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紅衣新郎：人面蜘蛛雄蛛體色功能初探

A bridegroom in red: function of body coloration of

male giant wood spider *Nephila pilipes*

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A bridegroom in red: function of body coloration of
male giant wood spider *Nephila pilipes*

本論文係周顓海（r99b44013）在國立臺灣大學生態學與演化生物學研究所完成之碩士學位論文，於民國103年6月11日承下列考試委員審查通過及口試及格，特此證明

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所長

摘要

　　吸引獵物假說過去在很多結網性蜘蛛的研究上得到證實，這些結網性蜘蛛會利用身上鮮艷的體色吸引昆蟲靠近蛛網。不過相關研究都僅針對雌性蜘蛛，而對雄性蜘蛛體色的研究則相當缺乏。性成熟之後的結網性蜘蛛雄蛛，在行為上和雌蛛有很大的差異，這些差異可能導致即使同樣在吸引假說的預期下，雄蛛的體色功能會有有別於雌蛛體色功能的目的。大人面蜘蛛雄蛛性成熟後會變成鮮艷的橘紅色，並且一直待在雌蛛網上等待交配機會。根據吸引假說，我預測大人面蜘蛛雄蛛鮮艷的體色可以吸引昆蟲靠近雌蛛的網，增加雌蛛的捕食率，進而延長雌蛛在該結網地停留的時間，最終可以提升雄蛛自己的交配成功率。我利用黑色塗料改變大人面蜘蛛雄蛛的體色訊號，並用攝影機在白天和晚上記錄昆蟲與蜘蛛網和雄蛛體色的互動，藉以探討雄蛛體色是否具有吸引昆蟲的功能。而為了確認吸引的效果是來自體色，不是其他因子，我製作蜘蛛紙片模型模擬大人面蜘蛛雄蛛的體色，進行相似的實驗。除了攝影外，我也持續追蹤雌蛛在同一個結網地停留的天數，以探討雄蛛體色對雌蛛結網地停留時間的影響。實驗結果顯示，雄蛛的體色在白天確實可以吸引昆蟲，而模型實驗則證實吸引的效應是來自於顏色，但是吸引效應並沒有影響雌蛛結網地的停留時間。或

許後續需要更多研究來探討是什麼選汰壓力促使大人面蜘蛛雄蛛演化

出鮮豔的體色來吸引昆蟲。

Abstract

Prey attraction hypothesis had been tested on many orb web spider species in recent years, and the results show that conspicuous coloration of spiders may attract insects to the webs. However, all of these studies focus on female spiders rather than males. After reaching maturity, male spiders behave differently from females, so the body coloration of male spiders probably functions in ways different from that of female spiders . Male *Nephila pilipes* is conspicuous orange-red color and it seldom build its own web after reaching maturity but lives on female's web waiting for copulating with female. I hypothesize that the conspicuous coloration of male *N. pilipes* may attract insects to female's web and then increase the web site tenacity of female to increase male's opportunity of mating. I manipulated the coloration of male *N. pilipes* and monitored the webs with male spiders by video cameras day and night and I also recorded the number of days a female stayed in a particular web site. In order to confirm if the attraction effect was caused by coloration instead of other factors, I made spider dummies resembling male *N. pilipes* in appearance and color. Results showed that the conspicuous coloration of male *N. pilipes* attracted insects to female's web during day time, and similar results was found in dummy experiment. However, the prey attraction effect did not increase the web site tenacity of female spiders. Results of my study demonstrate the attraction function of body coloration of male *N. pilipes*. More

researches are needed to realize the factors facilitating the evolution of conspicuous

body colors in male *N. pilipes*.

Key words: *Nephila pilipes*, prey attraction hypothesis, body coloration, web site

tenacity.

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Introduction

As a direct visual communication signal, animal body coloration plays an important role in surviving, foraging, and mating for animals. The well-known hypothesis used to explain the function of animal body coloration was crypsis hypothesis (Ruxton 2004). Crypsis hypothesis suggests that a lot of animal conceal themselves by matching the color of environmental background. However, there are some other animals which have conspicuous body coloration which has high contrast against environmental background or another part of body coloration. Unlike the crypsis body coloration that tend to hide, conspicuous body coloration has evolved to deliver many kinds of visual signals to different receivers, and the complex interaction between signalers and receivers has drawn lots of attention (methodology: Endler 1990; function and mechanism: Ruxton 2004). The hypothesis explaining the functions of conspicuous body coloration could be classified by receivers (such as predator versus. prey, or sex of organisms (intraspecies versus intrasexual groups). In aposematic coloration, predators were the signal receivers (Harvey et al. 1981; Leimar et al. 1986; Mappes et al 2005), while in disruptive coloration prey's outline is broken to prevent predators from identifying prey (Stevens and Merilaita 2009). When body coloration serves as a sexual signal in intersexual interactions, it usually has a relationship with mating behavior and

consequently is under the pressure of sexual selection (Pruett-Jones and Pruett-Jones

1990).
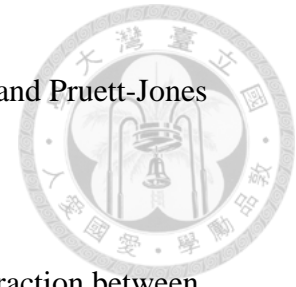
In recent years, there was a new hypothesis focusing on the interaction between

signalers and prey in terrestrial ecosystem - the attraction hypothesis. The attraction

hypothesis suggests that the conspicuous body coloration will attract prey to approach

the signaler and increase the feeding rate, especially in web spiders. No matter diurnal

or nocturnal, many web spider species have conspicuous coloration on their body, and

such coloration has been shown to attract insects to approach spiders' web and increase

prey interception rate in many species (diurnal: Craig and Ebert 1994; Hauber 2002;

Tso et al. 2002, 2004, 2006; Chuang et al. 2007; nocturnal: Tso et al. 2007; Chuang et al.

