Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes

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Summary

Many orb-weaving spiders in the tropics forage in open sites during the day and some of them have both bright and dark colourations. The conspicuous UV-reflective colour markings of these spiders have been reported to be attractive to visually oriented prey and thus could increase the spiders' foraging success. Using a combination of field and laboratory studies, we examine whether or not the body colouration of orb-weaving spiders exhibits optical properties that are attractive to insect prey from the viewpoint of insect visual physiology. We compared the prey interception rates and colour contrasts of the typical and melanic morphs of the giant wood spider, *Nephila pilipes*. Results of the field study showed that the typical morph caught significantly more insects than the melanic morph. Colour contrasts calculated from spectral reflectances of the background and body surface of spiders showed that the brightly coloured body parts of the typical morph exhibited rather high values, but those of the dark body parts were below the discrimination threshold. The differential colour contrasts of body parts generated a visual signal unlike that of a spider but rather like certain forms of food resources. On the other hand, the melanic morphs did not have bright colouration and the colour contrasts of every part of the body were significantly higher than the threshold, making the contour of spiders quite clear to bees.

Key words: colour contrast, visual signal, *Apis mellifera*, *Nephila pilipes*, polymorphism.

Introduction

Various diurnal orb-weaving spiders in the tropics exhibit both bright and dark markings, and recently these bright markings have been considered to be important in predator–prey visual interactions. Many spiders are active at night and their colourations are usually dark, grey or brown, to reduce the spiders' visibility during daytime (Oxford and Gillespie, 1998). However, some orb-weaving spiders of the families Araneidae and Tetragnathidae forage during the day and many of them exhibit conspicuous colour patterns (Yaginuma, 1986). The bright colour patterns of these diurnal orb-weaving spiders have recently been proposed to be able to increase foraging success by providing attractive visual signals to prey. For example, the brightly coloured dorsum of *Argiope argentata* in Panama was demonstrated to be more attractive to insects than the spiders' brown ventrum (Craig and Ebert, 1994). The spiny spiders *Gasteracantha foricata* in Australia also exhibit bright colouration on their dorsum. Covering this colouration with paint significantly reduced the spiders' foraging success (Hauber, 2002). The brightly coloured giant wood spider, *Nephila pilipes*, in Asia caught significantly more insects than its melanic conspecifics, and the reason for this was suggested to be the spiders' ultraviolet (UV)-reflecting markings (Tso et al., 2002). However, even though these studies have all demonstrated that the brightly coloured markings of diurnal orb-

weaving spiders helped increase spiders' foraging success by being attractive to insects, it is still not clear how these markings are perceived by prey and why they are attractive.

Many researchers attributed the attractiveness of spiders' body colouration to the UV-reflecting properties. However, insects see by detecting the colour contrast between the objects they are looking at and the background of that object using a combination of several receptor signals (Chittka and Menzel, 1992; Vorobyev and Brandt, 1997; Briscoe and Chittka, 2001). Insects do not rely solely on UV signals but instead use light signals reflected from the objects and backgrounds for visual detection (Kevan et al., 2001). In the honeybee, chromatic vision and achromatic vision are involved in the detection of colour targets, depending on the subtended visual angle of the target. While only contrast to the L (long-wavelength)-receptor is used for detecting targets with subtending small visual angles (Giurfa and Vorobyev, 1998), the chromatic visual system of the honeybee, which receives input from all three photoreceptor types, is responsible for detecting targets with large visual angles (Giurfa et al., 1996, 1997; Niggebrügge and Hempel de Ibarra, 2003). Recently, the way in which hymenopteran insects perceive crab spiders (Family: Thomisidae) on flowers was assessed by calculating the colour contrasts derived from the reflectance spectra of the spiders and

the petals (Chittka, 2001; Théry and Casas, 2002; Heiling et al., 2003). So far, this approach has not been used to assess the visual signals of diurnal orb-weaving spiders. In the present study, we examined how the colour markings of spiders were viewed by insects, by measuring their reflectance spectra, and then calculated the colour contrasts as perceived by hymenopteran insects.

