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從視覺生態角度探討蜘蛛捕食者與昆蟲獵物間之行為互動

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1 **Visual interactions between spider predators and insect prey:**
2 **Perspectives from insect visualphysiology**

3
4 **Abstract** Bright body colorations of orb-weaving spiders have been hypothesized to be
5 attractive to insects and thus function to increase foraging success. However, the colour
6 signals of these spiders are also considered to be similar to those of the vegetation
7 background, thus the colorations function to camouflage the spiders. In this study, we
8 evaluated these two hypotheses by field experiments and by quantifying the spiders' visibility
9 to insects. We first compared the insect interception rates of orbs constructed by the orchid
10 spider *Leucauge magnifica* with and without the spider. Orbs with spiders intercepted
11 significantly more insects than orbs without. Such a result supported the prey attraction but
12 not the camouflaging hypothesis. We then tested whether bright body colorations were
13 responsible for *L. magnifica*'s attractiveness to insects by manipulating the spiders' colour
14 signals with paint. Alteration of colour signals significantly reduced *L. magnifica*'s insect
15 interception and consumption rates, indicating that these spiders' bright body parts were
16 attractive to insects. Congruent with the finding of field manipulations were the colour
17 contrasts of various body parts of these spiders. When viewed against the vegetation
18 background, the green body parts were lower but the bright parts were significantly higher
19 than the discrimination threshold. Results of this study thus provide direct evidence that
20 bright body colorations of orb weavers function as visual lures to attract insects.

1 INTRODUCTION

2
3 Various diurnal orb-weaving spiders exhibit brightly coloured markings on their
4 body surface, and the roles of these colorations are still under debate. Many spiders
5 hunt nocturnally and their colorations are usually dark, gray or brown to reduce the
6 spiders' visibility during daytime (Oxford & Gillespie, 1998). However, some
7 orb-weaving spiders of the families Araneidae and Tetragnathidae forage actively
8 during the day and many of them exhibit conspicuous color patterns (Yaginuma
9 1986). In this study, we evaluated the prey-attraction and camouflaging functions of
10 bright body coloration of the orchid spider *Leucauge magnifica* by conducting field
11 experiments and by quantifying their visibility to insects. First, we manipulated the
12 presence of spiders on webs to see whether such treatment would affect the insect
13 interception rates. Secondly, we manipulated the colour signals of orchid spiders to
14 see whether their coloration is responsible for their attractiveness. Finally, we
15 quantified how orchid spiders were seen by insects. The colour contrasts of various
16 body parts of orchid spiders against vegetation backgrounds were calculated by the
17 colour hexagon model of Chittka (1992) to assess whether these brightly coloured
18 spiders were visible to their prey.

19 20 METHODS

21 The Study site and the spider

22 Field manipulative studies were conducted in the summers of 2004 and 2005 at
23 Lien-Hwa-Chih Research Center operated by the Taiwan Forestry Research Institute
24 in Yu-Chi, Nantou County, Taiwan. The study site consisted of a mixture of primary
25 broadleaf forests and Taiwanese fir plantations. A stable population of orchid spiders
26 *Leucauge magnifica* Yaginuma 1954 (Araneae: Tetragnathidae) was found in the
27 neighborhood of the research center. Orchid spiders construct horizontal webs on
28 herbaceous plants along the margin of trails in the study site throughout the year.
29 The prosoma and legs of orchid spiders are green, but their opithosoma are brightly
30 coloured. The dorsum is silver with thin longitudinal black stripes (Fig. 1A). On the
31 ventrum are two distinct yellow stripes embedded in a dark green area (Fig. 1B). In
32 this study, only female orchid spiders were used because their body coloration is
33 brighter and they forage much more actively compared with males (I. M. Tso,
34 personal observations).

1 **Testing the effect of spiders on prey interception:**

2 In this part of the study, we evaluated whether the presence of an orchid spider will
3 affect the prey interception rates of the web. Each day before the experiment we
4 randomly assigned spiders into two groups, experimental and control. In the
5 experimental group, the spiders were carefully removed from the webs and in the
6 control group the spiders were left on the webs. Spider body length, hub diameter,
7 orb radius from four cardinal directions and number of radii were measured to the
8 nearest mm with a digital caliper. The catching area of the orb was estimated by the
9 formula in Herberstein and Tso (2000). The prey interception rates (number of
10 insects hitting the web per hour) were measured by video cameras. Ten video
11 cameras were set up in the study site, five in each group. We placed the video
12 cameras 2 m away and made recordings with an angle of 45° to the left or right side
13 of the webs (depending on the microhabitat nearby). The recordings were conducted
14 daily from 0600 to 1400 between April 1 and 6, 2005. Prey interception data were
15 estimated by averaging the number of prey intercepted by webs during 8 hours of
16 monitoring.

