

Contents

Contents	1
Chapter1 (A nocturnal predator attracts prey with visual lure)	2
中文摘要	3
Abstract	4
Introduction	5
Materials and Methods	12
Results	22
Discussion	23
Acknowledgments	31
References	32
Tables	37
Figures	41
Chapter2 (Diurnal and nocturnal hunting of a conspicuously-colored sit-and-wait predator)	49
中文摘要	50
Abstract	51
Introduction	53
Materials and Methods	59
Results	68
Discussion	73
References	81
Tables	86
Figures	89

Chapter 1

A nocturnal predator attracts prey with visual lure

一種利用視覺誘餌吸引獵物的夜行性捕食者

中文摘要

本研究從夜行性昆蟲視覺之角度來探討夜行性結圓網蜘蛛其體色是否具有可吸引昆蟲之光訊號，進而了解在光線微弱環境下視覺在捕食者與獵物互動中所扮演之角色。在前人研究結果中顯示，日行性蜘蛛會藉著鮮豔的體表來提供吸引獵物的視覺訊號以增加捕食成功率。茶色姬鬼蛛 (*Neoscona punctigera*) 是夜行性的結圓網蜘蛛，其體色為不醒目的褐色，與其日間所藏匿之環境顏色相似。但在蜘蛛身體腹部的腹面卻具有特別明亮的斑點，且茶色姬鬼蛛步足之腿節常呈現暗紅色。本研究探討在茶色姬鬼蛛腹部之明亮斑點與暗紅色腿節改變其光訊號時是否會影響捕食率。首先以攝影機的夜視模式紀錄有無蜘蛛的網子其獵物攔截率，並將蜘蛛帶回實驗室測量其身體各部位反射光譜，以模擬在獵物視覺中蜘蛛各部位之顏色訊號是否可從背景中被辨識。結果顯示，當網子上有茶色姬鬼蛛時其獵物攔截率顯著高於網子上無蜘蛛的處理組；因此，茶色姬鬼蛛本身似乎能吸引夜行性昆蟲而能提高捕食率。利用色差之計算而模擬獵物視覺之結果發現，昆蟲無法從茶色姬鬼蛛所在的背景中區分出蜘蛛棕色部份的身體，但其明亮的腹部對昆蟲而言卻是很醒目。而夜間視覺模型顯示，從蛾的角度而言，茶色姬鬼蛛腹部亮點之光訊號與夜間開放之花類似。此外，在對蜘蛛腹部之亮點進行塗色處理後發現其獵物攔截率明顯下降，顯示茶色姬鬼蛛腹部亮點在夜間具有吸引獵物的功能。本研究證明茶色姬鬼蛛的亮點為可吸引夜行性昆蟲的視覺誘惑物。

Abstract

In this study the importance of the visual interactions between nocturnal predators and their prey was assessed by investigating whether body color of nocturnal orb weaving spiders were attractive to their prey. *Neoscona* spiders hunt during the night and most parts of their body are inconspicuously brown, which is similar to the color of their diurnal perching sites. However, the ventrum of various species of *Neoscona* exhibits bright color spots in ventrum and deep red femurs, both are distinct from the brown body. I manipulated the color signals of bright ventrum spots and red femurs to see if such treatments would affect their prey interception rates. In the first part of the study, I used the night shoot mode of video camera to record the prey interception rates of webs with or without *N. punctigera*. Then I measured the reflectance spectra of various body parts of those spiders and their typical perching sites to assess how these colors were viewed by diurnal and nocturnal insects. Webs with *N. punctigera* intercepted significantly more insects than those without spiders, indicating that the spiders constituted an attractive signal to nocturnal insect. A comparison of color signals of the spiders and their background using diurnal visual models showed that hymenopteran insects could not distinguish the brown body color of *N. punctigera* from that of bark. However, the bright ventrum spots of *N. punctigera* were highly visible to insects when viewed against the vegetation background. Results of analyzing color signals in the nocturnal context show that spider's ventrum spots exhibited high color contrasts and were similar to those flowers blossoming during night time. Furthermore, when the color signal of the bright spots was altered by paint, spider's prey interception rates decreased significantly. Such results demonstrated that bright spots of *N. punctigera* function as visual lures mimicking the color signals of flowers to attract nocturnal prey.

Introduction

Animals use various ways to communicate and the signals they used include olfactory, visual, auditory, touching, and even electric (Krebs & Davies 1997).

Among these modalities, visual signals are transmitted more directly and quickly than others and they can be delivered to the receiver without medium (Krebs & Davies 1997). However, the visual communications of animals are not always useful and safe. Many signalers (both conspecifics or heterospecifics) produce fake signals to the receiver to increase their own fitness at the expenses of those of receivers (Hasson 1994). For example, the crab spiders inhabiting the flowers of *Chrysanthemum frutescens* attract pollinator prey visually by their high contrast body color (Heiling et al. 2003).

While discussing the visual interactions between animals, most focus are placed on diurnal species than nocturnal species. Several reasons are responsible for such bias. First, there are significant differences in light environment between day and night. The light intensity in the day is higher than the night and therefore it is much easier for researchers to identify and analyze visual interactions. Secondly, the dim light environment in the night has lower signal-to-noise ratio (Warrant 2004).

Whether or how visually-orientated nocturnal animals cope with these two problems is still poorly understood. It is until very recently do researchers realize that

nocturnal vision does exist in a number of organisms (Kelber & Roth 2006). Results of recent studies show that body colorations of diurnal spiders have many functions. For instance, certain crab spiders can change their body coloration to match that of the flowers on which they are perching (They & Casas 2002). Some crab spiders, on the other hand, exhibit a high contrast body coloration which is attractive to insect pollinators (Heiling et al. 2003). Many spiders resemble the appearance of ants and such mimicking may reduce their predation risk for ants are generally avoided by numerous predators (Oxford 1998).

The body colorations of several genera of diurnal orb weaving spiders are very colorful. To date, there are several hypotheses about why diurnal orb weaving spiders have conspicuous body coloration. The prey attraction hypothesis proposes that bright body coloration is attractive to insects and it functions to increase prey interception rate of spiders. The camouflaging hypothesis suggests that color signals of bright body are similar to those of vegetation background thus body coloration functions to conceal the spiders from prey or predators (Merilaita & Lind 2005, Vaclav & Prokop 2006). In addition to these two hypotheses, others such as warning predators, attracting mate, intraspecific recognition had been proposed but those hypotheses lack direct evidence (Hauber 2002). Among these hypotheses, prey attraction hypothesis has received relatively more support. For example, the

Australian spiny orb weaving spider has conspicuous yellow and black stripes. Hauber (2002) applied black paint on spiny spiders' bright yellow dorsal strips and such treatment significantly reduced spiders' prey interception rates. The bright body coloration of the Asian giant wood spider *Nephila pilipes* has also been demonstrated to function as prey attractant (Tso et al. 2002, 2004). In the field, *N. pilipes* exhibiting typical black-and-yellow body coloration caught significantly more prey than their melanic conspecifics (Tso et al. 2002). Tso et al. (2004) assessed how *N. pilipes* was viewed by insects by calculating the color contrasts of various body parts of spiders. They found that only the bright body parts were visible to insects and they proposed that the coloration pattern made the spider looked like some form of resources rather than predators (Tso et al. 2004). Nevertheless, the brightly-colored orchid spider *Lecauge magnifica* had been shown to attract prey with body coloration. Tso et al. (2006) found that webs with orchid spiders intercepted more prey than webs without spiders. When the color signal of conspicuous body parts were altered, the prey interception and consumption rates were reduced significantly. While there is empirical evidence supporting prey attraction hypothesis, support for camouflaging hypothesis is few. Vaclav and Prokop (2006) fixed the diurnal *Argiope bruennichi* and nocturnal *Larinioides cornutus* on artificial webs. Although traps fixed with dulled-colored nocturnal *L. cornutus* intercepted

less prey than those fixed with brightly-colored *A. bruennichi*, the interception rate of the later was similar to that of traps without spiders. Vaclav and Prokop (2006) thus concluded that bright body coloration of spiders might help reduce detectability of spiders to insect, thus increase their hunting success. Concluding from the above review, although these two hypotheses were each supported by empirical evidence and therefore the functions of those diurnal orb weaving spiders are still under debate, prey attraction hypothesis receives more support. So far, all studies examining visual interactions between spiders and their prey focus on diurnal species. No one has assessed the function of body coloration of nocturnal spiders. Whether visual interactions also exist between nocturnal spider and their prey is poorly understood. Most nocturnal spiders, no matter wanderer or weaver, have inconspicuous coloration. The nocturnal orb weavers hunt by building an orb during night time and hide on bark or leaf in the daytime. Most parts of their body are inconspicuously brown and are similar to the color of their diurnal perching sites. However, the ventrum of various species of *Neoscona* and *Araneus* exhibits bright spots, and the femurs of their legs are dark red. In general, there will be two or four ventrum spots, although the form and number vary among species (Fig.1). Only during nighttime will the spiders expose the bright ventrum spots and deep red femurs, during daytime these colorful structures will be fully concealed (Chuang, personal observations).

During the past few decades several behavioral studies had been conducted on nocturnal orb weavers but none of them examined the functions of these spiders' body colorations. Several studies had been conducted to examine the prey composition of nocturnal orb weaving spiders (Pascoe 1980) and some species were found to exhibit prey specialization (Ceballo et al. 2005; Yamanoi & Miyashita 2005). Some studies focused on web site preference of nocturnal orb weaver. The food quality could affect *Araneus trifolium* to select suitable web site (Olive 1982). Nakamura and Yamashita (1997) found that the nocturnal *A. ventricosus* had positive phototaxes. Heiling (1999) further demonstrated that *Larinioides sclopetarius* would actively choose habitats with more light because preys in such environments tend to be more abundant. Finally, some researchers focused on the relationship between web structures of nocturnal spiders and prey catching efficiency. Herberstein and Heiling (1999) demonstrated that nocturnal spiders not only change the web structure by wind and light direction, but also choose suitable site according to these stimuli.

Concluding from the above review, so far all studies on foraging behaviors of nocturnal orb weaving spiders focus on prey specialization, foraging site preference or catching efficiency of trap. No one has examined whether body coloration of nocturnal spiders plays any role in predator-prey visual interactions. While relevant studies had been conducted on diurnal spiders more than a decade ago, the lack of

studies on visual interaction in the nocturnal system might reflect the general belief that visual signal does not play important role in the nocturnal system.

Recent studies show that visual signals are significantly involved in the interactions between nocturnal organisms. For example, many nocturnal vertebrate predators such as owls, geckos, and toads had been demonstrated to use vision to detect prey (Warrant 1999). In the terrestrial ecosystem, the major invertebrate predators are insects and spiders (Gullan & Cranston 2004). However, most predacious insects are diurnal (Gullan & Cranston 2004), and spiders comprise the major invertebrate nocturnal predator (Wise 1993). According to whether they build webs or not, nocturnal spiders could be categorized into two groups, wandering spiders and weavers. While wandering spiders can actively switch foraging sites, weavers must stay on their webs waiting for prey. So how to increase prey catching rate is very important for nocturnal orb weaving spiders (Hauber 2002). To date, no study had investigated how nocturnal orb weaving spiders increase prey catching rate, the mechanisms they use, and the type of prey they specialize on. Recently, more and more scientists found that nocturnal insects could use color vision to detect food resource at night. Nocturnal insects usually possess superposition compound eyes, which combine the light signal of hundreds of ommatidium to increase the photon numbers (Kelber et al. 2003). Kelber et al. (2002) found that hawkmoth *Deilephila*

elpenor could use color vision to discriminate color stimuli at night. Rafuso & Willis (2005) further found *Menduca sexta* to use both vision and olfaction to detect food resource at night. They demonstrated that either visual or olfactory cues alone could attract moths to fly toward the nectar resource. However, only when both visual and scent signals appear will moths perform foraging behavior. Results of those studies show that some nocturnal insects could use vision to search for food resources at night. Is it possible that nocturnal orb weaving spiders could use color signal to lure these insects, as those colorful diurnal spiders do to their prey? In this study, we test the hypothesis that nocturnal spider predator (*Neoscona* and *Araneus*) attract prey with visual lures mimicking the visual signal of food resource and attract prey by testing the followings: (1) Does the dull body coloration of *N. punctigera* function to camouflage the spider in the daytime? (2) Does the presence of nocturnal orb spider on webs affect prey interception rates at night? (3) Do those conspicuous spots of nocturnal orb weaving spiders function to attract prey at night? (4) How are the conspicuous ventrum spots of these spider viewed by their nocturnal prey?

Materials and Methods

Color contrast calculation using diurnal visual model:

We simulated how various body parts of *N. punctigera* were viewed by their insect prey or predator by calculating the color contrasts. Six female *N. punctigera* were collected from Taiwan Endemic Species Research Institute, Chi-Chi, in Nantou County, Taiwan. S2000 spectrometer (Ocean Optics, Inc., Dunedin, Florida, U.S.A.) was used to measure the reflectance spectra of five different body parts of *N. punctigera* (Fig. 1). The reading probe was vertically placed 5mm above the regions to be measured. Since wasp is the major diurnal predator of orb weaving spiders (Blackledge et al. 2005), so we used the visual model developed from Hymenoptera to calculate the color contrast. Since during the day *N. punctigera* usually perched on twig or bark nearby their web sites, we measured the reflectance spectrum of bark and used it as the background light signal. To determine whether the color signal of an object could be identified against certain background, first the quantity of light stimuli received by each photoreceptor must be estimated by the following equation (Stavenga et al. 1993; equation 1):

$$P = R \int_{350}^{700} I_s(I) S(I) D(I) dI \quad (1)$$

Where P is quantum catches that is absorbed by each photoreceptor, function I_s is spectral reflectance of stimulus, function S is spectral sensitivity of honeybee

photoreceptor, function D is the spectral reflectance of illumination. Function R is the sensitivity factor and can be calculated by the following equation:

$$R = 1 / \int_{350}^{700} I_B(\lambda) S(\lambda) D(\lambda) d\lambda \quad (2)$$

Where function I_B is the spectral reflection of background.

