Function of being colorful in web spiders: attracting prey or camouflaging oneself?

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Bright body colorations of orb-weaving spiders have been hypothesized to be attractive to insects and thus function to increase foraging success. However, the color signals of these spiders are also considered to be similar to those of the vegetation background, and thus the colorations function to camouflage the spiders. In this study, we evaluated these 2 hypotheses by field experiments and by quantifying the spiders' visibility to insects. We first compared the insect interception rates of orbs constructed by the orchid spider, *Leucauge magnifica*, with and without the spider. Orbs with spiders intercepted significantly more insects than orbs without. Such a result supported the prey attraction but not the camouflaging hypothesis. We then tested whether bright body colorations were responsible for *L. magnifica*'s attractiveness to insects by manipulating the spiders' color signals with paint. Alteration of color signals significantly reduced *L. magnifica*'s insect interception and consumption rates, indicating that these spiders' bright body parts were attractive to insects. Congruent with the finding of field manipulations were the color contrasts of various body parts of these spiders. When viewed against the vegetation background, the green body parts were lower, but the bright parts were significantly higher than the discrimination threshold. Results of this study thus provide direct evidence that bright body colorations of orb weavers function as visual lures to attract insects. *Key words:* color contrast, *Leucauge magnifica*, orchid spider, visual ecology. *[Behav Ecol 17:606–613 (2006)]*

Brightly colored animals have fascinated many researchers and have been the subject of numerous studies. The studies of animals' bright coloration can be broadly categorized as intraspecific and interspecific. Studies of animal coloration in the context of intraspecific interactions have mostly focused on behavioral or morphological traits relevant to sexual selection, such as species identification (Rutowski 1988), mate preference (Petrie and Halliday 1994; Andersson and Amundsen 1997; Johnsen et al. 1998; Grether 2000; Rodd et al. 2002), and mate quality assessment (McGraw and Hill 2000; Doucet and Montgomerie 2003; MacDougall and Montgomerie 2003). Most studies in the context of interspecific interactions have focused on antipredation adaptations such as aposematism, crypsis, or mimicry (Stuart-Fox et al. 2003; Ruxton et al. 2004). To date, there have been few direct empirical tests of the role bright body colorations play in the context of foraging (Craig and Ebert 1994; Hauber 2002; Tso et al. 2002, 2004). In this study, we assessed how bright body coloration is involved in the prey capture of spiders, the most abundant invertebrate predators in the terrestrial ecosystem (Wise 1993; Nyffeler 2000).

Various diurnal orb-weaving spiders exhibit brightly colored markings on their body surface, and the roles of these colorations are still under debate. Many spiders hunt nocturnally, and their colorations are usually dark, gray 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 actively during the day, and many of them exhibit conspicuous color patterns (Yaginuma 1986). One group of researchers regarded the bright color patterns of these diurnal orb-weaving spiders as a function to increase foraging success by providing attractive visual signals to prey. For example, the brightly colored dorsum of *Argiope argentata* of Panama was demonstrated to be more attractive to insects than the spiders' brown ventrum (Craig and Ebert 1994). The spiny spiders, *Gasteracantha fornicata*, of Australia also exhibit bright coloration on their dorsum. Covering this coloration with paint significantly reduced the spiders' foraging success (Hauber 2002). The brightly colored giant wood spider, *Nephila pilipes*, of Asia caught significantly more insects than its melanic conspecifics (Tso et al. 2002). Tso et al. (2004) examined how these 2 morphs of *N. pilipes* were seen by hymenopteran insects by calculating the color contrasts of various body parts against the vegetation background. They found the bright color bands of *N. pilipes* to be highly visible to hymenopteran insects, and they regarded this to be the reason for the attractiveness of the typical morph.

The camouflaging hypothesis, on the other hand, regards the bright coloration of orb-weaving spiders as functioning to conceal the spiders against the vegetation background. This hypothesis proposes that because the reflectance spectra of the spiders' body surface are similar to those of the background vegetation, the spiders are not easily perceived by insects. The vegetation background in which these spiders build their webs is usually a complex mosaic consisting of green vegetation, fallen leaves, and bark exhibiting complex UV signals (Blackledge 1998; Zschokke 2002). Because the bright body colorations of spiders also reflect UV, spiders may blend well with the vegetation background and thus are difficult to detect by their prey or predators. Although the functions of the crab spider body coloration had been demonstrated to be either attracting prey (Heiling et al. 2003, 2005) or concealing the spiders (Chittka 2001; Théry and Casas 2002), to our knowledge, there is no empirical study to simultaneously test these 2 alternative explanations. Evidence from several studies has shown that altering the color signals of orb-weaving spiders reduced their insect-catching rate (Craig and Ebert 1994; Hauber 2002), and therefore, this seems to provide

direct support for the prey attraction hypothesis. However, such results could also be interpreted as being congruent with the camouflaging hypothesis because the alteration of body coloration in the treatment might have destroyed the camouflaging pattern, thus rendering the spider more visible against the background and therefore lowering the insect-catching rate. Therefore, to test these 2 alternative hypotheses, it is not sufficient to merely compare the insect interception rates between the bright orb-weaving spiders and their color-manipulated conspecifics. Rather, a comparison in insect interceptions between orbs with or without spiders is needed. If the bright coloration of spiders serves as camouflaging device, then orbs with or without spiders will have similar insect interception rates. On the other hand, if the body coloration serves as an attractant, then orbs with spiders will intercept more insects than those without spiders.