A polymorphic population of the giant wood spider, *Nephila pilipes* (formally *N. maculata*), on Orchid Island, Taiwan had been demonstrated previously to exhibit colour-associated foraging success (Tso et al., 2002). Typical morph female *N. pilipes* have an olive-green prosoma and a yellowish-black abdomen decorated with a transverse white band, two longitudinal yellow bands and numerous yellow spots (Fig. 1). However, some of the females are totally dark,
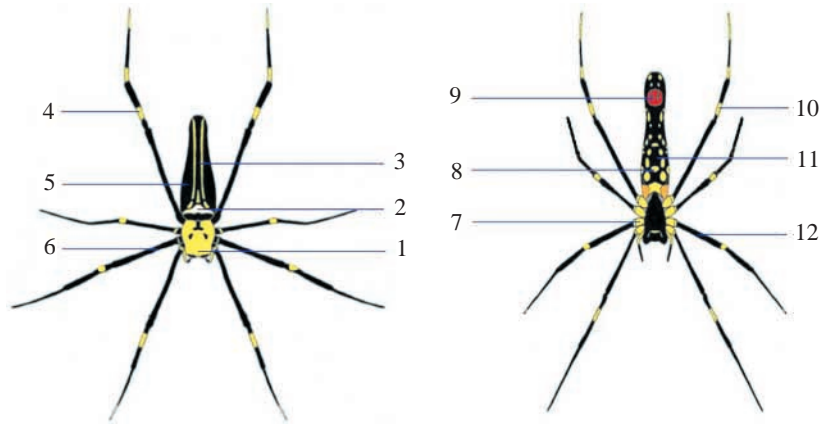

Fig. 1. Schematic drawings illustrating the colour markings of the typical morph giant wood spider *Nephila pilipes*. Reflectance spectra were recorded from the areas specified (see Figs 5, 6).

and allozyme data has demonstrated that both morphs are members of an interbreeding population (Tso et al., 2002). A previous study on this population has shown that the typical morphs caught almost twice as much prey as the melanic morphs (Tso et al., 2002). In the present study, we compared the prey interception rates of two morphs of *N. pilipes* again to confirm whether or not a bright colouration will render a higher foraging success. Moreover, we calculated the colour contrasts of these two morphs in the colour space of honey bees by measuring spectral reflectance of body surfaces and background light environment in the study site to assess how these spiders are perceived by insects.

Materials and methods
Field census of prey interception rate

To examine whether the body colouration of *Nephila pilipes* (Fabricus 1793) may provide an attractive signal to insects, field censuses were conducted between 19 and 30 June 2002 on Chung-Ai Bridge of Orchid Island (22°03′ N, 121°32′ E), Taitung County, Taiwan. Tso et al. (2002) give a detailed description of the study site. We marked the web sites of 18 typical and five melanic morphs of female *N. pilipes* by fastening a tape on vegetation near by. Each day before 08.00 h, we measured the horizontal and vertical web diameters as well as the hub diameter of all marked webs. Catching areas of orbs were calculated by the 'adjusted radii-hub' formula provided by Herberstein and Tso (2000). The marked spiders were monitored once each hour each day between 08.00 h and 18.00 h, and web damage, number and taxonomic order of prey caught by spiders were recorded. The prey interception data fitted well with a Poisson distribution (Pearson χ^2 test, $P<0.05$; Steel et al., 1997). Therefore, we used the Poisson regression to examine the relationship between insect interception rate, catching area and spider morphs. Categorical variables included catching area and spider morphs. Catching areas were ranked according to the following categories: <2000, 2000–3000, 3000–4000, 4000–5000,

5000–6000, 6000–7000, 7000–8000, 8000–9000 and >9000 cm^2. The Poisson model was expressed as:

$$\log \mu_N = \log N(Xi) + Xi\beta , \tag{1}$$

where μ was the expected value, Xi represented catching area or spider morphs, β was probability and N was total number of individuals.