Although the quantum catches are received by the photoreceptor, they will not be directly accepted by the insect brain. Therefore the quantum catches P must be transformed to effective signal that could be accepted by the brain by the following equation (Naka & Rushton 1966; equation 3):

$$E = P / (1 + P) \quad (3)$$

Where E is excitation maximum value, P is quantum catches of each photoreceptor.

Then the planar coordinate was used to express signals. Each stimulus could generate three E values: E_g , E_{uv} and E_b respectively. Where E_g is the excitation value of green photoreceptor of honeybee, E_b is that of blue photoreceptor and E_{uv} that of ultraviolet photoreceptor. To integrate these three excitation values, we used the following color hexagon model of Chittka (1996; equation 4):

$$X = \sqrt{3} / 2 (E_g - E_{uv}) \quad (4)$$

$$Y = E_b - 0.5(E_{uv} + E_g)$$

The Euclidean distances (ΔSt) of X and Y , which is the color contrast, can be calculated by the following equation (equation 5):

$$\Delta St = \sqrt{(\Delta X)^2 + (\Delta Y)^2} \quad (5)$$

For honeybees, color contrast discrimination threshold is estimated to be 0.05 (They & Casas 2002). We used one tail t-tests to examine whether the color contrasts of five body parts were significantly higher than the discrimination threshold value.

Calculating color contrast using nocturnal visual model:

The video recordings showed that moth was the major prey of *N. punctigera*. Therefore, we used nocturnal visual model developed for moth to assess how *N. punctigera* was viewed by their prey. The reflectance spectra of spiders and vegetation background were those used previously. In addition, in order to realize what kind of resources the bright spot of *N. punctigera* were mimicking, we measured the reflectance spectra of the following flowers: *Hedychium coronarium* Koenig (butterfly ginger), *Bidens alba* Sherff (big bidens) and *Sambucus formosanum* Nakai (Formosan elderberry). During the study these flowers were quite abundant in the study site. The visual model used by Johnsen et al. (2006) was followed to calculate the achromatic contrasts of different body parts of *N. punctigera*. The following equation was used to calculate the quantum catches of one ommatidium of moth (Warrant & Nilsson 1998).

$$N = 1.13(p/4)n\Delta P^2 D^2 \Delta t \int_{350}^{700} kt(1 - e^{-kRi(I)l})L(I)dI \quad (5)$$

Where n is the effective facets in the superposition, P is the photoreceptor acceptance angle, D is the diameter of a facet lens, t is the integration time of a photoreceptor, η is the quantum efficiency of transduction, t is the fractional transmission of the eye media, k is the absorption coefficient of the rhabdom, l is the rhabdom length doubled by tapetal reflection, $R_i(\lambda)$ are the absorbance spectra of each photoreceptor, $L(\lambda)$ is the reflectance spectra of object multiplied by the reflectance spectra of light environment and then divide by p (Johnsen 2006). The difference of object of interest and the background, the achromatic contrast, can be estimated by the following equation:

$$C = \frac{N_x - N_{green}}{N_x + N_{green}} \quad (6)$$

Where N_x is quantum catches of object, and N_{green} is quantum catches of green vegetation background (Johnsen et al. 2006). Currently, the discrimination threshold value of nocturnal color contrast is still not available.

Therefore, we compared the contrast values of various body parts of *N.*

punctigera and flowers using *t*-tests to determine whether the ventrum spots

were more conspicuous than other body parts, and whether they mimicked

the color signal of flowers.

In addition to achromatic contrast, I also calculated chromatic color contrast of various body parts of *N. punctigera* when viewed by moth during nighttime. First,

the quantum catches of one ommatidium (N) was calculated, and the N values of each photoreceptors were estimated to generate N_{uv} , N_b and N_g . Then q_{uv} , q_b and q_g , the relative quantum catches of each type of photoreceptor, were calculated by the following equations (Johnsen et al. 2006):

$$q_{uv} = \frac{N_{uv}}{N_{uv} + N_b + N_g} \quad (7)$$

$$q_b = \frac{N_b}{N_{uv} + N_b + N_g} \quad (8)$$

$$q_g = \frac{N_g}{N_{uv} + N_b + N_g} \quad (9)$$

Then values of each stimulus were used to calculate relative distances in the color triangle by the following equations (Johnsen et al. 2006):

$$X_1 = \frac{1}{\sqrt{2}}(q_g - q_b) \quad (10)$$

$$X_2 = \frac{\sqrt{2}}{\sqrt{3}}(q_{uv} - \frac{q_g + q_b}{2}) \quad (11)$$

X_1 and X_2 were the distances on the X axis and Y axis, which represented the relative intensity of three types of photoreceptors in the 2D color space. The distance of two

color stimuli on the color space was the color contrast (Johnsen et al. 2006). So far, no one had developed theoretical discrimination threshold value for the nocturnal chromatic visual model. Therefore, I used ANOVA tests to compare the chromatic color contrasts of different body parts of *N. pilipes* and the dark paint when viewed by moths against the green vegetation background.

Manipulating the color signal of spiders in the field :

In this part of study, we manipulated the color signal of *N. punctigera* to see whether such treatment would reduce insect catching rates. The field experiments were conducted in June 2005 in Taiwan Endemic Species Research Institute, Chi-Chi, Nantou County, Taiwan. In this research institute, the major woody plant is *Cinnamomum camphora* Nees and common forb like *Hedychium coronarium* Koenig (butterfly ginger), *Bidens alba* Sherff (big bidens) and *Sambucus formosanum* Nakai (Formosan elderberry). Female *N. punctigera* with carapace width larger than 0.5 cm were used. In the first experiment, I manipulated the presence of *N. punctigera* to see whether spider itself was attractive to prey. Each day after sunset when *N. punctigera* had emerged and completed web building, I randomly chose spiders and divided them into two groups. In the first group the spiders were carefully removed from their webs without damaging the orb. In the second group

the spiders were left on their webs. Since web area was known to influence prey catching rate of webs (Herberstein & Tso 2000), we also estimated the area of orb built by *N. punctigera* a covariable. In addition to determining whether presence of spiders would affect prey interception rate of webs built by *N. punctigera*, we then assessed whether the ventrum spots were responsible for the attractiveness. Each night before the recording *N. punctigera* were randomly assigned into two groups. In the first group, the experimental group, we used brown paint to alter the color signal of ventrum spots. Before the brown paint was applied on spiders, we measured its reflectance spectrum by S2000. The reflectance spectrum of brown paint was similar to that of brown body coloration of *N. punctigera* (Fig. 3F) and they did not differ in color contrast (achromatic, $t = 0.277$, $p = 0.79$; chromatic, $t = 2.66$, $p = 0.024$). In the second group, the control group, same amount of paint was applied on the brown ventrum near the spots. Before the application of paint the spiders were carefully removed from the web without damaging the orb and were anesthetized by CO₂ for 5 minutes. After the spiders recovered they were gently released back to their original web. The measurement of web parameters and the recording of interception events were similar to those mentioned previously. In addition to ventrum spots, I also manipulated the color signal of the red femur to see whether that would also affect attractiveness of *N. punctigera*. Female *N.*

punctigera were randomly assigned into two groups, one received brown paint on red femurs while another on the brown part of legs. All the rest of operations were similar to those described previously. The prey interception rates of webs with and without *N. punctigera* were measured using the night shot function of Sony HR118 Hi-8 video cameras. The video cameras were placed 1~2 m away from the web, depending on the vegetation nearby. The prey interception rates of webs were monitored for 8 hours (from 2000 to 0400 hours) each night for a total of 9 nights. After the experiment was completed the video tapes were brought back to the laboratory for subsequent analysis. The number of insects intercepted by webs was recorded and the taxonomic order of prey was also determined. During the field study each day before video recording we measured web radius, hub radius, length of hub, spiral number, radii number from four cardinal directions. These web parameters were used to calculate effective web area following the equations of Herberstein and Tso (2000).

Analysis of covariance (ANCOVA) was used to assess the effect of treatment on prey interception rates using orb area as covariance, if the data was normally distributed. If the data followed a Poisson distribution, then a Poisson regression would be used. When the data was not congruent with either normal or Poisson distribution, then nonparametric tests were used. Finally, the χ^2 test of homogeneity

was used to test the prey composition between different treatment groups.

Result

Color contrast calculation using diurnal visual model:

The reflectance spectrum measurements covered the range from 350 nm to 700 nm. Most body parts of *N. punctigera* had a low reflectance across the wavelengths measured. However, the bright spots on ventrum exhibited a high reflection at the area of 500~700 nm (Fig. 3E). Beside the bright spots, the other body parts had similar reflectance spectrum pattern (Fig. 3A~D). Both achromatic and chromatic contrasts of bright spot calculated by the diurnal visual model when viewed against bark by hymenopteran insects were significantly higher than the discrimination threshold value of 0.05 (Table 1, Fig. 4).

Color contrast calculation using nocturnal visual model:

Color contrasts of various body parts of *N. punctigera* calculated by nocturnal visual model followed the pattern of those derived from diurnal model. The achromatic contrast of bright spots was significantly higher than the other body parts (Fig. 5). Color contrasts of the other four body parts did not differ significantly among each other (Fig. 5). The achromatic contrasts of three species of flowers differed significantly (Fig. 6). The contrast of ventrum spot was significantly higher than that of *S. formosanum*, similar to that of *H. coronarium* and lower than that of *B.*

alba (Fig. 6). Such results indicate that the ventrum spots of *N. punctigera* and the flowers examined in this study were quite distinctive to moth when viewed against vegetation during the night. The chromatic color contrasts of various body parts of spiders and flowers also showed similar a pattern. The chromatic color contrast of bright spots was significantly higher than others body parts (Fig. 5). The other body parts did not differ significantly in nocturnal chromatic contrasts. The chromatic color contrasts of bright spots and *H. coronarium* were significantly lower than that of *B. alba*, but significantly higher than that of *S. formosanum* (Fig. 6).

Manipulating the color signal of spiders in the field :

When *N. punctigera* were present, the number of prey intercepted by the web was significantly higher than that of webs without spiders (Table 2). The mean prey interception rate of webs with spiders was 2.5 times that of webs without. This result indicated that *N. punctigera* itself could serve as an attractant to prey. The results of manipulating spider color signals demonstrated that the ventrum spots were responsible for such attractiveness. The prey interception rate of the experimental group (brown paint on ventrum spots) was significantly lower than that of the control group (brown paint on brown ventrum) (Table 3). When the color signal of ventrum spots was altered, the prey interception rate of *N. punctigera* reduced to one third that

of the control group (Fig. 8). In addition to prey interception rate, alteration of ventrum spot color signal also significantly changed the composition of prey ($X^2 = 11.5, P < 0.05$, Fig. 9). The major taxonomic order of intercepted insects in the control group was Lepidoptera (63%). However, in the experimental group the dominance of Lepidoptera in the diet reduced dramatically (Fig. 9). Although the color of femur of *N. punctigera* was quite different from that of brown body part, it did not seem to serve as a visual attractant. Compared with the prey interception rate of the experimental group (brown paint on femur), that of the control group (brown paint on brown part of legs) was not significantly higher (Table 4, Fig. 10). Finally, during 784 hours of video monitoring, we did not observe any attack event on *N. punctigera*.

Discussion

Most members of the genera *Neoscona* and *Araneus* have bright spots on the ventrum and our results showed that such feature serves as a visual lure to nocturnal prey. Here we propose that the bright spots of numerous nocturnal web spiders (such as *Neoscona* and *Araneus*) probably also function to attract nocturnal insect and to increase spider's prey encounter rate. Results of this study also show that while *Neoscona* spiders deliberately display their visual lure during the night; they minimize the visibility to predator morphologically and behaviorally during daytime. During daytime these spiders tear down their web and sit on the twig or bark nearby with all legs drawn close to the body, greatly alter the contour of the spiders. Moreover, the color contrast of spider's dorsum when viewed against the bark does not exceed the discrimination threshold of the hymenopteran insects. Therefore, it should be very difficult for wasps to visually detect *Neoscona* hiding on bark during daytime. The use of visual lure to attract nocturnal prey and inconspicuous body color to camouflage oneself during daytime might be *Neoscona* and *Araneus* spiders' adaptations to high predation pressures of parasitoid hymenopteran and dipterans. The great majority of these parasitoid insects are diurnal and many of them are visually orientated (Gullan & Cranstan 2004). For nocturnal orb weaving spiders, totally switching the foraging to nocturnal might lose the opportunity of catching

diurnal prey. However, the benefit of avoiding diurnal predator might have outweighed the cost of losing diurnal prey intake. Congruent with such hypothesis is that during 748 hours of video recording, we did not find any event of attack on spiders.

Results of this study showed that the nocturnal color contrast of ventrum spots of *N. punctigera* was high but those of the rest of body parts were low. Such results indicate that when *N. punctigera* are viewed by moths against the vegetation background, the ventrum spots will be quite distinctive while the rest of body will be relatively indistinguishable from the vegetation background. Therefore, from the eyes of moths the color signals of *N. punctigera* are perceived as something other than predators. Results of this study also demonstrated that the ventrum spots might be mimicking the color signal of moths' food resources. Both the flowers examined and ventrum spots of *N. punctigera* have high color contrasts and the values between spots and *H. coronarium* were quite similar. Results of previous studies show that the body colorations of diurnal orb weaving spiders might mimic the color signal of prey's food resources such as nectar or new leaves thus are attractive to insects (Heiling et al. 2003, Tso et al. 2004). Results of this study further demonstrate that such luring also occurs in the nocturnal context. By exhibiting body coloration resembling the color signal of flowers open at night, nocturnal orb weaving spiders

visually attract prey to fly toward them to increase foraging success.

Results of this study show that bright spot function as a visual lure to attract nocturnal insect, and it could increase foraging success of *N. punctigera*.