17 **Testing the effect of spider body coloration on prey interception and**
18 **consumption:**

19 In this part of the study, we evaluated whether altering the colour signals of the
20 orchid spiders would affect their prey interception as well as consumption rates.
21 Each day before the experiment, female spiders were assigned into four groups. In
22 the first group, the dorsal silver bands of the spider were covered with green paint of
23 known reflection wavelength (Fig. 4F). In the second group, the green paint was
24 applied on the ventral yellow stripes. In the third group, the green paint was applied
25 on both the dorsal and ventral sides of the spiders. In the fourth group, the control
26 group, the green paint was applied to the green parts of the abdomen (the areas
27 between the silver dorsum and yellow stripes) to serve as a control. Spider body
28 length, hub diameter, orb radius from four cardinal directions and number of radii
29 were measured to the nearest mm. The numbers of insects intercepted by the orbs
30 and those consumed by spiders were also measured by video cameras. Twelve video
31 cameras were used in the experiment, three placed in each group. The recordings
32 were conducted daily from 0600 to 1400 for a total of 19 recording days in August
33 and September, 2004. Rates of prey interception and consumption were estimated by
34 averaging the number of prey intercepted by webs or consumed by the spiders
35 during 8 hours of monitoring.

1 **Calculation of color contrasts:**

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

18 Colour signals were generated by multiplying the surface reflectance function
19 and the illumination function of the habitat (Wandell 1995). The fraction of the light
20 reflected by the surfaces of the spiders or plants is the surface-reflectance function.
21 The daylight illumination function of the forest understory was obtained from Tso,
22 Lin & Yang (2004). We chose the spectral sensitivity functions of the honeybee to
23 determine the photoreceptor excitation for each measured spectra. Therefore, colour
24 contrasts of spiders estimated from visual systems of honeybees should be quite
25 representative. The calculations of color contrasts against various backgrounds
26 followed the method of Chittka (1992; 1996; 2001). One-tailed *t*-tests were used to
27 compare the colour contrast values with the discrimination threshold value of 0.05
28 estimated for hymenopteran insects (Thery & Casas 2002). In this study, the colour
29 contrasts were calculated under these two conditions to examine how prey see the
30 orchid spiders against the vegetation background under different chromatic systems.

31 **RESULTS**

32 **Testing the effect of spiders on prey interception:**

33
34 In this part of the study, data were only included in the analysis when spiders
35 stayed in their orbs for more than 5 hours during the video camera monitoring. Valid
36 insect interception data was obtained from 288 hours of video recording. Among
37 them, 176 were from the control (n = 22 spiders) and 112 were from the
38

1 experimental group (n = 14 spiders). When the orb area was considered, the insect
2 interception rates of webs in the control group were significantly higher than those
3 of the experimental group (Table 1). Compared with the webs without spiders, those
4 with spiders intercepted almost twice as many insects per hour (Fig. 2).

6 **Testing the effect of spider body coloration on prey interception and** 7 **consumption:**

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

23 **Calculation of colour contrasts:**

24 Mean reflectance spectra of various body parts of the orchid spider and the
25 leaves of various plants in the study site were used in the calculations of colour
26 contrasts. The green body parts of orchid spiders such as legs, carapace and ventrum
27 had very similar chromatic properties. All of them exhibited low reflectance across
28 all wavelengths measured (Fig. 4C, D). Such a reflectance pattern was very similar
29 to that of the vegetation background (Fig. 4B). On the contrary, the dorsal silver
30 bands of orchid spiders reflected a considerable amount of light across all
31 wavelengths measured (Fig. 4E). The green paint used had a high reflectance at
32 wavelengths between 400 and 550 nm (Fig. 4F). Colour contrasts of various body
33 parts of orchid spiders viewed against the vegetation background under achromatic
34 vision were significantly higher than the discrimination threshold (Table 4).
35 However, under chromatic vision, colour contrasts of various green body parts of
36 orchid spiders against the vegetation background were low (Fig. 5) and were not
37 significantly greater than the discrimination threshold (Table 3). This result indicates
38 that hymenopteran prey could not distinguish the color signals of green body parts

