wavelengths for *P. labiata* to locate the decorated webs.

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Many animals are known to have eyes that possess photoreceptors sensitive to ultraviolet (UV: <400 nm) light (reviewed in Tovée 1995), and numerous studies have demonstrated that these animals use UV as cues in inter- and intraspecific communication (Tovée 1995; Cuthill et al. 2000). This has led to the hypothesis that UV may often be more important than other spectral wavelengths in animal communication. This hypothesis, however, remains controversial (Stevens & Cuthill 2007). Most recent empirical and theoretical studies have mainly focused on the role of UV in mate choice, particularly in birds (Hunt et al. 2001; Hausmann et al. 2003; Eaton 2005; Håstad et al. 2005; reviewed in Stevens & Cuthill 2007). Animals may also use UV as cues in foraging (reviewed in Tovée 1995; Honkavaara et al. 2002), and empirical studies have demonstrated this not only in birds (Viitala et al. 1995; Church et al. 1998; Hunt et al. 2001; Siitari et al. 2002), but also in other animals, including spiders (Chittka 2001; Théry & Casas 2002; Heiling et al. 2003, 2005; Li & Lim 2005; Théry et al. 2005).

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Many food items such as fruits and flowers absorb, scatter or reflect strongly in UV (Silberglied 1979; Burkhardt 1982; Willson & Whelan 1989; Altshuler 2001). In contrast, many types of leaves, bark and soil, which serve as the natural backgrounds for food items, reflect no or little UV (Endler 1993; Finger & Burkhardt 1994), increasing the contrast between the food item and its background (Regan et al. 1998; Hausmann et al. 2003). Thus, UV cues may enhance a predator's ability to detect prey (Tovée 1995). Many terrestrial arthropods such as insects (e.g. Lepidoptera) and spiders, which are potential prey for many predatory arthropods, reptiles and birds, also reflect in UV (Silberglied 1979; Vane-Wright & Boppre 1993; Oxford & Gillespie 1998; Lim & Li 2006b; Li et al. 2008a). Recent studies have provided demonstrations of the effects of UV cues on the foraging behaviour of predators (Viitala et al. 1995; Church et al. 1998; Siitari et al. 1999, 2002; Honkavaara et al. 2002; Théry & Casas 2002; Heiling et al. 2003, 2005; Li & Lim 2005; Théry et al. 2005). However, whether the reflectance in UV is more important as a cue than the reflectance in other wavelengths in the foraging of a predator for prey is poorly understood (Maddocks et al. 2001).

A recent study in which different parts of the spectrum (300–700 nm) corresponding to the different single cone types were removed showed that the reflectance in UV is not more important as

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#### METHODS

Study Species

finches, *Taeniopygia guttata* (Maddocks et al. 2001). However, there is considerable variation among species in the abundance of photoreceptor types, and this relates to the ecology of the species, such as the light characteristics of the foraging environment (Hart 2001). More studies are needed to investigate systematically the relative importance of different photoreceptors in various species of predators with different colour visual systems so as to determine whether the reflectance in UV as a cue is more important than human-visible colours in assisting predators in detecting prey. In this study, we investigated whether the UV reflectance of silken web decorations built by *Argiope versicolor*, an orb-web spider (Araneidae), is more important as a cue than reflectance in other wavelengths of decorations for an araneophagic jumping spider, *Portia labiata* (Salticidae), to detect the web-decorating spiders.