2008; Blamires et al. 2012). However, these studies all focus on female spiders but no

male spiders have been studied. In fact, male spiders of many spider species exhibit

conspicuous body coloration (e.g., *Herenia* spp, *Leucauge* spp, *Nephila* spp), but they

did not receive much attention for many reasons. First, almost all web spiders are sexual

size dimorphic in which females are much larger than males (Hormiga 2000), especially

in genus *Nephila*, which body size of females are ten times larger than males (Kuntner

and Coddington 2009), and consequently they are usually misidentified in the field.

Secondly, the body of male spiders is too small to observe. Because the behaviors of

female and male spiders different greatly, I predict that the conspicuous body coloration might function in ways different from that of female spiders.
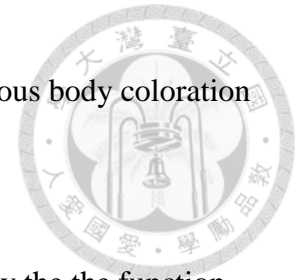
In this study, I used *Nephila pilipes* as my target species to study the the function of male spider body coloration. Male *N. pilipes* changed its body coloration when it completes the last molting and reaches maturity. During such process the color changes from a green base with yellow stripe on dorsal ventrum to orange-red on the whole body (Figures.1, 2). According to the timing that male *N. pilipes* changes its coloration, I predict that the coloration after maturity might play an important role in mating behavior. After reaching maturity, male spiders seldom weave its own web (Robinson and Robinson 1973). Instead, it would continually find a female's web and stay on the upper side of the web to wait for mating. Cohn and Christenson (1987) showed that no matter how starving a male spider was, it tended to mate first if it had a chance. In other words, mating has become the most important thing when male spiders reach maturity. Danielson-François et al. (2012) found that female molting was significantly related with mating success of male spider, and the longer the males can stay on females' webs the more likely it could copulate with females. However, how long a male spider could stay on the web is decided by the female. If a female spider leaves the web site because of various reasons (Rittschof, Ruggles 2010), it was difficult for the male spider to follow the same female. In addition to great variation in mobility between females and

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males due to size difference, there is also high mortality for a male when searching for a

female (Kasumovic 2006). Since previous studies showed a positive relationship

between local prey abundance and web site tenacity of spiders (Vollrath 1985; McNett

and Rypstra 1997; Chmiel et al. 2000; Rittschof and Ruggles 2010), therefore, I

hypothesize that the conspicuous body coloration of male *N. pilipes* may function to

attract insects to females' webs and increase the web site tenacity of females. In this

study, I ask the following two questions: (1) whether the conspicuous body coloration

of male *N. pilipes* attracts insects; and (2) whether the effect of conspicuous body

coloration increases the web site tenacity of female *N. pilipes*.

Material and method
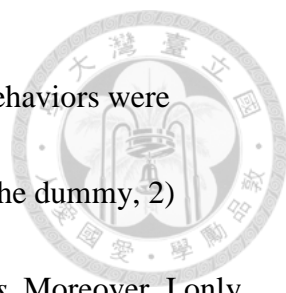
Field experiment

Dummy experiment

My study was divided into two experiments, the dummy experiment and the living spider experiment. The dummy experiment was conducted from August 20 to 23 and 27 to 30 in 2012, and the living spider experiment was from July 8 to 12 and 19 to 23 in 2013. Both experiments were interrupted by a typhoon, so I waited for few days to resume the experiments. The study site was located in a forest trail in Huoyan Mountain nature reserve in Sanyi, Miaoli County, Taiwan in which area there are abundant *Nephila pilipes* during summers. In the dummy experiment, I used dummies to simulate the body coloration of male *N. pilipes* to test the attraction hypothesis. In the field work, I searched along both sites of the trail for the female *Nephila pilipes* which constructed webs below 2 meters above the ground. I measured the body length of female *N. pilipes* and the following parameters to estimate the capture area of the webs: the upper and lower vertical radii, the horizontal diameter, the upper vertical hub radius and the lower vertical hub radius (Herberstein and Tso 2000). I also recorded the number of male *N. pilipes* and kleptoparasitic spiders on webs. Female *N. pilipes* used to construct their webs at the edge of forest (Fan et al. 2009), and the orientation of the web will be vertical to the forest edge and the trail with the ventral side of spider facing the trail.

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This phenomenon was observed by a previous study conducted in the same site and also by me (Fan et al. 2009), so I only included female spiders which ventral side facing to the trail in my experiment to avoid the possible interactions between background and ventral or dorsal spider body coloration. After the measurements, I removed all male *N. pilipes* and kleptoparasitic spiders, and then placed the dummy spiders on webs. Each dummy spider was placed on the end of a green iron wire, and another end of the wire was fixed on branches nearby the web to hang the dummy spiders in front of the web at a distance of about 5 centimeters. In each web I placed 3 dummy spiders. The dummy spiders were made by cardboards which were cut into the appearance of male *N. pilipes* with body length of 6 mm. The choice of cardboards was based on chromatic analysis to make sure that the color signal of the cardboard used was similar to that of male *N. pilipes* in insects' vision(see details in **Reflectance spectrum and color contrast**). In order to test the prey attraction hypothesis, in the experimental group I covered the coloration of dummies by black poster paint. I painted on a leaf nearby the web with same amount of poster paint in the control group to control the olfactory effect. I used video cameras (Sony CX-700 and Sony CX-720) to monitor the interactions between insects and the spider webs. The video cameras were placed 1 meter from the webs and the monitoring was conducted from 8:00 to 13:00 and from 18:00 to 01:00. Each web was monitored at least for four hours. In the video tapes, I recorded the interaction

between insects, spiders and spider webs, and three kinds of insect behaviors were

defined as insect attraction event to analysis: 1) insects flew around the dummy, 2)

insects intercepted by spider web, 3) insect eaten by female *N. pilipes*. Moreover, I only

included the events occurred in ventral side in my analysis, and it is acceptable because

the number of events happened in ventral side of the females were higher than the

dorsal side. Besides attraction event, I also recorded insect order and insect body length

which obtained by the relative body length of female *N. pilipes* I had already measured

in the field.