In this study, we evaluated the prey attraction and camouflaging functions of bright body coloration of the orchid spider, *Leucauge magnifica*, by conducting field experiments and by quantifying their visibility to insects. Firstly, we manipulated the presence of spiders on webs to see whether such treatment would affect the insect interception rates. Secondly, we manipulated the color signals of orchid spiders to see whether their coloration is responsible for their attractiveness. Finally, we quantified how orchid spiders were seen by insects. The color contrasts of various body parts of orchid spiders against vegetation backgrounds were calculated by the color hexagon model of Chittka (1992) to assess whether these brightly colored spiders were visible to their prey.

METHODS

The study site and the spider

Field manipulative studies were conducted in the summers of 2004 and 2005 at Lien-Hwa-Chih Research Center operated by the Taiwan Forestry Research Institute in Yu-Chi, Nantou County, Taiwan. The study site consisted of a mixture of primary broadleaf forests and Taiwanese fir plantations. A stable population of orchid spiders, *L. magnifica* (Araneae: Tetragnathidae), was found in the neighborhood of the research center. Orchid spiders construct horizontal webs on herbaceous plants along the margin of trails in the study site throughout the year. The prosoma and legs of orchid spiders are green, but their opithosoma are brightly colored. The dorsum is silver with thin longitudinal black stripes (Figure 1A). On the ventrum are 2 distinct yellow stripes embedded in a dark green area (Figure 1B). In this study, only female orchid spiders were used because their body coloration is brighter and they forage much more actively compared with males (I-M Tso, personal observations).

Testing the effect of spiders on prey interception

In this part of the study, we evaluated whether the presence of an orchid spider will affect the prey interception rates of the web. Each day before the experiment, we randomly assigned spiders into 2 groups, experimental and control. In the experimental group, the spiders were carefully removed from the webs, and in the control group, the spiders were left on the webs. Spider body length, hub diameter, orb radius from 4 cardinal directions, and number of radii were measured to the nearest millimeter with a digital caliper. The catching area of the orb was estimated by the formula in Herberstein and Tso (2000). The prey interception rates (number of insects hitting the web per hour) were measured by video cameras. Ten video cameras were set up in the study site, 5 in each group. We placed the video cameras 2 m away and made recordings with
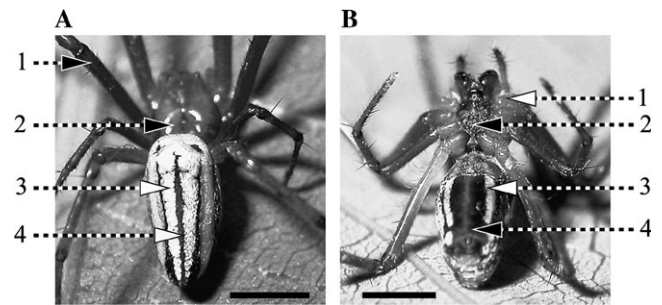
Figure 1
Dorsal (A) and ventral (B) views of the female orchid spider, *Leucauge magnifica*, showing various brightly colored body parts. The scale bars are 5 mm. (A) 1, green legs; 2, green prosoma; 3, silver dorsum; 4, black longitudinal stripes. (B) 1, green coax; 2, black sterna; 3, yellow stripes; 4, dark green ventrum.

an angle of 45° to the left or right side of the webs (depending on the microhabitat nearby). The recordings were conducted daily from 06:00 AM to 02:00 PM between 1 and 6 April 2005. Prey interception data were estimated by averaging the number of prey intercepted by webs during 8 h of monitoring. We defined an interception event as prey bumping into the web and being entangled for at least 5 s. Prey that passed through webs without touching the silk was not included in the analyses. The insect interception data set fitted well with the Poisson distribution (Pearson χ^2 test, $P = 0.4196$) (Steel et al. 1997). Therefore, we used the Poisson regression to examine the relationship between prey interception rate, orb area, and the presence/absence of spiders. In this analysis, the probability of events (such as insect interceptions) under various conditions (such as different treatments or orbs of different area) was compared. An iterative reweighted least squares method was used to obtain the maximum likelihood estimate of the ratio between probabilities of different events. A χ^2 test was then used to evaluate whether such ratio (the difference) between probabilities of events reached statistical significance (Steel et al. 1997). The Poisson model is

$$\log\mu_N = \log N(X_i) + X_i\beta,$$

where μ is the expected value, X represents the explanatory variables (spider presence/absence or orb area), β is the probability, and $N(X)$ is the total number of individuals. The web area was designated as a categorical variable due to a small sample size. We ranked web areas into the following 3 categories: <100, 100–200, and 200–300 cm^2.

