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Nocturnal hunting of a brightly coloured sit-and-wait predator

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Many studies have shown that colour signals are important in spider–insect interactions. The bright body coloration of certain orb-weaving spiders seems to serve as a visual lure to diurnal prey. However, no studies have examined whether this coloration affects spiders' nocturnal hunting. Some nocturnal lepidopteran pollinators use colour vision to locate their food resources, so orb-weaving spiders' bright coloration may also be attractive to visually oriented nocturnal insects. To assess the role of body coloration of the orchid spider, *Leucauge magnifica*, in luring nocturnal prey, we investigated whether: (1) these spiders actively hunt during the night; (2) nocturnal prey comprise a significant proportion of total prey intake; and (3) altering body colour signals significantly affect the nocturnal prey capture rate. Round-the-clock monitoring of *L. magnifica* activity patterns showed that they hunt more actively at night. Owing to the presence of relatively large moths in their diet at night, *L. magnifica* consumed higher prey biomass during nocturnal hunting, although this was not statistically significant owing to large variability. Painting over the spiders' yellow ventrum stripes significantly reduced their moth capture rate. These results show that certain orb-weaving spiders with bright body coloration attract nocturnal prey, and they obtain larger prey from nocturnal hunting.

Keywords: colour contrast; colour signal; *Leucauge magnifica*; orchid spider; visual ecology

The function of bright body coloration in animals has received much attention in the literature. Recently, most studies have investigated the role of bright body coloration in the context of sexual selection, such as species identification (Rutowski 1998), mate preference (Petrie & Halliday 1994; Andersson & Amundsen 1997; Johnsen et al. 1998; Grether 2000; Rodd et al. 2002) and mate quality assessment (McGraw & Hill 2000; Doucet & Montgomerie 2003; Heindl & Winkler 2003; MacDougall & Montgomerie 2003). Other researchers have studied bright body coloration in the context of antipredation adaptations, such as aposematism, crypsis or mimicry (Stuart-Fox et al. 2003; Ruxton et al. 2004). There have been few direct empirical tests of the role of bright body coloration in prey capture, and almost all relevant studies have been conducted in diurnal systems. In this study, we assessed how bright body coloration is involved in the prey capture of a sit-and-wait predator, especially at night.

Many spiders hunt only at night and their coloration is usually dark grey or brown reducing the spiders' visibility during daytime (Oxford & Gillespie 1998). Nocturnal spiders seem to rely heavily on olfactory cues to attract or locate prey. Haynes et al. (2002) showed that a nocturnal moth specialist, the bolas spider, *Mastophora hutchinsoni*, uses chemical mimicry of the moth sex pheromone to attract prey. The sac spider, *Chiracanthium mildei*, a nocturnal wandering spider, was reported to use pheromone to locate dipteran prey (Kaspi 2000). However, some spiders hunt actively during the day and many of them have conspicuous colour patterns (Yaginuma 1986), which may function as a visual lure to insects. For example, the brightly coloured dorsum of *Argiope argentata* of Panama is more attractive to insects than the spiders' brown ventrum (Craig & Ebert 1994). The spiny spiders, *Gasteracantha foricata*, of Australia also have bright coloration on their dorsum; painting over this coloration significantly reduced the spiders' foraging success (Hauber 2002). The

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brightly coloured giant wood spider, *Nephila pilipes*, of Asia catches significantly more insects than its melanic conspecifics (Tso et al. 2002). Tso et al. (2004) quantified how these two morphs of *N. pilipes* were viewed by hymenopteran prey insects by calculating the colour contrasts of spiders' various body parts against the vegetation background. The bright colour bands of *N. pilipes* were highly visible to hymenopteran insects and Tso et al. (2004) regarded that to be the reason for the higher foraging success of the typical morph. In addition to the body coloration of orb-weaving spiders, that of nonweavers is also attractive to insects. While crab spiders' body coloration is traditionally regarded as functioning to camouflage the spiders (Chittka 2001; Théry & Casas 2002), Heiling et al. (2003, 2005) showed that the body coloration of *Thomisus spectabilis* is attractive to hymenopteran insects. Thus, one major function of spiders' bright body coloration seems to serve as a visual lure when they hunt during the daytime. However, does their body coloration play any role at night?