a cue in foraging than reflections in other wavelengths in zebra

Many orb-web spiders, including A. versicolor (Seah & Li 2002), add conspicuous silken decorations to their webs (Herberstein et al. 2000). These decorations reflect light ranging from UV to humanvisible wavelengths (300-700 nm; e.g. Herberstein et al. 2000). As a visual cue, silken decorations make the web conspicuous to both prey and predator (but see Blackledge 1998; Blackledge & Wenzel 1999, 2000). Therefore, silken decorations have been hypothesized to increase a spider's foraging success by attracting UV-oriented insects to the webs and/or reduce predation risk by concealing or by increasing the apparent size of the spider (reviewed in Herberstein et al. 2000). However, building web decorations is also costly because, as a visual signal, web decorations may be exploited by unintended predators such as the jumping spider P. labiata (Seah & Li 2001), the praying mantis Archimantis latistylus (Bruce et al. 2001) and wasps (Cheng & Tso 2007). Salticids are well known for their complex eyes and spatial acuity (Land 1969; Blest et al. 1990; Land & Nilsson 2002) and their ability to discriminate visually between different prey, predators and conspecifics (Harland & Jackson 2004; Cross & Jackson 2006). Although colour vision has been studied in only four salticid species, there is considerable interspecific variation in the numbers of photoreceptors in their principal eyes that are sensitive to different wavelengths. Phidippus regius has three photoreceptors (360, 532 and 370 + 525 nm; DeVoe 1975), *Menemerus confusus* has four (360, 480-500, 520-540 and 580 nm; Yamashita & Tateda 1976), Plexippus validus has two (360 and 520 nm; Blest et al. 1981) and Maevia inclemens has photoreceptors sensitive to UV and green (520-550 nm) and possibly cells with peak sensitivity between 400 nm and 530 nm (Peaslee & Wilson 1989). Other species are known to have the ability to distinguish and respond to different colours (Nakamura & Yamashita 2000), including UV (Lim & Li 2006a; Lim et al. 2007, 2008; Li et al. 2008b).

Recent studies have provided empirical evidence that P. labiata is more often attracted to A. versicolor webs with silken decorations (Seah & Li 2001). Li & Lim (2005) showed that blocking the UV reflectance of silken decorations built by A. versicolor significantly reduced P. labiata's tendency to approach the decorated webs. However, it is unclear whether the UV reflectance of silk decorations is more important as a cue than the reflectance in other wavelengths of decorations for *P. labiata* to locate the decorated webs built by A. versicolor. Here, we addressed this question by experimentally removing the reflectance of silken decorations in UV and other human-visible wavebands within the visual spectral range of a salticid. We predicted that if the reflectance in UV from web decorations is more important as a cue than the reflectance in other human-visible wavelengths for P. labiata to locate the decorated webs, then the removal of the reflectance in UV from the silk decorations built by A. versicolor would affect the ability of P. labiata to detect the decorated webs more than the removal of any other range of wavelengths (blue, yellow or red).

The individual *P. labiata* (hereafter *Portia*) and *A. versicolor* (hereafter *Argiope*; Fig. 1) used in this study were collected as needed from the field in Singapore where *P. labiata* and *A. versicolor* are sympatric. Spiders were kept individually in plastic cages (for *Portia*, plastic cylindrical cage:  $100 \times 80$  mm; for *Argiope*, plastic frame cages with removable glass sides:  $200 \times 200 \times 50$  mm), which were housed in a laboratory with controlled environmental conditions (temperature:  $25 \pm 1$  °C; relative humidity: 80-90%; photoperiod: 12:12 h light:dark, lights on: 0800 hours; light intensity:  $332.8 \pm 4.3$  lx). Forty-eight adult *Portia* and 20 adult *Argiope* females were used in this study.

Adult *Argiope* females usually build cruciform (cross-like) silken decorations with one, two, three or four arms (Seah & Li 2002). In this study, only cruciform decorations with four arms were used (Fig. 1). Since web characteristics might influence *Portia*'s behaviour, we obtained 192 webs and divided them into four groups at random (see below). For each web we took several measurements from which we estimated capture area, total capture thread length and mean mesh size using the same procedure as described in Li & Lee (2004) and using the same formulae used in Heiling et al. (1998) and Tso (1996). A MANOVA revealed no significant differences in any web characteristic or the total web decoration length between the four experimental groups (Wilks's  $\lambda = 0.925$ ,  $F_{12,490} = 1.223$ , P = 0.264; Table 1). No webs were used more than once. *Portia* were kept without food for a week prior to the trials.

Illumination was provided by 10 equidistant (10 cm intervals) 1.8 m, 110 W Truelite tubes (Voltarc Ultra Light, Voltarc Technologies Inc., Waterbury, CT, U.S.A.), suspended 1 m above the chamber, which were powered by 120 V 50/60 Hz electronic ballasts (SUPER-TEK, Naturallighting.com, Houston, TX, U.S.A.). The main purpose of these light tubes was to provide a stable full-spectrum illumination (300–700 nm), which includes the UV and human-visible wavelengths typical of natural light habitats (Endler 1993; see Figure 2a in Maddocks et al. 2001).