Theoretically, the size of such visual lure should be large to maximize the attractiveness. However, the ventrum spots of *Araneus* and *Neoscona* were not large and they only occupy a small part of the ventrum (Fig. 1). Why *Neoscona* and *Araneus* spiders exhibit small rather than large visual lures? Two reasons might be responsible for such small visual lures. First, the size of ventrum spots might be constrained by strong predation pressure. During daytime when the parasitoid insects are most abundant *Neoscona* or *Araneus* spiders usually sit on bark with bright ventrum spots well concealed. However, if the size of ventral spots expands too much it will make spider difficult to conceal them and thus increase the detectability of the spiders. Secondly, the small size of bright spot might have evolved to cheat prey. When nocturnal prey such as moths detected spiders' ventrum spots, they might mistakenly regard the signal of potential food resources as being far away and consequently accelerate toward them. As the fast flying prey approached the spider and suddenly detected the predator, it might be difficult for them to perform appropriate avoidance maneuvering and they eventually collided into the webs.

From the video recording, moths were frequently observed to pass through the web or

pass by the margin of web then fly directly toward the spider (Fig. 11). Therefore, the small sized ventrum spots of nocturnal orb weaving spider might be generated by selection to achieve a better luring of prey.

In the field experiments, webs with spiders intercepted more prey and those with spiders' ventrum painted caught much fewer insects. The attractiveness of the spiders is considered as generated by the visual signals of the highly distinctive ventrum spots. When the color signals of ventrum spots were altered by paint, their luring effect was severely reduced. However, in addition to night color vision, moths also exhibit excellent olfactory senses (Hansson 2002). Was it possible that the ventrum spots were actually emitting some sort of prey-attracting olfactory signal, and the application of paint blocked the release of such substances? The possibility that *N. punctigera*'s ventrum spots actually serve as olfactory lures is low. Because, when those ventrum spots were carefully examined under the microscope there were no openings on them. The brightly pigmented area was covered by a continuous sheet of cuticle that covered the whole ventrum (Chuang, personal observation). On the other hand, it was also unlikely that the observed results were generated by nocturnal insects being attracted by the paint used to alter color signals. In this study we applied the same amount of brown paint on spiders of the control and experimental treatments. If the brown paint could attract moth, the prey interception

rates of control and experimental treatments should be similar. Therefore, the attractiveness of ventrum spots should be resulting from visual signal they generated. Alteration of such signals by paint will severely reduced their effectiveness as visual lures. Although the color of femurs of *N. punctigera* was different from the rest of body, they do not exhibit visual attractiveness to insects. We propose that the color difference between femurs and the other body parts may be related to *N. punctigera*'s camouflaging posture. During the day *N. punctigera* will sit on the twig or bark with all legs drawn near it body. While the body of *N. punctigera* is covered by brown spines or hairs, the surfaces of femurs have no hairs and thus are quite smooth. The lack of spines/hairs on femurs enables spiders to draw them tightly under the body to effectively change the contour of the spider. We had compared the red femur and the other parts of leg under the microscope and found that the redness of femurs simply reflects the original coloration of the spider. The brownish appearance of *N. punctigera* is generated by numerous brown hairs and spines rather than the cuticle of the spider. In addition to *Neoscona* and *Araneus*, other nocturnal orb weavers such as *Poltys* also exhibit red femurs (Chuang, personal observations). More study is needed to realize whether red femurs of these nocturnal orb weavers simply function to draw legs tightly together, or there are other functions.

In this study, the night shoot function of Hi-8 video cameras was used to record

the prey catching events of spiders. To make recording in the darkness, infrared beam was emitted from the video camera and the light reflected from the objects was used to generate images. Because most insects do not have infrared photoreceptors (except for some ants) (Briscoe & Chittka 2001), the infrared light of video camera should be invisible to prey of spiders (Depickere et al. 2004). Therefore, it should be the natural light signal reflected from ventrum spot of *N. punctigera* that attracted nocturnal insects, instead of the infrared light emitted from the video camera. On the other hand, one may argue that the infrared light reflected from the ventral spots might generate heat thus made the control spiders attractive to insects. In this study we did not measure the amount of heat generated from *N. punctigera* in the spot-painted and control groups. Therefore, it was not clear whether spiders in two treatment groups differed in the quantity of heat reflected. However, although most insects have thermoreceptors in the antenna, most insects could not detect the heat source (Gullan & Cranston 2004). There are a few studies demonstrating with direct evidence that insects such as cockroach, large moth, and beetles can detect heat. Some insects, such as beetles, could only detect heat which intensity is as large as forest fire (Gullan & Cranston 2004). The field experiments of this present study were conducted in a subtropical study site during summers, and the ambient temperatures usually exceeded 30°C. Therefore, it is unlikely the heat generated

from infrared reflection attracts nocturnal insects and thus affected the results of field experiments.

So far very few studies had investigated the predator-prey visual interactions in the nocturnal context. Our lack of understanding on nocturnal color vision makes most people consider that visual signals do not play significant role during night time. Recently, more and more studies found that nocturnal insect had excellent color vision (Kelber 2002, Warrant 1999). Results of this study demonstrated that a nocturnal terrestrial predator could use visual lures to attract prey. Therefore, predator-prey visual interactions also occur in the nocturnal light environment. This study is the first to simulate how the body color signal of a nocturnal predator is viewed by their prey. The nocturnal vision model I used was proposed by Warrant (1999), and was initially used to simulate how the color signals of nocturnal flowers were viewed by nocturnal pollinators. We used this nocturnal vision model to demonstrate our hypothesis. Although several previous studies used diurnal vision model to investigate how diurnal predators were viewed by their prey (Tso et al. 2004, They & Casas 2002), no study has used the color contrast approach to study predator-prey visual interactions in the nocturnal system.

Both moth and most nocturnal insect had superposition compound eyes. In order to aggregate the weak light signal and assemble it to only one ommatidium, the

superposition eye had possessed specific structures (Warrant 1999). Besides, superposition eyes have longer rhabdom than apposition eyes. The longer rhabdom helped to improve the problem of low signal-to-noise ratio characteristic of nocturnal light environment (Kelber & Roth 2005). One implication of this study is that perhaps in addition to moths many insects may also have nocturnal vision. To date, although only a few nocturnal insects are demonstrated to possess nocturnal color vision, nocturnal insects exhibit excellent nocturnal color vision might be quite abundant than we currently know. We believe that visual signal should play a very significant role in the nocturnal system in aspects such as foraging communication, mating, or intraspecific recognition. In the past, because of the limitation on research equipment and methodologies, the visual interactions of nocturnal animals are generally ignored. In the future, we should place much emphasis in the role color visions played in the nocturnal system.

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Table 1. The result of *t*-tests comparing the achromatic and chromatic color contrasts of various body parts of *N. punctigera* with the discrimination threshold of 0.05 estimated for honeybee (*Apis mellifera*).

Color contrast	Bright spot	Abdomen	Black area	Leg	Femur	Brown paint
Achromatic						
<i>t</i>	17.615	0.491	-0.896	-2.908	0.081	-0.909
<i>P</i>	<0.001	0.644	0.411	0.033	0.938	0.530
Chromatic						
<i>t</i>	17.615	0.491	-0.896	-2.908	0.081	0.081
<i>P</i>	<0.001	0.644	0.411	0.033	0.938	0.938

Table 2. The results of Poisson regression comparing the prey-interception rates of *N. punctigera* in the with spider and without spider groups.

Parameter	DF	Estimate of β	SE	χ^2	p
Intercept	1	-4.949	0.596	68.84	<.001
Web area 0-100	1	-0.514	0.575	0.800	0.371
Web area 100-200	1	-0.394	0.569	0.480	0.488
Web area 200-300	1	0.068	0.579	0.010	0.906
Treatment With-spider	1	0.851	0.325	6.840	0.008
Treatment Without-spider	0	0	0	-	-

Table 3. The result of Poisson regression comparing the prey interception rates of *N. punctigera* in the experimental (ventrum spot painted) and control (body ventrum painted) groups.

Parameter		DF	Estimate of β	SE	χ^2	p
Intercept		1	-6.637	0.773	73.610	<.001
Web area	0-100	1	0.759	0.758	1.000	0.316
Web area	100-200	1	0.726	0.731	0.990	0.320
Web area	200-300	1	0.571	0.759	0.570	0.452
Web area	300-400	1	0.853	0.768	1.230	0.267
Treatment	Control	1	1.364	0.313	18.900	<.001
Treatment	Experiment	0	0	0	-	-

Table 4. The result of Poisson regression comparing the prey interception rates of *N. punctigera* in experimental (red femur painted) and control (brown leg painted) groups.

Parameter	DF	Estimate of β	SE	χ^2	p
Intercept	1	-5.230	0.581	81.040	<.001
Web area 0-100	1	0.003	0.630	0.000	0.996
Web area 100-200	1	-0.215	0.659	0.110	0.743
Web area Control	1	-0.255	0.363	0.490	0.482
Web area Experimental	0	0	0	-	-

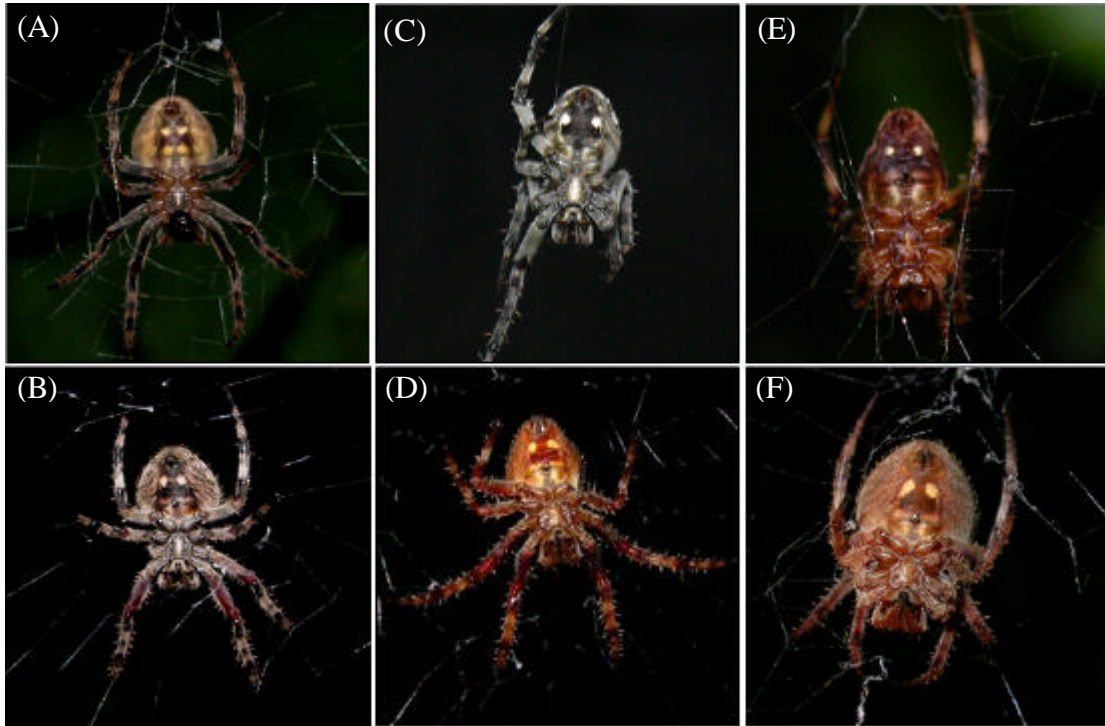


Figure 1. Different forms of ventrum bright spots in nocturnal orb weaving spiders. A and B: *Neoscona punctigera*; C: *N. nautical*; D: *Araneus lugubris*; E: *N. Scylla*; F: *A. rufofemoratus*.

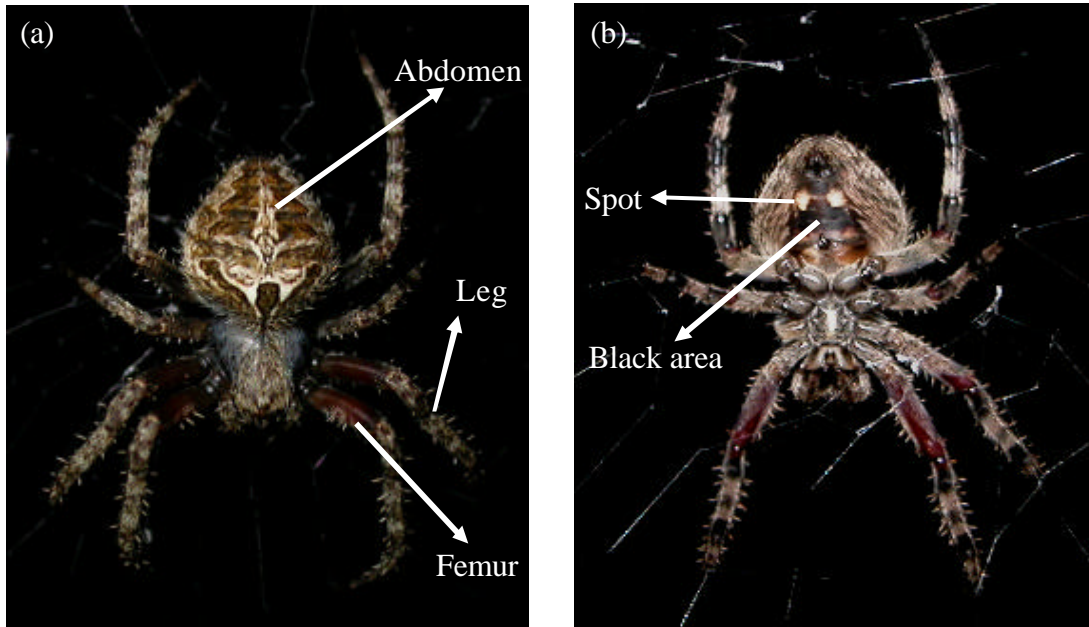


Figure 2. Dorsal (a) and ventral (b) views of *Neoscona puntigera*. Body parts from which reflectance spectra were measured were specified.