Traditionally, numerous species of brightly coloured orb-weaving spiders have been regarded as diurnal predators. However, few researchers have actually followed the spiders for 24 h to investigate their temporal hunting patterns. At least for some brightly coloured orb-weaving spiders, their prey catching may not be limited to the daytime. For example, *N. pilipes* and the orchid spider, *Leucauge magnifica*, have frequently been observed consuming wrapped prey on webs just before sunrise (I.-M. Tso, personal observation). Such observations indicate that some brightly coloured spiders also seem to hunt successfully at night. Parallel with such observations is the recent finding that certain nocturnal insects rely heavily upon colour signals in activities such as foraging, courting, orientation and predator avoidance. Some nocturnal insects have colour vision (Warrant 1999; Land & Osorio 2003). For example, nocturnal moths are able to distinguish different colours in dim light conditions (Kelber et al. 2002, 2003; Balkenius & Kelber 2004). The nocturnal hawkmoth, *Manduca sexta*, uses both colour and olfactory cues to locate food resources (Raguso & Willis 2002, 2005). Therefore, at least certain lepidopteran insects use colour vision to search for food resources at night. Since the body coloration of some spiders appears to resemble the colour signal of food resources and thus is attractive to diurnal insects (Craig 1994; Craig & Ebert 1994; Hauber 2002; Tso et al. 2002, 2004), these colour markings may also lure visually oriented nocturnal insects.

In this study, we investigated: (1) whether the brightly coloured orchid spider *L. magnifica* hunts nocturnally; (2) the contribution of nocturnal hunting to these spiders' overall prey intake; and (3) whether spiders' body coloration would enhance the capture of nocturnal prey. First, we monitored *L. magnifica*'s activity pattern round the clock to determine whether these spiders actively hunt at night. Second, we recorded the prey-catching and consumption rates of diurnal and nocturnal hunting and compared them to determine their contribution to the spiders' overall prey intake. Finally, we carried out a field manipulation to see whether altering the colour signal of *L. magnifica* would reduce the nocturnal hunting success of the spiders.

METHODS

Study Site and Spider

We conducted field studies in the summer of 2004 at Lien-Hua-Chih Research Centre operated by the Taiwan Forestry Research Institute in Yu-Chi, Nantou County, Taiwan. The study site consisted of a mixture of primary broadleaf forest and Taiwanese fir plantation. A stable population of *L. magnifica* (Araneae: Tetragnathidae) was found in the neighbourhood of the research centre. Orchid spiders construct horizontal webs on herbaceous plants along the margin of trails in the study site throughout the year. The prosoma and legs of orchid spiders are green, but the opisthosoma is brightly coloured. The dorsum is silver with thin longitudinal black stripes (Fig. 1a). On the ventrum are two distinct yellow stripes embedded in a dark green area (Fig. 1b). Reflectance spectra of various body parts of *L. magnifica* are given in Tso et al. (2006). In this study, only female orchid spiders were used because their body coloration is brighter and they hunt more actively than males (I.-M. Tso, personal observation).

Temporal Activity Patterns

We surveyed the temporal activity pattern of a population of orchid spiders for 7 days between 12 and 18 September 2004. In the study site, a transect line 20 m long was established along the trail and we counted *L. magnifica* webs on either side of the line every 2 h (from 0100 to 2300 hours). Only when spiders built a functional orb web and stayed in the hub were they included in the analysis. A Kruskal–Wallis test was used to compare the number of spider webs in these time intervals.