Living spider experiment

In the living spider experiment, the process was similar to dummy experiment

except I used the living male *N. pilipes* instead of dummies. After removing male *N.*

pilipes and kleptoparasitic spiders, I measured the body length of male *N pilipes* and

used a black marking pen to paint on the ventral opisthosoma to cover the body

coloration of spiders in the experimental group. I also placed paint on the dorsal

opisthosoma in control group spiders to control for the olfactory effect. According to

my observation, almost all male *N. pilipes* would stay on the same side of web with the

female, so I called the experimental group "black group", and the control group "red

group" based on the side the video camera faced. The definition of insect attraction

event was the same to the dummy experiment, and insect order and body length were

recorded in the video tape too. In addition to monitoring spider webs by video cameras,

I also recorded the number of days a female stayed in a particular web site in this

experiment.

Reflectance spectrum and color contrast

To calculate the color contrast of objects in this experiment (e.g. dummies, spiders,

black paint, black marking pen), I measured the reflectance spectra of each object first

by spectrometer from 300nm to 700nm with an interval of 5 nm (S4000; Ocean Optics,

Inc., Dunedin, FL, USA). To estimate diurnal color contrast, I used honey bees, *Apis*

mellifera (Briscoe and Chittka, 2001), as model insects to represent the diurnal insects.

The equation to estimate the relative quantum flux absorbed by each type of

photoreceptor, P, was as follows:

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

where $I_S(\lambda)$ is the spectral reflectance function of each object, $S(\lambda)$ is the spectral

sensitivity function of honey bee photoreceptors, and $D(\lambda)$ is the measured daylight

illuminating spectrum from the forest understory. The sensitivity factor R was

determined by the following equation:

$$R = \frac{1}{\int_{300}^{700} I_B(\lambda)S(\lambda)D(\lambda)d\lambda},$$
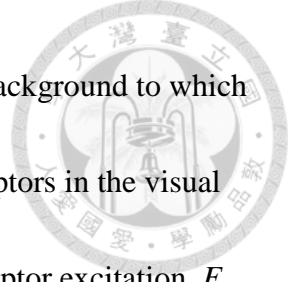
where $I_B(\lambda)$ is the spectral reflection function of the environmental background to which the photoreceptors are adapted. There are three kinds of photoreceptors in the visual system of honey bees, UV, blue and green, and the equation of receptor excitation, E,

$$\text{was:} E = \frac{P}{P+1}.$$

The receptor excitation on the hexagon space (Chittka, 1992) can be plotted by the following equations:

$$x = \sin 60°(E_G - E_{UV})$$

and
$$y = E_B - 0.5(E_{UV} + E_G),$$

where E_G, E_{UV} and E_B indicated the receptor excitation signal of three types of photoreceptors of the honey bee visual system. The distances between two dots on the hexagon space represented the value of color contrast and were called Euclidean distances (ΔS_t), which could be determined by:

$$\Delta S_t = \sqrt{(\Delta x^2) + (\Delta y^2)}$$

In the calculation of color distance under chromatic vision, I involved all three receptor excitation equations, and only green receptor excitation signal, E_G was involved while calculating achromatic contrast. One-sample t-tests were used to compare the color contrast values with discrimination threshold by Dyer et al. (2012) under conditions such as absolute conditioning (0.11) and differential conditioning (0.04).

To calculate nocturnal color contrast, I used hawk moths as the model insects because it had been reported that moths were the major order caught by spiders at night time (Tso et al. 2007). I calculated color contrast by following the equation reported by Johnsen et al. (2006):

$$N = 1.13(\pi/4)n\Delta P^2 D^2 \Delta t \int_{300}^{700} \kappa\tau\left(1 - e^{-kR_i(\lambda)l}\right)L(\lambda)d\lambda$$

It was used to calculate the quantum catches of one ommatidium of moth (Warrant and Nilsson 1998), where n is the effective facets in the superposition, ΔP is the photoreceptor acceptance angle, D is the diameter of a facet lens, Δt is the integration time of a photoreceptor, κ 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, and $L(\lambda)$ is the color signal of the object, which is the multiplication of reflectance spectra of objects and that of nocturnal light environment. The quantum catch values of each of three types of photoreceptors in the visual system of hawk moths, UV, blue, and green, could be used to estimate the relative quantum catch q as:

$$q_{UV} = \frac{N_{UV}}{N_{UV}+N_B+N_G},$$

$$q_B = \frac{N_B}{N_{UV}+N_B+N_G},$$

$$q_G = \frac{N_G}{N_{UV}+N_B+N_G},$$

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and then the chromatic color contrast could be calculated as relative distances in the

color triangle by:

$$X_1 = \frac{1}{\sqrt{2}}(q_G - q_B),$$

$$X_2 = \sqrt{\frac{2}{3}}(q_{UV} - q_B),$$

where 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 triangle color space.

Achromatic color contrast could be calculated by the following equation:

$$C = \frac{N_X - N_{GREEN}}{N_X + N_{GREEN}},$$

Where N_X is quantum catches of object of interest and N_{GREEN} is quantum

catches of environmental background. So far, there is no theoretical discrimination

threshold for the nocturnal visual model of hawk moths. Therefore, the color contrast

values of males were compared to different body parts of female *N. pilipes*, because the

female spider was the nearest object to the male spider and the color contrast of

different body parts of female *N. pilipes* had been evaluated in hawk moth vision to

show that the body coloration of female *N. pilipes* also functioned at night (Chuang et

al., 2007).

Statistical analysis

The diurnal color contrast values were compared with the absolute conditioning and differential conditioning thresholds by one-sample t-tests. The nocturnal color contrast values were compared by analysis of variance tests and Duncan's new multiple range test. The insect attraction data was a count data, and previous studies showed that insect interception data fitted well with a Poisson distribution (Chuang et al. 2007, Fan et al. 2009), so I used Poisson regression models to test the effect of treatments. The monitoring time was set as offset to transform the insect attraction data into rate data, and I also included web size, body length of male *N. pilipes*, body length of female *N. pilipes* and the amount of insects passed through the view of video camera representing background insect abundance into my model as variable. The data of insect weight in the dummy experiment and living spider experiment was not normally distributed by the test of Kolmogorov-Smirnov normality test (dummy experiment $P < 0.01$, live spider experiment $P < 0.01$), so I transformed the insect weight by logarithmic transformation to approach normal distribution, then using two-sample t-test to compare the experimental group and control group in this two experiments. The data of how long the female *N. pilipes* stayed in a particular web site did not follow a normal distribution; therefore, I tested the web site tenacity of female *N. pilipes* by U-test. The insect order was also recorded as ratio data and insect order composition were compared between the experimental group and control group by χ^2-test.