## **Experimental Procedure**

All trials were carried out in an apparatus that was cross-shaped (Fig. 2) as described in Bennett et al. (1996) and Maddocks et al. (2001). The apparatus mainly consisted of five chambers: a central chamber with four adjacently located chambers of



Figure 1. Adult Argiope versicolor female and its cruciform decorations with four arms.

| $Mean \pm 5E$ of characteristics of webs built by adult Argiope versicolor used in the choice tests |           |           |          |          |                                    |  |  |  |
|---|-----------|-----------|----------|----------|------------------------------------|--|--|--|
|   | UV-       | SW-       | MW-      | LW-      | ANOVA                              |  |  |  |
| CA (mm <sup>2</sup> )   | 1164±30   | 1166±32   | 1123±26  | 1095±25  | F <sub>3,188</sub> =1.465, P=0.226 |  |  |  |
| MM (mm)   | 3.0±0.1   | 3.1±0.1   | 3.0±0.1  | 2.9±0.1  | F <sub>3,188</sub> =0.811, P=0.489 |  |  |  |
| CTL (m)   | 34.5±0.9  | 33.9±0.6  | 33.1±0.6 | 33.4±0.6 | F <sub>3,188</sub> =0.722, P=0.540 |  |  |  |
| TDL (cm)  | 5 89+0 14 | 5 89+0 13 | 584+013  | 547+014  | $F_{2,199}=2.189 P=0.091$          |  |  |  |

Table 1Mean  $\pm$  SE of characteristics of webs built by adult Argiope versicolor used in the choice tests

CA: capture area; MM: mean mesh size; CTL: total capture thread length; TDL: total decoration length. Also shown is a summary of an ANOVA testing the variations in web characteristics and web decoration of web used in four light-filtering conditions (UV–, SW–, MW– and LW–).

identical dimensions. All inner surfaces were covered by a thin layer of black matt vinyl sheeting (ORACAL 651 Intermediate black, ORACAL, Black Creek, GA, U.S.A.) to minimize any background reflection. We acknowledge that actual perceived colour signals from 'black' backgrounds might be very different from colour signals from natural backgrounds (i.e. green vegetation), but this provides a maximal colour contrast between the full-spectrumreflecting web decoration and the 'black' background. The filters and test procedures used here were similar to those described in Hunt et al. (2001) and Maddocks et al. (2001).

We used four types of coloured filters that are designed to block particular wavelengths of the spectrum that correspond approximately to the sensitivities of *M. confusus*'s four photoreceptor classes (e.g. 360, 480–500, 520–540 and 580 nm; Yamashita & Tateda 1976). The colour visual system of *Portia* spp. is unknown, although UV is known to affect *Portia*'s behaviour (Li & Lim 2005). *Menemerus confusus* was chosen as a proxy for *P. labiata* because it is known to have four types of photoreceptors (Yamashita & Tateda 1976). Some studies have found fewer receptor types for other salticid species (DeVoe 1975; Yamashita & Tateda 1976; Blest et al. 1981; Peaslee & Wilson 1989) but more evidence is needed to confirm that these species do not have four types of photoreceptors. The rationale is that if some types of photoreceptors that are



**Figure 2.** Top view of the experimental set-up, consisting of a central chamber and four stimulus chambers. One *Portia* (predator), held in the glass vial (indicated by v) connected to the bottom of the centre of the central chamber, was allowed to approach decorated webs held onto an opaque black frame, each vertically placed in one of the stimulus chambers. Colours of webs were manipulated by the various colour filters which were horizontally placed over each stimulus chamber (see Fig. 3). Full-spectrum-transmitting glass dividers placed in front of each web permitted *Portia* to view the decorations illuminated under different filters but prevented any physical and chemical contact.

present in *M. confusus* were absent in *P. labiata*, we could expect that blocking the reflectance from web decorations to which these photoreceptors are sensitive would not affect how *P. labiata* used such signals to locate the webs. However, if we used a species with fewer photoreceptor types as a proxy for *P. labiata*, we might not fully understand whether UV light might be more important than the wavelengths that were not tested.