Nocturnal Hunting

We monitored diurnal and nocturnal hunting of orchid spiders between 25 and 30 June 2004. Eight Sony TRV 128 Hi8 video cameras were set up 2 m away from eight web sites of female spiders to monitor their prey capture. The daytime recording began at sunrise (at approximately 0600 hours) and ended at sunset (at about 1800 hours). The night-time recording began when the sun was totally set (at about 1900 hours) and ended at dawn of the next day (at about 0500 hours). While monitoring the spiders at night we used the night-shoot function of the video camera, which generated images with infrared light. Each day before recording we measured spider body length, hub diameter, orb radius from the four cardinal directions and the number of radii. The catching area of the orb was estimated by the formula given in Herberstein & Tso (2000). While viewing the videotapes in the laboratory, we recorded spiders' activity patterns, prey capture rates and prey taxonomic orders. We used the body size of the spiders to estimate the body length of the trapped prey and a two-tailed Mann–Whitney *U* test to compare the body length of insects caught by *L. magnifica* during diurnal and nocturnal hunting. The body length–dry weight regression formulae provided by Schoener (1980)

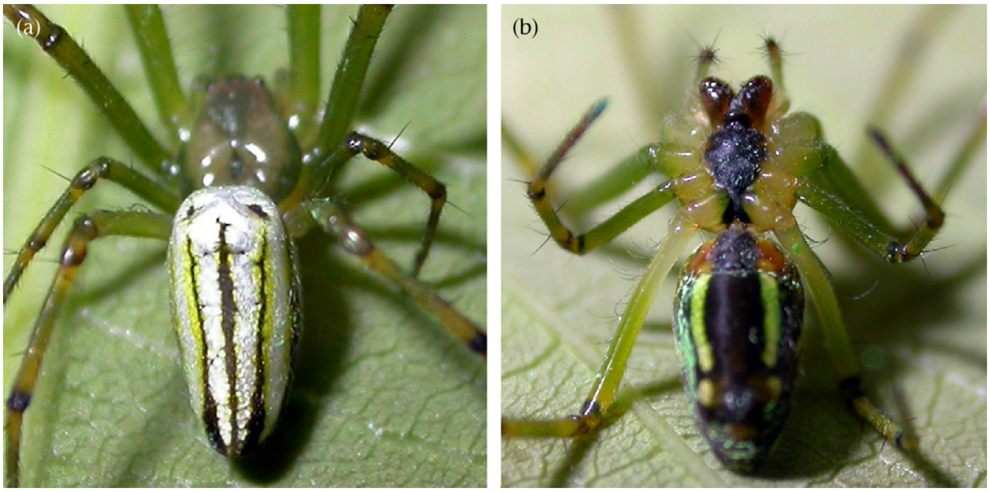

Figure 1. (a) Dorsal and (b) ventral views of the female orchid spider *Leucauge magnifica* showing various brightly coloured body parts.

were used to estimate the biomass of the trapped prey. Orb area correlates positively with prey capture rates (Higgins & Buskirk 1992; Sherman 1994), so to control this factor, we divided the prey data by the orb area to generate unit area prey interception (number of prey/h per 100 cm^2 of orb area) and consumption rates (mg/h per 100 cm^2 of orb area). Two-tailed Mann–Whitney *U* tests were then used to compare the unit area prey interception and consumption rates determined from spiders' diurnal and nocturnal hunting and to compare the total number of prey intercepted and biomass consumed per 100 cm^2 of orb area recorded during the day and at night. We used nonparametric tests as prey data deviated significantly from either normal or Poisson distributions (Steel et al. 1997), even after being transformed in various ways.

Colour Manipulation

We performed a field experiment to assess whether altering the colour signals of the orchid spiders would reduce their nocturnal hunting success. Each night before the experiment we randomly selected 10 female spiders and assigned them to three groups. In the first group, the dorsal silver bands of the spider were covered with green paint (Acrylic paint no. 53, Alphacolors, Korea) with a reflection peak between 450 and 550 nm which was used in Tso et al. (2006). In the second group, the green paint was applied on the ventral yellow stripes. In the third group, the control group, the green paint was applied to the green parts of the abdomen (the areas between the silver dorsum and yellow stripes) to serve as a control for the application of paint. Spider body length, hub diameter and orb radius from four cardinal directions and number of radii were measured (±1 mm) with a digital caliper. The catching area of the orb was estimated by the formulae of Herberstein & Tso (2000). The number and taxonomic order of insects intercepted by the orbs were determined by video cameras. The recordings were conducted daily from 1800 to 0200 hours for a total of 19 recording days in August and September 2004. We estimated prey interception rate by averaging the number of prey intercepted by webs during the monitoring. Prey data in this part of the study again deviated significantly from either a normal or a Poisson distribution, so we also used nonparametric methods to analyse the effects of colour manipulation on prey capture rate. We divided the prey interception rates by the orb area to generate the unit area prey interception rate (number of prey/h per 100 cm^2 of orb area). A Kruskal–Wallis test was then used to compare the unit area prey interception rates of spiders in the three treatment groups.

