



A nocturnal cursorial predator attracts flying prey with a visual lure



Shichang Zhang^a, Hong-Lin Chen^a, Kuan-Yu Chen^a, Jian-Jun Huang^a, Chia-Chen Chang^a,
Dakota Piorkowski^a, Chen-Pan Liao^a, I-Min Tso^{a, b, *}

^a Department of Life Science, Tunghai University, Taichung, Taiwan

^b Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung, Taiwan

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Body coloration has been known to play an important role in animal visual communication. Attraction of prey by visual signals, such as bright body coloration, has been mainly observed in diurnal predators. For nocturnal cursorial predators, however, this foraging tactic has been largely ignored, because one would not expect it to occur under low ambient illumination at night and because of the technical constraints of conducting research in dim light conditions. Metabolic constraints prevent most cursorial spiders moving continuously for a long time to improve prey encounter rate. Any adaptation that induces prey to orient towards these cursorial predators would greatly enhance their foraging success. Bright body coloration of certain nocturnal invertebrates may play such a role. In this study, we investigated colour-mediated prey attraction in a nocturnal cursorial predator, the brown huntsman spider, *Heteropoda venatoria*, which has a conspicuous moustache-like white stripe on the forehead. We conducted field experiments using dummy and real spiders and monitored with infrared video cameras the responses of nocturnal prey to treatment groups with the white stripe intact or removed. The results showed that in both dummy and real spiders the presence of the white stripe can significantly increase prey attraction rate. Nocturnal flying insects such as moths comprised the majority of attracted prey. We conclude that cursorial invertebrate predators can visually lure prey, especially flying insects such as moths, by their conspicuous body coloration at night.

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Animals use acoustic, seismic, chemical or visual signals to communicate intra- or interspecifically (Smith & Harper, 2003). Many animals display conspicuous body coloration, which functions as visual communication signals to attract opposite-sex conspecifics (Baker & Parker, 1979; Milinski & Bakker, 1990), aposematic or warning coloration to deter predators (Summers & Clough, 2001; Sword, 1999) or disruptive coloration to avoid predators (Stevens & Merilaita, 2011). Most studies investigating animal body coloration have focused on the effects of coloration in increasing reproductive success or decreasing predation pressure. However, studies examining how coloration is employed as a visual lure to enhance foraging success are relatively few. In vertebrates, organisms such as the sidewinder rattlesnake, *Crotalus cerastes* (Reiserer & Schuett, 2008), viper, *Cerastes vipera* (Heatwole & Davison, 1976), leaf frog, *Phyllomedusa burmeisteri* (Bertoluci, 2002) and the toad *Chaunus marinus* (Hagman & Shine, 2008) have been reported to visually attract prey by their conspicuous

body coloration. The visual signals may mimic food or potential mating partners, thus luring prey deceptively (Reiserer & Schuett, 2008).

In addition to the aforementioned reptiles and amphibians, most empirical reports of prey being lured by body coloration have been in terrestrial invertebrates, such as the orchid mantis, *Hymenopus coronatus* (O'Hanlon, Holwell, & Herberstein, 2014), and especially web-building spiders. Some spiders' conspicuous body coloration functions as camouflage (Heiling, Chittka, Cheng, & Herberstein, 2005; Théry & Casas, 2002), predator avoidance (e.g. crypsis; Hoese, Law, Rao, & Herberstein, 2006), male quality assessment (Li et al., 2008; Lim, Land, & Li, 2007) and predator deterrence (e.g. aposematic coloration; Oxford & Gillespie, 1998). The prey attraction function of spider body coloration, however, has only recently been discovered, mainly in the web-building spiders. Several web-building spiders increase the web interception rate of insects through brightly coloured body parts as has been shown in a diverse array of genera such as *Argiope* (Bush, Yu, & Herberstein, 2008) and *Gasteracantha* (Hauber, 2002) of the family Araneidae, *Nephila* of the family Nephilidae (Fan, Yang, & Tso, 2009; Tso, Lin, & Yang, 2004; Tso, Tai, Ku, Kuo, & Yang, 2002) and *Leucauge* of the

* Correspondence: I-Min Tso, Department of Life Science, Tunghai University, Taichung 40704, Taiwan.