Each of the four types of filters was placed horizontally above each of the four stimulus chambers. In this way, each filter created a different illumination (i.e. light environment; Fig. 3) in each chamber that held a decorated web (Fig. 4), allowing us to manipulate how the web decorations appeared to Portia. These filters were then classified according to the spectral regions of the wavebands that were removed: UV-blocking (UV-; Photonitech Pte Ltd, Singapore), short-wave-blocking (SW-; Rosco Supergel filter 14; Rosco, Stamford, CT, U.S.A.), medium-wave-blocking (MW-; Rosco Supergel filter 339) and long-wave-blocking (LW-; Rosco Supergel filter 73). Using these filters that blocked UV wavelengths, short wavelengths (SW), medium wavelengths (MW) and long wavelengths (LW), we examined the effects of the presence and absence of these hues on Portia's tendency to approach the decorated webs. However, different filters have different quantum fluxes (the total amount of light transmitted between 300 nm and 700 nm or, more or less, what is usually meant by intensity; see Bennett et al. 1996), which may also influence how Portia locate the webs. To control for the effects of the changes in intensity, we adjusted the attenuation of the filters using multiple layers of filter material such that the filters used for each chamber were approximately similar in the transmission of total quantum flux (the exact ratios of quantum flux for the four treatments were: UV-: SW-: MW-: LW-: 1.23: 1.09: 1.12: 1.00; see Hunt et al. 2001; Maddocks et al. 2001).

Each trial consisted of two consecutive 30 min test phases with two 5 min acclimation periods during which the test Portia was held in an opaque vial. (1) Control phase: no test web was present in any stimulus arm of the cross chamber. The rationale for this was to determine whether Portia, independent of seeing web decorations, was more inclined to enter particular chambers. (2) Experimental phase: Portia was given a choice of four light conditions to approach. Before commencing the trial, one test Portia was placed inside an opaque black vial (5 cm in height and 1 cm in diameter) stopped with a cork, with the opening of the vial in the central chamber. The test spider was kept in the vial for 5 min before the cork was removed. Usually within 1 min after removal of the cork, the test Portia climbed up the vial and into the central chamber of the apparatus, where it could view the four stimulus chambers, each of which contained one stimulus web with a cruciform decoration. Once Portia had climbed up and reached the top of the vial (i.e. the base of the central chamber), where it could see all four arms of the cross chamber, the trial started. Both of the test phases ended either when the Portia made a choice by entering one of the arms, or when 30 min had elapsed, whichever came first. The spider was placed back into the vial after the control phase and given another 5 min acclimation period before the experimental

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Figure 3. Transmission of the four filters used. (a) UV-blocking (UV-) filter; (b) yellow-coloured filter blocking short wavelengths (SW-); (c) pink-coloured filter blocking medium wavelengths (MW-); and (d) violet-coloured filter blocking long wavelengths (LW-).

phase. We also wiped the chamber with 70% ethanol to ensure that all secretions or pheromone deposited by the previous Portia was removed. No spider was used in more than one two-phase test. A total of 48 trials were conducted. A chi-square test for goodness of fit was performed for the frequency data from both the control phase and the experimental phase. However, when analysing the frequencies from the experimental phase, we used the frequencies from the control phase as the expected values and the frequencies from the experimental phase as the observed values, and a chisquare test for independence was used. Then we carried out four chi-square tests for independence to compare the frequencies of Portia approaching the webs with the decorations between the control and experimental phase for each light condition to determine the effects of the removal of particular wavelengths (i.e. UV-, SW-, MW- or LW-) reflected from silken decorations. For statistical analyses we use SPSS 19.0 (SPSS Inc., Chicago, IL, U.S.A.).



**Figure 4.** Normalized reflectance spectra of the cruciform decorations built by *Argiope versicolor* measured in the chambers without filters (solid line) and with ultravioletblocking (UV–), short-wave-blocking (SW–), medium-wave-blocking (MW–) and long-wave-blocking (LW–) filters (dashed lines).