RESULTS

Temporal Activity Pattern

The results of bihourly monitoring of the number of actively hunting *L. magnifica* in the transect showed that the number of spiders varied significantly during the day (Kruskal–Wallis test: $H_{11} = 40.04$, $P = 0.0001$; Fig. 2). Although *L. magnifica* has traditionally been regarded as a diurnal hunter, considerably more actively hunting individuals were found at night. The number of spiders peaked

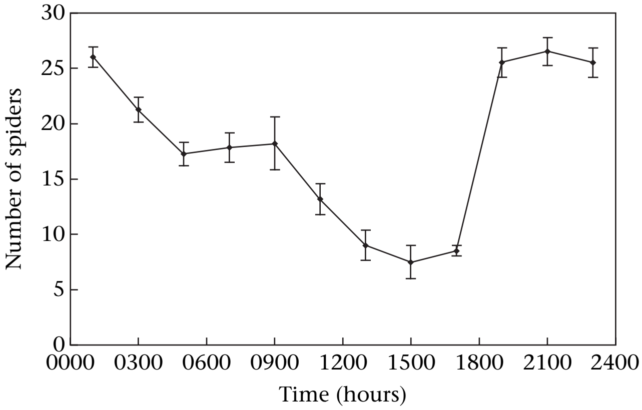

Figure 2. Mean ± SE number of actively hunting *Leucauge magnifica* in a transect throughout the day estimated from bihourly monitoring.

between 1900 and 0100 hours and dropped from about 25 to 17 as the sun gradually rose in the early morning. As midday approached, the number of spiders dropped to fewer than 10. At this time, other spiders were still in the transect, but most of them were resting in the vegetation nearby. During the initial stage of the study, when spiders left the webs we let the video camera run and monitored the web without the spider. When we viewed these videos we found that under such conditions insects occasionally bumped on to the webs but the spiders would not respond to the trapped prey. Therefore, it was probably that *L. magnifica* would stop monitoring the web when they were not on it. The number of actively hunting spiders abruptly rose after sunset and remained constant throughout the first half of the night.

Nocturnal Hunting

The monitoring of *L. magnifica*'s diurnal and nocturnal hunting was conducted for a total of 321 spider-hours. Orchid spiders actively hunted on their webs day and night and prey interception and consumption occurred during both time periods. However, when it rained or during the hot hours of the afternoon, spiders would leave their webs and hide in the vegetation nearby. Under such circumstances, the monitoring had to be stopped temporarily and therefore the mean recording time ± SE was 7.6 ± 0.65 h for diurnal hunting ($N = 35$) and 7.67 ± 1.32 h for nocturnal hunting ($N = 11$). No significant difference in unit area prey interception rate was found between diurnal and nocturnal hunting (Mann–Whitney *U* test: $U = 172.50$, $N_1 = 35$, $N_2 = 11$, $P = 0.601$; Fig. 3a). The unit area insect biomass intake rate of spiders' nocturnal hunting was considerably higher than that from diurnal hunting (Fig. 3b). However, owing to the high variance in nocturnal insect biomass intake, the results did not reach a significant level ($U = 147.50$, $N_1 = 35$, $N_2 = 11$, $P = 0.242$). The total number of insects intercepted per unit orb area did not differ significantly between diurnal and nocturnal hunting ($U = 176.00$, $N_1 = 35$, $N_2 = 11$, $P = 0.666$; Fig. 4a). However, the insects caught by *L. magnifica* during nocturnal hunting ($N = 40$) were significantly larger than those from diurnal hunting ($N = 97$; $U = 661.50$, $N_1 = 40$, $N_2 = 97$, $P = 0.0001$; Fig. 4b). The overall biomass of prey obtained during nocturnal hunting was nine times higher than that from diurnal hunting, although significance was not achieved owing to a high level of variation ($U = 149.50$, $N_1 = 35$, $N_2 = 11$, $P = 0.264$; Fig. 4c).