Testing the effect of spider body coloration on prey interception and consumption

In this part of the study, we evaluated whether altering the color signals of the orchid spiders would affect their prey interception as well as consumption rates. Each day before the experiment, female spiders were assigned into 4 groups. In the first group, the dorsal silver bands of the spider were covered with green paint of known reflection wavelength (Figure 4F). In the second group, the green paint was applied on the ventral yellow stripes. In the third group, the green paint was applied on both the dorsal and ventral sides of the spiders. In the fourth group, the control group, the green paint was applied to the green parts of the abdomen (the areas between the silver dorsum and yellow stripes) to serve as a control. Spider body length, hub diameter, orb radius from 4 cardinal directions, and number of radii were measured to the nearest millimeter. The numbers of insects intercepted

by the orbs and those consumed by spiders were also measured by video cameras. Twelve video cameras were used in the experiment, 3 placed in each group. The recordings were conducted daily from 06:00 AM to 02:00 PM for a total of 19 recording days in August and September 2004. Rates of prey interception and consumption were estimated by averaging the number of prey intercepted by webs or consumed by the spiders during 8 h of monitoring. Because the insect interception data fitted well with a Poisson distribution (Pearson χ^2 test, $P = 0.7138$) (Steel et al. 1997), we also used Poisson regression to examine the relationship between prey interception rate, orb area, and various spider body color treatments. In this analysis, web areas were ranked into the following 4 categories: 200–300, 300–400, 400–500, and 500–600 cm^2.

Calculation of color contrasts

Color contrast is the contrast caused by the spectral difference between 2 objective areas, which can only be detected by a visual system with at least 2 photoreceptor types. To calculate color contrast, the illuminance spectrum (the spectrum of the light source), the reflectance spectrum of the objects, and the spectral sensitivities of all photoreceptor types in the visual system were needed. By multiplying the illuminance spectrum with the reflectance spectrum of the object, the color signal of the objective area can be obtained. The spectral sensitivity of each type of photoreceptors was integrated with the color signal to obtain the relative absorption of each photoreceptor type to the color signals. The excitation rate of the photoreceptor was multiplied by a sensitivity factor and further transformed to the theoretical voltage excitation, E, as the nonlinearity of photoreceptor response to light stimulus is considered. With the color hexagon model by Chittka (1992), the locus of each color signal in the model and the distance between 2 loci of color signals can be calculated as the chromatic contrast.

Seven mature female orchid spiders were collected from the study site, and the reflectance spectra of the various parts of their body were measured with a spectrometer (S2000, Ocean Optics, Inc., Dunedin, Florida) in the laboratory. For each measurement, the illumination leg of the reflection probe (with 6 illumination fibers) was attached to a light source (450 W, xenon arc lamp) and the read leg (with one read fiber) to the spectrometer. The tip of the probe was placed vertically 5 mm above the sample. We measured legs, carapace, green bands on the side and ventrum of the abdomen, the dorsal silver bands, and the green paint used in the field manipulative study. Four measurements of reflectance spectra were made on each body part of each *L. magnifica*. The means were used in the subsequent calculations of color contrasts. Those of herbaceous vegetations collected from the study sites were obtained in a similar way. We chose 6 species of plants commonly seen in the study sites to assess the color signals of the vegetation background. From each plant species, reflectance spectra were measured from 6 leaves. Data from the 6 plant species were averaged and used in the calculation of color contrasts of spiders' body colorations.

Color signals were generated by multiplying the surface reflectance function and the illumination function of the habitat (Wandell 1995). The fraction of the light reflected by the surfaces of the spiders or plants is the surface reflectance function. The daylight illumination function of the forest understory was obtained from Tso et al. (2004). We chose the spectral sensitivity functions of the honeybee to determine the photoreceptor excitation for each measured spectra. Honeybee exhibits UV, blue, and green receptors, and such trichromatic color vision is found in almost all major taxa of insects (see review by Briscoe and Chittka 2001). Therefore, color contrasts

of spiders estimated from visual systems of honeybees should be quite representative. *Leucauge magnifica* builds horizontal webs in forest understory, and the background will be ground vegetation when the spider is viewed from the above or from the side. On the other hand, the background will be canopy when the spider is viewed from below. Therefore, the color contrasts of most body parts of the orchid spiders were calculated using vegetation as the background. However, because the 2 yellow stripes were embedded in a patch of dark green abdomen (Figure 1B), in calculating the color contrasts of these yellow stripes and the paint applied on them, the dark green patch in ventrum was used as the background. The calculations of color contrasts against various backgrounds followed the method of Chittka (1992, 1996, 2001). One-tailed *t*-tests were used to compare the color contrast values with the discrimination threshold value of 0.05 estimated for hymenopteran insects (Théry and Casas 2002). Previous studies showed that hymenopterans adopt achromatic vision by using green receptor signal alone when searching for an object far ahead and adopt chromatic vision by using green, blue, and UV receptor signals when approaching the object (Giurfa et al. 1997; Spaethe et al. 2001; Heiling et al. 2003). In this study, the color contrasts were calculated under these 2 conditions to examine how prey see the orchid spiders against the vegetation background under different chromatic systems.

RESULTS

Testing the effect of spiders on prey interception

In this part of the study, data were only included in the analysis when spiders stayed in their orbs for more than 5 h during the video camera monitoring. Valid insect interception data were obtained from 288 h of video recording. Among them, 176 were from the control ($n = 22$ spiders) and 112 were from the experimental group ($n = 14$ spiders). When the orb area was considered, the insect interception rates of webs in the control group were significantly higher than those of the experimental group (Table 1). Compared with the webs without spiders, those with spiders intercepted almost twice as many insects per hour (Figure 2).

