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Diurnal and nocturnal prey luring of a colorful predator

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Summary

While animal color signaling has been studied for decades, we have little knowledge of the role conspicuous body coloration plays in the nocturnal context. In this study we explored animal color signaling in both diurnal and nocturnal contexts to arrive at a more comprehensive understanding of its function. We quantified how the brightly colored giant wood spiders *Nephila pilipes* are viewed by nocturnal insects, and performed field manipulations to assess the function of a spider's coloration in both diurnal and nocturnal conditions. Seen through the eyes of moths, the conspicuous body parts of spiders are quite distinctive from the vegetation background. The presence of *N. pilipes* significantly increased the diurnal as well as the nocturnal prey interception rates of their webs, but these rates were significantly reduced when the conspicuous color signals of *N. pilipes* were altered by black paint. A comparison of the diurnal and nocturnal hunting performances of spiders showed that their conspicuous coloration had a higher luring effect under dim light conditions. These results demonstrate that the conspicuous body coloration of *N. pilipes* functions as a visual lure to attract both diurnal and nocturnal prey. It seems that nocturnal insects are the major target of this colorful sit-and-wait predator. We suggest that the selection pressure to effectively exploit the color vision of nocturnal prey could be one of the major forces driving the evolution of spider coloration.

Key words: spider, *Nephila pilipes*, color contrast, visual ecology.

Introduction

Deceptive or cheating messages are commonly involved in the communication between organisms (Hasson, 1994). Especially in predator–prey interactions, numerous predators use misleading signals to lure prey. The use of light signals to visually lure prey is common in marine ecosystems such as the deep sea because, when the ambient light intensity is low, bioluminance can achieve very effective luring (Munk, 1999). In terrestrial ecosystems, some predators also use deceptive visual signals to lure prey. For example, many species of orb spider which hunt during the day have conspicuous body colorations. Through the eyes of insects, the bright parts of these spiders are quite distinct from the vegetation background (Tso et al., 2004; Tso et al., 2006). When the color signals of these bright body parts are altered, the spiders' prey-catching ability is reduced greatly (Hauber, 2002; Tso et al., 2006). Researchers have proposed that the spiders' body coloration pattern makes them look like some form of food resource and thus makes them attractive to diurnal insects (Craig and Ebert, 1994).

In the night the light is dim and the signal-to-noise ratio is low (Warrant, 2004). Most studies on the cues used by interacting nocturnal organisms focus on acoustic or olfactory signals (Schneider, 1974; Suga, 1990; Konishi, 1993; Fullard, 1997; Kaspi, 2000; Haynes et al., 2002). While color signaling is considered an important ecological process in the diurnal conditions of terrestrial systems (Bruce et al., 2003), the role color signaling plays in the nocturnal context does not receive much attention. It was not until appropriate research techniques were available that researchers began to realize that visual signals are important cues for certain nocturnal organisms (Kelber and Roth, 2006). Many nocturnal insects have specialized eyes that enable them to discriminate color stimuli (Kelber et al., 2002) and to detect food resources at night (Raguso and Willis, 2005). The superposition compound eyes of numerous nocturnal insects combine the light signal received by hundreds of ommatidia. The signal intensity can thus be greatly magnified, thereby solving the problem of low light intensity in dim light environments (Kelber et al., 2003a). In addition, the rhabdoms of superposition eyes are longer than those of apposition eyes and so can help to improve the signal-to-noise ratio (Kelber and Roth, 2006). The visual sensitivity of nocturnal insects is furthered structurally by wide pupil aperture and physiologically by spatial/temporal summation of visual channel neural outputs (Warrant, 1999). Since numerous insects use vision to search for color signals of resources during the night, it is possible that predators evolve ways to exploit the prey's nocturnal vision. In the present paper we show that such exploitation does occur in the interaction between a colorful sit-and-wait spider predator and its nocturnal prey.

Nephila pilipes, the giant wood spider, is a large colorful orb spider (Fig. 1) commonly seen in the forests of East and Southeast Asia (Platnick, 2007). Previous studies have shown