1 of orchid spiders from the background vegetation from a short distance. Under
2 chromatic vision, colour contrasts of the dorsal silver bands of orchid spiders against
3 the vegetation background were high (Fig. 5) and were significantly higher than the
4 discrimination threshold (Table 4). The ventral yellow stripes when viewed against
5 the dark green ventrum also exhibited a very high colour contrast (Table 4; Fig. 5).
6 The colour contrast of green paint used was also significantly higher than the
7 threshold no matter whether it was seen against the vegetation background or the
8 dark green ventrum (Table 4; Figure 5).

10 **DISCUSSION**

11 Results of this study showed that the colorful spider itself can serve as a visual
12 lure to its prey. In this study, compared with orbs without orchid spiders, those with
13 spiders intercepted almost twice as many insects. Such a result is not congruent with
14 the camouflaging hypothesis, which predicts a similar prey interception rate between
15 orbs with and without spiders. Results of this and previous studies thus demonstrate
16 that orb-weaving spiders do not passively wait for accidentally trapped prey, but use
17 various ways to lure prey. Orb weavers such as the spiny spider (Hauber 2002), giant
18 wood spider (Tso et al. 2002; Tso, Lin & Yang 2004), garden spider (Craig & Ebert,
19 1994) and hunters such as crab spiders (Heiling, Herberstein & Chittka 2003;
20 Heiling et al. 2005) use their bright body coloration to lure prey. Various species of
21 the genus *Argiope*, *Cyclosa* and *Octonoba* incorporate silky structures called
22 decoration in their web to serve as visual lures (Herberstein et al. 2000). Bolas
23 spiders (Haynes et al. 2002) use chemicals mimicking the sex pheromone of their
24 moth prey as attractant, while *Nephila* spiders deposit half-digested prey on webs to
25 attract insects (Bjorkman-Chiswell et al. 2004). Therefore, the traditional view of
26 categorizing orb-weaving spiders as aerial filter feeders that passively sieve prey
27 from the air current flow through their orbs should be reconsidered.

28 Results of this study also demonstrate that the attractiveness of orchid spiders
29 to their prey is achieved by their bright body coloration. When either the dorsal
30 silver bands or ventral yellow stripes of orchid spiders were painted, the insect
31 interception and consumption rates were reduced but did not reach significance level.
32 However, when the color signals of both dorsum and ventrum were altered, the
33 insect interception and consumption rates were further reduced and the difference
34 was statistically significant. Such results indicate that both the dorsal silver bands
35 and ventral yellow bands are attractive to insects. When the color signal on either
36 side of the abdomen was altered, that on the other side was still functioning. Thus,
37 the insect attractiveness was somewhat lowered but not significantly. However,
38 when all the color signals were altered, the attractiveness of the spiders was reduced

1 dramatically. It was unlikely that the odor of the paint was responsible for the
2 observed result, since in the control group we also applied green paint on the green
3 part of the abdomen. In all treatment groups, there was paint on the body of spiders
4 and therefore the observed variation in prey capture among them should be
5 irrelevant with the odor of paint.

6 The attractiveness of the orchid spider's body coloration seems to be achieved
7 by the properties of the colour signal, rather than the visibility of the spider. In the
8 early stage of this study, when choosing appropriate paint with which to alter the
9 color signal of the spider, we purposely used a paint exhibiting a reflectance
10 spectrum different from that of the spiders. The colour contrasts of green paint
11 viewed either against the vegetation background or spiders' dark green ventrum
12 were significantly higher than the discrimination threshold, indicating that the paint
13 used could be readily seen by the insects. However, given such high visibility, those
14 painted spiders still intercepted and consumed far fewer insects than the control
15 group. Such results indicate that the reflectance properties of orb-weaving spiders'
16 body coloration are quite critical to their insect interception. The properties of their
17 colour signal have been fine-tuned by selection to achieve the best attractiveness to
18 their prey. Once such property was altered, even though the changed coloration was
19 still quite visible, they were no longer attractive to insects. Currently, it is not clear
20 why the color signals of these body colorations are attractive to insects. The color
21 signals of orb weaving spiders may be similar to those of flowers and new leaves
22 (Propoký & Owens 1983); thus, these spiders are perceived by their prey as some
23 form of resource. It is necessary to conduct field studies to find out what resources
24 those colorations are mimicking to determine whether these orb-weaving spiders are
25 exploiting the visual system of their prey.