Testing the effect of spider body coloration on prey interception and consumption

In this part of the study, data were only included in the analysis when spiders stayed in their orbs for more than 5 h during the video camera monitoring. Valid data were available from a total of 448 h of video recording. Among them, 128 were from the control ($n = 16$ spiders), 112 from the dorsum-painted ($n = 14$ spiders), 112 from the ventrum-painted ($n = 14$ spiders), and 96 from both sides–painted groups ($n = 12$ spiders). Compared with the insect interception and consumption rates of the control group, those in the dorsum-painted and ventrum-painted groups were lower (Figure 3). However, the differences between these groups did not reach statistical significance (Tables 2 and 3). When considering the orb area, the insect interception and consumption rates of spiders painted on both dorsal and ventral sides were significantly lower than those of the control group (Tables 2 and 3). Compared with spiders whose dorsal and ventral color signals were altered by paint, those in the control group intercepted and consumed 3 times as many insects per hour of monitoring (Figure 3).

Calculation of color contrasts

Mean reflectance spectra of various body parts of the orchid spider and the leaves of various plants in the study site were used in the calculations of color contrasts. The green body

Table 1

Results of Poisson regression comparing prey interception rates of orchid spiders estimated by video recordings between experimental (spiders removed) and control group (spider remained)[a,b]

Poisson regression

Parameters		df	Estimate of β	SE	χ^2	P
Intercept		1	−1.2548	0.1097	9.38	0.0022
Experimental	Without spider	1	−0.9002	0.3147	8.18	0.0042
Control	With spider	0	0	0	—	—
Web area	200–300	1	0.8346	0.5172	2.61	0.1065
Web area	100–200	1	0.9916	0.437	5.15	0.0233
Web area	0–100	0	0	0	—	—

SE, standard error.

[a] The β of the control group and the orb area 0–200 size category were arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

[b] The ratio between probabilities of 2 certain events was e^{β}.

parts of orchid spiders such as legs, carapace, and ventrum had very similar chromatic properties. All of them exhibited low reflectance across all wavelengths measured (Figure 4C,D). Such a reflectance pattern was very similar to that of the vegetation background (Figure 4B). On the contrary, the dorsal silver bands of orchid spiders reflected a considerable amount of light across all wavelengths measured (Figure 4E). The green paint used had a high reflectance at wavelengths between 400 and 550 nm (Figure 4F). Color contrasts of various body parts of orchid spiders viewed against the vegetation background under achromatic vision were significantly higher than the discrimination threshold (Table 4). However, under chromatic vision, color contrasts of various green body parts of orchid spiders against the vegetation background were low (Figure 5) and were not significantly greater than the discrimination threshold (Table 3). This result indicates that hymenopteran prey could not distinguish the color signals of green body parts of orchid spiders from the background vegetation from a short distance. Under chromatic vision, color contrasts of the dorsal silver bands of orchid spiders against the vegetation background were high (Figure 5) and were significantly higher than the discrimination threshold (Table 4). The ventral yellow stripes when viewed against the dark green ventrum

also exhibited a very high color contrast (Table 4 and Figure 5). The color contrast of green paint used was also significantly higher than the threshold, no matter whether it was seen against the vegetation background or the dark green ventrum (Table 4 and Figure 5).

DISCUSSION

Results of this study showed that the colorful spider itself can serve as a visual lure to its prey. In this study, compared with orbs without orchid spiders, those with spiders intercepted almost twice as many insects. Such a result is not congruent with the camouflaging hypothesis, which predicts a similar prey interception rate between orbs with and without spiders. Results of this and previous studies thus demonstrate that orb-weaving spiders do not passively wait for accidentally trapped prey but use various ways to lure prey. Orb weavers such as the spiny spider (Hauber 2002), giant wood spider (Tso et al. 2002, 2004), garden spider (Craig and Ebert 1994), and hunters such as crab spiders (Heiling et al. 2003, 2005) use their bright body coloration to lure prey. Various species of the genus *Argiope*, *Cyclosa*, and *Octonoba* incorporate silky structures called decoration in their web to serve as visual lures
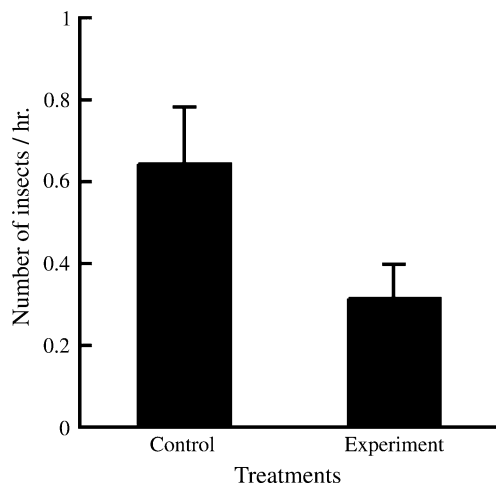
Figure 2
Mean (±standard error) prey interception rates (number of insects per hour) of *Leucauge magnifica* in the experimental (spider removed) and control (spider remained) groups estimated from video recording.
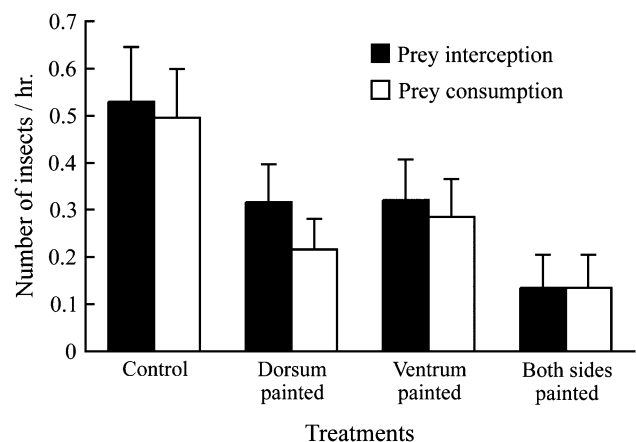
Figure 3
Mean (±standard error) prey interception (number of insects per hour) and consumption (number of insects consumed per hour) rates of *Leucauge magnifica* in the control (green part painted) and experimental (dorsum or ventrum or both sides painted) groups estimated from video recording.