Colour Manipulation

The video recording sometimes had to be temporarily stopped owing to occasional rain. Therefore, the data were included in the analysis only when spiders were monitored cumulatively for more than 3 h. Prey data were available for 448 h of video recording: 128 h were from the control ($N = 20$), 112 from the dorsum painted ($N = 23$) and 112 from the ventrum painted ($N = 13$) groups. The overall unit area insect interception rates did not differ significantly between the three groups (Kruskal–Wallis test: $H_2 = 1.883$, $P = 0.390$; Fig. 5a). However, the unit area moth interception rates were significantly lower for spiders painted on the ventrum of the abdomen than for those of the other two groups ($H_2 = 6.854$, $P = 0.032$; Fig. 5b). Compared with spiders whose ventral colour signals were painted, those in the control group intercepted three times as many moths/h of monitoring per 100 cm^2 of orb area.

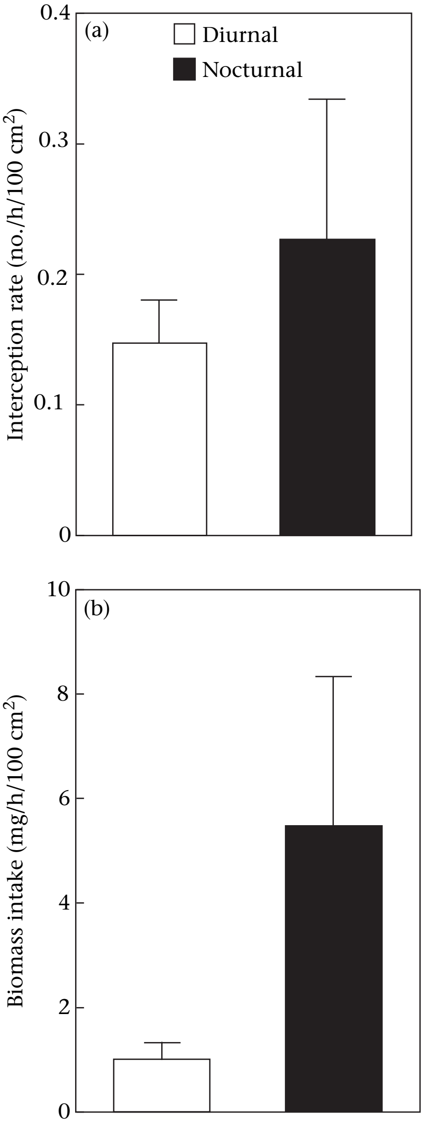

Figure 3. Mean ± SE (a) prey interception and (b) biomass intake rates of *Leucauge magnifica*'s diurnal and nocturnal hunting.

DISCUSSION

Our results showed that the orchid spider, *L. magnifica*, hunts actively during the night and its bright body coloration seems to serve as a visual lure. The field survey showed that the number of actively hunting *L. magnifica* at night was two to three times higher than that during the day. A comparison of orchid spiders' diurnal and