E-mail address: spider@thu.edu.tw (I.-M. Tso).

family Tetragnathidae (Tso, Liao, Huang, & Yang, 2006), although a few studies do not support the visual lure hypothesis (Gawryszewski & Motta, 2012; Vanderhoff, Byers, & Hanna, 2008). In addition to web spiders, some cursorial spiders have also been demonstrated to visually lure prey. For example, the UV-reflective body coloration of Australian crab spiders can attract prey (e.g. bees) to the flowers on which they are positioned (Heiling & Herberstein, 2004; Heiling, Herberstein, & Chittka, 2003; Herberstein, Heiling, & Cheng, 2009).

Most of the limited number of studies exploring the colour-mediated foraging function of body coloration have been conducted in the diurnal context. For nocturnal arthropods, however, visual signalling has been largely ignored because of the low ambient illumination at night, technical constraints of conducting research in dim light conditions and the dull body coloration of nocturnal organisms in general (Blamires et al., 2012). But there is growing evidence that various nocturnal trap-building predators can visually attract insects at night by conspicuous signals on their body. For example, the conspicuous body parts of the giant wood spider, *Nephila pilipes* (Chuang, Yang, & Tso, 2007), orchid spider, *Leucauge magnifica* (Tso, Huang, & Liao, 2007) and the garden spider, *Neoscona punctigera* (Blamires et al., 2012; Chuang, Yang, & Tso, 2008) have been shown to function as visual lures for nocturnal prey.

The brown huntsman spider, *Heteropoda venatoria* (Araneae: Heteropodidae), is a large nocturnal cursorial predator (Fig. 1a) with a moustache-like white stripe across its forehead region (Fig. 1b) that

perches on the ground, tree trunks or rocks to hunt for prey (Edwards, 2009). Most cursorial spiders are unable to improve prey encounter rate through increased locomotion, because of metabolic constraints (Foelix, 2011). Therefore, any adaptation that induces prey to orient towards these cursorial predators would greatly improve foraging success. In the field, *H. venatoria* can jump and snatch flying insects out of the air when prey approach close enough for a quick attack (S. Zhang personal observation). Thus, we hypothesized that the conspicuous white stripe of the brown huntsman spider functions to attract nocturnal insects. To test this hypothesis, we manipulated the colour signal of the white stripes by using live spiders and paper dummies, and monitored nocturnal prey responses to different treatment groups in the field using infrared video cameras.

METHODS

Field Experiments Using Dummy Spiders

Field experiments using dummy spiders were conducted between 24 and 27 August, 2013 in an abandoned air defence tunnel (ca. 100 m) under a road on the campus of Tunghai University (120°9'56"E, 24°18'00"N), where *H. venatoria* were found perching on the wall at night (more than 30 individuals within 50 m). The tunnel is minimally disturbed and its microenvironment is close to the wild. We made paper dummies that were the same size, shape and colour as adult female *H. venatoria* (Fig. 1a) using body length and width measurements and photographs of live spiders. We measured the chromatic properties of selected sheets of brown and white dummy construction paper across a 300–700 nm spectrum using a USB4000 spectrophotometer (Ocean Optics, Dunedin, FL, U.S.A.; Chuang et al., 2008). The spectral properties across a 300–700 nm spectrum were also measured for the body (palps, carapace and abdomen) and the white stripe of live female *H. venatoria* collected from Tunghai University ($N = 5$) so as to compare spectral properties between corresponding dummy and live spider body parts. Preliminary observations showed that moths were the major prey of *H. venatoria*. Therefore, to quantify how the colour of the dummy and live body parts of *H. venatoria* was viewed by the moths, a visual neuroethological model developed for hawkmoths (Johnsen et al., 2006) was followed to calculate the nocturnal achromatic and chromatic contrasts. We measured the following parameters from Johnsen et al. (2006): (1) moth photoreceptor acceptance angle; (2) facet lens diameter; (3) photoreceptor integration scoring time; (4) quantum transduction efficiency; (5) eye fractional transmission; (6) absorption coefficient of the rhabdom; (7) absorbance spectra of each photoreceptor; and (8) tapetal reflection. The mean full moonlight illumination function across the 300–700 nm waveband was assumed equivalent to that reported by Somanathan, Borges, Warrant, and Kelber (2008) and the background reflectance spectrum was obtained by measuring the reflectance spectrum of pieces of concrete collected from the tunnel.