Table 2

Results of Poisson regression comparing rates of prey interception of orchid spiders estimated by video recordings between experimental (bright bands on dorsum and/or ventrum painted) and control groups (green body parts on both sides of abdomen painted)[a,b]

Poisson regression

Parameter		df	Estimate of β	SE	χ^2	P
Intercept		1	0.1995	0.2617	0.58	0.446
Experimental	Both side painted	1	−0.7817	0.3921	3.97	0.0462
Experimental	Ventrum painted	1	−0.1976	0.3058	0.42	0.5182
Experimental	Dorsum painted	1	−0.2529	0.265	0.91	0.3398
Control	Green part painted	0	0	0	—	—
Web area	500–600	1	−0.9942	0.3341	8.35	0.0039
Web area	400–500	1	−1.0869	0.3471	9.8	0.0017
Web area	300–400	1	−1.4969	0.3977	14.16	0.0002
Web area	200–300	1	−0.8198	0.3283	6.24	0.0125
Web area	100–200	0	0	0	—	—

SE, standard error.

[a] The β of the control group and the orb area 100–200 size category were arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

[b] The ratio between probabilities of 2 certain events was e^β.

(Herberstein et al. 2000). Bolas spiders (Haynes et al. 2002) use chemicals mimicking the sex pheromone of their moth prey as attractant, whereas *Nephila* spiders deposit half-digested prey on webs to attract insects (Bjorkman-Chiswell et al. 2004). Therefore, the traditional view of categorizing orb-weaving spiders as aerial filter feeders that passively sieve prey from the air current flow through their orbs should be reconsidered.

Results of this study also demonstrate that the attractiveness of orchid spiders to their prey is achieved by their bright body coloration. When either the dorsal silver bands or ventral yellow stripes of orchid spiders were painted, the insect interception and consumption rates were reduced but did not reach significance level. However, when the color signals of both dorsum and ventrum were altered, the insect interception and consumption rates were further reduced, and the difference was statistically significant. Such results indicate that both the dorsal silver bands and ventral yellow bands are attractive to insects. When the color signal on either side

of the abdomen was altered, that on the other side was still functioning. Thus, the insect attractiveness was somewhat lowered but not significantly. However, when all the color signals of the spiders were altered, the attractiveness of the spiders was reduced dramatically. It was unlikely that the odor of the paint was responsible for the observed result because in the control group, we also applied green paint on the green part of the abdomen. In all treatment groups, there was paint on the body of spiders, and therefore, the observed variation in prey capture among them should be irrelevant with the odor of paint.

The attractiveness of the orchid spider's body coloration seems to be achieved by the properties of the color signal, rather than the visibility of the spider. In the early stage of this study, when choosing appropriate paint with which to alter the color signal of the spider, we purposely used a paint exhibiting a reflectance spectrum different from that of the spiders. The color contrasts of green paint viewed either against the vegetation background or spiders' dark green

Table 3

Results of Poisson regression comparing rates of prey consumption of orchid spiders estimated by video recordings between experimental (bright bands on dorsum and/or ventrum painted) and control groups (green body parts on both sides of abdomen painted)[a,b]

Poisson regression

Parameter		df	Estimate of β	SE	χ^2	P
Intercept		1	−0.0372	0.2983	0.02	0.9008
Treatment	Both sides	1	−1.0221	0.4330	5.57	0.0183
Treatment	Ventrum painted	1	−0.2780	0.3235	0.74	0.3902
Treatment	Dorsum painted	1	−0.4735	0.2920	0.74	0.3902
Treatment	Control	0	0	0	—	—
Web area	500–600	1	−0.9246	0.4218	5.29	0.0214
Web area	400–500	1	−0.9354	0.3906	5.73	0.0166
Web area	300–400	1	−1.2387	.4350	8.11	0.0044
Web area	200–300	1	−0.4746	0.3598	1.74	0.1873
Web area	100–200	0	0	0	—	—

SE, standard error.