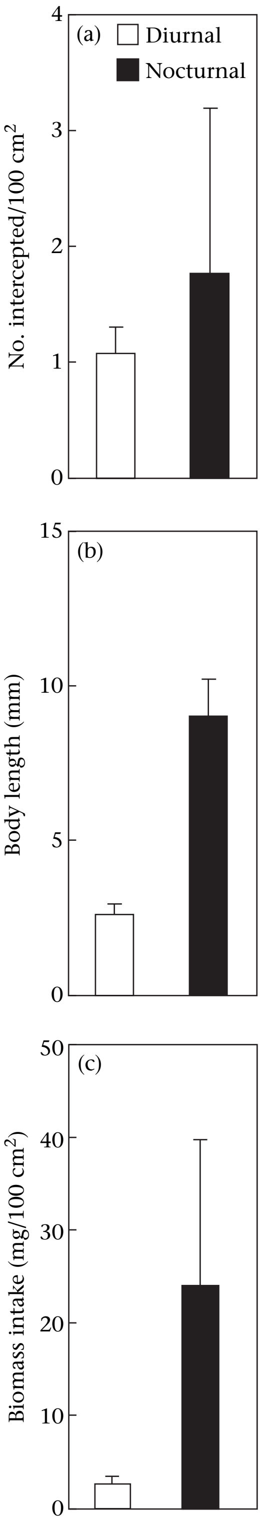

Figure 4. Mean ± SE (a) total number of prey intercepted, (b) size of intercepted prey and (c) total biomass intake of *Leucauge magnifica*'s diurnal and nocturnal hunting.

nocturnal hunting performance recorded by video cameras also revealed that their prey intake was higher from nocturnal hunting, although not significantly so, owing to the high level of variation. Although the overall number of insects caught by orchid spiders between diurnal and nocturnal hunting did not differ significantly, the insects caught at night were considerably larger. Therefore, nocturnal hunting seems to be the primary source of prey intake for orchid spiders, although success varied greatly. Our results also show that the bright body coloration of the orchid spider serves as a visual lure to nocturnal insects. When the colour signals of the ventral yellow stripes of the *L. magnifica* were painted, the moth interception rate was reduced significantly.

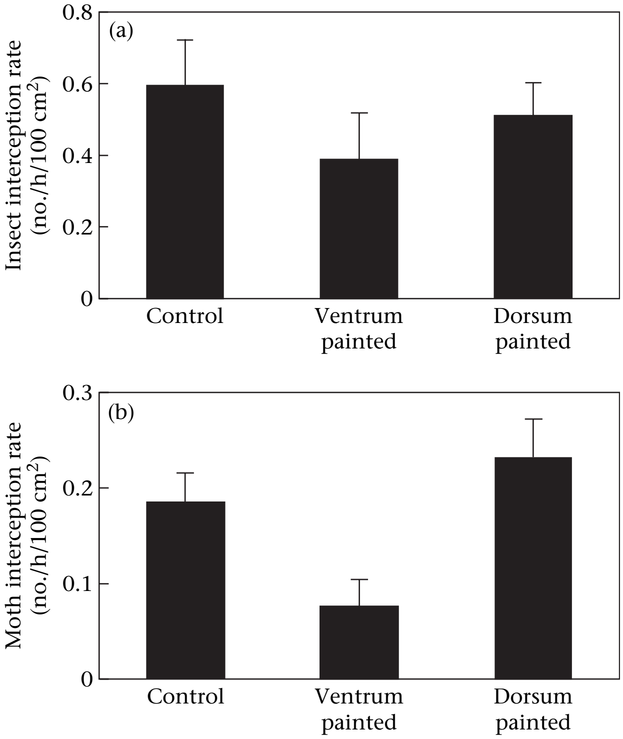

Figure 5. Mean ± SE (a) insect and (b) moth interception rates of *Leucauge magnifica* in the experimental (dorsum painted and ventrum painted) and control groups.

Our results indicate that the bright yellow abdominal stripes on the ventrum of *L. magnifica* function as a visual lure, especially to nocturnal moths. Why were the moths attracted by these yellow stripes? The abdominal yellow stripes have a relatively high reflectance between 500 and 650 nm (Tso et al. 2006) as do colours of some other orb-weaving spiders, such as *N. pilipes* (Tso et al. 2004). Many insects associate yellow colour signals with food resources such as flowers or new leaves (Prokopy & Owens 1983; Chittka 1996; Craig 2003). The abdominal yellow stripes of *L. magnifica* may thus resemble the colour signals of food resources of the moth and thus be attractive to such prey. The abdominal dorsum silver bands of *L. magnifica*, although distinctive, did not seem to function as a lure to nocturnal insects, perhaps because they did not resemble food resources of nocturnal insects. Instead, they might serve as a thermal regulator by reflecting sunlight during the hot hours of the day.