Results

**Reflectance spectrum and color contrast**

The reflectance spectra of (1) ventral opisthosoma of male *N. pilipes* (2) dummy spider (3) black poster paint (4) black marking pen was shown in Figure 3. The chromatic color contrast between ventral opisthosoma of male *N. pilipes* and environmental background was 0.135 ± 0.01 (mean $\pm$ SE, $t_{4,0.11} = 2.5$, $P = 0.0333$ when compared with absolute conditional threshold 0.11 and $t_{4,0.04} = 9.48$, $P = 0.0003$ for differential conditional threshold of 0.04). This result demonstrated that the coloration of ventral opisthosoma of male *N. pilipes* was conspicuous against environmental background when viewed by hymenopteran insects. The chromatic color contrast between dummy spiders and ventral opisthosoma of male *N. pilipes* was 0.032 ± 0.0004 (mean $\pm$ SE, $t_{2,0.11} = -147.54$, $P < 0.0001$ for absolute conditional threshold and $t_{2,0.04} = -15.46$, $P = 0.0021$ for differential conditional threshold). This result demonstrated that the coloration of dummy was similar to the body coloration of male *N. pilipes* when viewed by hymenopteran insects. The color contrast between black poster paint and environmental background was 0.109 ± 0.007 (mean $\pm$ SE, $t_{4,0.11} = -0.04$, $P = 0.4835$ for absolute conditional threshold and $t_{4,0.04} = 9.79$, $P = 0.9997$ for differential conditional threshold). The color contrast between black marking pen and environmental background was 0.122 ± 0.012 (mean $\pm$ SE, $t_{4,0.11} = 0.97$, $P = 0.7829$ for absolute

conditional threshold and $t_{4,0.04} = 6.42$, $P = 0.9883$ for differential conditional

threshold)(table 1). The nocturnal chromatic color contrast values of objects were

significantly different when viewed against environmental background (ANOVA test,

$F_{5,16} = 162.07$, $P < 0.0001$, Figure 4). The yellow spots on ventral basal leg segment of

female *N. pilipes* were the most conspicuously colored among all body parts (Figure 4).

There were no significant difference when comparing the chromatic color contrasts of

opisthosoma of male *N. pilipes*, dummies, black paint and black marking pen (Figure 4).

The black parts on ventral opisthosoma of female *N. pilipes* were the least conspicuous

coloration among all of these objects (Figure 4). The achromatic color contrast values

were also significantly different when viewed against environmental background

(ANOVA test, $F_{5,16} = 33.96$, $P < 0.0001$, Figure 4). The yellow spots on ventral basal

leg segment of female *N. pilipes*, opisthosoma of male *N. pilipes* and the dummies had

the highest achromatic color contrast values among all of these objects, and followed by

the black paint and black marking pen (Figure 4). The black parts on ventral

opisthosoma of female *N. pilipes* had the lowest achromatic color contrast values among

all of these objects.

Field experiment

Dummy experiment
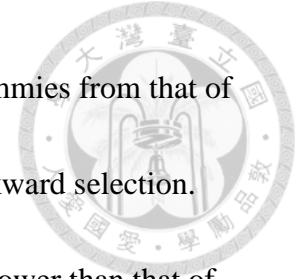
When I compared the insect attraction rate of webs with red dummies from that of webs with black dummies, only treatment effect was chosen by backward selection. Prey attraction rates of webs with black dummies was significantly lower than that of webs with red dummies (Poisson regression, β = -1.5652, Wald χ^2 = 15.95, P < 0.0001, table 2). Moreover, the weight of insects attracted by webs with red dummies was also significantly higher than that of webs with black dummies (two sample t-test, $t_{22,0.05}$ = 7.29, P = 0.0037, Figure 3).

Living spider experiment

In the second experiment using living male *N. pilipes*, two parameters were selected in the diurnal insect attraction model, the first was amount of background insect (β = 0.185, Wald χ^2 = 28.24, P < 0.0001, table 3), another parameter selected was treatment effect. The result of analysis showed that the insect attraction rate of red group was significantly higher than that of the black group (β = -0.5473, Wald χ^2 = 4.10, P < 0.0429, table 3). However, the insect weight between red and black group was not significantly different (two sample t-test, $t_{27,0.05}$ = -0.83, P = 0.4134, Figure 4). The composition of insect orders between two group was significantly different (contingency table, $\chi^2_{3,0.05}$ = 9.02, P = 0.029, table 4). There was no parameter selected in nocturnal insect attraction model. Web site tenacity of female spiders did not differ significantly between two groups (Mann–Whitney U-test, P = 0.9721, Figure 5).
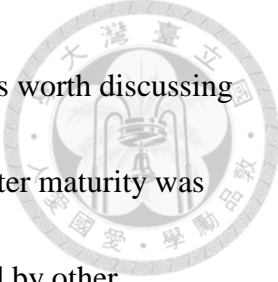
Discussion

This is the first study to investigate the function of body coloration of male orb web spiders, and I found that the body coloration of male *N. pilipes* could attract insects to the females' webs in the day time and this result was the same in both dummy and living spider experiments. However, when I compared the weight of insects attract to webs, I found no significant difference in the living spider experiment. My results show that male spiders attracted smaller insects (table 4). The difference of biomass between insects was very large, so the result of insect weight comparison could be considerably affected by a small amount of large insects. The results of insect weight comparison in dummy experiment and living spider experiment differed. It might be caused by the difference in amount of male spiders or dummies I used in these two experiments. In the dummy experiment, I placed three dummies in one female's web, but there was only one male spider on a female's web in the living spider experiment. Fan et al. (2009) showed that when increasing the intensity of attraction signal of *N. pilipes* dummies in the day time, it would significantly increase the prey attraction rate. Moreover, many studies showed that on the webs of female *N. pilipes* up to seven males could be found (Robinson and Robinson, 1973; Danielson-François et al. 2012). Therefore, multiple male spiders on a web could possibly increase the intensity of attraction signal and attract more insects to the female's web. However, I still had to consider the effect of

male-male competition that could affect the interaction between spiders and insects

(Rittschof and Ruggles 2010).