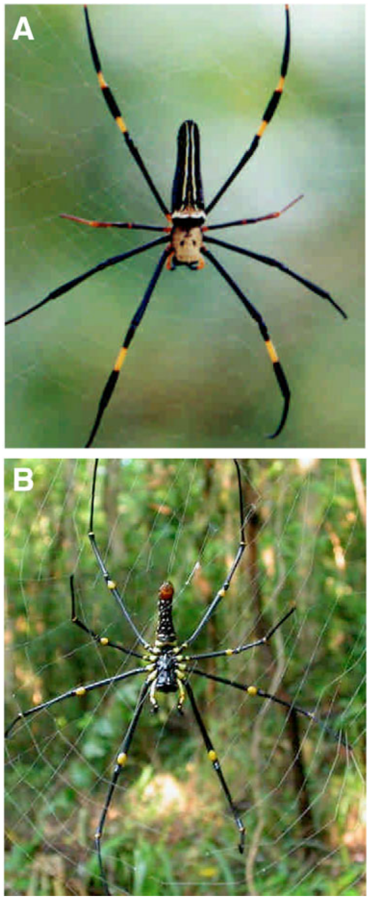

Fig. 1. Dorsal (A) and ventral (B) views of a colorful sit-and-wait predator, the giant wood spider *Nephila pilipes* (Araneae: Tetragnathidae).

that through the eyes of hymenopteran insects only the conspicuous yellow but not the black body parts of *N. pilipes* can be distinguished from the background vegetation (Tso et al., 2004). Their coloration pattern seemed to make the spiders resemble some form of food resource and thus was attractive to diurnal insects. From a round-the-clock survey we found that in addition to diurnal hunting, *N. pilipes* also actively hunts for prey during the night. In this study, we evaluated the role conspicuous body coloration plays in this spider's diurnal as well as nocturnal hunting. First, by calculating nocturnal color contrast values we quantified how this spider was viewed by nocturnal insects. Second, field manipulations were conducted to examine the attractiveness of the spider's body coloration to insects under both diurnal and nocturnal conditions. Our results show that the conspicuous body coloration of *N. pilipes* functions better during night-time, and that large nocturnal prey might be the major targets of these colorful predators.

Materials and methods

Quantifying how N. pilipes are viewed by nocturnal insects

We calculated nocturnal color contrast values to quantify how the various body parts of *N. pilipes* were viewed by nocturnal insects. Color contrast is the contrast caused by the spectral difference between two objective areas, which can only be detected by a visual system with at least two photoreceptor types (Chittka, 1992). In recent years, studies quantifying how orb spiders are viewed by insect prey have all been conducted in a diurnal context (Tso et al., 2004; Tso et al., 2006), using neuroethological models developed from the visual systems of diurnal insects (Chittka, 1992). Nocturnal insects such as moths generally have UV, blue and green photoreceptors (Kelber et al., 2003b). Similar types of receptor are also found in numerous diurnal insects (Briscoe and Chittka, 2001). However, while moths can distinguish color signals at night, diurnal insects are color blind in dim light conditions (Kelber et al., 2003b). Therefore, we cannot use the diurnal neuroethological models to quantify how the coloration of an organism is viewed under dim light conditions. Since the results of our preliminary survey showed that moths were the major nocturnal prey of *N. pilipes*, we used the model developed for the hawkmoth (Johnsen et al., 2006) to calculate nocturnal color contrast values. According to the review by Briscoe and Chittka (Briscoe and Chittka, 2001), the spectral sensitivities recorded from most moth species, including Sphingidae and Pyralidae, reveal three photoreceptor types, i.e. UV, blue and green, and all have similar spectral sensitivity functions. In addition to the three common receptor types, a red receptor type was recorded from Noctuidae moths but only from two species, i.e. *Spodoptera exempta* and *Mamestra brassicae*, so far (Briscoe and Chittka, 2001). Thus, the spectral sensitivity curves of *Deilephila elpenor* were chosen as a general model for color contrast calculation to represent most moths, but not all, in the present study.

Six female *Nephila pilipes* (Fabricius 1793) were collected from a secondary forest in Sanyi, Miaoli County, in central Taiwan. In the hawkmoth neuroethological model, the quantum response of a moth ommatidium, N, is estimated by Eqn 1, according to the method of Warrant and Nilsson (Warrant and Nilsson, 1998):

$$N = 1.13(\pi/4)n\Delta P^2 D^2 \Delta t \int_{350}^{700} \kappa\tau(1-e^{-kR_i(\lambda)l})L(\lambda)\mathrm{d}(\lambda)\,, \quad (1)$$

