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Deceptive color signaling in the night: a nocturnal predator attracts prey with visual lures

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The role color signaling plays in the nocturnal condition of the terrestrial ecosystem is currently poorly understood. In general, arthropods active in the night are inconspicuously colored. However, in addition to inconspicuously colored dorsum, several genera of nocturnal orb spiders also have conspicuous ventrum spots. In this study, we tested whether the inconspicuously colored dorsum functioned to reduce spiders‘ visibility to diurnal predators while the spiders were perching on bark with ventrum spots well concealed. We also evaluated when spiders sit on webs with conspicuous ventrum spots fully exposed, would they serve as deceptive color signals to lure visually orientated nocturnal prey. We first quantified how diurnal hymenopteran predators viewed the dorsum and nocturnal lepidopteran prey viewed the ventrum spots of nocturnal orb spiders *Neoscona punctigera* by calculating color contrasts. The diurnal color contrast of spiders’ dorsum when viewed by hymenopteran insects against bark was lower than the discrimination threshold. However, the nocturnal color contrasts of spiders‘ ventrum spots when viewed by moths were high. In the field, webs with *N. punctigera* intercepted significantly more insects than those without. When the color signal of ventrum spots was altered by paint, webs’ prey interception rates decreased significantly. These results demonstrate that even in the nocturnal condition certain terrestrial organisms exhibit visual lures to attract prey. *Key words:* color contrast, *Neoscona punctigera*, spider, visual ecology. *[Behav Ecol 19:237–244 (2008)]*

While discussing the color signaling between animals, most focus is placed on the diurnal system. The first reason for such bias is that the daylight intensity is higher than that of nighttime. Second, the dim light environment in the nighttime has very high noise-to-signal ratio (Warrant 2004). Therefore, it is easier to identify and analyze various forms of color signaling in the diurnal condition. Although color signaling is considered as an important ecological process in the diurnal system (Bruce et al. 2003), the role it plays in the nocturnal system is still poorly understood. Researchers traditionally focus on acoustic or olfactory cues while studying the interactions between nocturnal animals in the terrestrial ecosystem (Schneider 1974; Suga 1990; Konishi 1993; Fullard 1997; Kaspi 2000; Hansson 2002; Haynes et al. 2002). Only since appropriate research techniques and information became available have researchers gradually realized that the color signal is an important cue for certain nocturnal organisms (Warrant 1999; Kelber and Roth 2006).

Most nocturnal orb spiders hunt by building an orb during the nighttime and hiding on bark or leaf in the daytime (Yin et al. 1997). Most parts of their body are inconspicuously brown to match the color of their diurnal perching sites (Oxford and Gillespie 1998) (Figure 1A). However, the ventrum of various species of *Neoscona* and *Araneus* exhibits 2–4 bright spots (Yaginuma 1986). During nighttime, the spiders will sit in the center of the orb web and expose the bright ventrum spots (Figure 1B–D), but during daytime, these colorful structures are fully concealed (Figure 1A). Why does a sit-and-wait predator that is only active during the night has such conspicuous body coloration? Many species of spiders that hunt during the day also have conspicuous body colorations. One group of researchers regards the bright coloration of orb-weaving spiders as functioning to conceal the spiders against the vegetation background (Hoese et al. 2006; Václav and Prokop 2006). This hypothesis proposes that because the reflectance spectra of the spiders‘ body surface are similar to those of the background vegetation (Blackledge 1998; Zschokke 2002), the spiders are not easily perceived by insects. To test this hypothesis, Tso et al. (2006) compared the insect interception rates of orbs constructed by the orchid spider *Leucauge magnifica* with and without the spiders. If the bright coloration of spiders serves as camouflaging device, then orbs with or without spiders will have similar insect interception rates. Tso et al. (2006) found that orbs with spiders intercepted significantly more insects than orbs without, indicating that at least in orchid spiders bright body coloration did not seem to function to conceal the spiders. Another group of researchers, however, regarded the bright color patterns of these diurnal spiders as a function to increase foraging success by providing attractive visual signals to prey. From the eyes of insects, the bright parts of these spiders are quite distinctive from the vegetation background (Heiling et al. 2003; Tso et al. 2004, 2006). When the color signals of these bright body parts are altered, the spiders’ prey-catching ability reduced greatly (Craig and Ebert 1994; Hauber 2002; Tso et al. 2002, 2006). Results of these studies indicate that bright body colorations of orb weavers function as visual lures to attract insects, at least in the diurnal condition. Is it possible that the conspicuous ventrum spots of nocturnal orb spiders also serve as visual lures to attract visually orientated prey in the dim light condition, as does the conspicuous body coloration of those diurnal orb-weaving spiders?