The experiment in the night time failed to find a significant result, even though

many studies have found empirical evidence supporting the attraction hypothesis in

nocturnal spiders (Tso et al. 2007; Blamires et al. 2012). However, there are some

behavioral differences between male *N. pilipes* and other nocturnal spiders. Female *N.*

pilipes still catch prey at night but male usually would leave the original position near

the upper side of web and move to the end of web then climb on structural threads

connecting nearby vegetation. Such behavior would extremely decrease the attraction

effect not only because the increase of distance between the male and web hub, but

some male spiders even hide behind the leaves. Tso et al. (2007) showed that insects

were more abundant in night time, so why during night time male spiders did not stay

on web, but chose to leave and rest behind the leaves? It might be because more females

molted in the day time, and it represented more mating opportunities for the males, so in

the night time the males leave the web to avoid the risk of being eaten by the female

spider. Such cannibalism has been observed in many spider species, and it frequently

occurs during mating process (Elgar 1991; Herberstein et al. 2002). However, whether

female *N. pilipes* actively attacked male spiders when the male spiders stay close with

females still needs more observation to confirm.

My experiment did not exclude the alternative hypothesis, so it is worth discussing

another possible hypothesis here. The coloration of male *N. pilipes* after maturity was

orange-red, and it was very similar to aposematic coloration exhibited by other

organisms used as warning signal (Mappes et al 2005). However, I have to quantify

how these coloration is viewed by the vision of animals which interacted with the

spiders (Endler 1990). Usually, animals would have to experience a stimulation to learn

if it was a warning signal (Ruxton et al. 2004), and the stimulation could origin from the

signaler itself or from the mimics to show the unpalatability (Ruxton et al. 2004). There

was no evidence to determine whether male *N. pilipes* was poisonous or mimic of

another unpalatable animal. Therefore, it is unlikely that the coloration of male *N.*

pilipes function as a warning signal. Sexual selection was another mechanism of the

evolution of conspicuous body coloration especially in animals exhibiting sexual

dimorphism or color changing in the mating season (Hill and McGraw 2006; Girard et

al. 2011). Nonetheless, web spiders mainly communicate by the vibration of the silk

(Maklakov et al. 2003), and it had been reported that male *N. pilipes* will vibrate the silk

threads as an intersexual interaction signal when it came to a female's web first.

Therefore, the role male body coloration plays in the courtship of *N. pilipes* is doubtful.

I did not found a positive connection between insect attraction and web site

tenacity of female *N. pilipes*. However, foraging events were rare for male *N. pilipes*

(personal observation; Kasumovic 2006 for male *N. plumipes*), therefore the insects

attracted by male *N. pilipes* were mostly not for itself. The results of my experiments

demonstrated that although number of insects intercepted by webs differed between

different treatment groups, web site tenacity did not differ between them. Rittschof and

Ruggles (2010) argued that the male harassment might have a negative effect on web

site tenacity of female spiders. In my experiment, in both treatment groups each web

had the same number of male spiders, so the effect of male harassment had been well

controlled in my study. Typhoon could be an important factor to affect the web site

tenacity, because it dramatically wiped out the original population at the study site, and

the new population needed more time to obtain habitat information to estimate the food

resource around the whole habitat (Herberstein and Elgar 2000). There was an

alternative hypothesis to explain why male *N. pilipes* attracts insects to female's web, it

is the molting hypothesis. Previous study showed that the increase in food resource

could increase the molting rate (Higgins 1992). Female molting has been shown to be

one of the most important variables to affect the mating success of male *N. pilipes*

(Danielson-François et al. 2012). If male spider could speed up the molting of female

spiders, then it could shorten the waiting time on the female's web and also decrease the

risk of female leaving or other unpredictable factors. Moreover, female *N. pilipes* have

been reported to be able to molt even after maturity (Kuntner et al. 2012). Therefore,

increasing foraging intake of female *N. pilipes* to induce them to molt earlier is

beneficial to males. However, more efforts are needed to verify such hypothesis.
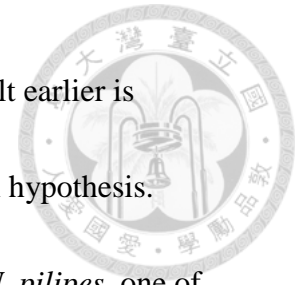
There was a group of spiders which look very similar to male *N. pilipes*, one of

them is kleptoparasitic spider, the *Argyrodes miniaceus* (Figure 6). Its body coloration

was also orange-red, and the body size was similar to that of male *N. pilipes*. *A.*

miniaceus was a kleptoparasitic spider and it was often observed to forage on *N. pilipes*

webs searching for small prey. It will be interesting to investigate if the body coloration

of *A. miniaceus* has prey attraction function similar to that of male *N. pilipes*, and the

interaction between these two kinds of spiders. Peng et al. (2013) showed that another

Argyrodes species, *A. fissifrons*, attracts insects to its host, and the prey size of *A.*

fissifrons was highly significantly different from its host. Orange-red body coloration of

A. miniaceus probably has the same function as silvery coloration of *A. fissifrons*.

Before reaching maturity, the body coloration of male *N. pilipes* was similar to that

of juvenile females (Figure 1). However, when I examined the pattern of body

coloration in the genus *Nephila*, I found that some of *Nephila* species looked quite

different between females and males, and in several *Nephila* species the body

colorations of males are very similar. Moreover, these species were not monophyletic

(Kuntner et al. 2013), and it seems that the observed convergent body coloration pattern

was generated by similar selection pressures. To solve this question, I needed more

ecological observation about male *Nephila* spiders and kleptoparasitic spiders on

Nephila spider's webs and the result of my study provides the first step toward such

goal.