## RESULTS

In the control phase, during which there were no webs in the stimulus chambers, there was no significant difference in how often *Portia* entered particular chambers (chi-square test for goodness of fit:  $\chi^2_{0.05,3} = 0.67$ , N = 48, P = 0.88; Fig. 5). However, in the experimental phase, blocking the particular reflectance from the web decorations significantly affected *Portia*'s tendency to approach the webs (chi-square test for goodness of fit:  $\chi^2_{0.05,3} = 17.833$ , N = 48, P < 0.0001; Fig. 5). Pairwise tests showed that fewer *Portia* approached the decorated webs when the reflectance in UV from the decorations was blocked (i.e. UV–) than when the reflectance in MW (i.e. MW–;  $\chi^2_{0.05,1} = 13.37$ , N = 27, P < 0.0001) and in LW wavelengths (i.e. LW–;  $\chi^2_{0.05,1} = 5.556$ , N = 18, P = 0.018). There was also a significant difference in *Portia*'s tendency to approach the webs between SW– and MW– conditions ( $\chi^2_{0.05,1} = 8.533$ , N = 30, P = 0.003). However, there was also no significant difference in *Portia*'s tendency to approach the webs between UV– and



**Figure 5.** The number of *Portia* (N = 48) approaching the webs with silken decoration at each filter-treated arm of the chamber: ultraviolet-blocking (UV–), short-wave-blocking (SW–), medium-wave-blocking (MW–) and long-wave-blocking (LW–). Open bar: control phase (i.e. webs were not present); solid bar: experimental phase.

SW– conditions ( $\chi^2_{0.05,1} = 0.818$ , N = 11, P = 0.366), between SW– and LW– ( $\chi^2_{0.05,1} = 2.333$ , N = 21, P = 0.127) and between MW– and LW– conditions ( $\chi^2_{0.05,1} = 2.189$ , N = 37, P = 0.139).

When we used the frequencies from the control (no webs present) as the expected values and the frequencies from the experimental trials (webs present) as the observed values, the removal of a particular range of wavelengths had an overall significant effect on how often *Portia* approached the webs with decorations (chi-square test for independence:  $\chi^2_{0.05,3} = 12.53$ , N = 48, P = 0.006; Fig. 5). The removal of the UV (UV–) significantly reduced the number of *Portia* approaching the webs under UV– ( $\chi^2_{0.05,1} = 4$ , N = 16, P = 0.046). The removal of the medium wavelengths (MW–) increased the number of *Portia* approaching the webs by 64%, but this increase was not significant ( $\chi^2_{0.05,1} = 2.189$ , N = 37, P = 0.139). The removal of short wavelengths (SW–;  $\chi^2_{0.05,1} = 0.529$ , N = 17, P = 0.467) and long wavelengths (LW–;  $\chi^2_{0.05,1} = 0.154$ , N = 26, P = 0.695) had no significant effects on the number of *Portia* approaching the webs.

## DISCUSSION

Previous work demonstrated that blocking the reflectance in UV (i.e. UV-) from silken decorations spun by A. versicolor results in fewer P. labiata approaching the decorated webs, compared to normal full-spectrum (UV+) decorated webs (Li & Lim 2005). The experiment reported here, which involved simultaneously presenting the decorated webs under UV-, SW-, MW- and LWconditions, demonstrates that the reflectance in UV from silken decorations built by Argiope is a more important visual cue than reflections in short, medium and long wavelengths in assisting Portia in locating Argiope. As expected, fewer Portia initiated predatory sequences when the webs with silk decorations were illuminated under a UV-blocking (UV-) filter, but more Portia chose the webs lacking medium wavelengths (MW-), whereas the removal of the short and long wavelengths (LW-) did not seem to affect Portia's response, although there was no significant difference in Portia's tendency to approach the decorated webs between UV- and SW- conditions. Thus, under the experimental conditions used here (e.g. artificial light and black background), UV as a visual cue is relatively more important than human-visible wavelengths for Portia in locating Argiope. The colour signal of black background used in the laboratory is very different from that (i.e. green vegetation) in the natural habitat of spiders; thus Portia may respond very differently to the treatments created in the laboratory and to colour signals in nature. Future studies should repeat the experiments using natural background to see whether such a conclusion is still valid.