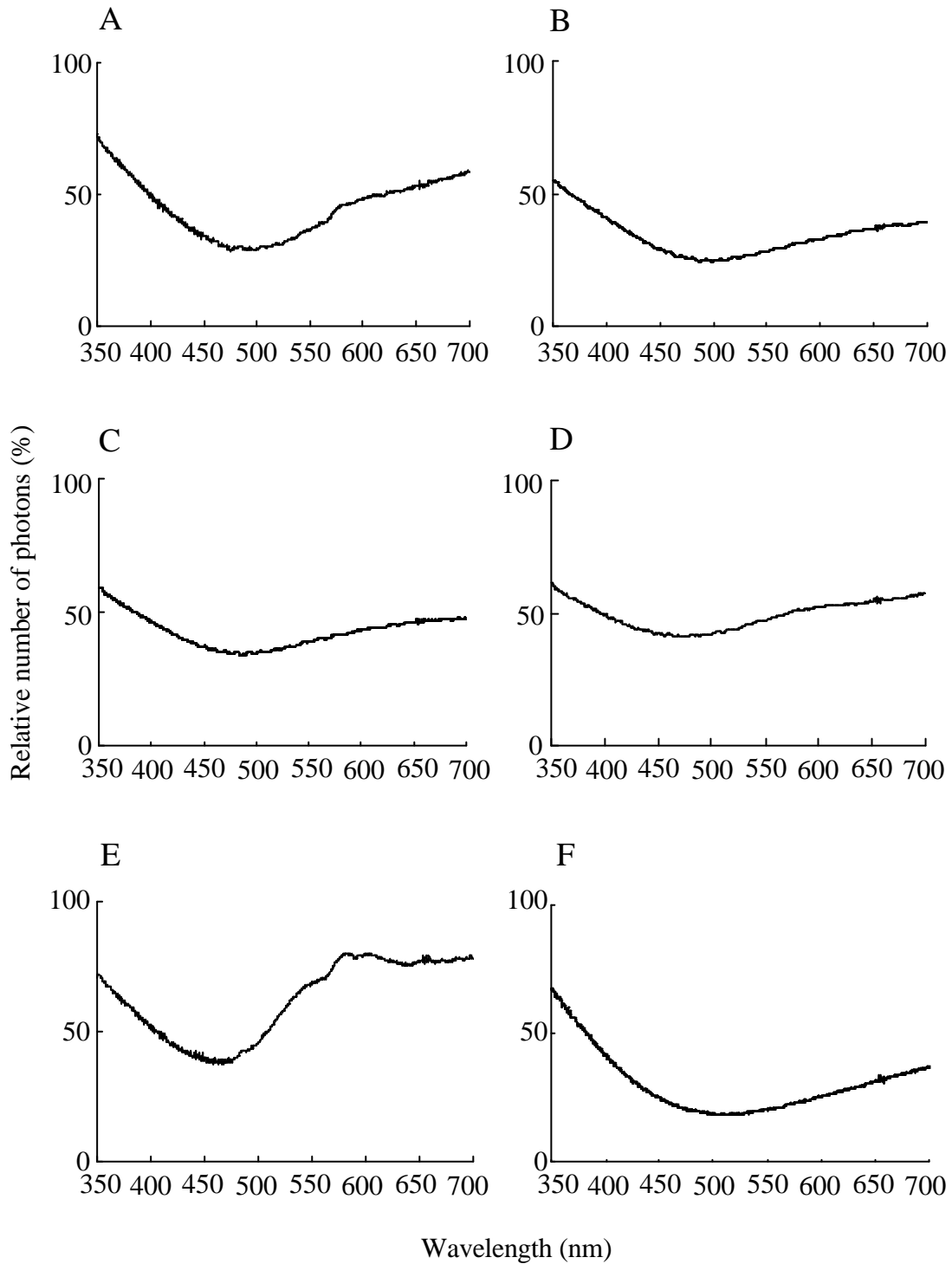


Figure 3. The reflection spectra of various body parts of *Neoscona punctigera*. A: femur, B: the black area on the ventrum, C: leg, D: abdomen, E: bright spot, F: brown paint used in altering body color signal.

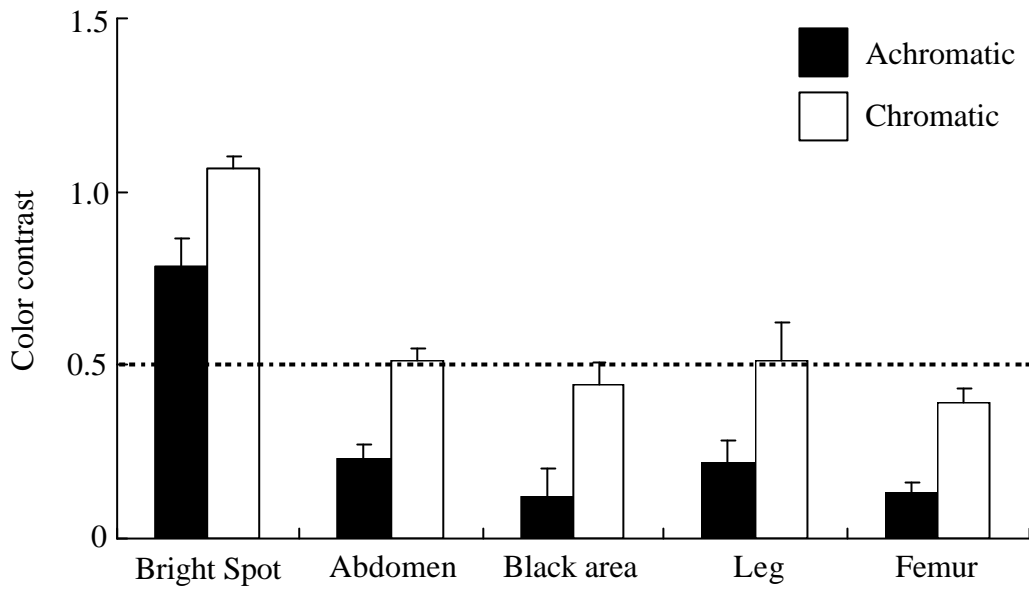


Figure 4. Mean (\pm SE) color contrasts of different body parts of *Neoscona punctigera* calculated by diurnal visual model. The broken line is the discrimination threshold estimated for honeybee (0.05).

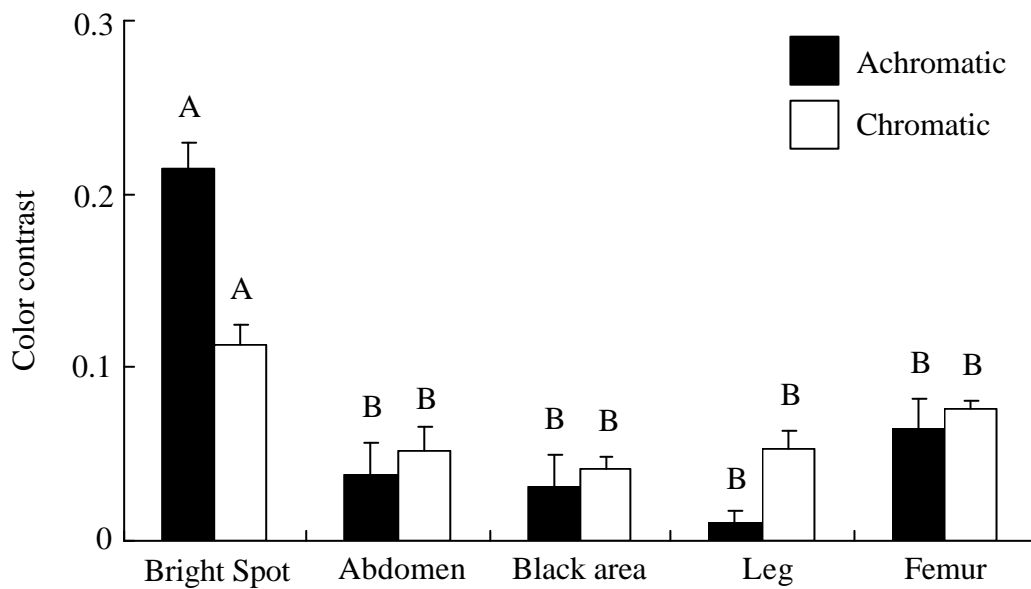


Figure 5. Mean (\pm SE) color contrasts of different body parts of *Neoscona punctigera* calculated by nocturnal visual model. Capital letters represent results of ANOVA test LSD mean comparisons.

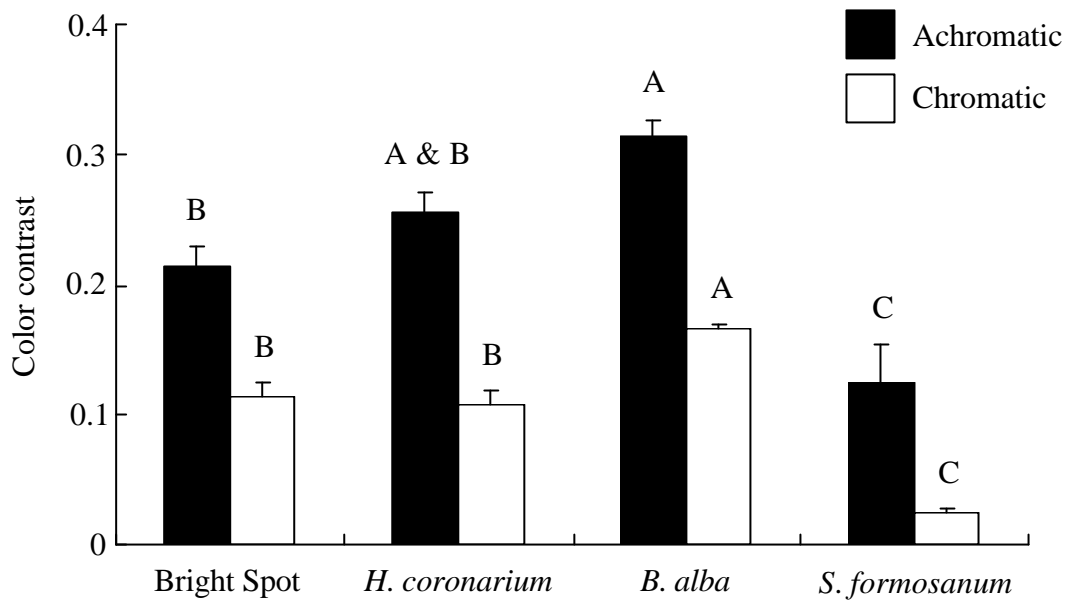


Figure 6. Mean (\pm SE) color contrasts of bright spots of *Neoscona punctigera* and various flowers calculated by nocturnal visual model. Capital letters represent results of ANOVA test LSD mean comparisons.

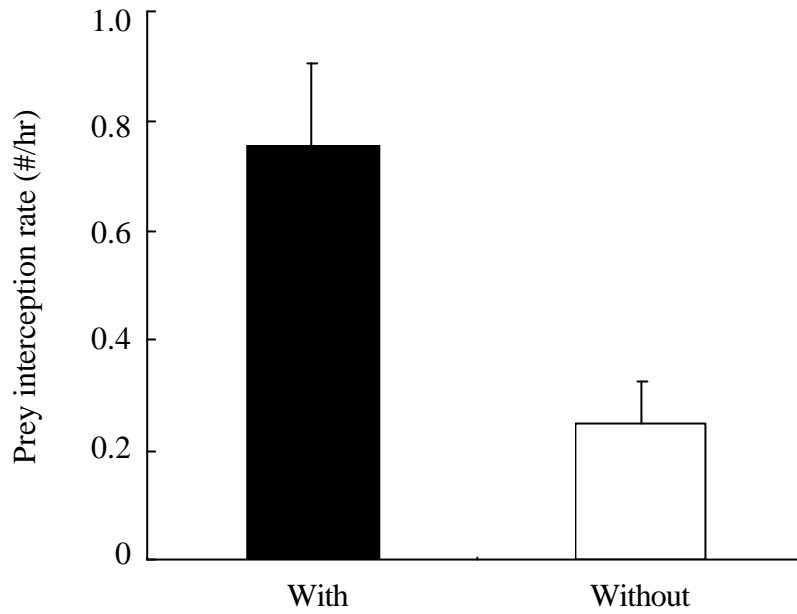


Figure 7. Mean (\pm SE) prey interception rates of webs built by *Neoscona punctigera* with and without spiders.

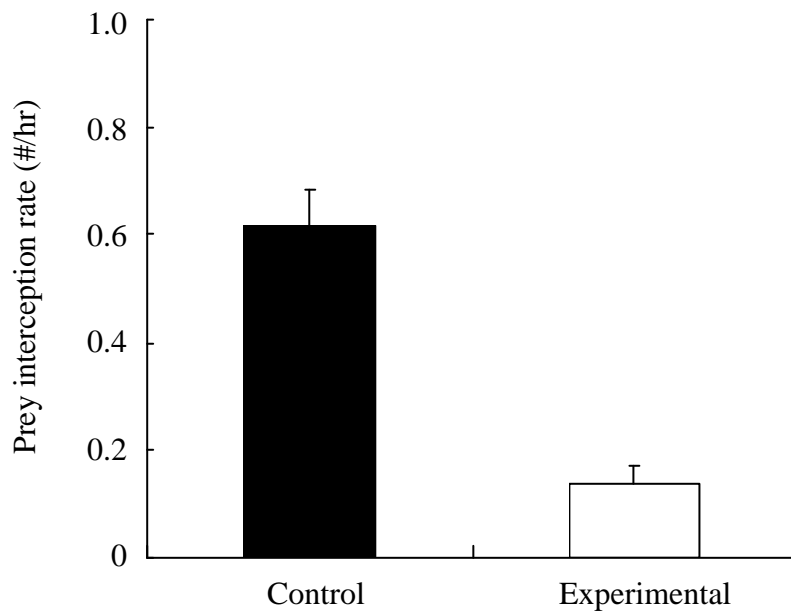


Figure 8. Mean (\pm SE) prey interception rates of webs built by *Neoscona punctigera* in the control (paint on body part) and experimental (paint on bright ventrum spot) groups.