Many nocturnal insects have specialized eyes that enable them to discriminate color stimuli (Kelber et al. 2002) and

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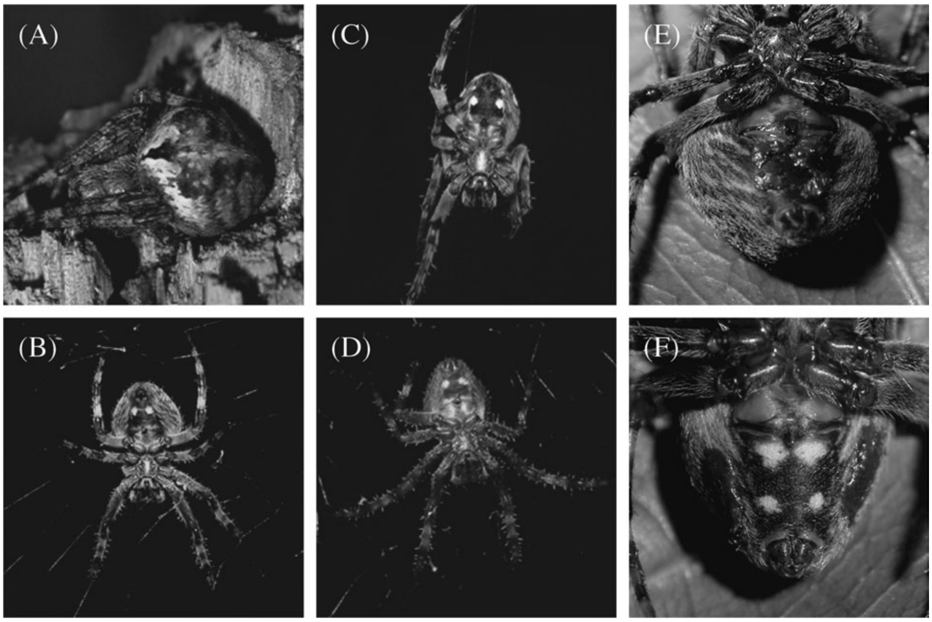

Figure 1
Dorsal view of *Neoscona punctigera* perching on the bark (A), conspicuous ventrum spots in various species of nocturnal orb weaving spiders (B: *N. punctigera*; C: *N. nautica*; D: *Araneus lugubris*), and ventral view of *N. punctigera* used in the altering spider color signal treatments (E: ventrum spot painted; F: brown ventrum painted).

to detect food resource 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 be greatly magnified, and therefore, the problem of low light intensity in dim light environments can be solved (Kelber et al. 2003). Besides, the rhabdoms of superposition eyes are longer than those of apposition eyes, and this can help to improve the signal-to-noise ratio (Kelber and Roth 2006). We wonder whether certain orb spiders exploit the nocturnal vision of their prey by exhibiting body coloration mimicking the color signal of the prey's food resources. To test this hypothesis, we first quantified how *Neoscona punctigera*, a nocturnal orb spider commonly seen in East Asia (Yin et al. 1997), was viewed by its lepidopteran prey. We also conducted field experiments to see whether manipulating the color signals of ventrum spots would affect spiders' insect-catching rates. So far, all studies examining visual interactions between spiders and their prey focus on diurnal species and none has assessed the function of body coloration of nocturnal spiders. Our results show that the nocturnal sit-and-wait predator *N. punctigera* attracts prey with deceptive visual lures mimicking the color signals of prey's food resources.

METHODS

Quantifying how spiders are viewed nocturnally and diurnally

Six female *N. punctigera* were collected from the Taiwan Endemic Species Research Institute (TESRI) in central Taiwan. A spectrometer (detection range: 200–1100 nm; USB2000-UV-VIS, Ocean Optics, Inc., Dunedin, FL) connected to a notebook computer was used to measure the reflectance spectra of ventrum spots, brown abdomen, and legs of spiders. A reflection probe (R400-7-UV-SR, Ocean Optics, Inc.) with 1 read fiber connected to the spectrometer and 6 illumination fibers connected to a deuterium–tungsten halogen light source (DT-1000, Ocean Optics, Inc.) was placed 5 mm vertically above the sample. All measurements were performed in a dark room. The spectrometer operating software (OOIBase32, Ocean Optics, Inc.) was used to access online measurement. Reflection is expressed as the percentage ($\%R_\lambda$) relative to the reflection from a standard reference (WS-1, Diffuse Reflectance Standard, Ocean Optics, Inc.):

$$\%R_\lambda = \frac{S_\lambda - D_\lambda}{R_\lambda - D_\lambda} \times 100\%,$$

where S is the sample intensity at wavelength λ, D is the dark intensity at wavelength λ, and R is the reference intensity at wavelength λ.