[a] The β of the control group and the orb area 100−200 size category were arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

[b] The ratio between probabilities of 2 certain events was e^β.
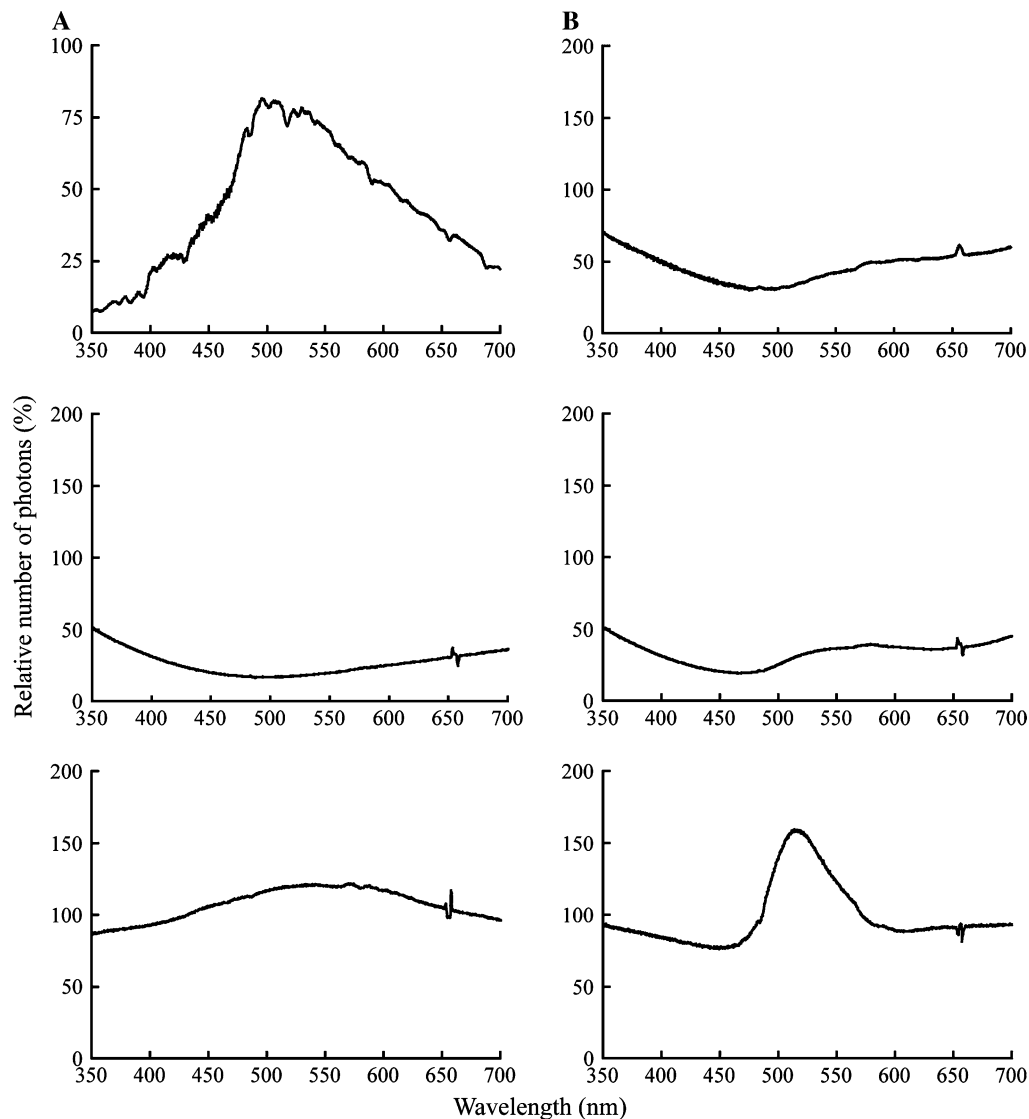
Figure 4
Mean reflectance spectra of various body parts of the orchid spider *Leucauge magnifica*. (A) The forest understory daylight illuminating spectrum, (B) vegetation background, (C) carapace and leg, (D) green stripes on abdomen, (E) silver band on the dorsum, and (F) the green paint used in the experimental group.

ventrum were significantly higher than the discrimination threshold, indicating that the paint used could be readily seen by the insects. However, given such high visibility, these painted spiders still intercepted and consumed far fewer insects than the control group. Such results indicate that the reflectance properties of orb-weaving spiders' body coloration are quite critical to their insect interception. The properties of their color signal have been fine-tuned by selection to achieve the best attractiveness to their prey. Once such property was altered, even though the changed coloration was still quite visible, they were no longer attractive to insects. Currently, it is not clear why the color signals of these body colorations are attractive to insects. The color signals of orb-weaving spiders may be similar to those of flowers and new leaves (Propoky and Owens 1983); thus, these spiders are perceived by their prey as some form of resource. It is necessary to conduct field studies to find out what resources these colorations are mimicking to determine whether these orb-weaving spiders are exploiting the visual system of their prey.