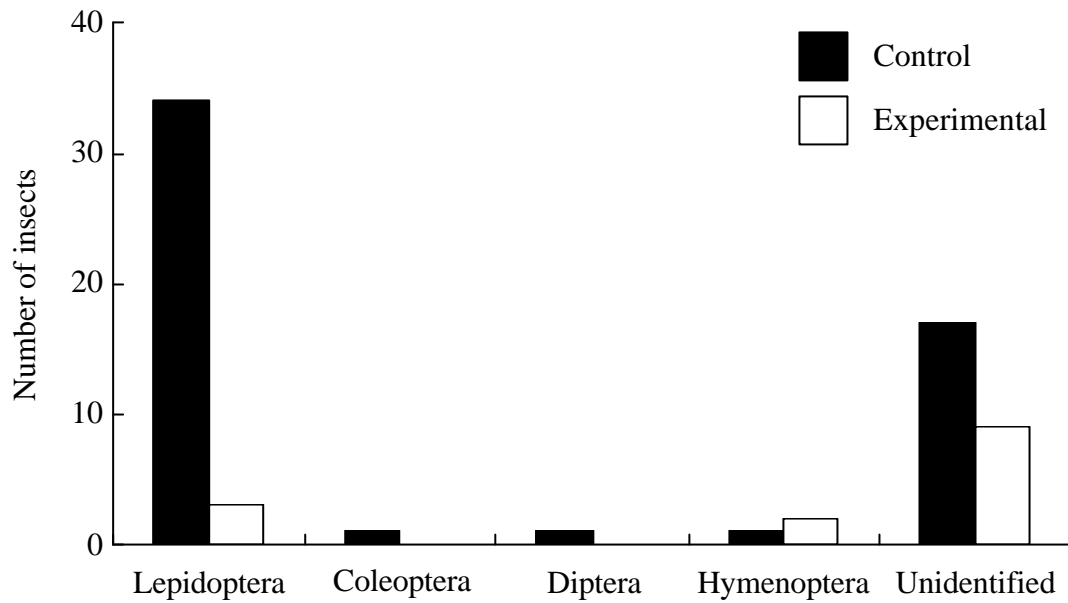


Figure 9. Composition of insects (in taxonomic orders) intercepted by *Neoscona punctigera* in the control (paint on body part) and experimental (paint on right ventrum spot) groups.

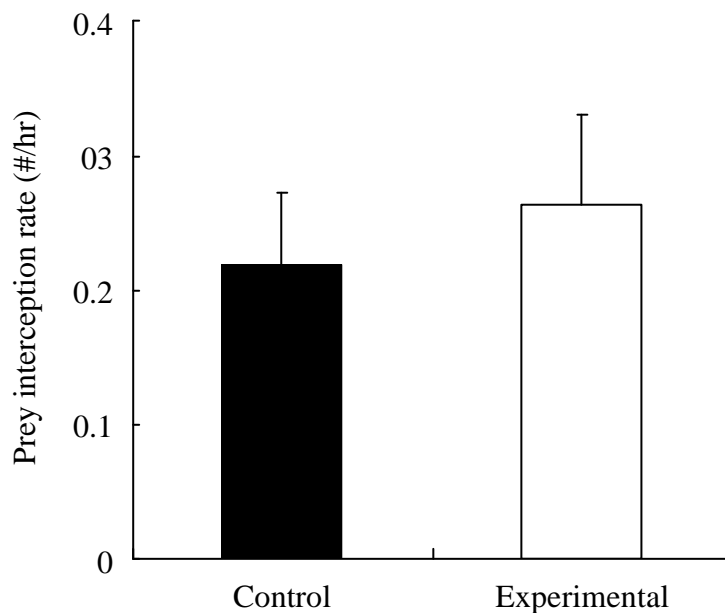


Figure 10. Mean (\pm SE) prey interception rates of webs built by *Neoscona punctigera* in the control (body part painted) and experimental (red femur painted) group.

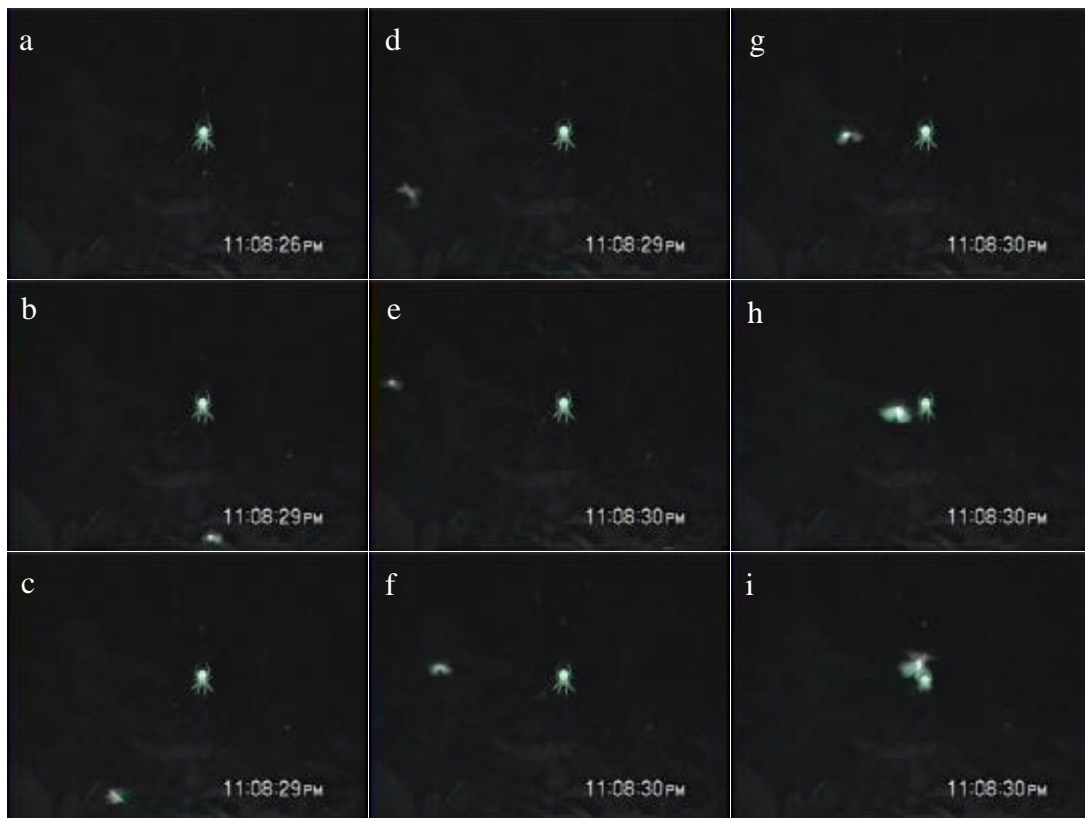


Figure 11. Consecutive images from video recording showing a moth initially passed by the margin of web (a~d) but changed direction and oriented toward the spider (e~i).

Chapter 2

Diurnal and nocturnal hunting of a
conspicuously-colored sit-and-wait predator

體色鮮艷之伏擊型捕食者其日夜捕食行為探討

中文摘要

本實驗利用人面蜘蛛 (*Nepila pilipes*) 為材料，探討其身體黑黃相間之斑紋是否可直接吸引昆蟲；或藉形成輪廓破碎化而使昆蟲不易察覺。此外，有些動物會因環境變動或捕食、競爭等壓力而改變其活動時間，但是同時於日間與夜間進行覓食的動物卻很少見。因此本研究也比較人面蜘蛛在日間與夜間的捕食量及食物組成是否有所差異。在野外實驗中，我同時在日間與夜間進行網子上有無蜘蛛的處理，以探討蜘蛛的存在是否會增加網子之昆蟲攔截率。接著我也在日間與夜間藉操縱人面蜘蛛體表顏色訊號來驗證其鮮豔斑紋是否會吸引昆蟲而增加捕食率。利用顏色相似於蜘蛛身體黑色部位的顏料，人面蜘蛛被區分為控制組(保留蜘蛛鮮豔的顏色)與實驗組(將蜘蛛全身塗成黑色)。實驗結果顯示不論是在日間或夜間，有蜘蛛的處理其獵物攔截率顯著高於無蜘蛛的處理。而在塗色處理中，當蜘蛛的顏色訊號被黑色顏料去除後其獵物攔截率明顯下降。研究結果顯示人面蜘蛛的體色不論在日間或夜間皆有吸引獵物的功能；而且其夜間獵物攔截率或是捕獲率皆顯著高於日間。本實驗證明人面蜘蛛其鮮豔體色之功能為吸引獵物，而且人面蜘蛛雖為一種日夜皆覓食的捕食者，夜間的捕食活動對其而言更為重要。

Abstract

In this study, I investigated whether the body coloration of *Nephila pilipes* functions to attract prey or to camouflage the spider. Besides, previous studies show that some animals could change their temporal activity patterns in response to the environmental changes or pressures from predators or competitors. It is not common that animals will forage both in the daytime and at night, but *N. pilipes* is just one such organism. Therefore, in this study I also investigated whether the diurnal and nocturnal huntings of *N. pilipes* differed in prey catching success and composition. Field manipulations were conducted both during daytime and nighttime to test the effectiveness of *N. pilipes*'s body colorations in different light environments. I first manipulated the presence of *N. pilipes* to see whether the spider itself served as prey attractant both in the daytime and at nighttime. Then I altered the color signals of spiders by paint to evaluate whether the conspicuous body coloration was responsible for *N. pilipes*'s attractiveness both in the daytime and at nighttime. Presence of spiders significantly increased diurnal as well as nocturnal prey interceptions, but these rates were significantly reduced when the conspicuous color signals of *N. pilipes* were altered. These results demonstrated that the conspicuous body coloration of *N. pilipes* functioned as visual lures to attract insects both in the daytime and nighttime. Furthermore, *N. pilipes* were also found to catch and consume

significantly more prey during their nocturnal hunting. Such results indicate that while the conspicuously-colored *N. pilipes* are usually regarded as diurnal predators, nocturnal hunting might be their major source of prey intake. Therefore, the intended recipient of conspicuously colored spiders might not be diurnal insects but nocturnal prey.

Introduction

The interaction patterns of predator and prey are very diverse and complicated. While the resources or environmental conditions deteriorate, the organisms must change their habitat, food resource or temporal activity pattern to cope with the problems (Schoener 1974). For example, the temporal activity of the rodent degu (*Octodon degus*) in Chile was affected by environmental conditions, such as high temperatures (Bozinovic et al. 2004). Besides, predation pressure could also affect the foraging success of the individuals (Werner & Anholt 1993). Resource limitation and predation pressure would force organisms to change their niches. In the past, relevant studies about changes in niche type generally examine how organisms use different habitats, different food resources, and exhibit different activity patterns. However, few studies have discussed temporal activity partitioning (Noga & Dayan 2003). Because the composition of food resource or presence of predators vary throughout the day, foraging in different time periods could avoid interspecific competition or predation pressure (Gullan & Cranston 2004). The temporal partitioning of resource use could also be regarded as a kind of niche (Noga & Dayan 2003).

False or cheating messages are usually involved in the communication between organisms (Hasson 1994). Especially in predator-prey interactions, numerous

predators use cheating signals to lure prey. The anglerfish (*Melanocetus johnsoni*) in the deep sea exhibits esca photophores that serve as a visual lure to attract prey (Munk 1999). The use of light signals to visually lure prey is very common in deep sea, because in the very dim environment the bioillumination can achieve a very effective luring. The use of lures to attract prey also occurs in the terrestrial system. For example, bolas spider (*Mastophora longipes*) is a nocturnal predator which uses olfactory lure mimicking the sex pheromone of particular species of moth to attract prey (Yeorgan 1994). In addition to olfactory cue, terrestrial predators also use the body coloration as visual lure to attract prey. Recent studies show that the conspicuous body colorations of numerous orb-weaving spiders are attractive to their prey. Since orb-weaving spiders are sit-and-wait predators so they can not actively move from place to place to search for prey, there might be strong selection pressure for them to evolve means to make prey move toward them. For example, the spiny spider *Gasteracantha fornicate* in Australia has yellow-and-black striped conspicuous coloration. Hauber (2002) applied dark paint on the conspicuous yellow stripes and such treatment generated a significant reduction in spider's foraging success. While Hauber (2002) found that the reduction of conspicuousness would reduce spiny spider's foraging success, Tso et al. (2006) demonstrated that exhibiting the appropriate color signal was also important. Tso et al. (2006) applied conspicuous

paint on the brightly-colored stripes of the orchid spider, *Leucauge magnifica*, to evaluate the effects on spiders' foraging success. Although the application of paint did not change the conspicuousness of the spider but simply alter the color signals, the foraging success of *L. magnifica* was significantly reduced. Furthermore, they simulated how the spiders were viewed by diurnal insects and they found that the conspicuous part of spider body coloration was very bright and distinctive (Tso et al. 2006).