26 Insects see by detecting the contrasts between objects and their environments
27 and all kinds of colour receptors and signals are involved (Chittka & Menzel 1992;
28 Vorobyev & Brandt 1997; Briscoe & Chittka 2001). We suggest that all types of
29 receptor signals should be considered when exploring the visual interactions
30 between predators and prey. Numerous studies have tried to manipulate the UV
31 signal of the system and they did find that in some cases the attractiveness of the
32 spider body coloration or silk decorations were affected (Craig & Bernard 1990; Tso
33 1996; Watanabe 1999; Li et al. 2004). The results of these studies can be interpreted
34 such that manipulation altered the insects' perception thus they were no longer
35 attracted by the altered colour signal. In this study, however, we did not alter the UV
36 signal of the spider but used paint with a strong reflectance in the yellow-green
37 spectra. Such treatment was equally effective in reducing the attractiveness of orchid
38 spiders' body coloration. This result indicates that when the colour signal is altered,

1 no matter whether the change is in the UV, green or blue spectra, such alternation
2 will affect the relative excitations of receptors. Subsequently, the recipient organism
3 have a different perception of the signal perceived and alter their behavioral
4 responses.

5 Various body parts of orchid spiders differ considerably in brightness and
6 colour contrasts and such a pattern is commonly seen in numerous genera of orb
7 weaving spiders such as *Nephila*, *Argiope* and spiny spiders (Yaginuma 1986). We
8 suggest that the co-occurrence of low and high colour contrast body parts in these
9 orb weaving spiders may be an adaptive morphological trait. Because the bright
10 coloration of orb weaving spiders is attractive to insects, if the whole body is
11 covered by high contrast coloration, the contour of the spider will be more than
12 obvious to insects. Prey will quickly learn to associate that with danger by
13 recognizing the shape of the images. The presence of low contrast colorations,
14 however, changes the appearance of the spiders. Break in contour due to low
15 contrast body colorations, plus the resource-mimicking color signals of high contrast
16 body color, make it difficult for insects to associate these spiders with predation risk.
17 Another advantage of such contour-breaking coloration might be to reduce predation
18 risk. Most predators of these orb-weaving spiders, such as birds and parasitoid
19 wasps (Coville 1987; Blackledge & Pickett 2000; Blackledge & Wenzel 2001) are
20 visually orientated. A spider covered by a large area of high contrast colorations
21 makes it easily detected by predators. Therefore, the presence of low contrast
22 coloration to break the contour of the body and high contrast coloration to attract
23 prey seems to be a product of various counteracting selection pressures involved in
24 spider-insect visual interactions.

25

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31

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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)^{1,2}.

Poisson regression						
Parameters		DF	Estimate of	SE	X^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	-	-

¹The of the control group and the orb area 0-200 size category was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

²The ratio between probabilities of two certain events was e^β .

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)^{1,2}.

¹The of the control group and the orb area 100-200 size category was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

Poisson regression					
Parameter	DF	Estimate of	SE	X^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	-	-

² The ratio between probabilities of two certain events was e^β .

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)^{1,2}.

Poisson regression						
Parameter	DF	Estimate of	SE	X^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	-	-	

¹The of the control group and the orb area 100-200 size category was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

²The ratio between probabilities of two certain events was e^β .

Table 4. Results of one-tailed t -tests comparing the colour contrasts of various body parts of the orchid spider *Leucauge magnifica* against vegetation background and against dark green ventrum of the spider seen by honey bees under chromatic and achromatic visions with the discrimination threshold of 0.05.

Vision	Areas examined						
	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

Figure 1. Dorsal (A) and ventral (B) views of the female orchid spider *Leucauge magnifica* showing various brightly-coloured 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 coxa; 2: black sterna; 3: yellow stripes; 4: dark green ventrum.

Figure 2. Mean (\pm SE) 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 (\pm SE) 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.

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.

Figure 5. Mean (\pm SE) colour contrasts of various body parts of the orchid spider *Leucauge magnifica* against the different vegetation backgrounds and the spiders' green ventrum seen by honey bees under chromatic and achromatic vision. Dashed line represents the threshold for colour contrast discrimination calculated for Hymenoptera.