The reflectance spectrum of background green vegetation was that used in Tso et al. (2004), which was estimated by averaging the spectra of 184 leaves from a random sampling of plant species. To determine whether ventrum spots mimicked the color signals of the resources of spiders' prey, we measured the reflectance spectra of flower petals of 3 species ($n = 6$ for each species) of herb plants frequently visited by moths (Chuang CY, personal observations). The plant species examined included *Hedychium coronarium* Koenig (butterfly ginger), *Bidens alba* Sherff (big bidens), and *Sambucus formosanum* Nakai (Formosan elderberry). The video recording of *N. punctigera*'s hunting showed that moth was the major prey of this spider. Therefore, to quantify how various parts of *N. punctigera* were viewed by moths, the visual neuroethological model developed for hawk moths (Johnsen et al. 2006) was followed to calculate the nocturnal color contrasts. The following equation was used to calculate the quantum catches of one ommatidium of moth (Warrant and Nilsson 1998):

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

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 (λ) 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. In addition to reflectance spectra, values of all the other variables and nocturnal illumination spectrum followed those reported in Johnsen et al. (2006). The difference of object of interest and the background, the achromatic contrast, was estimated by

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

where N_X is quantum catches of object and N_{green} is quantum catches of green vegetation background (Johnsen et al. 2006).

In addition to achromatic contrasts, we also calculated nocturnal chromatic contrasts following the methods given in Johnsen et al. (2006). First, the quantum catch values (N) of UV (uv), blue (b), and green (g) photoreceptors were each 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:

$$q_{\text{uv}} = \frac{N_{\text{uv}}}{N_{\text{uv}} + N_{\text{b}} + N_{\text{g}}},$$
$$q_{\text{b}} = \frac{N_{\text{b}}}{N_{\text{uv}} + N_{\text{b}} + N_{\text{g}}},$$
$$q_{\text{g}} = \frac{N_{\text{g}}}{N_{\text{uv}} + N_{\text{b}} + N_{\text{g}}}.$$

Then values of each stimulus were used to calculate relative distances in the color triangle by

$$X_1 = \frac{1}{\sqrt{2}}(q_{\text{g}} - q_{\text{b}}),$$
$$X_2 = \frac{\sqrt{2}}{\sqrt{3}}\left(q_{\text{uv}} - \frac{q_{\text{g}} + q_{\text{b}}}{2}\right),$$

where X_1 and X_2 were the distances on the x axis and y axis, which represented the relative intensity of 3 types of photoreceptors in the 2-dimensional (2D) color space. The distance of 2 color stimuli in the color space was the nocturnal chromatic color contrast (Johnsen et al. 2006). So far, the theoretical discrimination threshold value for the nocturnal chromatic neuroethological model is still not available. Therefore, the nocturnal achromatic and chromatic contrast values of various body parts of *N. punctigera* and those averaged from 3 species of flowers were compared by analysis of variance tests and least significant difference (LSD) mean comparisons. Results of these tests could help determine whether the ventrum spots were more conspicuous than other body parts and whether they were similar to those of flowers.

We also calculated diurnal color contrasts of *N. punctigera* when viewed against tree bark by hymenopteran predators to determine whether the inconspicuous body coloration can help camouflage the spiders. Because hymenopteran insects are the major diurnal predators of orb-weaving spiders (Blackledge et al. 2003), we used the diurnal color hexagon model for honey bees (Chittka 1992) to calculate the achromatic and chromatic contrasts. During the day, *N. punctigera* usually perched on twig or bark nearby their web sites; therefore, the reflectance spectrum of tree barks was used as the background light signal. The bark reflectance spectrum was estimated by averaging the spectra of 6 barks collected from a random sampling of dominant tree species in the study site. The daylight spectrum was that used in Tso et al. (2004), which was measured by placing the end of the probe of the spectrometer 5 mm above (90°) the standard white and recording the data each hour, each day from 0800 to 1800 h for 3 sunny days. We used spectral sensitivity functions of photoreceptors of the honey bee *Apis mellifera* (Briscoe and Chittka 2001) to determine the photoreceptor excitations for each measured spectra. The relative quantum flux absorbed by each type of photoreceptor P can be expressed as