Recently, Tso et al. (2002) reported that in addition to the typical black-and-yellow colored giant wood spider *N. pilipes*, sympatric with them were some melanic individuals which were totally dark. Tso et al. (2002, 2004) compared the foraging success of these two morphs of giant wood spiders and found that typical *N. pilipes* caught significantly more preys than the melanics. They also quantified how the spiders were viewed by hymenopteran insects and found that only the conspicuous yellow stripes but not the black body part of *N. pilipes* could be distinguished from the vegetation background (Tso et al. 2004). Tso et al. (2004) proposed that the coloration pattern of *N. pilipes* made the spiders similar to some form of food resources and thus were attractive to insects. However, Tso et al. (2004) did not provide direct evidence to demonstrate that the higher foraging success of typical *N. pilipes* was generated by their conspicuous body coloration. It is also

possible that the body color of typical *N. pilipes* serves as cryptic coloration. The body coloration of *N. pilipes* might break the contour of spiders, decrease the visibility of spiders to insects thus increase the probabilities that prey might accidentally bump into the web (Vaclav & Prokop 2006). Cryptic coloration means that body color of organism matches that of the environment thus makes others difficult to visually detect it (Endler 1998). Cryptic coloration can be achieved by either background matching or disruptive coloration (Merilaita & Lind 2005). For example, the marine isopods, *Idotea baltica*, have various colorations on their body. The function of such body coloration pattern were suggested to decrease this organism's detectability to predators by disruptive coloration (Merilaita 1998). The cuttlefish *Sepia officinalis* is well known to camouflage itself by disruptive colorations. This cuttlefish could change its coloration pattern according to different substrate of background (Chiao et al. 2005). The reef fish (*Pygoplites diacanthus*) camouflages by exploiting light spots in the coral reef. The body coloration of this fish mimics the light spots shining on the coral reef and thus could camouflage itself (Marshall 2000).

Concluding from the above, while typical morph of *N. pilipes* exhibits higher foraging success than the melanic, it is still not clear whether such difference is generated by typical morph being more attractive, or more invisible than the melanics.

In this study, field manipulative studies were conducted to simultaneously evaluate the prey attraction and cryptic coloration hypotheses. If the body coloration of typical *N. pilipes* functions to increase prey interception rates, then the presence of spider on the web would attract more prey to the web. On the other hand, if the body coloration of *N. pilipes* functions to decrease the visibility of spiders, there will be no difference in prey interception rates between webs with and without spiders.

In general, researchers tend to consider that ecological interactions involving conspicuous body coloration should occur in the diurnal context. Because, during the night the light environment is dim and signal-to-noise ratio is low (Warrant 2004). Therefore, researchers tend to regard conspicuous body coloration as unlikely to play significant ecological roles during night time. *Nephila pilipes* is a large colorful orb-weaving spider and is generally regarded as a diurnal predator. However, a round-the-clock survey showed that *N. pilipes* were actively foraging both in the daytime and nighttime. *N. pilipes* usually started making a web at about 0200 hours. It usually took them about an hour to weave a complete orb web. They would then stay on the hub hunting for prey until 2000 hours. *N. pilipes* actively hunts for prey in the day and night, and the light environments of these two time periods are quite different (Warrant 2004). Results of this study demonstrated that the bright body coloration of *N. pilipes* also functions well during nighttime, and the intended

recipient of body color signals of *N. pilipes* might be nocturnal rather than diurnal prey.

Material and Method

The study site and spiders:

The field manipulative studies were conducted in August, 2005 in Sanyi, Miaoli County, in central Taiwan. The study site was located in a secondary forest and giant wood spiders *Nephila pilipes* were commonly seen building webs along the trails. The secondary forest was dominated by tung oil tree (*Aluertes fordii*) and Taiwanese Acacia (*Acacia confuse*), which are common tree species in lowland areas of Taiwan. Mature female *N. pilipes* usually built orbs in the forest understory and the diameter usually exceeds one meter. They prefer to choose the edge of forest to build their webs.

Testing the attractiveness of spiders to prey:

In this part of study I evaluated the effectiveness of *N. pilipes* per se as prey attractant by comparing the prey interception rates of webs with and without spiders. This manipulative study was conducted both in the daytime (0600 to 1400 hours) and in the nighttime (0200 to 0530 hours) to realize *N. pilipes*' attractiveness in luring prey in different light environments. Individual spiders along the trails were randomly chosen and the distance between the individuals was at least five meters. Spiders chosen were randomly divided into two groups. In the first group the

spiders were carefully removed from the webs (without damaging the web) and in the second group the spiders were left intact on web. The sample size of spider removal group in daytime and nighttime was both 17. Those of the with spider group were 20 in the daytime and 19 in the nighttime.

Testing the attractiveness of spider coloration:

In this part of study I evaluated whether the conspicuous body coloration of *N. pilipes* was responsible for the spiders' attractiveness to insects. To test this hypothesis, the conspicuous color signals of *N. pilipes* were altered by dark paint with reflectance properties similar to those of spiders' black body part. This manipulative study was also conducted both in the daytime (0600 to 1400 hours) and in the night time (0200 to 0530 hours). To realize whether the dark paint used exhibited chromatic properties similar to those of *N. pilipes*'s black body coloration, I brought eight spiders back to the lab, applied dark paint on them and measured the reflectance spectra with a S2000 spectrometer. The reflectance spectra were used to calculate color contrasts to see whether the paint can be chromatically distinguished from spiders' black body parts. The chosen spiders were randomly assigned into two groups, the experimental and control. In the experimental group (N = 23 in daytime and 21 in nighttime experiments), dark paint was applied on the conspicuous carapace,

dorsal stripes and leg spots. In the control group (N = 16 in daytime and 16 in nighttime), same amount of dark paint was applied on the dark body parts to control for the effects of treatments. Before the application of paint, the chosen spiders were carefully removed from their webs (without causing any damage on orb) and were anesthetized by CO₂ (for about 5 min) to perform body color manipulations. Before recording prey interception events, for all the spiders and webs in four treatment groups the following variables were measured: spider body length, radius from four cardinal directions, number of radii and number of spirals from four cardinal directions. These variables were used to calculate capture area of the web following the formulae of Herberstein and Tso (2000). Sony Hi-8 video cameras were used to record the foraging success of *N. pilipes* in different treatment groups. The night-shot function of the video cameras was used while the recording was made during the night. The video cameras were placed at least 1 m in front of the webs monitored. The video tapes were brought back to the laboratory for further analysis. While viewing the video tapes I recorded the number of prey intercepted by each web. Prey interception rate was generated by dividing the number of prey intercepted by the web of each spider with number of recording hours that day. In addition, I also used body length of *N. pilipes* recorded during the field study to estimate the body length of intercepted prey. The body size of prey was used to calculate biomass

following the length-dry weight formulae provided by Schoener (1980). Prey biomass was used to estimate prey consumption rate of *N. pilipes* in different treatment groups. While analyzing the data, I first evaluated whether the prey interception and consumption rates were congruent with normal or Poisson distributions. Then either Analysis of Covariance or Poisson regression would be used, using capture area of the webs as the covariance. However, if the data did not fit both distributions, I would divide the prey interception and consumption rates with capture area to generate unit area prey interception/consumption rate, then analyzed by nonparametric *U*-tests.

Color contrast calculation using diurnal visual model:

We simulated how various body parts of *N. pilipes* were viewed by their insect prey or predator by calculating their color contrasts. Six female *N. pilipes* were collected from Sanyi, Miaoli County, in central Taiwan. The S2000 spectrometer (Ocean Optics, Inc., Dunedin, Florida, U.S.A.) was used to measure the reflectance spectra of black paint applying on spider body. The reading probe was vertically placed 5mm above the regions to be measured. I used the visual model developed from Hymenoptera to calculate the color contrast. I measured the reflectance spectrum of green leaf and used it as the background light signal. To determine

whether the color signal of an object could be identified against certain background, first the amount of light signals received by each photoreceptor must be estimated by the following equation (Stavenga et al. 1993; equation 1):

$$P = R \int_{300}^{700} I_s(I)S(I)D(I)dI \quad (1)$$

Where P is quantum catches that is absorbed by each photoreceptor, function I_s is spectral reflectance of stimulus, function S is spectral sensitivity of honeybee photoreceptor, function D is the spectral reflectance of illumination. Function R is the sensitivity factor and can be calculated by the following equation:

$$R = 1 / \int_{300}^{700} I_B(I)S(I)D(I)dI \quad (2)$$

Where function I_B is the spectral reflection of background.

Although the quantum catches are received by the photoreceptor, they will not be directly accepted by the insect brain. Therefore the quantum catches P must be transformed to effective signal that could be accepted by the brain by the following equation (Naka & Rushton 1966; equation 3):

$$E = P / (1 + P) \quad (3)$$

Where E is excitation maximum value, P is quantum catches of each photoreceptor.

Then the planar coordinate was used to express signals. Each stimulus could generate three E values, E_g , E_{uv} and E_b respectively. Where E_g is the excitation value of green photoreceptor of honeybee, E_b is that of blue photoreceptor and E_{uv} that of

ultraviolet photoreceptor. To integrate these three excitation values, we used the following color hexagon model of Chittka (1996; equation 4):

$$X = (\sqrt{3}/2)(E_g - E_{uv}) \quad (4)$$

$$Y = E_b - 0.5(E_{uv} + E_g)$$

The Euclidean distances (ΔSt) of X and Y , which is the color contrast, can be calculated by the following equation (equation 5):

$$\Delta St = \sqrt{(\Delta X)^2 + (\Delta Y)^2} \quad (5)$$

For honeybees, the estimated color contrast discrimination threshold is 0.05 (They & Casas 2002). We used one tail t -tests to examine whether the color contrasts of various body parts of *N. pilipes* were significantly higher than the discrimination threshold value.

Color contrast calculating using nocturnal visual model:

The video recordings showed that moth was the major nocturnal prey of *N. pilipes*. Therefore, I used nocturnal visual model developed for moth to assess how *N. pilipes* was viewed by their prey. The reflectance spectra of spiders and vegetation background were those used previously. The visual model used by

Johnsen et al. (2006) was followed to calculate the achromatic contrasts of different body parts of *N. pilipes*. The following equation was used to calculate the quantum catches of one ommatidium of moth (Warrant & Nilsson 1998).

$$N = 1.13(p/4)n\Delta P^2 D^2 \Delta t \int_{350}^{700} kt(1 - e^{-kR_i(I)l})L(I)dI \quad (5)$$

Where n is the effective facets in the superposition, P is the photoreceptor acceptance angle, D is the diameter of a facet lens, t is the integration time of a photoreceptor, ρ is the quantum efficiency of transduction, τ is the fractional transmission of the eye media, k is the absorption coefficient of the rhabdom, l is the rhabdom length doubled by tapetal reflection, $R_i(\lambda)$ are the absorbance spectra of each photoreceptor, $L(\lambda)$ is the reflectance spectra of object multiplied by the reflectance spectra of light environment and then divide by p (Johnsen et al. 2006). The difference of object of interest and the background, the achromatic contrasts, can be estimated by the following equation:

$$C = \frac{N_x - N_{green}}{N_x + N_{green}} \quad (6)$$

Where N_x is quantum catches of object, and N_{green} is quantum catches of green vegetation background (Johnsen et al. 2006). Currently, the discrimination threshold value of nocturnal color contrast is still not available. Therefore, we compared the contrast values of various body parts of *N. pilipes* and black paint using t -tests to determine whether the colorful body

parts were more conspicuous than other black parts.

In addition to achromatic contrast, I also calculated chromatic color contrast of various body parts of *N. pilipes* when viewed by moth during nighttime. First, the quantum catches of one ommatidium (N) was calculated, and the N values of each photoreceptors were estimated to generate N_{uv} , N_b and N_g . Then q_{uv} , q_b and q_g , the relative quantum catches of each type of photoreceptor, were calculated by the following equations (Johnsen et al. 2006):

$$q_{uv} = \frac{N_{uv}}{N_{uv} + N_b + N_g} \quad (7)$$

$$q_b = \frac{N_b}{N_{uv} + N_b + N_g} \quad (8)$$

$$q_g = \frac{N_g}{N_{uv} + N_b + N_g} \quad (9)$$

Then values of each stimulus were used to calculate relative distances in the color triangle by the following equations (Johnsen et al. 2006):

$$X_1 = \frac{1}{\sqrt{2}}(q_g - q_b) \quad (10)$$

$$X_2 = \frac{\sqrt{2}}{\sqrt{3}}\left(q_{uv} - \frac{q_g + q_b}{2}\right) \quad (11)$$

X_1 and X_2 were the distances on the X axis and Y axis, which represented the relative intensity of three types of photoreceptors in the 2D color space. The distance of two color stimuli on the color space was the color contrast (Johnsen et al. 2006). So far, no one had developed theoretical discrimination threshold value for the nocturnal chromatic visual model. Therefore, I used ANOVA tests to compare the chromatic color contrasts of different body parts of *N. pilipes* and the dark paint when viewed by moths against the green vegetation background.

Results

Testing the attractiveness of spiders to prey:

N. pilipes spiders in the study site were monitored for a total of 1000 hours.

However, I did not find any predation event on *N. pilipes*. The reason might be that during the time the field studies were conducted (August of the year) *N. pilipes* populations were composed of large adult spiders. Parasitoid predators such as wasps might avoid attacking those giant wood spider as big as a human hand. In this study, 670 hours of video recording were made on diurnal hunting of *N. pilipes*, and 330 hours of recording were made on nocturnal recording. Presence of *N. pilipes* on webs significantly increased the interception rate of prey, no matter in diurnal or nocturnal hunting. The prey interception data of this part of study fitted well with Poisson distribution (Pearson $\chi^2 = 3.168$, $p = 0.5049$), so Poisson regressions were used to compare the difference on prey catching rate between treatment groups while considering orb area. The diurnal prey interception rate of webs with spiders was seven times that of webs without spiders (Fig. 3, Table1a). The difference on nocturnal prey interception rate between two treatment groups was even more dramatic. The nocturnal prey interception rate of webs with *N. pilipes* was 20 times that of webs without the spider (Fig. 3, Table1b).