Under light resource $D(\lambda)$ and background reflectance spectrum $I(\lambda)$, photoreceptors in one ommatidium of the nocturnal elephant hawkmoth, *Deilephila elpenor*, per integration time of the photoreceptor, is given by:

$$N = 1.13 \left(\frac{\pi}{4} \right) n \Delta \rho^2 D^2 \Delta t \int_{300}^{700} \kappa \tau \left(1 - e^{-\kappa I R_i(\lambda)} \right) L(\lambda) d\lambda$$

where n is the number of effective facets in the superposition aperture (568); $\Delta \rho$ is the photoreceptor acceptance angle (3.0°); D is the diameter of a facet lens ($29 \mu\text{m}$); κ is the quantum efficiency

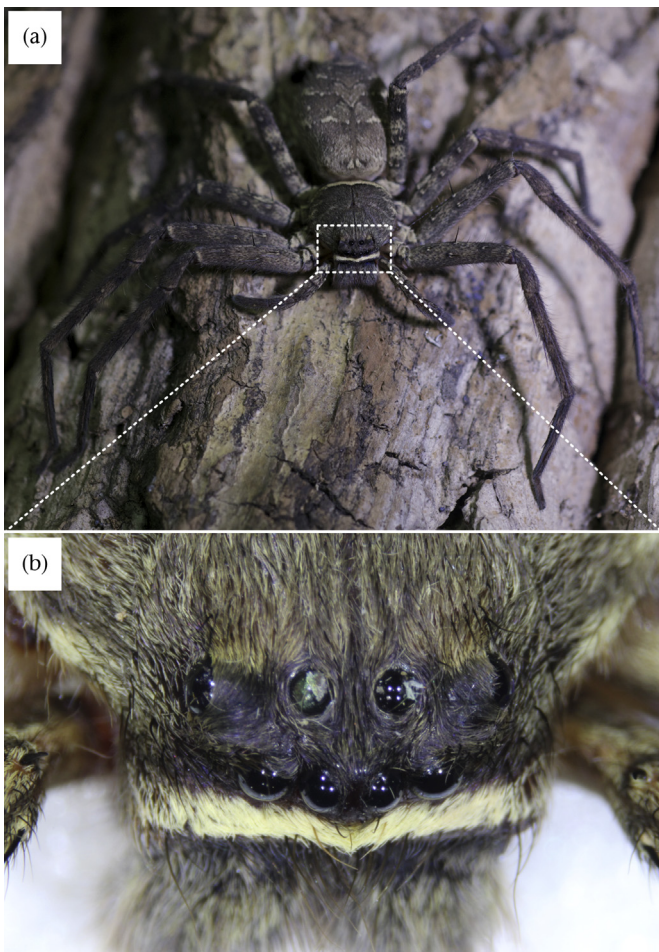


Figure 1. (a) Female brown huntsman spider, *Heteropoda venatoria*, with (b) the white stripe on the forehead region highlighted.