where n is the number of effective facets in the superposition aperture, 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, $R_i(\lambda)$ is the absorbance spectra of each photoreceptor, and $L(\lambda)$ is the color signal of the object, which is the multiplication of the reflectance spectra of objects by that of the nocturnal light environment (Johnsen et al., 2006). The reflectance spectra of various body parts of spiders and the vegetation background were those used previously (Tso et al., 2004). The yellow body parts of *N. pilipes* had a small reflectance in the UV region and a strong reflectance between 550 and 700 nm (Fig. 4A in Tso et al., 2004). In contrast, the dark body parts had a low reflectance across all wavelengths measured (Fig. 4B in Tso et al., 2004). The background vegetation spectrum was estimated by averaging the spectra measured from green leaves, fallen leaves and bark (Fig. 3B in Tso et al., 2004). All the other variables and nocturnal illumination spectra followed those reported previously (Johnsen et al., 2006). Since moonlight was the dominant nocturnal illumination during our field study, we used its spectrum, rather than that of starlight, to quantify how *N. pilipes* was viewed by nocturnal insects. The quantum response values of spider body parts and background green vegetation were used to calculate achromatic nocturnal contrast by Eqn 2 (Johnsen et al., 2006):

$$C = \frac{N_x - N_{\mathrm{green}}}{N_x + N_{\mathrm{green}}}\,, \tag{2}$$

where N_x is the number of quantum responses for the object and N_{green} is the number of quantum responses for the green vegetation background. Insects are assumed to use achromatic contrast when viewing objects from a long distance and chromatic vision when they come close to the object (Giurfa et al., 1997). Therefore, in addition to using green receptor signals to calculate achromatic contrast values, we used the signals of all receptor types to calculate the chromatic contrast values of the various body parts of *N. pilipes* when viewed by a moth during the night-time. To calculate chromatic contrast, the quantum response values (N) of UV, blue (b) and green (g) photoreceptors were first estimated to generate relative quantum responses of each type of photoreceptor (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 using Eqn 3–5:

$$q_{\mathrm{uv}} = \frac{N_{\mathrm{uv}}}{N_{\mathrm{uv}} + N_b + N_g}\,, \tag{3}$$

$$q_b = \frac{N_b}{N_{\mathrm{uv}} + N_b + N_g}\,, \tag{4}$$

$$q_g = \frac{N_g}{N_{\mathrm{uv}} + N_b + N_g}\,. \tag{5}$$

Relative quantum response values were used to generate relative distances in the color triangle using Eqn 6 and 7:

$$X_1 = \frac{1}{\sqrt{2}}\,(q_g - q_b)\,, \tag{6}$$

$$X_2 = \frac{\sqrt{2}}{\sqrt{3}}\left(q_{\mathrm{uv}} - \frac{q_g + q_b}{2}\right), \tag{7}$$

where X_1 and X_2 are the distances on the X and Y axis, which represents the relative intensity of three types of photoreceptor in 2D color space (Johnsen et al., 2006). The distance between two color stimuli in the color space is the nocturnal chromatic color contrast. To date, the discrimination threshold value of nocturnal color contrast is still not available. In this study we compared the nocturnal achromatic and chromatic contrast values of various body parts of *N. pilipes* by ANOVA and least significant difference (LSD) mean comparisons to determine whether the yellow body parts were more conspicuous than others when viewed against green vegetation under dim light conditions.

Quantifying the attractiveness of N. pilipes to diurnal and nocturnal insects

We conducted two field experiments to evaluate the prey-attraction function of spider coloration under both diurnal and nocturnal conditions. The field experiments were conducted between August 18 and 28, 2005, in Sanyi, Miaoli County, in central Taiwan. The study site was located in a secondary forest and *N. pilipes* were commonly seen building webs along the trails. Mature female *N. pilipes* usually built webs along the forest edges and the orb diameter usually exceeded 1 m. In the first experiment we compared the prey interception performance of the webs with and without *N. pilipes* to evaluate whether the colorful spiders were attractive to insects. Individual spiders along the trails were randomly chosen and the distance between the individuals was at least 5 m. 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 their webs. Before recording prey interception events, we measured spider body length, and hub and web radius from four cardinal directions to calculate the capture area, following the formulae of Herberstein and Tso (Herberstein and Tso, 2000). Sony HR118 Hi-8 video cameras were used to monitor the prey interception rates of *N. pilipes*. One machine was placed 1–2 m away from each web monitored. The monitoring was conducted both in daytime (06:00–14:00 h) and at night-time (02:00–05:30 h) to determine the attractiveness of *N. pilipes* in different light conditions. While recording nocturnal prey interception events, the infrared night view function of the video cameras was used. When viewing the videotapes, we recorded the number, type (lepidopteran *vs* non-lepidopteran) and length of prey intercepted by each web. The number of insects caught in the webs during diurnal or nocturnal monitoring was divided by the number of monitoring hours to generate prey interception rates.