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Figure 1. Dorsal view of juvenile male *N. pilipes*. The scale bar is 2mm.

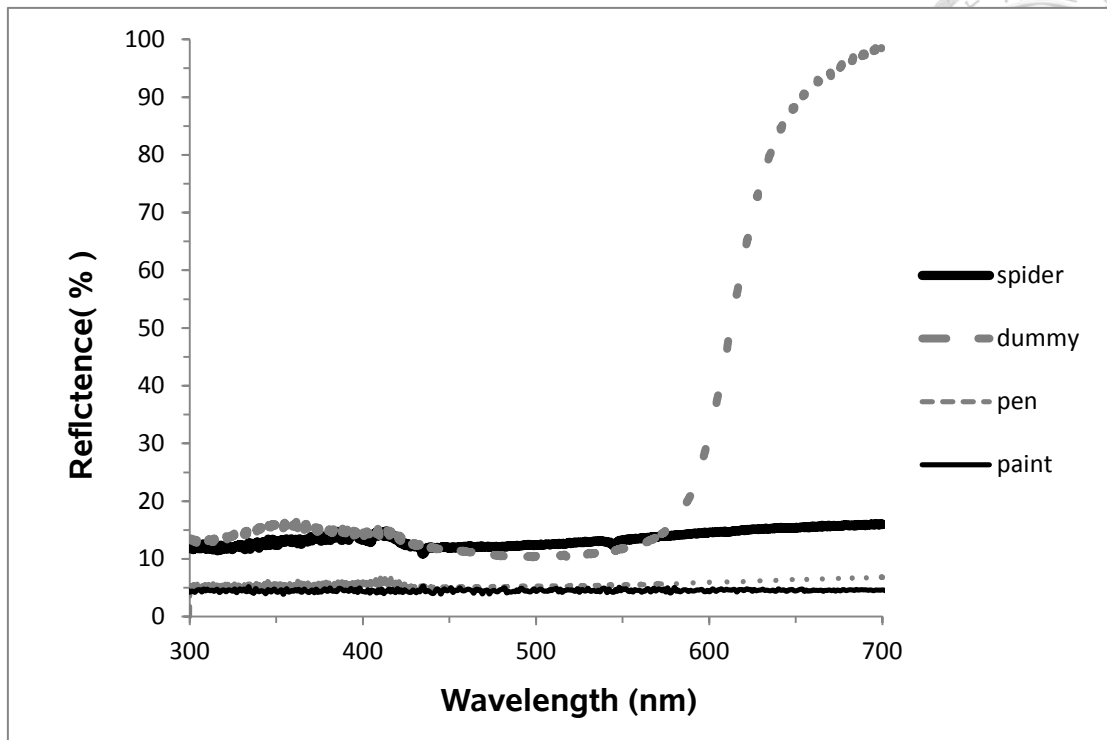Figure 2. Dorsal view of male *Nephila pilipes* after reaching maturity. The scale bar is 2mm.

Figure 3. Reflectance spectra of (1) ventral opisthosoma of male *Nephila pilipes* (bold line), (2) dummy spider (dash line), (3) marked pen (dotted line), (4) poster paint (solid line).
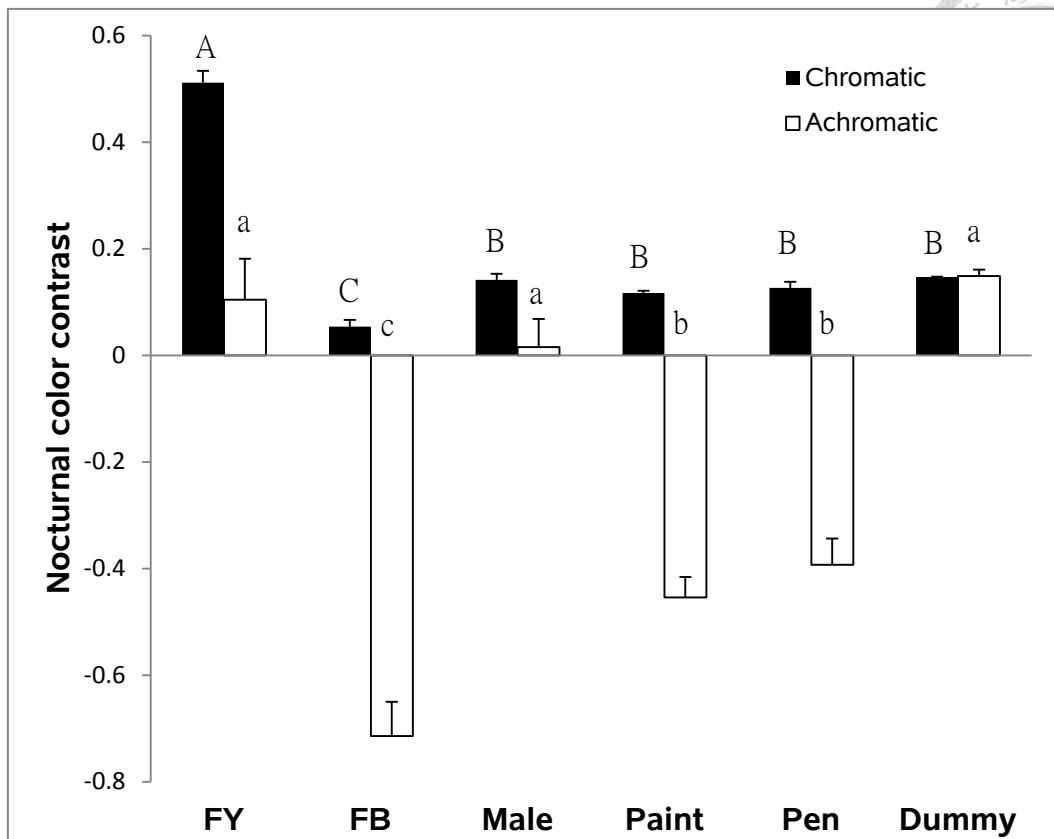
Figure 4. Mean (+ SE) nocturnal achromatic and chromatic color contrast values of (1)

yellow spots on ventral basal leg segment of female *Nephila pilipes* (FY) (2) black parts

on ventral opisthosoma of female *N. pilipes* (FB) (3) opisthosoma of male *N. pilipes* (4)

black paint (4) black marking pen (5) dummy viewed against environmental

background by lepidopteran insects. Letters represent results of analysis of variance and