of transduction (0.5); τ is the fractional transmission of the eye media (0.8); Δt is the integration time of a photoreceptor (0.036 s); k is the absorption coefficient of the rhabdom (0.0067 μm^{-1}); l is the rhabdom length, doubled by tapetal reflection (414 μm); and $L(\lambda)$ is the stimulus light intensity in photons/ m^2 per s per nm per steradian (Johnsen et al., 2006; Kelber, Balkenius, & Warrant, 2003). $R_i(\lambda)$ ($i = G, B, U$) are the absorbance spectra of the three visual pigments of *D. elpenor* (green, blue, UV), normalized to a peak of 1 (Warrant, 2004). The quantum catch values for the papers and their representative spider body parts were plotted onto a hawkmoth UV–blue–green visual triangle (Johnsen et al., 2006; Warrant, 2004) and their Euclidean positions were used to calculate their chromatic contrast values (see Kelber, Vorobyev, & Osorio 2003 for more details). The relative photons absorbed by different photoreceptors can be calculated by

$$Q_j = N_j / (N_{Gj} + N_{Bj} + N_{Uj}).$$

The coordinates in the spider colour hexagon were calculated by

$$\begin{pmatrix} x_j \\ y_j \end{pmatrix} = \begin{pmatrix} \frac{1}{\sqrt{2}} (Q_{Gj} - Q_{Bj}) \\ \frac{\sqrt{2}}{\sqrt{3}} [Q_{Uj} - (Q_{Gj} + Q_{Bj})/2] \end{pmatrix}$$

Then, the colour contrast between objects 1 and 2 was calculated by the Euclidean distance in the color hexagon:

$$c = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2}$$

where x and y are the coordinates of the hexagon.

We also calculated the achromatic contrasts of the papers and their representative spider body parts when viewed against the background using the equation:

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

where N_x is the green photoreceptor quantum catch for the target (coloured paper or *H. venatoria* body parts) and N_{green} is the green photoreceptor quantum for the background. We assumed that green receptors extend over the entire length and width of the rhabdom and no lateral screening took place (Johnsen et al., 2006).

Dummies were constructed using brown cardboard cut into the shape of a spider. In the control group, white stripes were stuck on the forehead region of the dummies (Supplementary material, Fig. S1a) by water-soluble glue (Transparent School Glue, En-Yuan Chemical Co., Tainan, Taiwan). In the experimental group (Fig. S1b), we affixed equivalent-sized brown stripes on the forehead region of the dummies to control for the potential impacts of chemicals contained in the glue. Each dummy was used only once to avoid the chromatic property of the cardboard being changed by dew or other environmental factors. During the field experiments, the dummies used for each day of data collection were made on the previous day. In total, 63 spider dummies were constructed (32 with a white stripe and 31 without).

Dummies were randomly stuck on the wall of the tunnel with silicone gel. We used 30 video cameras with infrared night view scopes (Sony HDR-CX720V and DCR-SR100, Tokyo, Japan) to monitor the responses of prey to dummies. Video cameras were placed perpendicular to dummies at a distance of about 1 m. Each dummy was recorded simultaneously for 4 h (from 2000 to 2400 h) allowing confounding factors such as temporal changes in prey abundance over the course of night to have a uniform effect on all dummies. The video cameras were covered by rainproof caps, so the tiny red

recording lights on our machines were totally obscured to prevent potential impacts of artificial insect attraction by the lights. An 'attraction' event was defined as an insect flying or approaching within 5 cm of a dummy. We recorded the number and type (flying versus nonflying) of prey attracted by dummies from video footage. For each dummy monitored, the number of the prey attraction events was divided by monitoring time to calculate the prey attraction rate (number of prey attracted per hour of monitoring). Dummies with <3 h of available footage were excluded from the statistical analysis.