In the second experiment we evaluated whether the conspicuous body coloration was responsible for the spiders' attractiveness to insects. The conspicuousness of the yellow body parts of *N. pilipes* was altered by black acrylic paint (Alpha Acrylic Colors, Seoul, Korea). Before the field experiments were conducted, we brought eight spiders back to the lab, applied black paint to them and measured the reflectance spectra with a spectrometer (S2000, Ocean Optics, Dunedin, FL, USA). The reflectance spectrum data were used to calculate diurnal as well as nocturnal contrast values to determine whether the chromatic properties of the black acrylic paint used were similar to those of the black body parts of *N. pilipes*. We used Student's *t*-test to determine whether the diurnal color contrast of the paint when viewed against the black body parts was significantly higher than the discrimination threshold value of 0.05 estimated for hymenopteran insects (Théry and Casas, 2002). A *t*-test was also used to find out whether the paint's nocturnal contrast was similar to that of the black body parts. Spiders along the trail were randomly chosen and were divided into experimental and control groups. The spiders chosen were carefully removed from their webs (without causing any damage to the webs) and were anesthetized by CO_2 (for about 5 min) to allow us to perform body color manipulations. In the experimental group, black paint was applied to the conspicuous carapace, dorsal stripes and leg spots. In the control group, the same amount of black paint was applied to the black body parts to control for the effect of the treatment. The rest of the procedures were similar to those of the first field experiment.

Statistical analyses

Either Poisson regressions (Steel et al., 1997) or *U*-tests were used to compare the difference in prey interception rates between treatment groups while considering the capture area. In the Poisson regression, the probability of events (such as insect interceptions) under various conditions (such as different treatments or orbs of different area) was compared. An iterative re-weighted least squares method was used to obtain the maximum likelihood estimate of the ratio between probabilities of different events. A χ^2 test was then used to evaluate whether such a ratio (the difference) between probabilities of events reached statistical significance. The Poisson model is shown in Eqn 8:

$$\log\mu_N = \log N(X_i) + X_i\beta \,, \tag{8}$$

where μ is the expected value, X represents the explanatory variables (treatment groups or orb area), β is the probability and $N(X)$ denotes the total number of individuals. The web area was designated as a categorical variable due to the small sample size. We ranked capture areas into the following three categories: 0–200, 200–400 and 400–600 cm^2. To analyze those data that did not fit either normal or Poisson distributions, we divided prey interception rate by capture area to generate unit-area prey interception rates, then compared the treatment groups with a non-parametric *U*-test. χ^2 tests of homogeneity were used to compare the prey composition and *t*-tests were used to compare prey body length of various treatment groups.

Results

Nocturnal contrast values of N. pilipes

The nocturnal achromatic contrast values of conspicuous yellow body parts of *N. pilipes* when viewed against the vegetation background by lepidopteran insects were significantly higher than those of the black body parts (ANOVA test, F=12.062, P<0.001, Fig. 2). The yellow stripes on the dorsum of the abdomen had the highest achromatic contrast among all body parts. The achromatic contrast values of the yellow carapace and yellow spots on the 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 (Fig. 2). The nocturnal chromatic color contrast of various body parts of *N. pilipes* followed a trend similar to that of the achromatic contrast values. Various conspicuous yellow body parts exhibited contrast values significantly higher than those of the black body parts (ANOVA test, F=36.93, P<0.001, Fig. 2). Again, the yellow stripes on the dorsum exhibited the highest color contrast values, followed by the yellow carapace and yellow leg spots. The nocturnal chromatic color contrast values of the black body parts were considerably lower than those of the yellow body parts. These results indicate that when a giant wood spider hanging in front of green vegetation is viewed by a moth, the spider's yellow body parts are quite distinctive but the dark parts are relatively indistinguishable from the background.

Diurnal and nocturnal prey attraction of N. pilipes

N. pilipes in the study site were monitored by infrared video cameras for a total of 1000 h. Of that time, 670 h were spent on diurnal hunting and 330 h were spent on nocturnal hunting. The sample sizes of the spider-absent groups in the daytime and night-time were both 17. Those of the spider-present group were 20 in the daytime and 19 at night-time. The presence of *N. pilipes* on the webs significantly increased the prey interception rate, regardless of whether diurnal or nocturnal hunting was being monitored. The prey interception data of this part of our study fitted well with the Poisson distribution (Pearson χ^2=3.168, P=0.5049), so Poisson regressions were used to compare the difference in prey interception rate between treatment groups while considering the capture area. The diurnal prey interception rate of webs with spiders was seven times that of webs without spiders (Fig. 3A, Table 1A). The difference in the nocturnal prey interception rate between the 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. 3B, Table 1B).