Fig. 1

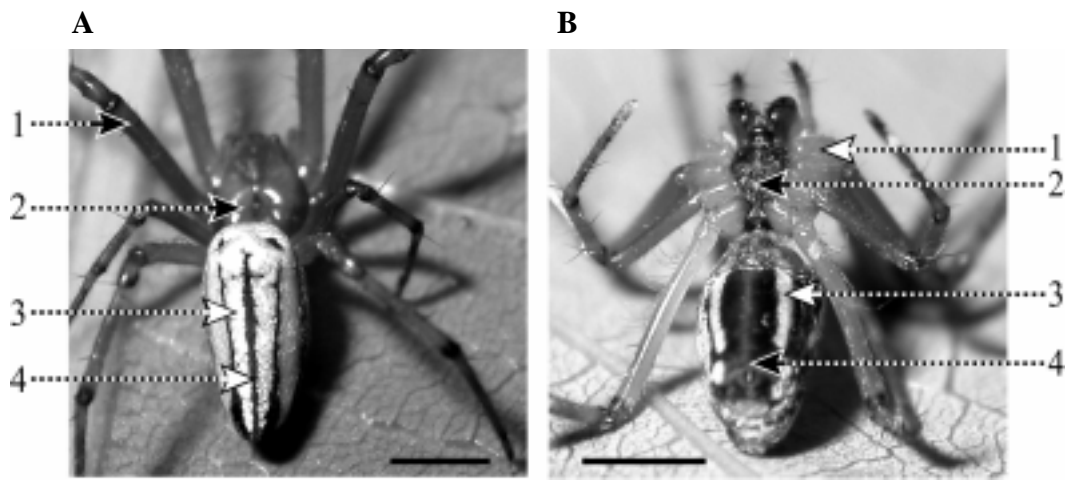


Fig. 2

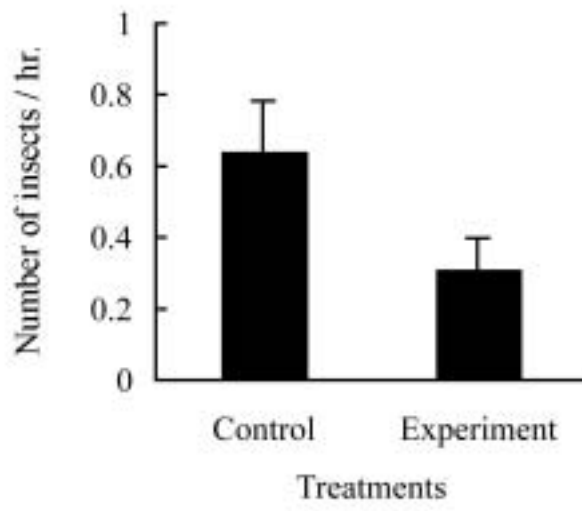


Fig. 3

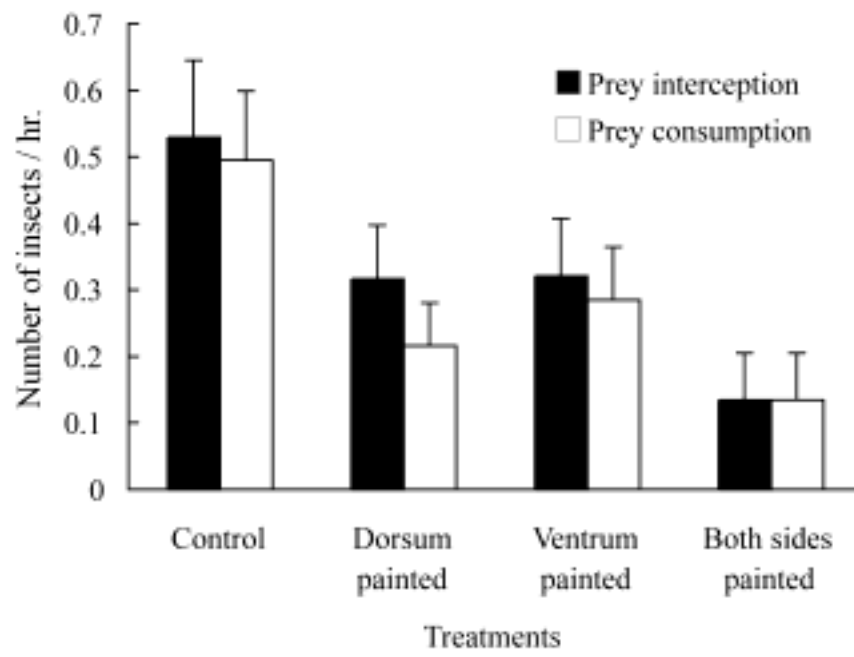


Fig. 4

註解: 沒有標註(A) (B) (C)...