Measurements of light environment and spectral properties

Reflectance spectra of the spiders, the background light environment and the illumination functions of the study sites were used to calculate the colour contrasts perceived by spiders' prey and predators (Chittka et al., 1994). We measured the reflectance spectra of various objects with a spectrometer (S2000; Ocean Optics, Inc., Dunedin, FL, USA). In the study site, giant wood spiders usually hang their webs in the forest understorey in front of dense vegetations. Therefore, the background light environment was estimated by averaging the reflectance spectra measured from green leaves, fallen leaves and bark (N=190 in total) collected from the field census site. The daylight spectrum of the forest understorey illumination was measured at the study site by placing the end of the probe of the spectrometer 5 mm above (90°) the standard white. The measurements were taken every day at hourly intervals from 08.00 h to 18.00 h for three sunny days. The means of these readings were used in the subsequent calculations of colour contrasts. Eight typical and six melanic morphs were brought to the laboratory to measure the reflectance spectra of various areas on their body (Fig. 1). All the reflectance spectrum measurements in this study followed the standard procedures described previously (Tso et al., 2002). The spectral reflectance measurements covered the range from 300 nm to 700 nm (increment 0.3 nm). For each wavelength, we measured reflectance 10 times and we plotted the mean against the wavelength.

Bees were reported to adopt achromatic vision by using the green receptor signal when searching for objects far ahead and to adopt chromatic vision by using green, blue and UV receptor

signals when approaching objects (Giurfa et al., 1997; Spaethe et al., 2001). Heiling et al. (2003) showed that the visibility of crab spiders on flowers to bees varied when different achromatic and chromatic neural channels were adopted. Therefore, colour contrasts of *N. pilipes* viewed by either achromatic or chromatic vision were calculated to assess how different morphs were perceived by bees during different stages of searching.

Calculation of colour contrasts

We calculated the colour contrasts of spiders and decorations by the colour hexagon model of Chittka (1992). To determine photoreceptor excitations for each measured spectra, we used spectral sensitivity functions of photoreceptors of the honey bee, *Apis mellifera* (Briscoe and Chittka, 2001), to determine the photoreceptor excitations for each measured spectra. The relative quantum flux absorbed by each type of photoreceptor, *P*, can be expressed as:

$$P = R \int_{300}^{700} I_S(\lambda)\, S(\lambda)\, D(\lambda)\, d\lambda \,, \qquad (2)$$

where $I_S(\lambda)$ is the spectral reflectance function of the spider colourations or web decorations, $S(\lambda)$ is the spectral sensitivity function of honey bee photoreceptors, and $D(\lambda)$ is the measured daylight illuminating spectrum from the forest understorey. The sensitivity factor, *R*, is determined by:

$$R = \frac{1}{\int_{300}^{700} I_B(\lambda)\, S(\lambda)\, D(\lambda)\, d\lambda} \,, \qquad (3)$$

where $I_B(\lambda)$ is the spectral reflection function of the vegetation background to which the photoreceptors are adapted. When photoreceptors are adapted by the vegetation background, we can assume that the photoreceptors display half their maximum response (Naka and Rushton, 1966). The non-linear transfer function relating the receptor excitation, *E*, with the quantum flux, *P*, follows:

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

The three excitation values in the honey bee's UV, blue and green photoreceptors can be depicted in a three-dimensional photoreceptor excitation space or in the colour hexagon (Chittka, 1996). With the three photoreceptor excitation values plotted at angles of 120°, the *x* and *y* coordinates in the colour plane are given by:

$$x = \sin 60° \, (E_G - E_{UV}) \qquad (5)$$

and

$$y = E_B - 0.5(E_{UV} + E_G) \,, \qquad (6)$$

where E_{UV}, E_B and E_G are the inputs from the three photoreceptors. When calculating the colour contrasts of objects viewed under chromatic vision, signals from all three photoreceptors were used. When calculating the colour contrasts of objects viewed under achromatic vision, only the green photoreceptor signal was used. Euclidean distances (ΔSt) between stimuli are calculated as:

$$\Delta St = \sqrt{(\Delta x)^2 + (\Delta y)^2} \,. \qquad (7)$$

The Euclidean distance (ΔSt) is the colour contrast in the colour space of honey bees. One-sample *t*-tests were used to compare the calculated values with the discrimination threshold for colour contrast detection estimated by Théry and Casas (2002) for honey bees.