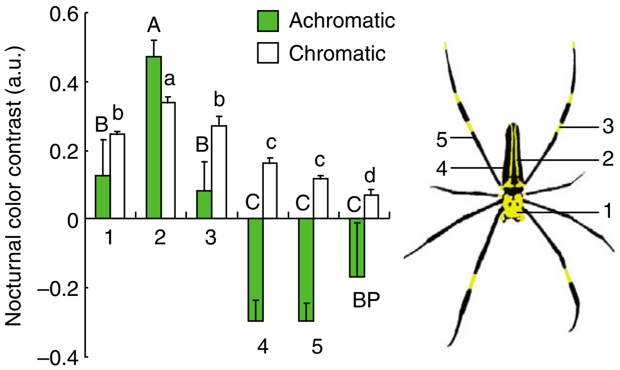

Fig. 2. Mean (±s.e.m.) nocturnal achromatic and chromatic contrast values (in arbitrary units, a.u.) of various body parts of *Nephila pilipes* viewed against green vegetation by lepidopteran insects. BP, black paint used to alter the color signals of body parts 1, 2 and 3. Letters represent results of ANOVA and LSD mean comparisons.

In the second field experiment, the effects of altering the color signals of the conspicuous yellow body parts of *N. pilipes* using black acrylic paint were significant. The chromatic and achromatic contrast values of the dark paint when viewed against *N. pilipes* black body parts 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). The achromatic contrast of the dark paint when viewed by nocturnal lepidopteran insects was also similar to that of the spiders' black body parts (Fig. 2). However, the nocturnal chromatic contrast of the dark paint was significantly lower than that of the black body part (Fig. 2). Therefore, the dark paint we used was able to effectively reduce the conspicuousness of the yellow body parts of *N. pilipes*. The prey interception rate of diurnal prey fitted well with a Poisson distribution (Pearson χ^2=3.1687, P=0.5843), so we used a Poisson regression to compare the prey interception rates between the experimental (conspicuous body parts painted) and the control (black body parts painted) groups while considering the capture area. The diurnal prey interception rate of the experimental group was significantly lower than that of the control group (Table 1C).

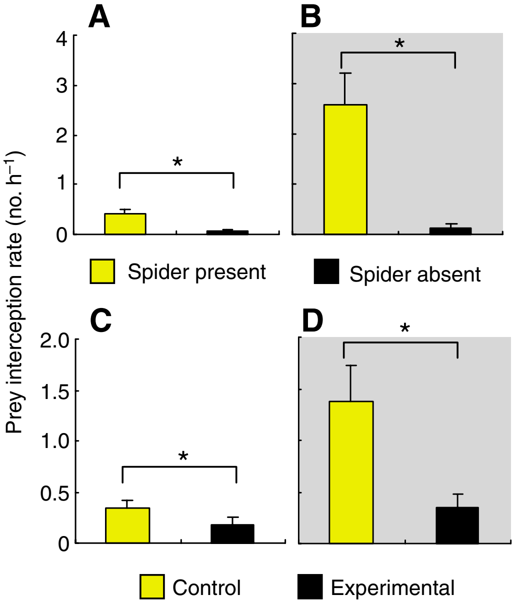

Fig. 3. Mean (±s.e.m.) diurnal (A,C) and nocturnal (B,D) insect interception rates of webs of *Nephila pilipes* in experiments manipulating spider presence (A,B) and color signal (C,D). *$P<0.05$.

Compared with the *N. pilipes* whose conspicuous body color signals were altered, the prey interception rate of the control group was twice as high (Fig. 3C). The nocturnal prey interception data did not fit either normal or Poisson distributions. Therefore, we divided the prey interception rate by the capture area to generate a unit area prey interception rate and then compared it with a non-parametric *U*-test. The prey interception rate of the control group was three times that of the experimental group (*U*-test statistic=226.500, $P=0.002$; Fig. 3D).

Manipulating the presence of *N. pilipes* color signals also significantly changed the composition and size of nocturnal prey intercepted by the webs. Among the nocturnal prey intercepted by the spider-present and control groups, the percentages of moths were high (33 and 60%, respectively). However, in the treatments with spiders removed, as well as those where the yellow body parts had been painted over, the percentages of intercepted moths were much lower (0 and 30%, respectively). These changes in nocturnal prey composition were statistically significant in both experiments (χ^2 test of homogeneity, $\chi^2=48.00$, $P<0.001$ for manipulating spider presence and $\chi^2=33.00$, $P<0.001$ for manipulating spider color signal experiments).