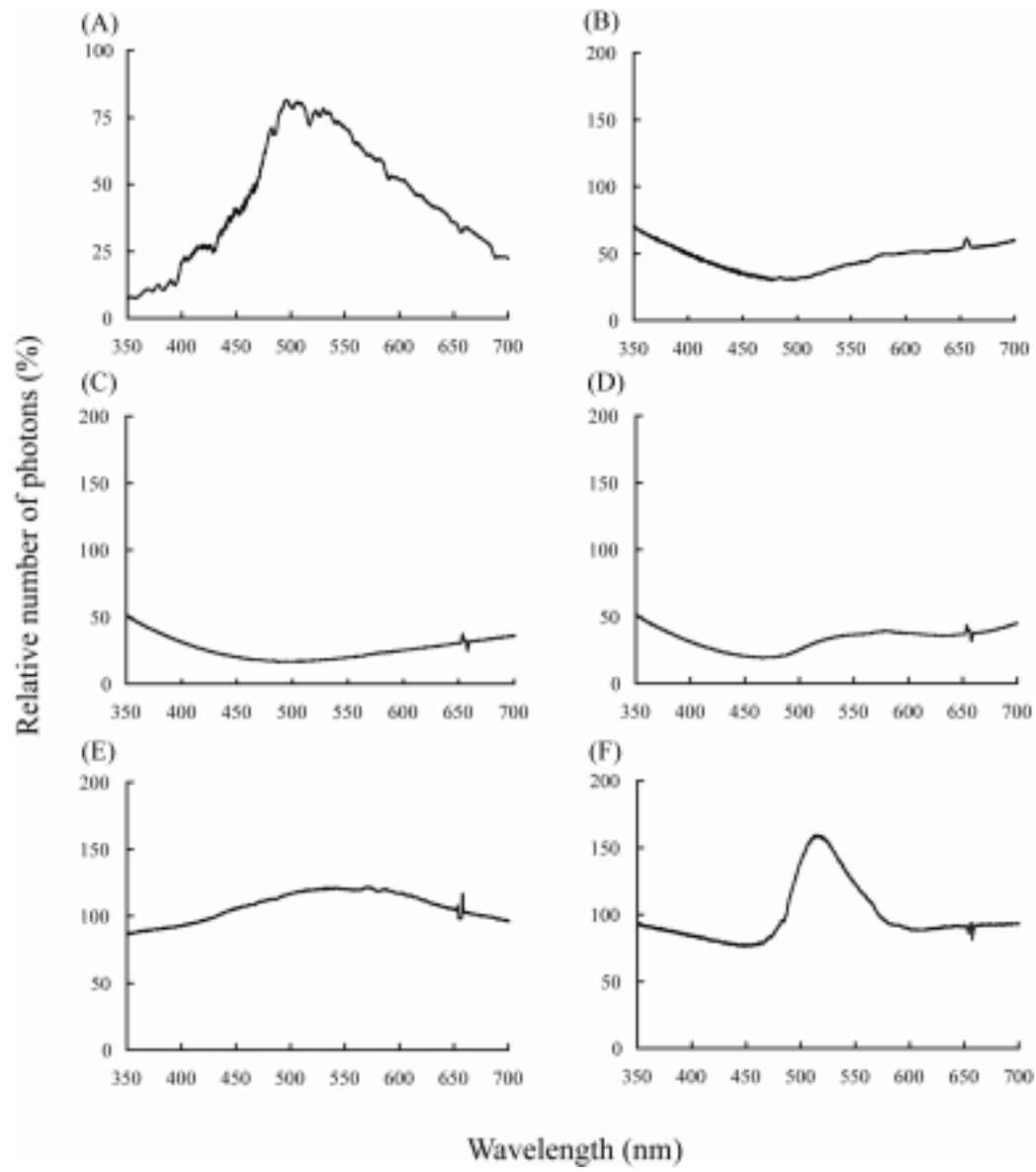


Fig. 5