Results
Insect interception rates

Among all the captured insects recorded, 49% were Hymenoptera (bees, wasps and ants), 19% were Coleoptera (beetles) and 16% were Diptera (flies). All these insects potentially relied on colour signals for their survival (Briscoe and Chittka, 2001). Results of Poisson regression comparing insect interception rates between different morphs of *Nephila pilipes* recorded from the field census showed that the typical morph intercepted significantly more insects than the melanics (Table 1). Similar to results reported by Tso et al. (2002), typical *N. pilipes* caught twice as many insects as melanics (Fig. 2). Although catching area was quite important in influencing the insect interception rate of *N. pilipes* in Tso et al. (2002), in the present study it was not a significant determinant of the dependent variable.

Reflectance properties and colour contrasts of Nephila pilipes

The daylight illuminating spectrum of the forest understorey

Table 1. *Results of Poisson regression comparing prey interception rates of typical and melanic* Nephila pilipes *on Orchid Island, Taiwan*

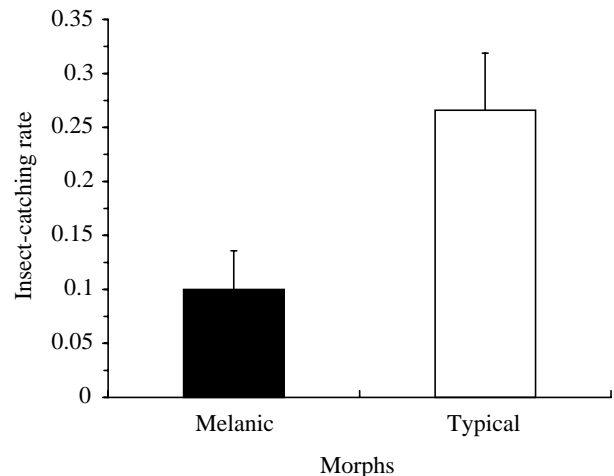| Variables	Mean	SE	χ^2	*P*
Intercept	−7.999	0.6986	131.09	<0.0001
Web	0.0001	0.0001	1.22	0.2697
Morph (typical)	−1.2082	0.6112	3.91	0.0481
Morph (melanic)	0.000	0.000	–	–

Fig. 2. Mean (± S.E.M.) insect interception rates (no. of insects per hour per web) of different morphs of *Nephila pilipes*.
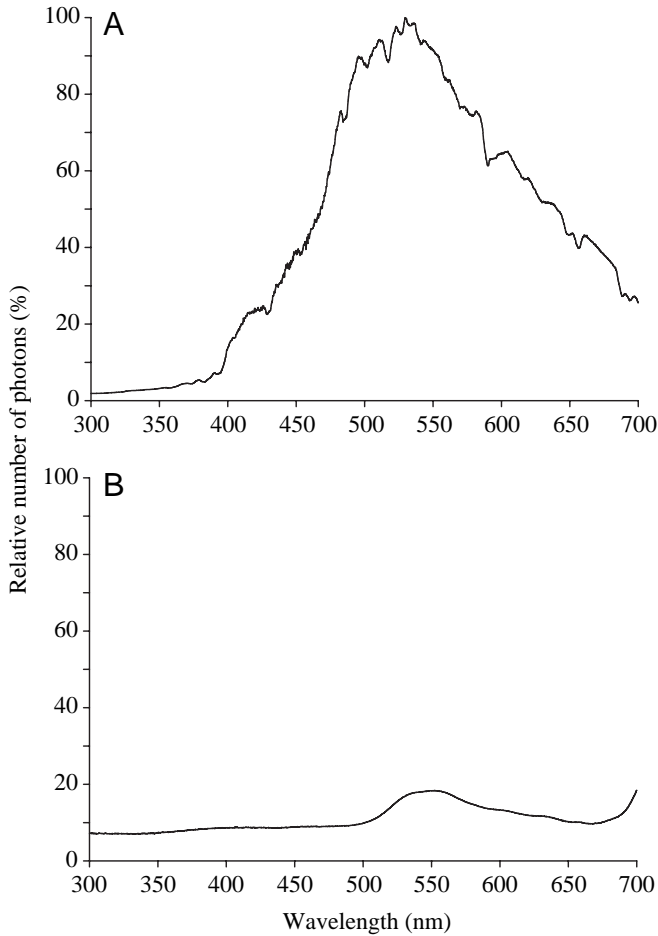
Fig. 3. (A) The forest understorey daylight illuminating spectrum in the study site in Orchid Island and (B) the spectral reflection of the background to which the photoreceptors are assumed to be adapted in the model calculations. The curve was the mean of the reflection functions of fresh leaves, fallen leaves and bark (N=190).