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

where $I_{\text{S}}(\lambda)$ is the spectral reflectance function of the spider colorations, $S(\lambda)$ is the spectral sensitivity function of honey bee photoreceptors, and $D(\lambda)$ is the daylight spectrum. The sensitivity factor R is determined by the equation:

$$R = \frac{1}{\int_{300}^{700} I_{\text{B}}(\lambda)S(\lambda)D(\lambda)\mathrm{d}\lambda},$$

where $I_{\text{B}}(\lambda)$ is the spectral reflection function of the vegetation background to which the photoreceptors are adapted. When photoreceptors are adapted by the vegetation background, we can assume that the photoreceptors display half their maximum response (Naka and Rushton 1966). The nonlinear transfer function relating the receptor excitation E with the quantum flux P follows:

$$E = \frac{P}{(P+1)}.$$

The 3 excitation values in the honey bee's UV, blue, and green photoreceptors can be depicted in a 3D photoreceptor excitation space or in the color hexagon (Chittka 1992). With the 3 photoreceptor excitation values plotted at angles of 120°, the x and y coordinates in the color plane are given by

$$x = \sin 60^{\circ}(E_{\text{G}} - E_{\text{UV}}),$$
$$y = E_{\text{B}} - 0.5(E_{\text{UV}} + E_{\text{G}}),$$

where E_{UV}, E_{B}, and E_{G} are the inputs from the 3 photoreceptors. When calculating the color contrasts of objects viewed under chromatic vision, signals from all 3 photoreceptors were used. When calculating this under achromatic vision, only the green photoreceptor signal was used. Euclidean distances (ΔSt) between stimuli are calculated as

$$\Delta\text{St} = \sqrt{(\Delta x)^2 + (\Delta y)^2}.$$

The Euclidean distance (ΔSt) is the color contrast. One sample *t*-tests were used to compare the diurnal contrasts of various body parts of *N. punctigera* with the discrimination threshold value of 0.05 estimated for hymenopteran insects (Théry and Casas 2002).

Manipulating spider color signal in the field

In this part of the study, we manipulated the presence and color signal of *N. punctigera* to see whether such treatments would reduce insect-catching rates. The field experiments were conducted in a secondary forest in TESRI in June 2005. Female *N. punctigera* with carapace width larger than 0.5 cm were used. In the first experiment, we 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, we randomly chose spiders and divided them into 2 groups. In the first group ($N = 10$), the spiders were carefully removed from their webs without damaging the orb. In the second group ($N = 12$), the spiders were left on their webs. The prey interception rates of

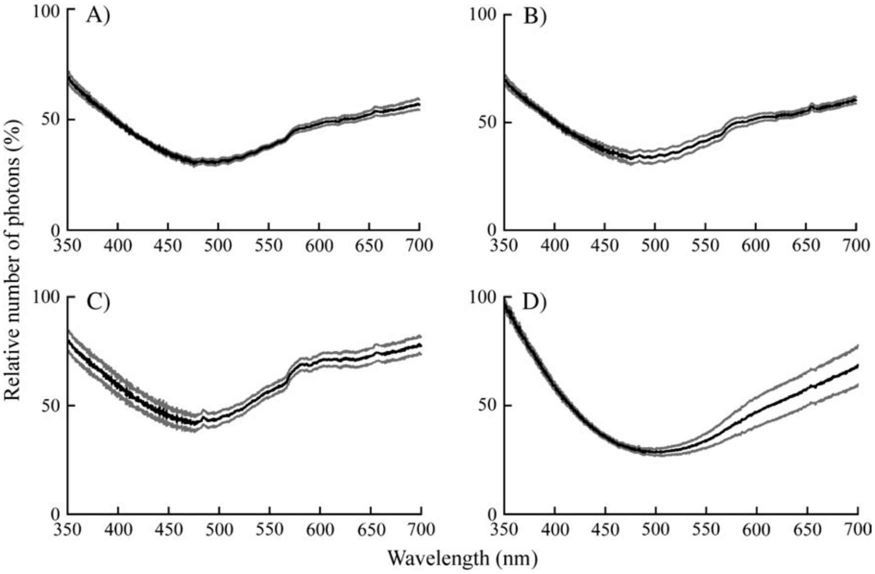

Figure 2
Mean (±standard error) reflectance spectrum curves of various body parts of *Neoscona punctigera*. (A) leg, (B) abdomen, (C) bright spot, (D) brown paint used in altering body color signal.