Field Experiments Using Live Spiders

Field experiments using similar-sized live female spiders were conducted at the Conservation Education Center, Taiwan Endemic Species Research Institute in Chi-Chi, Nantou county, Taiwan (120°48'03.1'E, 23°49'42.1'N), between 4 and 7 April 2014. We caught female *H. venatoria* from the trail at the Conservation Education Center and divided them into experimental and control groups. In the experimental group, spiders were anaesthetized with CO₂, then they were placed on a foam platform, and their white stripes were removed carefully by razor blade under a dissecting microscope. In the control group, spiders were also anaesthetized with CO₂ and we scraped their white stripes carefully with the blunt side of the blade so as not to damage them. We measured the spectrum of the manipulated forehead region using a USB4000 spectrophotometer after removing a spider's white stripe, to compare it with the spectrum prior to removal. After being 'shaved', spiders were individually introduced to a plastic cylinder (ca. 600 ml) for ca. 12 h to recover. Before the field experiments, spiders were placed randomly on the tree bark or the vertical surface of the artificial structures where we caught them. Each spider was monitored for prey attraction events by an infrared video camera (Sony HDR-CX720V and DCR-SR series, Tokyo, Japan) placed perpendicularly at a distance of ca. 1 m for 4 h (from 1900 to 2300 hours). To prevent spiders from running away, we tied one end of a cotton string (15 cm) to the abdomen of the spider, while the other end of the string was nailed to the substrate. Thus, the spiders were constrained in an activity area with a diameter of about 30 cm. The flying and nonflying prey attraction rates of each *H. venatoria* monitored were estimated in the laboratory at Tunghai University.

Statistical Analysis

The theoretical discrimination threshold value for the nocturnal chromatic neuroethological model is not yet available. Therefore, the nocturnal achromatic and chromatic contrast values of various papers and corresponding body parts of *H. venatoria* were compared by one-way ANOVA tests (with a Welch correction) and Games–Howell post hoc comparisons. Results of these tests could help determine whether the colours of papers used to construct dummies were similar to those of corresponding spider body parts when viewed by moths under nocturnal conditions with concrete as the background. The prey attraction data from the dummy experiment were fitted with a Poisson distribution (Pearson chi-square goodness-of-fit tests: $\chi^2 = 63.5$, $P = 0.154$ for flying prey and $\chi^2 = 58.9$, $P = 0.268$ for nonflying prey). Poisson regressions were used to compare the flying and nonflying prey attraction rates of dummies in the experimental and control groups. While viewing the video footage of field experiments using real spiders, we found that for the great majority of spiders monitored the number of prey attraction events was either zero or one. Fewer than 10% of spiders experienced multiple attraction events during monitoring. Therefore, a logistic regression was used to compare the flying and nonflying prey attraction events recorded from *H. venatoria* in the experimental and control groups.

RESULTS

Field Experiments Using Dummy Spiders

The reflectance spectrum of the white stripe differed from that of the brown body parts of live *H. venatoria* (Fig. 2). The nocturnal achromatic and chromatic contrast values of brown and white papers used to construct dummies did not differ significantly from that of the corresponding body parts of female *H. venatoria* (Fig. 3). Therefore, from the eyes of lepidopteran prey, the dummy coloration resembled that of real brown huntsman spiders.

A total of 252 h of video footage was obtained for dummy prey attraction: 128 h from the control and 124 h from the experimental group. Results of a Poisson regression showed that dummies with the white stripes attracted significantly more flying prey (per hour of monitoring) than those without (Table 1, Fig. 4a). Some control group dummies had a higher nonflying prey attraction rate than experimental ones (Fig. 4b). However, this difference was not statistically significant (Table 1). The great majority of flying prey were moths, while nonflying prey included ants, cockroaches and crickets.

Field Experiments Using Live Spiders

When the white hairs were shaved from the forehead region of female *H. venatoria*, the reflectance spectrum differed considerably from the natural one (Fig. 2). The achromatic and chromatic colour contrasts of the manipulated and intact forehead region differed significantly (Fig. 3).

A total of 240 h of video footage was obtained for live spider prey attraction with 120 h in each treatment group. Results of a logistic regression showed that compared with spiders with white stripes shaved, native state spiders were significantly more likely to attract flying prey, among which over 60% could be identified as moths (Table 2, Fig. 5a). In both treatment groups, compared to flying prey, the likelihood of attracting nonflying prey was much lower (Fig. 5b). Control and experimental treatment groups did not differ significantly in the likelihood of attracting nonflying prey (Table 2). The nonflying prey recorded in this part of the study included crickets, beetles and ants.

DISCUSSION

In this study, we examined the function of the moustache-like white stripe on the forehead of the brown huntsman spider, *H. venatoria*, and found that it can visually attract nocturnal prey.