Many nocturnal orb-weaving spiders have similar coloration patterns to those of *L. magnifica*. For example, various species of *Neoscona* and *Araneus* in East Asia have either two yellow stripes or two yellow spots on the ventrum of the abdomen (Yaginuma 1986). During the day, these spiders usually perch on twigs or barks near their webs with their brown-coloured dorsum facing upwards and the yellow abdominal markings obscured. However, at night while the spiders are sitting on their orb webs hunting, they fully expose the yellow markings. Orb-weaving spiders that hunt at night, such as *L. magnifica*, *Neoscona* and *Araneus*, all have two yellow markings on the ventrum of the abdomen. Since these genera are not phylogenetically closely related (Hormiga et al. 2000), this trait may have evolved convergently because of its function in attracting nocturnal prey. It would be interesting to investigate whether the yellow abdominal markings of strictly nocturnal hunters, such as *Neoscona* and *Araneus*, also serve as visual lures to nocturnal insects.

Our results show that the yellow ventrum stripes of *L. magnifica* increase the spiders' foraging success by functioning as a visual lure to attract nocturnal insect. Theoretically, such a visual lure should be large to maximize the attractiveness. However, the yellow ventrum stripes are not large and they occupy only a small part of the ventrum (Fig. 1b). There may be two reasons for such small visual lures. First, although the bright yellow body coloration of orchid spiders is attractive to nocturnal insects, if the whole body is covered by such coloration, the contour of the spider will be more obvious to insects. Prey will quickly learn to associate the colour with danger by recognizing the shape of the images. Second, the size of the ventrum stripes might be constrained by strong predation pressure. The major predators of orb-weaving spiders are dipteran or hymenopteran parasitoids (Coville 1987; Blackledge & Pickett 2000; Blackledge & Wenzel 2001), most of which are visually oriented diurnal predators. A large area of bright coloration on the spiders' body will make it easily detected by those predators. Therefore, the size of orchid spiders' yellow ventrum stripes seems to be a product of various counteracting selection pressures involved in spider–prey insect and spider–predatory insect visual interactions.

In the study of visual interactions between organisms, it is critical to know how visual signals are perceived by the intended recipients. Numerous recent studies have quantified how the colour signals of spiders are perceived by their prey or predators and the results of these studies have greatly expanded our view of spider–insect visual interactions. For example, several studies have investigated how diurnal spiders are viewed by hymenopteran insects (Chittka 2001; Théry & Casas 2002; Heiling et al. 2003; Tso et al. 2004, 2006; Chou et al. 2005; Heiling et al. 2005). Various visual physiological models used in these studies, such as the colour hexagon model (Chittka 1992; Chittka & Menzel 1992; Chittka et al. 1994), are based upon the visual system of diurnal honeybees, *Apis mellifera*. In our study, the major prey of *L. magnifica* during nocturnal hunting was moths, which in general have ultraviolet, blue and green photoreceptors (Kelber et al. 2003). Numerous diurnal insects such as honeybees have similar types of receptors (Briscoe & Chittka 2001). Nocturnal hawkmoths, however, can discriminate colour signals in dim light, whereas in such light conditions honeybees are colour blind (Kelber et al. 2003). Therefore, we cannot simply use existing bee visual physiological models to quantify how colour signals of spiders are perceived by moths in dim light conditions. Results of this and numerous studies have shown that colour vision is important in the nocturnal system. However, development of visual physiological models to quantify how colour signals are perceived by nocturnal organisms is needed.

Few researchers have considered the possibility that spider body coloration is involved in nocturnal spider–insect interactions. Yet our results show that the intended recipients and functions of these spiders' colour signals might differ from what we previously thought. Future studies on how colour signals are involved in nocturnal systems will greatly expand our view of predator–prey visual interactions.

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