Fig. 4. Mean reflectance spectra of (A) yellow and (B) black parts on the body of the typical morph *Nephila pilipes*.

in the study site is shown in Fig. 3A. This daylight illumination spectral curve was used in all the model calculations. The spectral reflection of the vegetation background averaged from fresh leaves, fallen leaves and bark is given in Fig. 3B. The reflectance spectra of bright and dark body parts of typical *Nephila pilipes* are given in Fig. 4. Various bright body parts
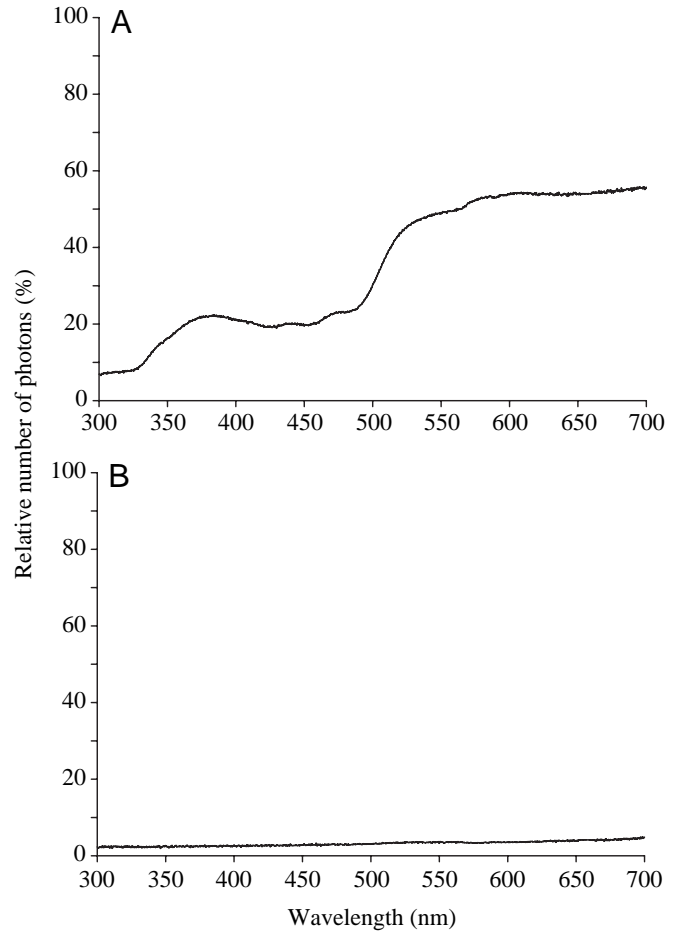
of *N. pilipes* had very similar reflectance properties. These areas exhibited a strong reflectance between 550 and 700 nm, which corresponded to the yellow to red region of the visible spectrum. In addition, bright body parts also had a small reflectance in the UV region of the spectrum (Fig. 4A). By contrast, various dark body parts of *N. pilipes* all had a very low reflectance across all wavelengths measured (Fig. 4B). The prosoma, two yellow bands on the abdomen, and spots on the legs and ventrum of typical *N. pilipes* all exhibited colour

Table 2. *Results of one-sample* t-*tests comparing colour contrasts of various body parts of typical* Nephila pilipes *viewed by honey bees under chromatic and achromatic vision with the discrimination threshold*

Vision	Areas examined											
	1	2	3	4	5	6	7	8	9	10	11	12
Chromatic												
t_7	4.626	0.074	3.656	3.322	0.922	1.382	2.125	3.156	6.239	1.382	0.922	2.125
P	<0.01	NS	<0.025	<0.01	NS	NS	NS	<0.05	<0.01	NS	NS	NS
Achromatic												
t_7	2.814	6.11	2.318	3.854	10.139	13.681	4.767	3.067	1.127	3.854	10.139	13.681
P	<0.05	<0.01	NS	<0.01	<0.01	<0.01	<0.01	<0.05	NS	<0.01	<0.01	<0.01

Numbers correspond to areas shown in Fig. 1.