Testing the attractiveness of spider body coloration to prey:

In this part of the study I tested whether the conspicuous body coloration of *N. pilipes* was responsible for its attractiveness to prey. The color signal of the dark paint used was similar to that of spiders' black body parts (Fig. 2). The chromatic and achromatic contrasts of dark paint when viewed against the black body part of *N. pilipes* by diurnal Hymenopteran insects were significantly smaller than the discrimination threshold value (one tailed *t*-test, $t = 0.476$, $p = 0.644$ for chromatic contrast, $t = 1.631$, $P = 0.129$ for achromatic contrast) (Fig.1). The achromatic contrasts of dark paint when view by nocturnal Lepidopteran insects was similar to that of the spiders' black body part (Table 2a, Fig. 2). However, dark paint's nocturnal chromatic color contrast was significantly smaller than that of the black body part (Table 2b, Fig. 2). Therefore, the dark paint I used should be able to effectively reduce the conspicuousness of the yellow body parts of *N. pilipes*.

The application of paint on conspicuous body parts of *N. pilipes* significantly reduced their foraging success. The prey interception rate of diurnal prey fitted well with a Poisson distribution (Pearson $\chi^2 = 3.1687$, $p = 0.5843$), so I used a Poisson regression to compare the prey interception rates between the experimental (conspicuous body part painted) and control (black body painted) groups while considering the orb area. The diurnal prey interception rate of the experimental

group was significantly lower than the control group (Table 3). Compared with that of *N. pilipes* whose conspicuous body color signal was altered, the prey interception rate of the control group was twice as high (Fig. 4). The effect of reducing conspicuousness by paint was even more dramatic in *N. pilipes*' nocturnal hunting. The nocturnal prey interception data did not fit either normal or Poisson distributions. Therefore, I divided prey interception rate with web area to generate unit area prey interception rates then compared with a nonparametric *U*-test. The prey interception rate of control treatment was significantly higher than that of the experimental treatment (*U*-test = 226.500, $p = 0.002$). The prey interception rate of the experimental groups was only one-third that of the control group (Fig. 4).

Relative importance of diurnal and nocturnal hunting:

To assess the relative importance of diurnal and nocturnal hunting in *N. pilipes*, I used the data from the with spider and control treatment groups. Because, the conspicuous body coloration of spiders in these two groups was not altered. In the with spider group, *N. pilipes* intercepted significantly more prey at nighttime than in the daytime (Table 3a). In the control group, the nocturnal prey interception rate was also significantly higher than that of diurnal prey (Table 3b). A similar trend was also found in prey consumption rates. Prey consumption rate data did not fit normal

or Poisson distributions, so I divided the consumption rate web orb area then analyzed with nonparametric *U*-tests. In with spider group, the biomass of nocturnal prey caught and consumed by *N. pilipes* was 8 times that of the diurnal prey (*U*-test = 75.5, $p = 0.01$, Fig. 5). Similarly, spiders in the control group also consumed significantly higher biomass of nocturnal prey than diurnal prey (*U*-test = 78.5, $p = 0.023$, Fig. 5). Therefore, insect from nocturnal hunting seems to be the major source of prey intake in *N. pilipes*.

Nocturnal chromatic and achromatic contrast:

The nocturnal achromatic contrasts of conspicuous yellow body parts of *N. pilipes* when viewed against vegetation background by lepidoteran insects were significantly higher than those of black body parts and black paint (ANOVA test, $F = 12.062$, $p > 0.001$, Fig. 2). The yellow stripes on dorsum of abdomen had the highest achromatic contrast among all body parts. The achromatic contrasts of yellow carapace and yellow spots on legs did not differ significantly. No significant difference in achromatic contrast values was found among various black body parts or the paint used to alter body color signals. The nocturnal chromatic color contrast of various body parts of *N. pilipes* followed a trend similar to that of achromatic contrasts. Various conspicuous yellow body parts exhibited contrast values

significantly higher than those of body parts (ANOVA test, $F = 36.93$, $p < 0.001$, Fig.

2). Again, the yellow stripes on dorsum exhibited the highest color contrast values,

followed by yellow carapace and yellow leg spots. Although the nocturnal

chromatic color contrasts of black body parts were considerably lower than those of

yellow body parts, they were significantly higher than the value of dark paint.

Discussion

Results of this study demonstrated that the conspicuous body coloration of giant wood spider *N. pilipes* function as visual lure to attract both diurnal and nocturnal prey. While most orb weaving spiders confine their hunting to either diurnal or nocturnal part of the day, *N. pilipes* hunt for in both light and dark hours of the day. Results of this study strongly indicate that the bright body coloration of orb weaving spider functions as prey attractant rather than to camouflage the spider. Following camouflaging hypothesis, if the coloration pattern makes spiders blending well with background vegetation, then webs with spiders will catch similar amount of prey than those without. Contrary to the predictions of camouflaging hypothesis, webs with *N. pilipes* present intercepted significantly more prey, indicating that spiders themselves serve as conspicuous visual lures to attract prey. This study also provides direct evidence that the conspicuous body coloration of *N. pilipes* is responsible for the spiders' attractiveness. While Tso et al. (2004) found the conspicuous typical *N. pilipes* to catch more prey than the melanic conspecifics, such result was congruent with the predictions of either prey attraction or camouflaging hypotheses. In this study, when the conspicuousness of *N. pilipes* was reduced by using dark paint exhibiting a color signal similar to that of black body parts, the attractiveness of spiders to prey was significantly reduced. While conspicuous body parts of *N.*

pilipes were attractive to diurnal insects, results of this study showed that they were also attractive to nocturnal insects. Moreover, nocturnal insects might be the major target of this conspicuously colored sit-and-wait predator. The amount of prey biomass consumed by *N. pilipes* from their nocturnal hunting was several times higher than that from diurnal hunting. Therefore, while the brightly-colored orb weaving spider are traditionally regarded as diurnal predators, results of this study demonstrate that at least in some species nocturnal hunting might be their major way of prey intake. Although the light intensity and signal-to-noise ratio of diurnal and nocturnal light environments differ significantly (Warrant 2004), my results indicated that the body color of *N. pilipes* serves as effective visual lure in both light conditions.

This study not only is the first to investigate the nocturnal hunting of a brightly-colored terrestrial predator, this is also the first study to assess how the body signals of spiders are viewed by nocturnal lepidopteran insects. The color contrasts of brightly-colored orb weaving spiders when viewed by diurnal hymenopteran spiders had been reported previously. Results of these studies showed that the dark or green part of spider body was indistinguishable from the vegetation background but the conspicuous parts were highly visible to insects (Tso et al. 2004, 2006). Such phenomenon also occurs when these spiders are viewed by nocturnal insects during the night. Through nocturnal achromatic vision, the black body parts of *N. pilipes*

was significantly smaller than various yellow body parts, suggesting that when *N. pilipes* are viewed by moths in the dim light environment from a long distance, the conspicuous body parts are be more visible than dark parts. As moths fly toward the spider and use chromatic vision, the conspicuous body parts are more visible than the dark parts. The combination of low and high contrast body colorations might make the appearance of spiders unlike that of a predator but some form of resource, as is suggested in other orb weaving spiders (Tso et al. 2004, 2006). The use of visual lure in nocturnal hunting might be more effective than in diurnal hunting. Although these spiders will be regarded as some form of resources by diurnal insects, when prey fly near the spider they will eventually detect the web then adopt escape manuvors. However, in the nocturnal condition when prey are attracted by the spiders and fly toward them, under such dim light environment if will be very difficult for them to detect the presence of the web. The difference in web visibility in two light environments might be one of the major reasons why *N. pilipes* intercepted higher number of prey from their nocturnal hunting.

Tso et al. (2006) also used paint to alter body color signal of spiders then investigated the consequences on prey attractiveness. The approach used in this study in altering spider body color signals is quite different from theirs. In Tso et al. (2006), they used a conspicuous paint to apply on the conspicuous body colorations of

orchid spiders *L. magnifica*. After such treatment the visibility of orchid spiders to their diurnal prey was not changed but the chromatic properties of the color signals were altered. In this study, I used a paint exhibiting a chromatic property that was similar to that of inconspicuous black body parts. Application of such paint on *N. pilipes* effectively reduced the conspicuousness of the yellow body parts. Both the treatments of this study and Tso et al. (2006) worked well in reducing the attractiveness of spider body coloration to their prey. Results of these two studies indicate that both the conspicuousness (the visibility) and the chromatic properties (such as reflectance properties) of the body coloration are important components of an effective visual lure. So far, we only realize that reducing the conspicuousness of body coloration would reduce the nocturnal hunting performance of *N. pilipes*. It is still not clear whether altering the chromatic properties but maintaining the visibility of the body coloration would affect spiders' attractiveness to nocturnal prey.

While most spiders hunt either during daytime or nighttime, *N. pilipes* conduct both diurnal and nocturnal hunting and the relative importance of the latter seems to be larger. In this study, *N. pilipes*'s hunting performances in daytime and nighttime were compared in two ways. The diurnal and nocturnal prey interception and consumption rates of spiders in the with spider treatment and control groups were compared respectively. For the spiders in both treatment groups, the foraging

success of nocturnal hunting was always much higher than that of diurnal hunting.

On average, about 85 % of prey biomass intake of *N. pilipes* was from their nocturnal hunting. Since results of this study show that the body coloration of *N. pilipes* functioned better at night and most prey intake come from nocturnal hunting, why this spider spend so much time hunt during the day? One of the reasons might be that *N. pilipes* were maximizing their prey intake. Compared with other web spiders, the body size of *N. pilipes* is much larger. To be able to obtain sufficient energy to meet the needs of growth and reproduction, large spiders such as *N. pilipes* require much more prey than other web spiders. Therefore, although the effectiveness of diurnal hunting is not that high, they still forage during the day to maximize their energetic need. However, while *N. pilipes* actively hunt throughout day, they will breakdown the web and rest for about 6~7 hours during the night (from about 2000 to 0200 hours). Since nocturnal hunting is much more efficient than diurnal hunting, why *N. pilipes* did not rest during the day, as numerous *Araneus* and *Neoscona* spiders do?

One major reason might be that during the day the threat from visually oriented predators is much more severe than during the night. Although *N. pilipes* is quite big and few predators are able to successfully attack them, staying on the web can help the spider detect and escape potential predators (Foelix 1996). Since for *N. pilipes* predation pressure is smaller during the night, the risk of lacking early warning

and protection from webs might be much smaller. In the field, juvenile *N. pilipes* seem to spend more time hunting than adult spider. There seemed to be a negative relationship between size of *N. pilipes* and foraging effort in terms of time spend hunting (Chuang, unpublished data). This result suggests that smaller spiders would try to maximize their prey intake to reach adult stage as soon as possible. Juvenile *N. pilipes* are probably severely impacted by predation pressures. Therefore, they will try to shorten their growth time to grow into certain size as soon as possible to relieve themselves from predation pressures (Orizaola & Brana 2005).

Recently, more and more orb weaving spiders have been demonstrated to attract nocturnal prey with visual lures. For example, the obligate nocturnal orb weavers of the genera *Neoscona* and *Araneus* are inconspicuously brown but exhibit bright spots on the ventrum of abdomen. These brightly-colored ventrum spots were demonstrated to serve as visual lures to nocturnal insects (Chuang, unpublished data). In addition, the bright body coloration of orchid spider *L. magnifica* was also shown to be attractive to nocturnal prey (Tso et al. acceptance pending revision). Therefore, it seems that even in the dim light condition of nocturnal system visual signals are significantly involved in the predator-prey interactions. Especially in less mobile sit-and-wait predators such as orb weaving spiders, they exhibit a diverse array of visual lures to attract prey. Results of the aforementioned studies demonstrate that

no matter the lures are composed of small ventrum spots or large dorsum stripes; they are all effective in attracting nocturnal insects. Recently, more and more nocturnal insects such as hawkmoths, nocturnal bees and dune beetles are shown to have nocturnal color visions (Warrant 1999). Limited by equipments and methodologies, it is until very recently do we begin to realize that in the dim light environment during the night color vision are actually quite common in numerous organisms (Kelber & Roth 2006). Since in the night there are so many insects using color signals to forage and to interact with each other, it is likely that predators such as orb weaving spiders might have evolved sensory exploitation and lure nocturnal prey with false signals (Hasson 1994). I expect that as further efforts are invested, more interesting visual interactions between nocturnal predator and prey will be discovered.

One implication of this study is that in future behavioral studies investigating interspecific signal transmission, especially those in the visual context, researchers should serious consider what organisms are the intended recipient of the signalers. In the past, in the terrestrial ecosystem color signals are generally considered to be used only by diurnal organisms. However, more and more studies demonstrated that various nocturnal organisms utilize color signals to locate food resources and mates (Kelber & Roth 2006). In the case of *N. pilipes*, their conspicuous body coloration actually attracts much more nocturnal than diurnal prey. Therefore, it might be the

selection pressures of effectively exploiting the color signal sensing of nocturnal prey that drives the evolution of orb weaving spider's body coloration. Another implication of this study is that while studying animal communications we should seriously consider under what conditions does the signal transmission really takes place. Traditionally, we usually think that conspicuous body coloration only functions in the diurnal context. However, results of this study strongly demonstrate that bright body coloration of *N. pilipes* visually lure both diurnal and nocturnal prey. Moreover, such visual lures function more effectively in spiders' nocturnal hunting. Finally, while studying the visual interactions between organisms, one should conduct a round-the-clock survey to realize the temporal activities of them. So far, almost all empirical studies on foraging behaviors of so-called "diurnal" web spiders only investigated spiders diurnal hunting. Numerous studies monitored the diurnal hunting of spiders for few hours then made conclusions accordingly (such as Tso 1996, 1998a, 1998b, 2002, 2004). In this study, it was until *N. pilipes* were monitored on a 24 hour basis and their temporal activity pattern fully realized then I realized that they also hunt during the night. If the color signals of one organism are most significantly involved in one light condition but researches are conducted in another, the conclusions subsequently made will not be able to reflect the realities.

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Table 1. Results of the Poisson regressions comparing diurnal (a) and nocturnal (b)

prey interception rates of webs with *Nephila pilipes* and without.