webs with and without *N. punctigera* were estimated using the night shot function of Sony HR118 Hi-8 video cameras. 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. The video cameras were placed 1–2 m away from the webs depending on the vegetation nearby. The prey interception rates of webs were monitored for 8 h (from 2000 to 0400 h) each night for a total of 9 nights. After the experiment was completed, the videotapes were brought back to the laboratory for subsequent analysis. While viewing the videotapes, the number of insects intercepted by webs was recorded and their taxonomic order was determined. Because web area was known to influence prey-catching rate of webs (Brown 1981; Craig 1989; Higgins and Buskirk 1992), we also estimated the area of orb built by *N. puntigera.* During the field study each day before video recording, we measured web radius, hub radius, length of hub, spiral number, and radii number from 4 cardinal directions. These web parameters were used to calculate effective web area following the equations of Herberstein and Tso (2000).

In the second field experiment, we assessed whether the ventrum spots were responsible for spiders' attractiveness to prey. Each night before the recording, *N. punctigera* were randomly assigned into 2 groups. In the first group, the experimental group ($n = 18$), we used brown acrylic paint (Alpha Acrylic Colors, # 26, Raw Sienna) to alter the color signal of ventrum spots (Figure 1E). Before the brown paint was applied on spiders, we measured the paint's reflectance spectrum by a spectrometer (S2000, Ocean Optics, Inc.). The reflectance spectrum of brown paint was similar to that of brown body coloration of *N. punctigera* (Figure 2D). In the second group, the control group ($n = 17$), same amount of paint was applied on the brown ventrum near the spots (Figure 1F). Before the application of paint, the spiders were carefully removed from the hub without damaging the orb and were anesthetized by CO_2 for 5 min. After the spiders recovered, they were gently released back to their original webs. The prey interception rates of webs were monitored for 8 h (from 2000 to 0400 h) each night for a total of 9 nights. The measurement of web parameters and the recording of interception events were similar to those mentioned previously.

The prey-catching data fitted well with Poisson distributions (Pearson's $\chi^2 = 5.175$, $P = 0.075$, for the spider-removal treatment and Pearson's $\chi^2 = 1.375$, $P = 0.715$, for altering color signal treatment). Therefore, Poisson regressions (Steel et al. 1997) were used to assess the effect of treatment on prey interception rates using orb area as covariance. The Poisson model is

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

where μ is the expected value, X represents the explanatory variables (treatments or orb area), β is the probability, and $N(X)$ is the total number of individuals. In this analysis, web areas were ranked into the following 3 categories: 0–100, 100–200, and 200–300 cm^2. Finally, a χ^2 test of homogeneity was used to compare the prey composition between different treatment groups.

RESULTS

Quantifying how spiders are viewed nocturnally and diurnally

The reflectance spectrum measurements covered the range from 350 to 700 nm. The reflectance of brown body parts of *N. punctigera* was low across the wavelengths measured (Figure 2A,B), but ventrum spots had high reflectance between 500 and 700 nm (Figure 2C). Color contrasts of the brown body parts did not differ significantly between each other (Figure 3A). The achromatic and chromatic nocturnal contrasts of ventrum spots and flowers were both significantly higher than those of spiders' brown body parts ($F = 23.211$, $P < 0.0001$ for achromatic contrast; $F = 3.367$, $P = 0.031$ for chromatic contrast). The contrast values of ventrum spots and flowers did not differ significantly (Figure 3A). Such results indicate that when *N. punctigera* are viewed by moths against the green vegetation background, the ventrum spots will be quite distinctive while the rest of the body is relatively indistinguishable from the vegetation background. Such a pattern also occurred when *N. punctigera* was viewed by their diurnal predators. Both achromatic and chromatic diurnal contrasts of spiders' ventrum spots were significantly higher, but those of brown body parts (dorsum and legs) were either similar to or significantly lower than the discrimination threshold (Figure 3B, Table 1). Therefore, it should be difficult for diurnal hymenopteran predators such as wasps to chromatically and achromatically discriminate the color signal of *N. punctigera* from that of barks.