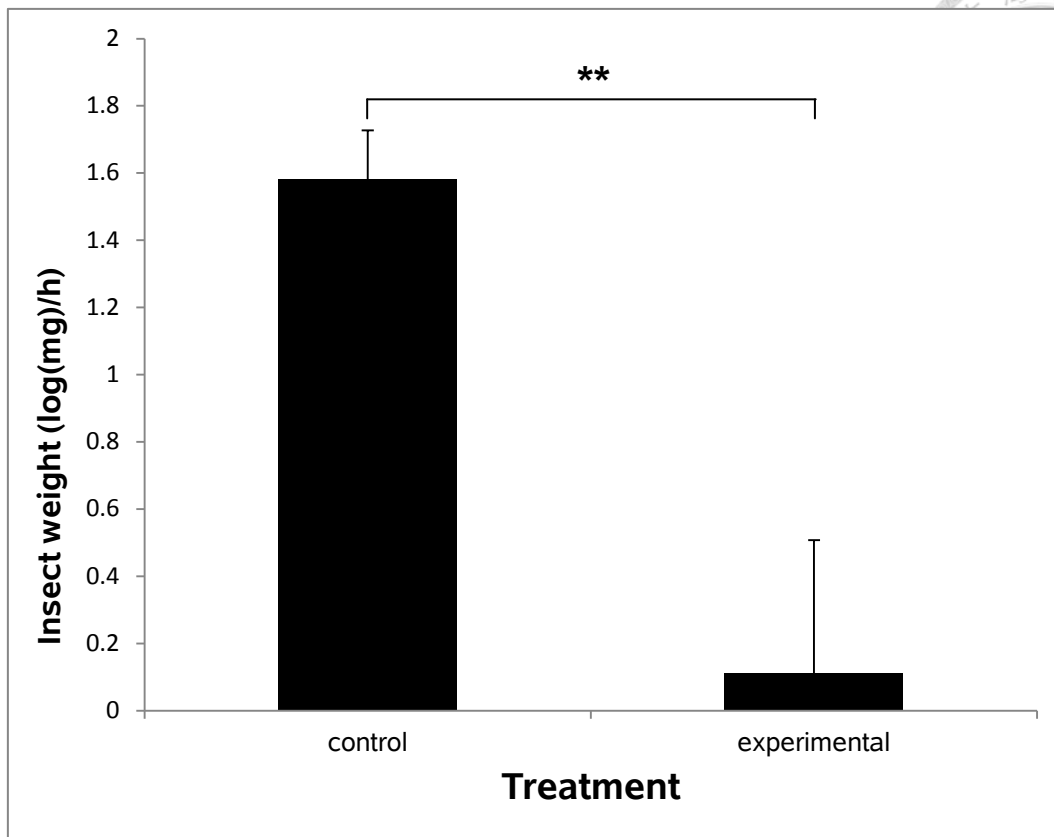Duncan's new multiple range test.

Figure 5. Mean (+ SE) weight of insects (log milligram of insect weight per hour)

attracted to webs containing control and experimental group dummies (**: *P*<0.01).
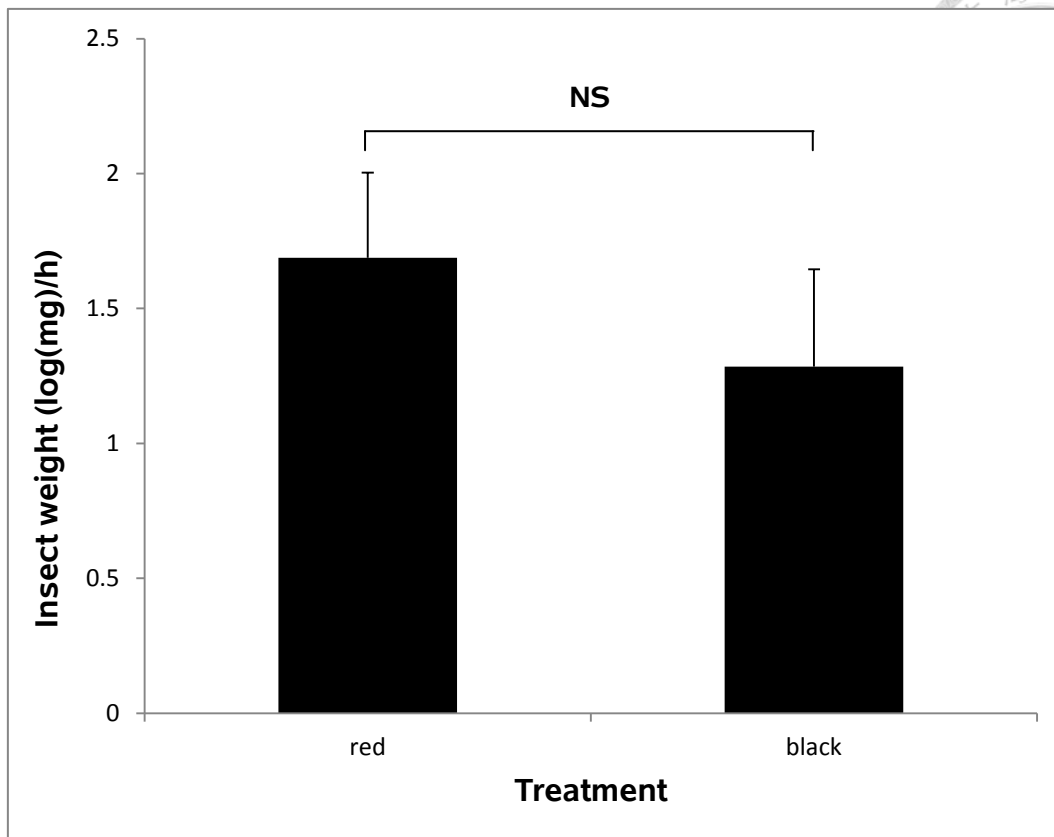
Figure 6. Mean (+ SE) weight of insects (log milligram of insect weight per hour)