Insects see by detecting the contrasts between objects and their environments, and all kinds of color receptors and signals are involved (Chittka and Menzel 1992; Vorobyev and Brandt 1997; Briscoe and Chittka 2001). We suggest that all types of receptor signals should be considered when exploring the visual interactions between predators and prey. Numerous studies have tried to manipulate the UV signal of the system, and they did find that in some cases the attractiveness of the spider body coloration or silk decorations was affected (Craig and Bernard 1990; Tso 1996; Watanabe 1999; Li et al. 2004). The results of these studies can be interpreted such that manipulation altered the insects' perception; thus, they were no longer attracted by the altered color signal. In this study, however, we did not alter the UV signal of the spider but used paint with a strong reflectance in the yellow–green spectra. Such treatment was equally effective in reducing the attractiveness of orchid spiders' body coloration. This result indicates that when the color signal is altered, no matter whether the change is in the UV, green, or blue spectra, such

Table 4

Results of one-tailed *t*-tests comparing the color contrasts of various body parts of the orchid spider, *Leucauge magnifica*, against vegetation background and against dark green ventrum of the spider seen by honeybees under chromatic and achromatic visions with the discrimination threshold of 0.05

Areas examined

Vision	Leg	Carapace	Dark green ventrum	Silvery dorsum	Ventrum stripes	Paint dorsum	Paint ventrum
Chromatic							
t_6	0.893	0.620	0.707	2.792	0.497	3.608	2.704
P	0.203	0.279	0.253	0.016	0.318	0.006	0.018
Achromatic							
t_6	16.618	11.721	16.585	21.276	0.052	5.435	3.758
P	<0.001	<0.001	<0.001	<0.001	0.48	<0.001	0.005

alternation will affect the relative excitations of receptors. Subsequently, the recipient organism has a different perception of the signal perceived and alters its behavioral responses.
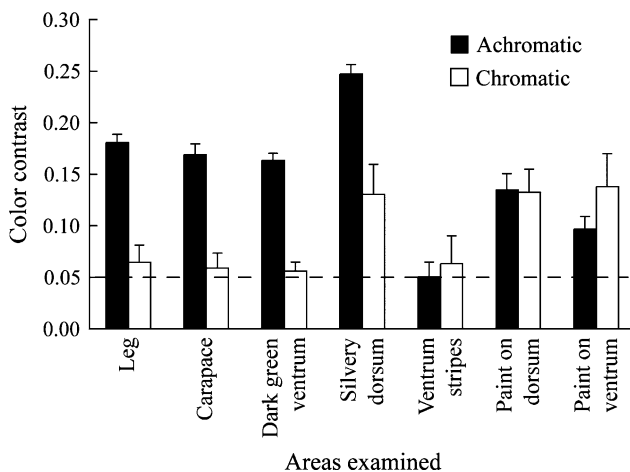
Various body parts of orchid spiders differ considerably in brightness and color contrasts, and such a pattern is commonly seen in numerous genera of orb-weaving spiders such as *Nephila, Argiope,* and spiny spiders (Yaginuma 1986). We suggest that the co-occurrence of low– and high–color contrast body parts in these orb-weaving spiders may be an adaptive morphological trait. Because the bright coloration of orb-weaving spiders is attractive to insects, if the whole body is covered by high-contrast coloration, the contour of the spider will be more than obvious to insects. Prey will quickly learn to associate that with danger by recognizing the shape of the images. The presence of low-contrast colorations, however, changes the appearance of the spiders. Break in contour due to low-contrast body colorations plus the resource-mimicking color signals of high-contrast body color make it difficult for insects to associate these spiders with predation risk. Another advantage of such contour-breaking coloration might be to reduce predation risk. Most predators of these orb-weaving spiders, such as birds and parasitoid wasps (Coville 1987; Blackledge and Pickett 2000; Blackledge and Wenzel 2001; Craig et al. 2001), are visually orientated. A spider covered by a large area of high-contrast

colorations makes it easily detected by predators. Therefore, the presence of low-contrast coloration to break the contour of the body and high-contrast coloration to attract prey seems to be a product of various counteracting selection pressures involved in spider–insect visual interactions.

REFERENCES

Andersson S, Amundsen T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. Proc R Soc Lond B Biol Sci 264:1587–91.

Bjorkman-Chiswell B, Kulinski MM, Muscat RL, Nguyen KA, Norton BA, Symonds MRE, Westhorpe GE, Elgar MA. 2004. Web-building spiders attract prey by storing decaying matter. Naturwissenschaften 91:245–8.

Blackledge TA. 1998. Signal conflict in spider webs driven by predators and prey. Proc R Soc Lond B Biol Sci 265:1991–6.

Blackledge TA, Pickett KM. 2000. Predatory interactions between mud-dauber wasps (Hymenoptera, Sphecidae) and *Argiope* (Araneae, Araneidae) in captivity. J Arachnol 28:211–6.

Blackledge TA, Wenzel JW. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasp. Behaviour 138:155–71.

Briscoe AD, Chittka L. 2001. The evolution of colour vision in insects. Annu Rev Entomol 46:471–510.

Chittka L. 1992. The colour hexagon: a chromaticity diagram based on photoreceptor excitation as a generalized representation of colour opponency. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 170:533–43.

Chittka L. 1996. Optimal sets of colour receptors and opponent processes for coding of natural objects in insect vision. J Theor Biol 181:179–96.

Chittka L. 2001. Camouflage of predator crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Hymenoptera: Apidae). Entomol Gen 25:181–7.

Chittka L, Menzel R. 1992. The evolutionary adaptation of flower colours and the insect pollinators' colour vision. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 171:171–81.