Although the light conditions created by filters that were used in our experiments may have affected the ability of *Portia* to detect and approach the webs, the results from the control phase (i.e. in the absence of web decorations) showed that *Portia* displayed no significant discrimination among the empty chambers. This reveals that *Portia*'s perception of colour signals from web decorations is independent of the differences in the illumination or the light environment of the different chambers. Moreover, none of the apparatus backgrounds in the experiments reflected UV, SW, MW or LW light, yet fewer *Portia* approached the webs with the UV wavelengths from the decorations blocked. Other factors (e.g. web area, mesh size and web symmetry) may affect the discrimination of *Portia* (Jackson 1995). However, in our study we ensured that there were no significant differences in the web characteristics, in particular the size of the cruciform decorations (Table 1).

In the experimental phase, *Portia*'s tendency to approach the four arms was significantly different. The web from which the UV light was filtered was the least approached, and the web from

which the reflectance in medium wavelengths was blocked was the most approached. As these colour-filtered silken decorations differed most in the UV transmission (Fig. 4), Portia generally more often approached the decorated webs with UV reflection (from highest to lowest UV refection: MW-, LW-, SW-) over those without UV reflection (UV-; Fig. 4), as has been reported in a previous study (Li & Lim 2005). The reason for this may be that the UV reflection of the decorations makes the webs appear more conspicuous or brighter to Portia, so that they can be easily distinguished and located. A few species of salticids are known to have cells sensitive to blue, red and, in particular, UV and green in their principal eyes (Land 1969; DeVoe 1975; Yamashita & Tateda 1976; Blest et al. 1981; Peaslee & Wilson 1989), which enable them to distinguish colours (Nakamura & Yamashita 2000). A possible reason why MW-blocked (MW-) webs were the most approached among the four treatments may be because, under these conditions, only UV-sensitive cells are stimulated. In this case, the UV waveband, without the accompanying blue and green wavebands, appeared to stand out more to the Portia. In other words, the contrast of what the Portia saw increased. The same reason for MW- webs may also be applied to the LW- webs, which were the second most approached when UV reflection was present. Another reason why the LW- webs were the second most approached may be that Portia are unable to see LW (red) light. Red receptors have only been reported in the salticid M. inclemens (Peaslee & Wilson 1989), but have not been confirmed in the other salticids that have been examined so far (Land 1969; DeVoe 1975; Yamashita & Tateda 1976; Blest et al. 1981). Even if Portia could see long wavelengths, UV may be a better medium for signalling over short distances because it is more rapidly degraded over long distances than are longer wavelengths owing to particle scatter (e.g. Hausmann et al. 2003). Finally, UV signals may have evolved via sensory exploitation to use a pre-existing sensory bias for them (Ryan 1990; Endler & Basolo 1998). It has been suggested, for example, that *P. regius* is particularly sensitive to UV wavelengths of light compared with other wavelengths (DeVoe 1975) and that salticids evolved UV vision in order to find prey (Li & Lim 2005) and/or mates (Lim et al. 2007, 2008; Li et al. 2008b). In either case, UV signalling would be favoured because salticids are biased to such signals (Ryan 1990; Endler & Basolo 1998).

Some studies have argued that silk decorations are cryptic to prey or predators because they are a part of flat, broadband reflectance (Blackledge 1998; Blackledge & Wenzel 2000). However, recent studies on the colour contrast of silk decorations have shown that silk decorations built by *Argiope* spiders have a strong contrast against a natural green background and they are therefore visible to hymenopteran prey and bird predators over both short and long distances (Bruce et al. 2005). In addition, if silk decorations are cryptic because they are a part of flat, broadband reflectance, the removal of any wavelengths should have had the same effect on *Portia*'s perception for decorated webs. Our results, however, showed that the removal of UV significantly reduced *Portia*'s tendency to approach the decorated webs. This suggests that *Portia* are able to distinguish colour, including UV (Li & Lim 2005).