Relative performance of diurnal and nocturnal hunting in N. pilipes

The performance of diurnal and nocturnal hunting in *N. pilipes* was compared using the data from the spider-present group in the first experiment and the control group in the second experiment, because the color signal of the conspicuous body coloration of spiders in these two groups was not altered. In the spider-present group the prey interception rate during diurnal hunting was significantly lower than that during nocturnal hunting (Fig. 4A, Table 2A). This same trend was found in the control group

Table 1. *Results of Poisson regressions comparing diurnal prey interception rates of webs with and without spiders (A), nocturnal prey interception rates of webs with and without spiders (B) and diurnal prey interception rates of webs in the spider-painted (experimental) and control groups (C)*

Parameter	d.f.	Estimate of β	s.e.m.	χ^2	*P*
(A) Diurnal prey interception rates of webs with and without spiders					
Intercept	1	–6.472	0.468	190.87	<0.001
Web area: 0–200 cm^2	1	–0.681	0.425	2.570	0.109
Web area: 200–400 cm^2	1	–0.223	0.334	0.450	0.504
Treatment: present	1	1.656	0.441	14.08	0.001
Treatment: absent	0	0	0	–	–
(B) Nocturnal prey interception rates of webs with and without spiders					
Intercept	1	–6.300	0.624	101.69	<0.001
Web area: 0–200 cm^2	1	–0.758	0.366	4.280	0.038
Web area: 200–400 cm^2	1	–0.045	0.282	0.030	0.873
Treatment: present	1	3.046	0.609	24.97	<0.001
Treatment: absent	0	0	0	–	–
(C) Diurnal prey interception rates of webs in the experimental and control groups					
Intercept	1	–6.385	0.651	96.230	<0.001
Web area: 0–200 cm^2	1	0.534	0.695	0.590	0.442
Web area: 200–400 cm^2	1	0.056	0.605	0.010	0.925
Web area: 400–600 cm^2	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	–	–

The β values of the spider-absent and experimental groups were arbitrarily designated as 0 to facilitate comparison of probabilities of different events. The ratio between probabilities of two certain events is e^{β}.

(Fig. 4B, Table 2B). The prey consumed by *N. pilipes* during diurnal and nocturnal hunting differed considerably in both composition and size. Significant differences were found between diurnal and nocturnal prey composition in both the spider-present (χ^2 test of homogeneity, χ^2=88.00, P<0.0001) and control (χ^2 test of homogeneity, χ^2=47.00, P<0.0001) groups. In the diurnal hunting of the spider-present and control groups, lepidopteran insects comprised less than 10% of prey consumed (6.5% in spider-present and 0% in control groups). However, 33% of nocturnal prey in the spider-present and 60% in the control groups were lepidopterans. The average size of the intercepted nocturnal prey was significantly larger than that of the diurnal prey in both the spider-present (*t*-test, t=3.167, P=0.02, Fig. 4C) and control (*t*-test, t=2.925, P=0.004, Fig. 4D) groups. The average size of the diurnal prey did not significantly differ from that of the nocturnal prey when the spiders were not present on their webs (*t*-test, t=0.253, P=0.807, Fig. 4E), or when their color signals were altered (*t*-test, t=0.966, P=0.346, Fig. 4F). These results indicate that large lepidopteran insects seem to be the major target of the colorful giant wood spiders during nocturnal hunting.

Discussion

While most orb-weaving spiders confine their hunting to either the diurnal or the nocturnal part of the day, *N. pilipes* hunt in both light conditions. In this study, when the conspicuousness of *N. pilipes* was altered by using black paint exhibiting chromatic properties similar to those of their black body parts, the attractiveness of the spiders to their prey was significantly reduced. These results indicate that the conspicuous body coloration of the giant wood spider *N. pilipes* functions as a visual lure to attract both diurnal and nocturnal prey. Moreover, the major target of this colorful sit-and-wait predator seems to be nocturnal insects. The rate of prey interception during *N. pilipes* nocturnal hunting was several times higher than that during diurnal hunting. Therefore, while the brightly colored orb-weaving spiders are traditionally regarded as diurnal predators, the results of this study demonstrate that at least in some species nocturnal hunting might contribute the major portion of their prey intake. Although the light intensity and signal-to-noise ratio of diurnal and nocturnal light environments differ significantly (Warrant, 2004), our results indicate that the body coloration of spiders can serve as an effective visual lure in both light conditions. The use of visual lures in nocturnal hunting might be more effective than in diurnal hunting. Although these spiders are regarded as some form of resource by diurnal insects, when prey flies near the spiders there will be a higher chance for them to detect the web and perform escape maneuvers (Craig and Freeman, 1991). However, in nocturnal conditions the light is dim and the web visibility is much lower, therefore it is much harder for prey to detect the web (Craig, 1986; Craig, 1988). The difference in web visibility in these two light environments might be one of the major reasons why *N. pilipes* has a much higher prey interception rate in their nocturnal hunting.