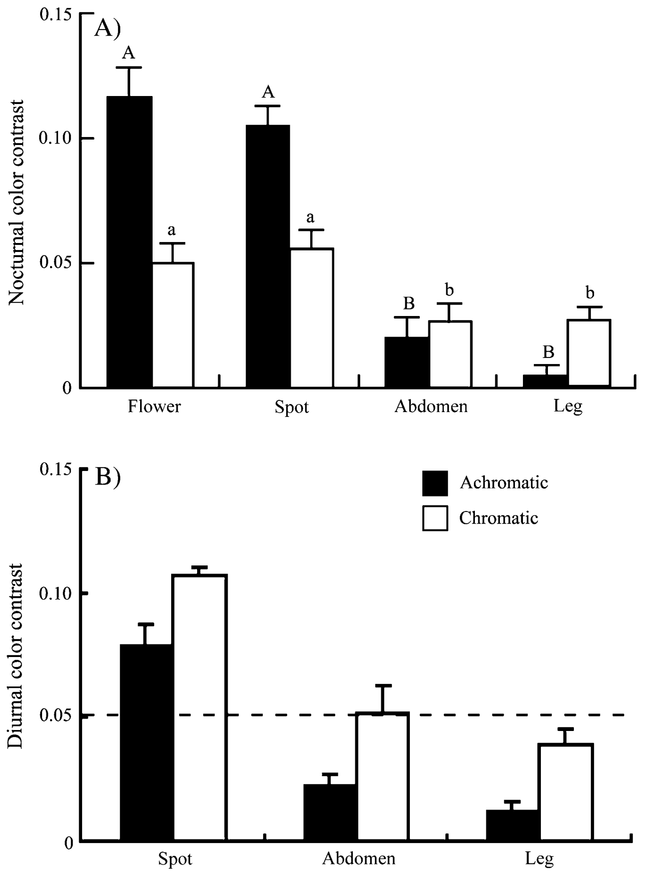

Figure 3
Mean (±standard error) nocturnal (A) and diurnal (B) color contrasts of different body parts of *Neoscona punctigera* and flowers. Dashed line in (B) represents the discrimination threshold of 0.05 estimated for hymenopteran insects. Letters represent results of analysis of variance test and LSD mean comparisons comparing achromatic (capital letters) and chromatic (lower case letters) contrasts of various spider body parts. Different letters mean that the contrast values were significantly different from each other at $\alpha = 0.05$ level.

Manipulating spider color signal in the field

In the study site, most *N. punctigera* built their webs in forest understory vegetation on both sides of trails with dorsum facing the vegetation and ventrum facing the open space. The vegetation was usually only several centimeters from the dorsum of spiders, and the great majority of prey came from the open space and approached the webs from spiders' ventrum.

Table 1

The results of 1-tailed *t*-tests comparing the achromatic and chromatic color contrasts of various body parts of *Neoscona punctigera* with the discrimination threshold of 0.05 estimated for hymenopteran insects

Color contrast	Ventrum spots	Abdomen	Leg
Achromatic			
t	17.615	0.491	−2.908
P	<0.001	0.644	0.033
Chromatic			
t	3.515	−7.02	−13.83
P	0.008	<0.001	<0.001