Although our study demonstrates the greater importance of UV than short, medium and long wavelengths for *Portia* foraging on spiders in webs with silken decorations, whether the reflectance in UV is more important as a cue compared with human-visible wavelengths may vary from species to species. For example, in an experiment with zebra finches using the procedure we followed, Maddocks et al. (2001) showed that UV light is less important than long-wave light for zebra finches foraging for seeds, as this species' preference for seeds was apparently most affected by the removal of long wavelengths (i.e. LW–). The relative importance of

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particular wavelengths may also depend on the context. Hunt et al. (2001) found that UV is not more important than other wavelengths in mate choice in zebra finches; instead, short-distance mate choice in zebra finches is a long-wavelength-dominant task. The inconsistent findings between birds and salticids may be because, for birds, signals reflecting relatively less light of shorter wavelengths are less likely to be affected by the manipulation of UV light than are signals that reflect fewer long wavelengths (Banks 2001; Stevens & Cuthill 2007). In salticids, UV photoreceptors may be more sensitive than green receptors, and thus UV cues may be especially detectable to these species. Another possibility for the inconsistent findings among studies of birds and salticids may be because different backgrounds (and thus different chromatic properties) were used in different studies.

The relative importance of UV light as a cue during predator—prey interactions has strong implications for future studies on colour perception during foraging and finding mates in salticids, and indeed in animals in general. Observations of behaviour under light that lacks a UV component may result in an incomplete assessment of inter- and intraspecific interactions if salticids have UV vision and exhibit UV colour patterns and sexual UV dimorphism (Lim & Li 2006a, b; Lim et al. 2007, 2008; Li et al. 2008a, b). Therefore, we should consider all of the wavelengths to which salticids are sensitive and all of the light environments (i.e. ambient light and background) in which behaviour occurs to carry out an accurate investigation of inter- and intraspecific interactions.

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## Appendix

### Silken decoration colour

We calculated the photon catches for each type of Portia photoreceptor when viewing web decorations under each filtering light condition to relate any effects of Portia's behavioural responses to the likely influence of filters on colour perception. To do so, we used a spectrophotometer to measure the spectral reflectance of the decorations in eight webs with the filters above them according to the filtering light conditions (Fig. 4). These data were used together with data on the spectral sensitivities of M. confusus's four types of photoreceptors, which were chosen as a proxy for Portia as described above: UV (maximum sensitivity at 360 nm), blue (480-500 nm), green (520-540 nm) and yellow cells (580 nm; Yamashita & Tateda 1976). We used the program AVICOL (this is a free program available from D. Gomez at dodogomez@yahoo.fr) to calculate the photon catches for each photoreceptor type. We then performed two-way ANOVAs with photoreceptor type and light condition as two main factors to determine the variations in the amount of photon catches among the receptors and among the filtered light conditions. Tukey's honestly significant difference, HSD, paired comparisons were performed if ANOVAs showed significant differences. SPSS 19.0 for Mac was used.

The calculated photon catches by salticid SW, MW and LW photoreceptors elicited by silk decorations were always higher than those of the UV photoreceptor in all four light conditions (Fig. A1, Table A1). The photon catches for all four types of salticid photoreceptors were higher under the UV–, SW– and LW– light conditions than the MW– light condition except that the photon catches of the UV receptor in UV– and SW– light conditions were lower than that of UV receptors in the MW– light condition (Table A1), but there was no significant difference in the photon catches among the UV–, SW– and LW– filter conditions (Tukey's HSD: P > 0.05 all paired comparisons; Table A1, Fig. A1). There was a significant effect of interaction between *Portia* photoreceptors and the filtering light conditions on the photon catches (Table A1).



**Figure A1.** *Portia*'s photon catches calculated for each photoreceptor (UV, SW, MW, LW) under each filtering condition (UV–, SW–, MW–, LW–).

#### Table A1

Summary of two-way ANOVA testing the effects of *Portia* photoreceptor type and filtering light condition on the photon catches of each *Portia* photoreceptor (UV, SW, MW or LW)

| Source                                  | df  | Mean square | F       | Р        |
|---|-----|-------------|---------|----------|
| Intercept                               | 1   | 76 437.207  | 485.997 | < 0.0001 |
| Photoreceptor type                      | 3   | 4578.769    | 29.112  | < 0.0001 |
| Filter light condition                  | 3   | 2980.889    | 18.953  | < 0.0001 |
| Photoreceptor*filter<br>light condition | 9   | 505.253     | 3.212   | 0.002    |
| Error                                   | 112 | 157.279     |         |          |
| Total                                   | 128 |             |         |          |