Table 3. *Results of one sample* t-*tests comparing colour contrasts of various body parts of melanic* Nephila pilipes *viewed by honey bees under chromatic and achromatic vision with the discrimination threshold*

Vision	Areas examined											
	1	2	3	4	5	6	7	8	9	10	11	12
Chromatic												
t_5	2.845	3.038	5.048	3.175	5.048	4.401	0.506	2.208	1.539	3.175	5.048	4.401
P	<0.05	<0.05	<0.01	<0.01	<0.01	<0.025	NS	NS	NS	<0.01	<0.01	<0.025
Achromatic												
t_5	4.626	0.074	3.656	3.322	0.922	1.382	2.125	3.156	6.239	1.382	0.922	2.125
P	<0.01	NS	<0.025	<0.01	NS	NS	NS	<0.05	<0.01	NS	NS	NS

Numbers correspond to areas shown in Fig. 1.

contrasts significantly higher than the discrimination threshold for colour contrast detection estimated for honey bees (Théry and Casas, 2002; Fig. 5A,B), regardless of whether they were viewed by chromatic or achromatic (Table 2) vision. The dark parts of the body (areas 5 and 11) had low colour contrasts that were not significantly different from the discrimination threshold when viewed by chromatic vision (Table 2, areas 5 and 11). However, they had colour contrasts significantly higher than the threshold when only green receptor signal was used (Table 2, achromatic vision). The melanic *N. pilipes* had weak but visible colour signals when viewed by chromatic vision (Fig. 6A,B). In most parts of the body, the colour contrasts were slightly but significantly higher than the discrimination threshold (Table 3). When viewed by achromatic vision, the colour contrasts of all body parts of melanics were even higher (Table 3; Fig. 6A,B).

Discussion

Many diurnal orb-weaving spiders exhibit dramatic patterns of colouration, with both bright and dark markings on their bodies. Results of this study demonstrate that the colour contrasts of the brightly coloured markings are high but those of dark colourations vary when perceived by different chromatic channels. When *Nephila pilipes* are perceived from a long distance, when bees are using the achromatic receptor signal, both the dark and bright markings are detectable. When bees detect the spider from a long distance, due to the limited resolution of the compound eyes, the whole contour of the spider is blurred, thus it is unlikely that the bees would recognize the signal as a predator. The high colour contrast of dark markings when viewed by achromatic vision from a long distance might be adaptive. When all body parts are visible, the strength of the visual signal increases; thus, the opportunity of being spotted by prey becomes higher. When bees orient toward the spider
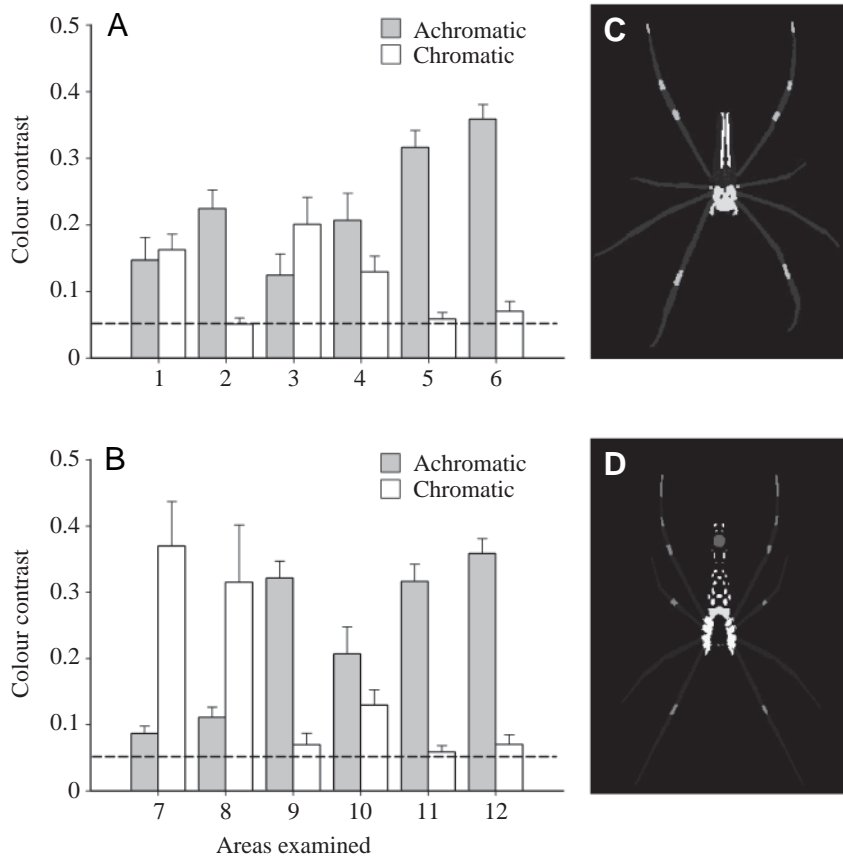