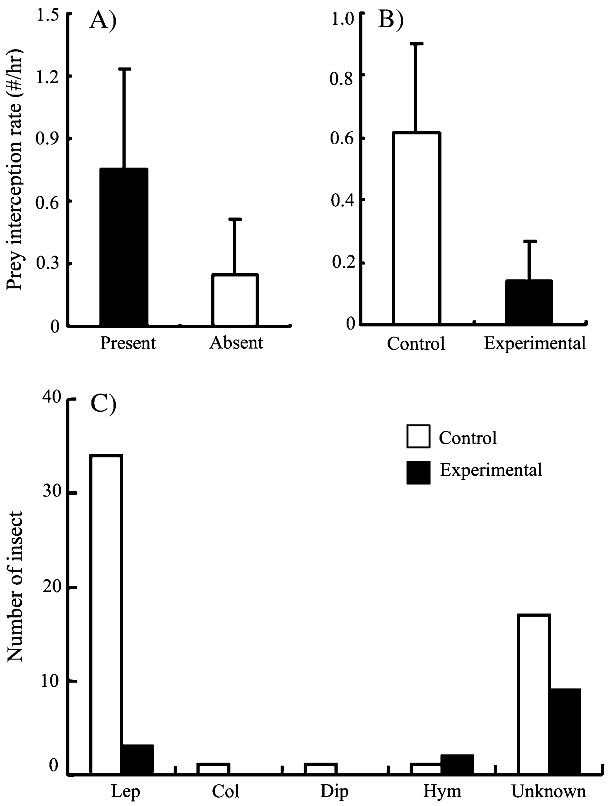

Figure 4
Mean (±standard deviation) prey interception rates of webs built by *Neoscona punctigera* with spiders present and absent (A) and those of the experimental (ventrum spot painted) and control (brown ventrum painted) groups (B). (C) Compositions of insects (in taxonomic orders) intercepted by webs built by *N. punctigera* in the control and experimental groups. (Lep: Lepidoptera; Col: Coleoptera; Dip: Diptera; Hym: Hymenoptera).

In the first field experiment, the presence of *N. punctigera* was manipulated to see whether the spider itself was attractive to prey. While considering the effect of orb area, the prey interception rate of webs with spiders was significantly higher than that of webs without (Figure 4A, Table 2). The mean prey interception rate of webs with spiders was 2.5 times that of webs without. From the video recordings, moths were frequently observed to pass by the margin of web then turn and fly directly toward the spider (Figure 5). In the second field experiment, we assessed whether the color signals of ventrum spots were responsible for the spiders' attractiveness. Altering the color signal of ventrum spots significantly reduced the prey interception rate of webs built by *N. punctigera* (Figure 4B, Table 3). The prey interception rate of *N. punctigera* in the experimental group was only one-third that of the control group. Altering the color signal of ventrum spots also significantly changed the composition of prey intercepted by the spiders' webs (χ^2 test of homogeneity, $\chi^2 = 11.500$, $P = 0.021$). 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 was much reduced (Figure 4C).

DISCUSSION

Members of the orb spider genera *Neoscona* and *Araneus* have bright spots on the ventrum, and our results showed that

Table 2

The results of Poisson regression comparing the prey interception rates of webs with or without *Neoscona punctigera* while considering the effect of web area

Parameter		df	Estimate of β	SE	χ^2	*P*
Intercept		1	−4.949	0.596	68.84	<0.001
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	—	—

SE, standard error; df, degrees of freedom. The web area was designated as a categorical variable due to a small sample size. The β of the without spider group was arbitrarily designated as 0 to facilitate comparison of probabilities of different events. The ratio between probabilities of 2 certain events was e^{β}.

such features may serve as visual lures to nocturnal prey. The ventrum spots seem to mimic the color signal of nocturnal insects' food resources because the nocturnal color contrasts of spots and flowers were similar. Results of this study thus suggest that nocturnal orb spiders may exploit the color vision of nocturnal insects by exhibiting visual lures resembling the color signal of flowers open at night. 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 that 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.

In addition to nocturnal 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 lure prey by olfactory cues is low. Because when those ventrum spots were carefully examined under the microscope, there were no openings on them and the whole area was covered by a continuous sheet of cuticle (Chuang CY, personal observations). On the other hand, it was 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 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 the visual signals they generated.

The ventrum spots of *Araneus* and *Neoscona* are not large, and they only occupy a small part of ventrum (Figure 1B–D). Many nocturnal insects have superposition eyes, and these eyes are extremely sensitive to very dim light signals. Such extraordinary sensitivity is achieved structurally by wide pupil aperture and physiologically by spatial/temporal summation of visual channel neural outputs (Warrant 1999). The sensitivity of superposition eyes is so high (theoretically estimated to be 10 000 times that of locust; Warrant 1999) that they can even perceive far-away point light source (Lythgoe 1979; Warrant 2006). Although the abdominal spots of *N. punctigera* are small, the color signal reflected from them should be easily perceived by nocturnal insects with superposition eyes. On the other hand, the size of ventrum spots might be constrained by strong predation pressure. During daytime when the major predators of orb spiders such as parasitoid insects (Blackledge et al. 2003) are most abundant (Gullan and Cranston 2004), *Neoscona* or *Araneus* spiders usually perch on bark with their bright ventrum spots well concealed. If the size of ventral spots is too large, they will be difficult to conceal and this will consequently increase the conspicuousness of spiders to predators.