(a) Diurnal hunting

Parameter	DF	Estimate of β	SE	χ^2	P
Intercept	1	-6.472	0.468	190.87	<.001
Web area 0-200	1	-0.681	0.425	2.570	0.109
Web area 200-400	1	-0.223	0.334	0.450	0.504
Treatment With	1	1.656	0.441	14.08	0.001
Treatment Without	0	0	0	-	-

(b) Nocturnal hunting

Parameter	DF	Estimate of β	SE	χ^2	P
Intercept	1	-6.300	0.624	101.69	<.001
Web area 0-200	1	-0.758	0.366	4.280	0.038
Web area 200-400	1	-0.045	0.282	0.030	0.873
Treatment With	1	3.046	0.609	24.97	<.001
Treatment Without	0	0	0	-	-

Table2. Results of the Poisson regression comparing prey interception rates of webs built by *Nephila pilipes* in the experimental (conspicuous body part painted) and control (black body part painted) groups.

Parameter		DF	Estimate of β	SE	χ^2	P
Intercept		1	-6.385	0.651	96.230	<.001
Web area	0-200	1	0.534	0.695	0.590	0.442
Web area	200-400	1	0.056	0.605	0.010	0.925
Treatment	400-600	1	0.278	0.961	0.080	0.771
Treatment	Control	1	1.211	0.402	9.060	0.002
Treatment	Experimental	0	0	0	-	-

Table 4. Results of Poisson regressions comparing diurnal and nocturnal prey

interception rates of *Nephila pilipes* in the with spider group (a) and control group (b) respectively.

(a) With spider group

Parameter	DF	Estimate of β	SE	χ^2	P
Intercept	1	-3.240	0.137	556.26	<.001
Web area 0-200	1	-0.981	0.322	9.240	0.002
Web area 200-400	1	0.000	0.213	0.000	0.999
Treatment Diurnal prey	1	-1.601	0.188	72.06	<.001
Treatment Nocturnal prey	0	0	0	-	-

(b) Control group

Parameter	DF	Estimate of β	SE	χ^2	P
Intercept	1	-4.353	0.411	112.09	<.001
Web area 0-200	1	0.703	0.519	1.830	0.175
Web area 200-400	1	0.770	0.432	3.180	0.074
Treatment Diurnal prey	1	-1.401	0.235	35.42	<.001
Treatment Nocturnal prey	0	0	0	-	-

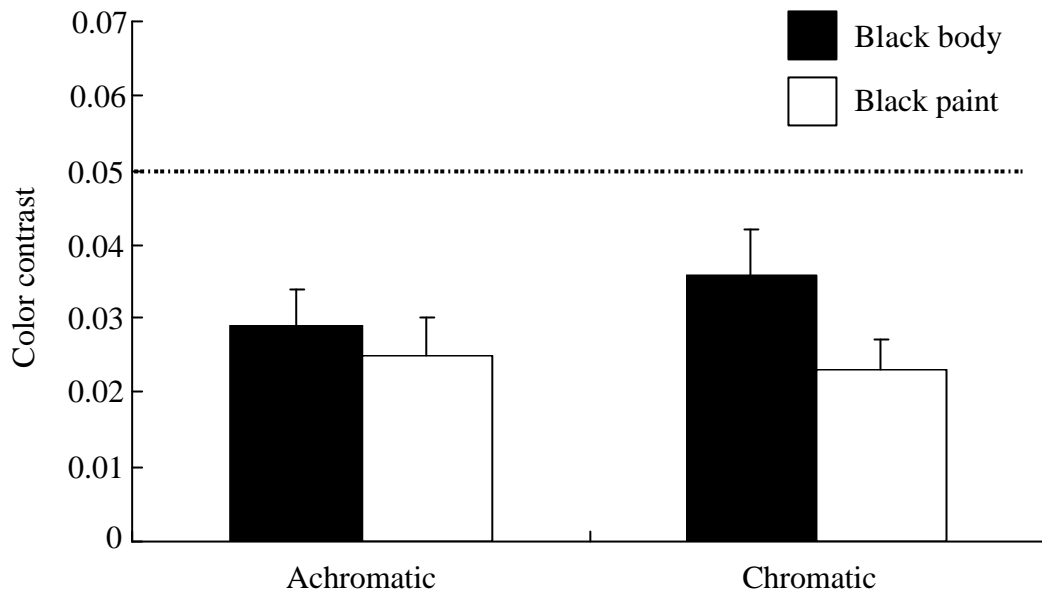


Figure 1. Mean (\pm SE) color contrasts of dark paint used to alter color signal of *Nephila pilipes* and the black body part of the spiders when viewed by diurnal hymenopterans insects. Dotted line represents the discrimination threshold of 0.05 estimated for hymenopterans.

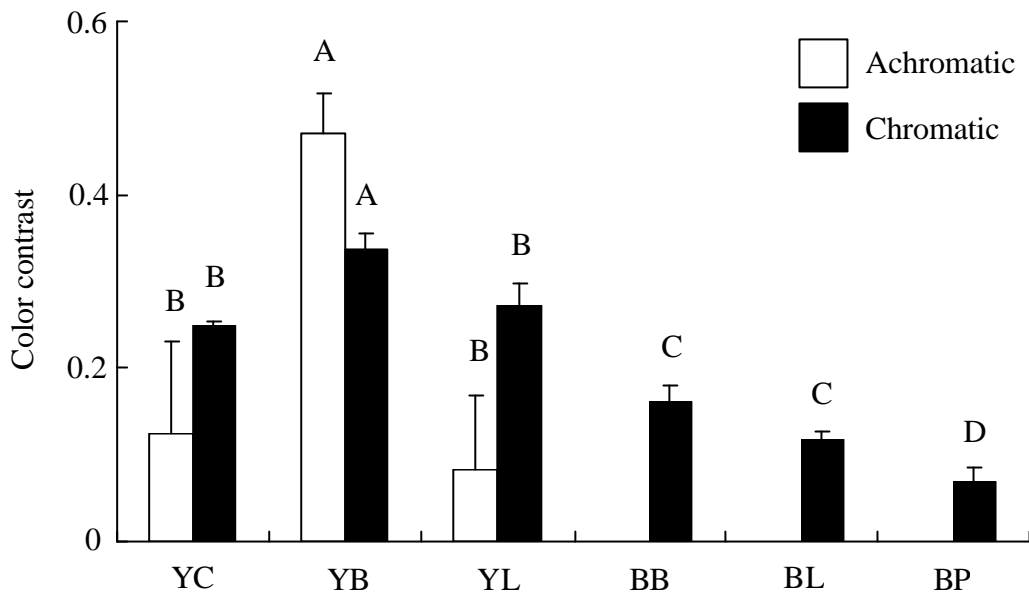


Figure 2. Mean (\pm SE) nocturnal achromatic and chromatic contrasts of various body

parts of *Nephila pilipes* viewed against vegetation background by

lepidopteran insects. YC: yellow carapace, YB: yellow stripes on dorsum,

YL: yellow spots on legs, BB: black body, BL: black legs, BP: black paint.

Capital letters represent results of ANOVA test LSD mean comparisons.

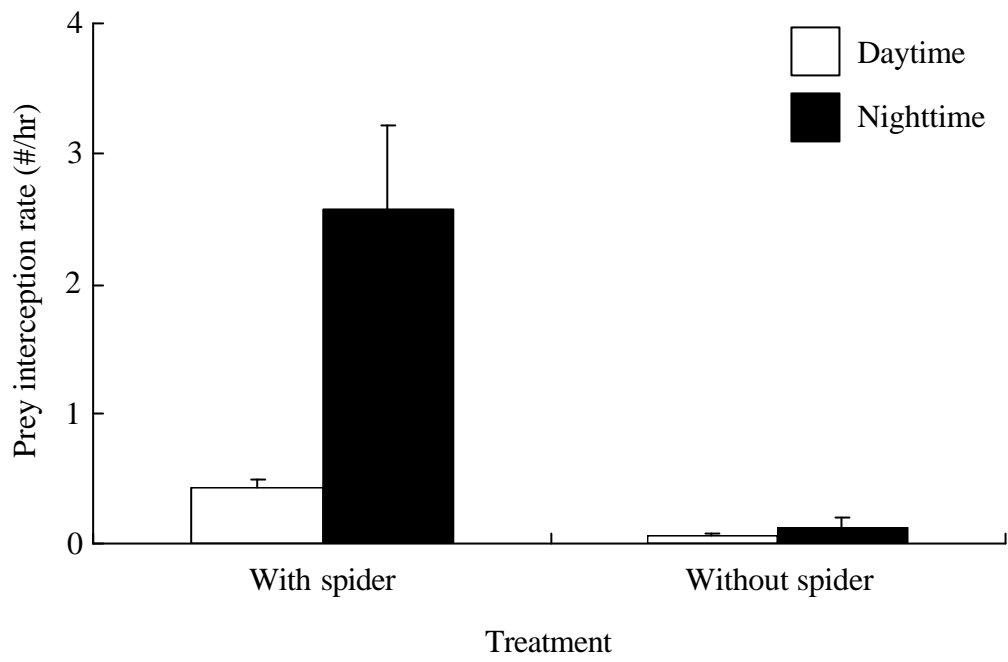


Figure 3. Mean (\pm SE) diurnal and nocturnal prey interception rates of webs built by *Nephila pilipes* with and without spiders.

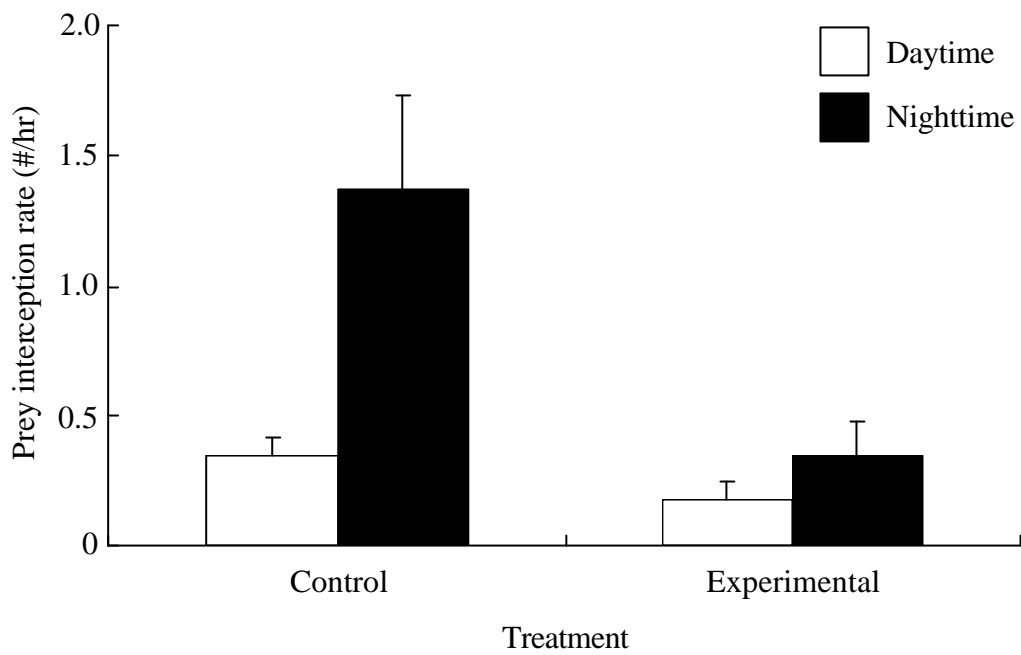


Figure 4. Mean (\pm SE) diurnal and nocturnal prey interception rates of webs built by *Nephila pilipes* in the experimental (dark paint on conspicuous body parts) and control (dark paint on black body parts) groups.

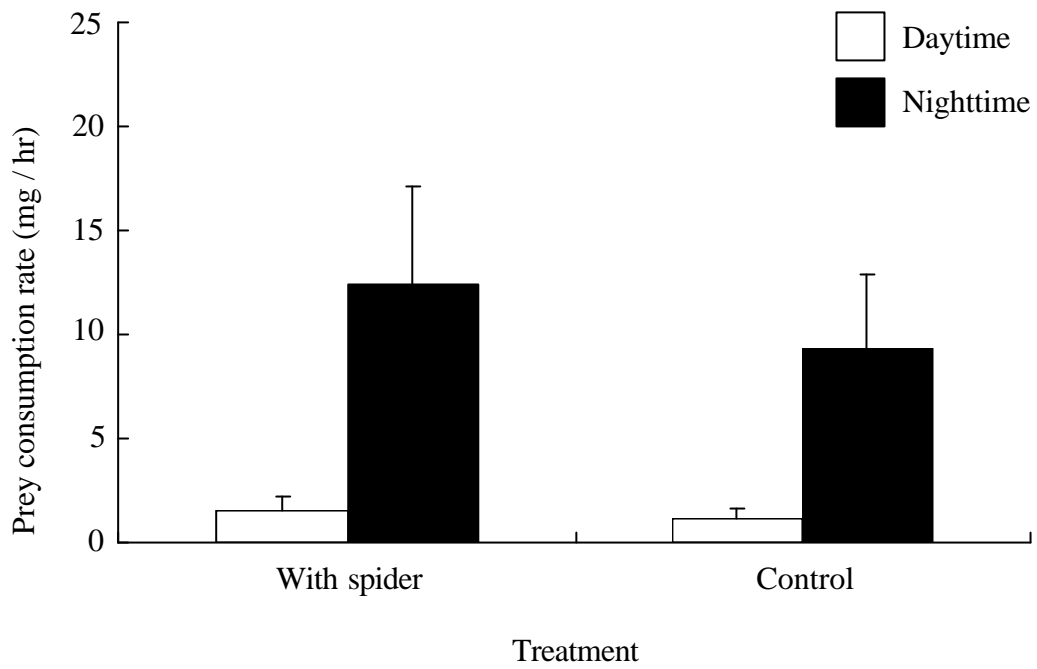


Figure 5. Mean (\pm SE) diurnal and nocturnal prey consumption rates of *Nephila pilipes* in the with spider and control treatment groups.