Fig. 5. (A,B) Mean (± S.E.M.) colour contrasts of different body parts of typical *Nephila pilipes* viewed by achromatic and chromatic vision. Broken lines indicate the threshold for colour-contrast detection estimated for honeybees. (C,D) Schematic drawings mimicking the (C) dorsum and (D) ventrum patterns perceived by bees using chromatic vision. Body parts whose colour contrasts were smaller than the discrimination threshold were given the same colour as the background, which was artificially designated as black. Those with significantly higher values were assigned different degrees of grey according to their contrast values. Numbers correspond to areas shown in Fig. 1.

and switch to chromatic vision, the brightly coloured markings are still visible but the dark parts become indistinguishable from the background. Those high-contrast bright and low-contrast dark markings are arranged in such a way that it greatly alters the contour of the spider and generates a signal unlike that of a predator (Fig. 5C,D). Most of the bright markings of *N. pilipes* are yellow. Many insects associate this colour signal with food resources such as flowers and new leaves (Prokopy and Owens, 1983). Therefore, the colouration patterns of the typical *N. pilipes* not only provide a signal perceivable to insects but also make the spiders similar to some forms of food resources in both appearance and visual properties.

The insect interception rates of typical yellow morphs and melanic morphs were significantly different. Compared with typical morphs, melanic *N. pilipes* do not have yellow markings but only dark body colour. Colour signals of the melanics were significantly different from those of dark markings of the typical morphs. The dark markings of typical morphs looked yellowish-black but those of melanics were shiny black. Excessive deposition of dark pigments might have caused such a dramatic change in appearance and colour signal. While the contrasts and thus the visibility of dark markings of typical morphs vary when viewed by different chromatic channels, melanics have high contrasts when viewed by either achromatic or chromatic visions. Although melanic morphs are visible to insects, the uniformly coloured body renders the contour of the spiders quite clear (Fig. 6C,D). Nevertheless, melanic morphs lacked colour signals mimicking those of insects' resources. Therefore, while the visual signals of the typical *N. pilipes* could both deceive and attract the insects, those of melanics exhibit no such properties. This might explain why the former caught significantly more prey than the latter in this and the previous study by Tso et al. (2002).