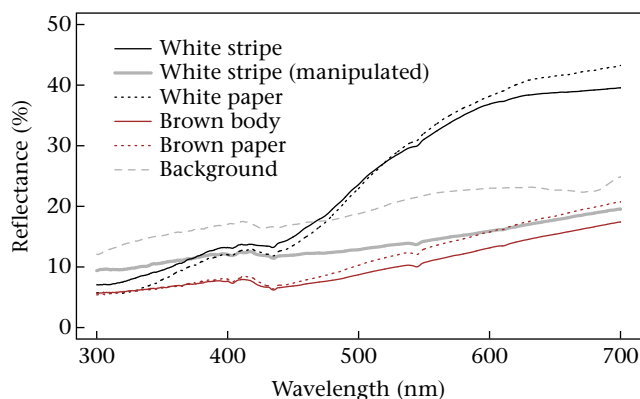


Figure 2. Reflectance spectra of the intact and manipulated body parts of the female brown huntsman spider and various types of paper used for constructing dummies.

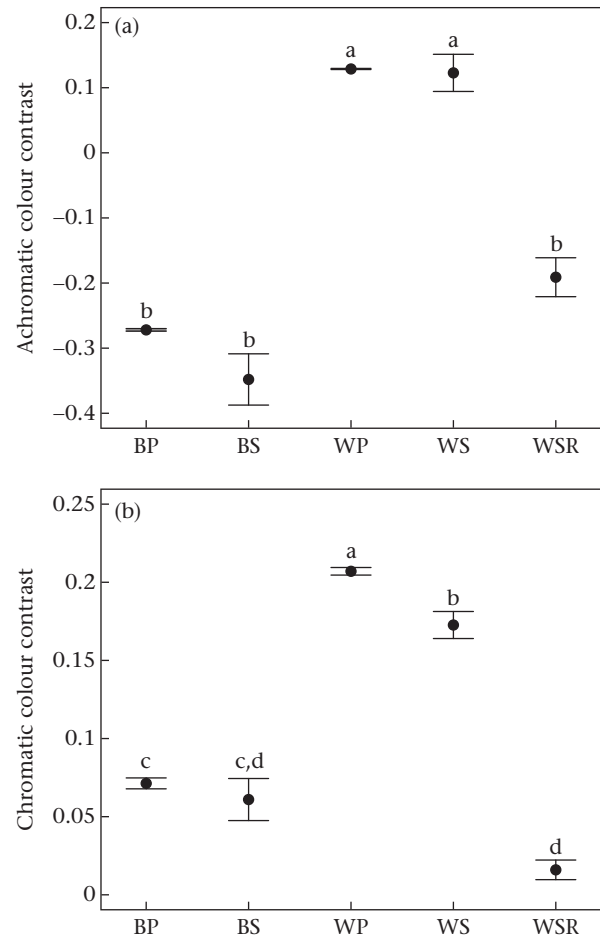


Figure 3. Mean \pm SE nocturnal (a) achromatic and (b) chromatic contrast values of intact and manipulated body parts of the female brown huntsman spider and the papers used for constructing dummies. Letters represent results of Games–Howell post hoc comparisons. The variances of achromatic and chromatic colour contrasts are not homogeneous ($\chi^2_4 = 22.326$, $P < 0.001$ for achromatic contrast and $\chi^2_4 = 9.947$, $P = 0.041$ for chromatic contrast). The achromatic and chromatic colour contrasts of the five types of object are significantly different ($F_{4,8,403} = 823$, $P < 0.001$ for achromatic contrast and $F_{4,8,943} = 320.2$, $P < 0.001$ for chromatic contrast). BP: brown paper; BS: brown spider body part; WP: white paper; WS: white stripe; WSR: white stripe removed.