This study is the first to quantify how a conspicuously colored spider is viewed by nocturnal lepidopteran insects. The color contrast of the brightly colored orb-weaving spider when viewed by diurnal hymenopteran insects has been reported previously. The results of these studies showed that the dark or green part of a spider's body was indistinguishable from the vegetation background but the conspicuous parts were highly visible to insects (Tso et al., 2004; Tso et al., 2006). This phenomenon also occurs when these spiders are viewed by nocturnal insects under dim light conditions. Through nocturnal achromatic vision, the black body parts of *N. pilipes* were significantly smaller than the 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 more visible than the dark parts. The combination of high and low contrast body colorations might make the appearance of spiders unlike that of a predator but rather like some form of resource. Many pollinator insects have an innate preference for symmetric and disruptive patterns (Rodríguez and Gumbert, 2004). Moreover, floral guides, stingless bee nest entrances and insectivorous pitchers all exhibit a similar dark center, radiating stripes and peripheral dots (Biesmeijer et al., 2005). The arrangement of body color patches on *N. pilipes* and their differential visual distinctiveness to insects may be because the overall signal resembles the aforementioned global visual attributes of a pollinator's resource. On the other hand, many nocturnal insects use the star pattern as a cue for open space or for orientation (Sotthibandhu and Baker, 1979), and the ventrum coloration pattern of *N. pilipes* (Fig. 1B) might be similar to certain celestial signals. More efforts regarding insect color and form vision are needed to verify why the body coloration pattern of *N. pilipes* is attractive to diurnal and nocturnal insects.

Tso et al. (Tso et al., 2006) also used paint to alter the body color signal of spiders and then investigated the consequences on prey attractiveness. In their study, a brightly colored paint was applied to the conspicuous body parts

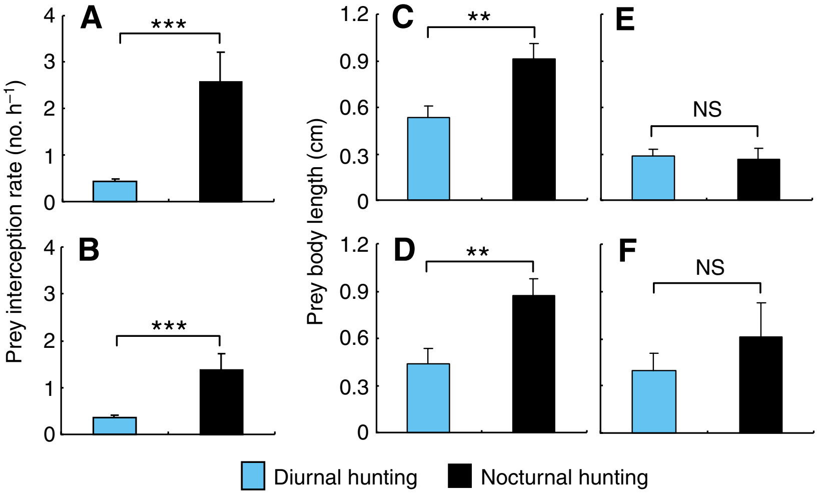

Fig. 4. (A,B) Mean (±s.e.m.) nocturnal prey interception rates of webs of *Nephila pilipes* in the spider-present (A) and control (B) groups. (C–F) Mean (±s.e.m.) body length of diurnal and nocturnal prey in the spider-present (C), control (D), spider-absent (E) and experimental (F) groups, in the first (C,E) and second (D,F) field experiments. NS, not significant; $^{**}P<0.01$, $^{***}P<0.0001$.

Table 2. *Results of Poisson regressions comparing diurnal and nocturnal prey interception rates of giant wood spiders in the spider-present group of the first field experiment (A) and the control group of the second field experiment (B)*

Parameter	d.f.	Estimate of β	s.e.m.	χ^2	*P*
(A) Spider-present group, first field experiment					
Intercept	1	–3.240	0.137	556.26	<0.001
Web area: 0–200 cm^2	1	–0.981	0.322	9.240	0.002
Web area: 200–400 cm^2	1	0.000	0.213	0.000	0.999
Treatment: diurnal prey	1	–1.601	0.188	72.06	<0.001
Treatment: nocturnal prey	0	0	0	–	–
(B) Control group, second field experiment					
Intercept	1	–4.353	0.411	112.09	<0.001
Web area: 0–200 cm^2	1	0.703	0.519	1.830	0.175
Web area: 200–400 cm^2	1	0.770	0.432	3.180	0.074
Treatment: diurnal prey	1	–1.401	0.235	35.42	<0.001
Treatment: nocturnal prey	0	0	0	–	–