Results of censuses conducted in 1997, 1999 (Tso et al., 2002) and 2002 (present study) demonstrate that the ratio of melanic to typical *N. pilipes* in the study site in Orchid Island was more or less constant (20–30%). Results of this study and that of Tso et al. (2002) indicate that melanic *N. pilipes* had a significantly low foraging success, which might result from their altered colour signals. However, given such a disadvantage, why does the melanic morph persist stably in the population in Orchid Island? Results of the present study show that colour contrasts of melanic *Nephila* were significantly higher than the discrimination threshold. This result indicates that melanics are actually highly visible to hymenopteran insects, especially under achromatic vision, when the predators are searching for prey from a long distance. Although Tso et al. (2002) suggested that one advantage enjoyed by melanics
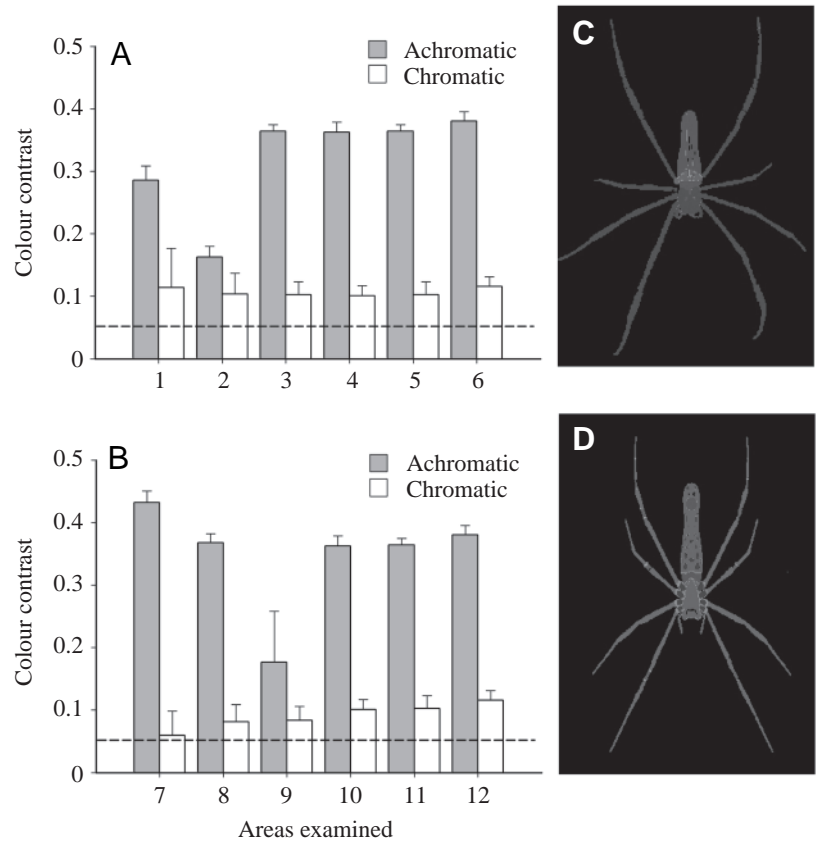

Fig. 6. (A,B) Mean (± S.E.M.) colour contrasts of different body parts of melanic *Nephila pilipes* viewed by achromatic and chromatic vision. Broken lines indicate the threshold for colour-contrast detection estimated for honeybees. (C,D) Schematic drawings mimicking the (C) dorsum and (D) ventrum patterns perceived by bees using chromatic vision following scenarios used in Fig. 5.

might be a lower mortality resulting from lower visibility to predators, the colour contrast data indicate that this is not the case. However, visibility is not the only determinant of predation pressure. Although melanics were visible to wasps, they did not have the bright colourations exhibited by the typical morphs. Perhaps hymenopteran predators use the bright colouration patterns as a cue and form a search image (Allen, 1988; Endler, 1988) for the more frequent typical *N. pilipes*. Melanics might benefit from a lack of bright colour signal and low frequency in population rather than a lower visibility generated by reflectance properties. Further field manipulative studies are needed to evaluate whether melanics have lower mortality and the underlying mechanisms.

Insects see by detecting contrast between objects and their environments, and all kinds of colour receptors and colour signals are involved (Chittka and Menzel, 1992; Vorobyev and Brandt, 1997; Briscoe and Chittka, 2001). Many relevant studies have only considered the UV component of the system when inferring the nature of insect–spider visual interactions (Craig and Bernard, 1990; Craig et al., 1994; Tso, 1996; Blackledge, 1998; Watanabe, 1999; Blackledge and Wenzel, 2000; Tso et al., 2002; Zschokke, 2002). However, all sorts of colour signals and receptors should be considered when

determining the colour signals of spiders. Compared with the traditional 'UV approach' (measuring the UV reflectance of organisms to infer the nature of visual interactions), the 'colour contrast approach' is more realistic because it takes into account all colour signals of the objects and the various receptors of the organisms. We suggest that all types of receptor signals should be considered when exploring the visual interactions between predators and prey.

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