Thus, we demonstrated that nocturnal cursorial predators can lure prey through conspicuous body coloration. Flying insects are a large fraction of the attracted prey, suggesting they are a primary prey resource for *H. venatoria*. Some nocturnal insects, especially bees and moths, possess excellent night vision by having superposition

Table 1
Poisson regressions comparing flying and nonflying prey attraction rates of dummy spiders in control and experimental groups

Coefficient	Estimate of β	SE	Z	P
Flying prey attraction rate				
Intercept	-0.330	0.162	-2.033	0.042
Treatment effect*	-0.659	0.324	-2.033	0.042
Nonflying prey attraction rate				
Intercept	-1.421	0.292	-4.866	<0.001
Treatment effect*	-1.121	0.584	-1.920	0.055

Control group: with white stripe on forehead region; experimental group: without white stripe on forehead region.

* The ratio of prey attraction probability of the experimental versus control group is e^β .

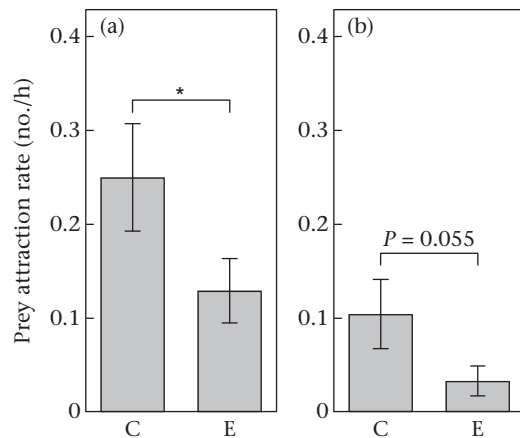


Figure 4. Mean \pm SE (a) flying and (b) nonflying prey attraction rates of dummies resembling the female brown huntsman spider in appearance and colour with (C) or without (E) the white stripe in the forehead region. * $P < 0.05$.

compound eyes (Warrant & Dacke, 2011), which, consequently, allow discrimination between different colour signals (Kelber, Balkenius, & Warrant, 2002; Kelber & Roth, 2006; Somanathan et al., 2008; Warrant & Dacke, 2011). The white stripe of *H. venatoria* reflected light from 300 to 700 nm, which can be well detected by nocturnal moths and bees (Höglund & Struwe, 1970; Kelber & Roth, 2006). However, it remains unclear why the white stripe of the brown huntsman spider is visually attractive to nocturnal moths.

Recent studies have demonstrated that, in addition to the white stripe of *H. venatoria*, various forms of colour signals exhibited by several spider taxa are also visually attractive to nocturnal insects. For example, the yellow spots on the abdomen and the legs of the giant wood spider *N. pilipes* (Nephilidae) (Chuang et al., 2007), the yellow ventrum stripes on the abdomen of the orchid spider *L. magnifica* (Tetragnathidae) (Tso et al., 2007), the paired ventrum spots on the abdomen of the orb weaver *N. punctigera* (Araneidae) (Blamires et al., 2012; Chuang et al., 2008) and the silvery abdominal spots on *Argyrodes fissifrons* (Theridiidae) (Peng, Blamires, Agnarsson, Lin, & Tso, 2013) all function as effective nocturnal visual lures. The shape and colour of visual lures exhibited by these trap-building or cursorial nocturnal predators are very diverse, rendering the identification of key visual elements of the deceptive signals difficult. So far, our knowledge of how visual signals are involved in terrestrial predator–prey interactions in the nocturnal context is limited. However, an increasing number of studies show that visual interaction in terrestrial ecosystems at night is actually much more common than originally thought. We suggest that more effort be given to resolve the ecological significance of the form and function of visual lures exhibited by

Table 2

Logistic regressions comparing flying and nonflying prey attraction events of spider *Heteropoda venatoria* in experimental and control groups

Coefficient	Estimate of β	SE	Z	P
Flying prey attraction rate				
Intercept	−0.872	0.306	−2.850	0.004
Treatment effect*	−1.476	0.612	−2.414	0.016
Nonflying prey attraction rate				
Intercept	−2.035	0.406	−5.013	<0.001
Treatment effect*	−0.325	0.812	−0.401	0.689

Control group: white stripe in forehead region intact; experimental group: white stripe in forehead region shaved.