In this study, the night shot function of Hi-8 video cameras were used to record the prey-catching events of spiders. Except for some ants (Depickere et al. 2004), most insects do not have infrared photoreceptor (Briscoe and Chittka 2001).

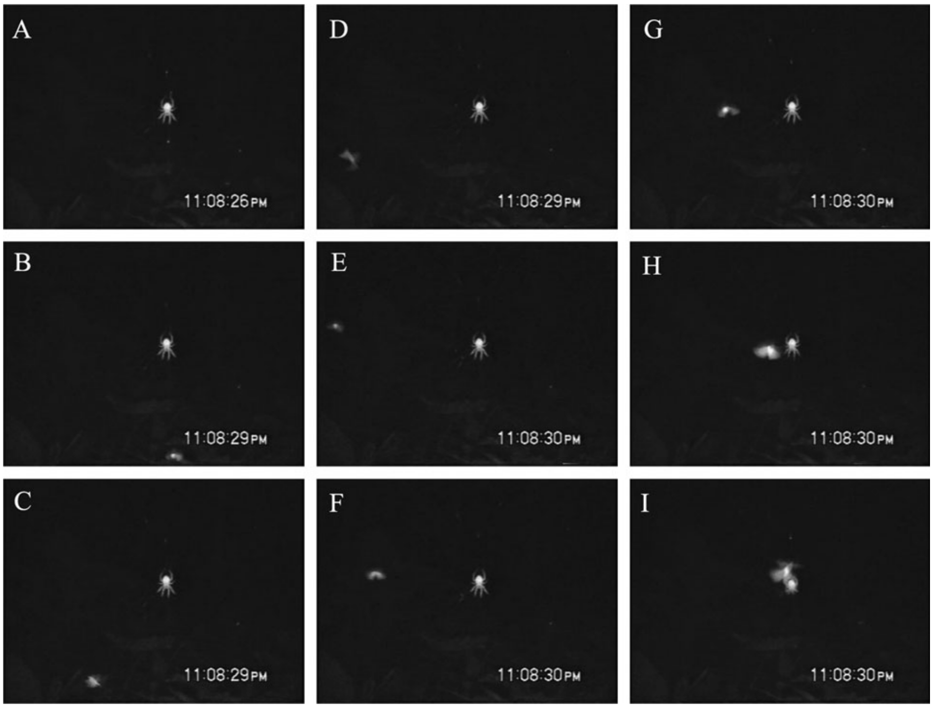

Figure 5
Consecutive images from video recording showing a moth initially passed by the margin of web (A–D) but changed direction and oriented toward the spider (E–I).

Table 3

The results of Poisson regression comparing the prey interception rates of *Neoscona punctigera* in the experimental (ventrum spot painted) and control (body ventrum painted) groups while considering the effect of web area

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	<0.001
Treatment	Experiment	0	0	0	—	—

SE, standard error; df, degrees of freedom. The web area was designated as a categorical variable due to a small sample size. The β of the experimental group was arbitrarily designated as 0 to facilitate comparison of probabilities of different events. The ratio between probabilities of 2 certain events was e^{β}.

Therefore, the infrared light emitted from the video camera should be invisible to prey of spiders. 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 projected on the ventral spots might generate heat that made the control spiders attractive to insects. However, the observed results were unlikely to be generated by heat effects because the heat-detection capability of most insects was not that sensitive (Gullan and Cranston 2004), and the ambient temperature in the study site during the experiment was high (around 30 °C).

During the past few decades, numerous studies had been conducted on nocturnal orb weavers but none of them examined the functions of these spiders' body colorations. Studies on foraging behaviors of nocturnal orb-weaving spiders focus on prey specialization (Pascoe 1980; Ceballo et al. 2005; Yamanoi and Miyashita 2005), foraging site preference (Olive 1982; Nakamura and Yamashita 1997; Heiling 1999; Adams 2000), or positioning of spiders on webs (Herberstein and Heiling 2001), but none investigated whether body coloration of nocturnal spiders played any ecological role. The lack of relevant studies on nocturnal spiders reflects our lack of knowledge and appropriate equipments to study color signaling in the nocturnal system. So far, the role color signaling plays in the nocturnal condition of the terrestrial ecosystem is poorly understood. Results of our study demonstrate that deceptive color signaling does occur in the dim light condition of the terrestrial ecosystem. We suggest color signals to be important cues used by numerous nocturnal terrestrial organisms in interactions of both intra- and interspecific context such as foraging, communication, mating, or conspecific recognition.

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