Coville RE. 1987. Spider-hunting sphecid wasps. In: Nentwig W, editor. Ecophysiology of spiders. Berlin, Germany: Springer-Verlag. p 309–27.

Craig C L, Bernard GD. 1990. Insect attraction and ultraviolet-reflecting spider webs and web decorations. Ecology 71:616–20.

Craig CL, Ebert K. 1994. Colour and pattern in predator-prey interactions: the bright body colours and patterns of a tropical orb-spinning spider attract flower-seeking prey. Funct Ecol 8:616–20.

Craig CL, Wolf SG, Davis JLD, Hauber ME, Maas JL. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is

Figure 5
Mean (±standard error) color contrasts of various body parts of the orchid spider, *Leucauge magnifica*, against the different vegetation backgrounds and the spiders' green ventrum seen by honeybees under chromatic and achromatic vision. Dashed line represents the threshold for color contrast discrimination calculated for Hymenoptera.

correlated with reduced survivorship and the presence of stingless bees, its primary prey. Evolution 55:986–93.

Doucet SM, Montgomerie R. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumages and bowers signal different aspects of male quality. Behav Ecol Sociobiol 14:503–9.

Giurfa M, Vorobyev M, Brandt R, Posner B, Menzel R. 1997. Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 180:235–43.

Grether GF. 2000. Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulate*). Evolution 54:1712–14.

Hauber ME. 2002. Conspicuous coloration attracts prey to a stationary predator. Ecol Entomol 27:686–91.

Haynes KF, Gemeno C, Yeargan KV, Millar JG, Johnson KM. 2002. Aggressive chemical mimicry of moth pheromones by bolas spider: how does this specialist predator attack more than one species of prey? Chemoecology 12:99–105.

Heiling AM, Chittka L, Chen K, Herberstein ME. 2005. Coloration in crab spiders: substrate choice and prey attraction. J Exp Biol 208:1785–92.

Heiling AM, Herberstein ME, Chittka L. 2003. Crab-spiders manipulate flower signals. Nature 421:334.

Herberstein ME, Craig CL, Coddington JA, Elgar MA. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. Biol Rev Camb Philos Soc 75:649–69.

Herberstein ME, Tso IM. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs. J Arachnol 28:180–4.

Johnsen A, Andersson S, Ornberg J, Lifjeld JT. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. Proc R Soc Lond B Biol Sci 265:1313–8.

Li D, Lim MLM, Seah WK, Tay SL. 2004. Prey attraction as a possible function of discoid stabilimenta of juvenile orb-spinning spiders. Anim Behav 68:629–35.

MacDougall AK, Montgomerie R. 2003. Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. Naturwissenschaften 90:464–7.

McGraw KJ, Hill GE. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. Proc R Soc Lond B Biol Sci 267:1525–31.

Nyffeler M. 2000. Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates. Bull Br Arachnol Soc 11:367–73.

Oxford GS, Gillespie RG. 1998. Evolution and ecology of spider coloration. Annu Rev Entomol 43:619–43.

Petrie N, Halliday T. 1994. Experimental and natural changes in the peacock's (*Pavo cristatus*) train can affect mating success. Behav Ecol Sociobiol 35:213–7.

Prokopy RJ, Owens ED. 1983. Visual detection of plants by herbivorous insects. Annu Rev Entomol 28:337–64.

Rodd FH, Hughes KA, Grether GF, Baril CT. 2002. A possible nonsexual origin of mate preferences: are male guppies mimicking fruit? Proc R Soc Lond B Biol Sci 269:475–81.

Rutowski RL. 1988. Mating strategies in butterflies. Sci Am 279: 64–9.

Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford: Oxford University Press.

Spaethe J, Tautz J, Chittka L. 2001. Visual constraints in foraging bumblebees: flower size and colour affects search time and flight behavior. Proc Natl Acad Sci USA 98:3898–903.

Steel RGD, Torrie JH, Dickey DA. 1997. Principles and procedures of statistics: a biometrical approach. New York: McGraw-Hill Press. p 558–61.

Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IPF. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Anim Behav 66:541–50.

Théry M, Casas J. 2002. Predator and prey views of spider camouflage. Nature 415:133.

Tso IM. 1996. A test of the insect attraction function of silk stabilimenta [PhD dissertation]. Ann Arbor, MI: University of Michigan.

Tso IM, Lin CW, Yang EC. 2004. Colourful orb-weaving spiders and web decorations through a bee's eyes. J Exp Biol 207: 2631–7.

Tso IM, Tai PL, Ku TH, Kuo CH, Yang EC. 2002. Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tragnathidae). Anim Behav 63:175–82.

Vorobyev M, Brandt R. 1997. How do insect pollinators discriminate colours? Isr J Plant Sci 45:103–13.

Wandell BA. 1995. Foundations of vision. Sunderland, MA: Sinauer Associates, Inc.

Watanabe T. 1999. Prey attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. Behav Ecol 5:607–11.

Wise DH. 1993. Spiders in ecological webs. Cambridge, UK: Cambridge University Press.

Yaginuma T. 1986. Spiders of Japan in colour. Osaka, Japan: Hoikusha Publishing Company (in Japanese).

Zschokke S. 2002. Ultraviolet reflectance of spiders and their webs. J Arachnol 30:246–54.