The β value of the nocturnal prey group was arbitrarily designated as 0 to facilitate comparison of probabilities of different events. The ratio between probabilities of two certain events is e^{β}.

of the orchid spiders *Leucauge magnifica*. After such treatment the visibility of the orchid spiders' conspicuous body parts to their diurnal prey was not changed but the chromatic properties were altered (Tso et al., 2006). In the study of Hauber (Hauber, 2003) and in the present study, the conspicuousness of the brightly colored body parts was reduced by using a paint exhibiting chromatic properties similar to those of the inconspicuous body parts. This treatment and that of Tso et al. (Tso et al., 2006) both worked well to reduce the attractiveness of spiders to their prey. The results of these studies thereby indicate that both the conspicuousness (visibility) and chromatic properties (such as reflectance spectra) of the body coloration are important attributes of a visual lure. Therefore, other than being conspicuous, exhibiting the right kind of color signal is also necessary in achieving effective prey attraction.

While most spiders hunt during either daytime or night-time, *N. pilipes* hunts during both with the night-time seeming to be more important. Considering the fact that the body coloration of *N. pilipes* functions better at night, why does this spider spend so much time hunting during the day? We surmise that one of the reasons might be that *N. pilipes* are maximizing their prey intake. Compared with other web spiders, the body size of *N. pilipes* is much larger (Yaginuma, 1986). 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. Although the effectiveness of diurnal hunting might not be that high, hunting during the day maximizes their energy needs. While *N. pilipes* stay on webs and hunt throughout the day, they break down their webs and rest for about 6–7 h during the night (from about 20:00 to 02:00 h). Once again, if nocturnal hunting is so much more profitable than diurnal hunting, why do *N. pilipes* not rest during the day, similar to numerous other nocturnal orb spiders (Nakamura and Yamashita, 1997; Heiling, 1999; Adams, 2000; Ceballos et al., 2005)? One major reason might be that most parasitoids are diurnal (Gullan and Cranstan, 2004), with the result that during the day the threat from visually oriented predators is much higher than during the night. For orb spiders, staying on the web can help them detect and escape from potential predators (Foelix, 1996). Since predation pressure is smaller during the night, breaking down and recycling the webs under dim light conditions can reduce the risk of lacking the early warning and protection that their webs provide.

Some researchers suggest that conspicuous body coloration functions to decrease the visibility of the spider (Zschokke, 2002). These spiders usually have both conspicuous and dull body colorations and such a pattern might break the contour of the spiders, thus decreasing their visibility to the prey (Hoese et al., 2006; Václav and Prokop, 2006). If the body coloration of spiders serves as a camouflaging device, then webs with or without spiders will have similar insect interception rates. On the other hand, if the body coloration serves as a visual attractant, then webs with spiders will intercept more insects than those without. The results of our field manipulation indicate that the bright body coloration of orb-weaving spiders functions as a prey attractant rather than a disruptive coloration to camouflage the spider. This is proven by the fact that webs with *N. pilipes* present intercepted significantly more prey. This result is incongruent with the predictions of the camouflaging hypothesis and indicates that spiders themselves serve as visual lures to attract prey.

The results of the present study indicate that while studying animal communication we should have a comprehensive view of the timing as well as the visual systems of all organisms involved in the interaction. If the color signaling of one organism functions in a range of light conditions but research is conducted only in a subset of them, the conclusions subsequently made might be biased. To date, almost all empirical studies on the foraging behaviors of so-called 'diurnal' web spiders have only investigated the diurnal hunting spiders. In this study, it was not until *N. pilipes* were monitored on a 24 h basis that we realized that they also hunt during the night. When we explored color signaling from both diurnal and nocturnal perspectives we found that the way in which the intended target organisms perceived their predator, and how they responded to it behaviorally, cannot be quantitatively predicted from what we know just about diurnal signaling. In the past, in the terrestrial ecosystem color signals were generally considered to be used only by diurnal organisms.

However, more and more studies have demonstrated that various nocturnal organisms utilize color signals to locate food resources and mates (Kelber and Roth, 2006). In the case of *N. pilipes*, their conspicuous body coloration actually attracts much more nocturnal than diurnal prey. Since orb-weaving spiders are sit-and-wait predators, they are under strong selection pressure to evolve ways to make prey orient toward them. Therefore, the selection pressure of effectively exploiting the color vision of large nocturnal prey might be one of the major forces driving the evolution of orb spider body coloration. We suggest that this same selection pressure to exploit the nocturnal color vision of signal receivers could be a major force driving the evolution of animal color signaling.

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