attracted to webs containing red and black group males in living spider experiment (NS:
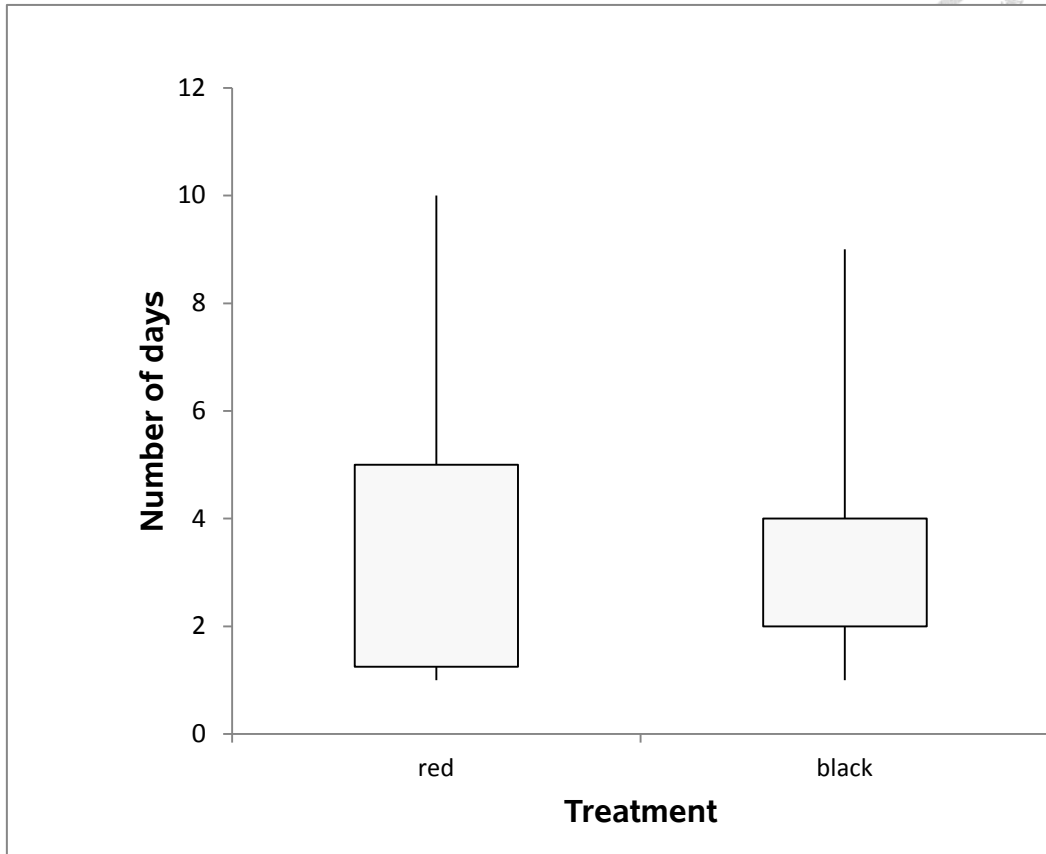
nonsignificant at α=0.05 level).

Figure 7. Box plot of web site tenacities of female *Nephila pilipes* containing red or

black group males on webs.

Table 1. Results of one-sample t-tests comparing diurnal chromatic color contrast values with absolute conditioning threshold and differential conditioning threshold values.

Group	Contrast values	t	*P*	t	*P*
		Absolute conditioning		Differential conditioning	
Opisthosoma of male *Nephila pilipes* against environmental background	0.135 ± 0.01	2.5	0.0333	9.48	0.0003
Opisthosoma of male *Nephila pilipes* against dummies	0.032 ± 0.0004	-147.54	0.0001	-15.46	0.0021
Black paint against environmental background	0.109 ± 0.007	-0.04	0.4835	9.79	0.9997
Black marking pen against environmental background	0.122 ± 0.012	0.97	0.7829	6.42	0.9883

Table 2. The results of Poisson regression comparing the insect attraction rate of webs

containing experimental and control group male dummies[a]

Parameter	DF	Estimate of β	SE	Chi-Square	P
Intercept	1	0.0706	0.169	0.17	0.6762
Treatment experimental	1	-1.5652	0.3919	15.95	<.0001

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

Table 3. The results of Poisson regression comparing the insect attraction rate of webs

containing red and black group males while considering background insect abundance

in the living spider experiment[a]

Parameter		DF	Estimate	SE	Chi-Square	*P*
Intercept		1	-2.0468	0.3219	40.42	<.0001
BI		1	0.185	0.0348	28.24	<.0001
Treatment	Black	1	-0.5473	0.2703	4.1	0.0429

BI, Background insect.

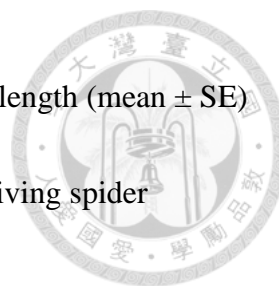[a] The ratio between probabilities of 2 certain events is e^{β}.

Table 4. The taxonomic order composition (in percentage) and body length (mean ± SE) of insect attracted by webs containing red and black group males in living spider experiment.

Groups	Lepidoptera	Hymenoptera	Diptera	Unidentified
Red	0.21	0.10	0.00	0.69
	35.40 (±4.85)	18.15 (±3.98)	-	5.33 (±0.92)
Black	0.33	0.19	0.10	0.38
	34.85 (±7.81)	20.71 (±6.51)	6.3	7.10 (±1.32)