* The odds ratio between the experimental and control group is e^{β} .

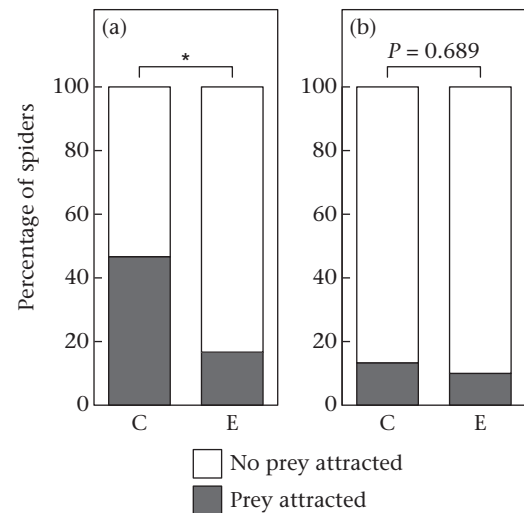


Figure 5. Mean \pm SE (a) flying and (b) nonflying prey attraction rates of female brown huntsman spiders with the forehead white stripe intact (C) or experimentally removed (E). * $P < 0.05$.

nocturnal predators. It is also possible that the conspicuous white stripes of *H. venatoria* may also attract the attention of potential predators, such as geckos, that have good night vision (Roth & Kelber, 2004; Warrant, 2004). Therefore, the body coloration of *H. venatoria* may have been shaped by a compromise between prey attraction and predator avoidance, in a way similar to that reported for *N. pilipes* (Chuang et al., 2007; Fan et al., 2009). On the other hand, as many wandering spiders have good vision (Uhl & Elias, 2011), it is possible that the conspicuous stripe of *H. venatoria* has a role in species identity or mate choice. In salticids, it has been documented that bright visual signals in the ‘face’ area are ‘sexy’ characters, which can significantly influence mate choice (Taylor & McGraw, 2013).

As high diversity and abundance of nocturnal lepidopterans evolved, many predators developed various adaptations to exploit these new food resources (Stephens, Brown, & Ydenberg, 2007). According to current knowledge, predators that are able to subdue nocturnal flying moths either exhibit excellent flying ability (such as insectivorous bats) or construct aerial traps (such as nocturnal web spiders). On the one hand, with high aerial mobility, nocturnal insectivorous bats detect and target moths through echolocation (Waters & Jones, 1995). On the other hand, sedentary trap-building nocturnal spiders exhibit either visual (Blamires et al., 2012; Chuang et al., 2007) or chemical lures (Eberhard, 1977; Stowe, Tumlinson, & Heath, 1987) to attract and entangle moths in webs. During field experiments, we found that after attracting and orienting flying insects towards the white stripe, the spider would jump and snatch prey out of the air (S. Zhang personal observation). This behaviour may have been triggered by moths’ airflow stimuli sensed by the trichobothria on the body surface of *H. venatoria*, in a way similar to the prey-catching mechanism of another nocturnal cursorial predator, the wandering spider *Cupiennius salei* (Barth, 2002). Results of our study show that terrestrial nocturnal predators that cannot fly and do not build aerial traps can also effectively hunt for flying moths as a major source of prey through conspicuous body coloration. Therefore, we find that aerial mobility or trap building are not prerequisites for catching nocturnal flying moths.

Across Araneae, various lineages have evolved dramatically different foraging modes, yet similar colour-mediated strategies to hunt for nocturnal moths appear to exist. Orb-weaver spiders build either 2D (Blamires et al., 2012; Chuang et al., 2007, 2008; Tso et al.,

2007) or 3D (Blamires, Hou, Chen, Liao, & Tso, 2014; Peng et al., 2013) aerial traps and lure moths into them with their conspicuous body parts. Our findings indicate that taxa adopting a cursorial hunting mode also lure moths to fly towards them but detect and target them, probably through trichobothria on body parts such as legs. In our study, the achromatic contrast of the white stripe was significantly higher than that of the chromatic contrast (Fig. 3), suggesting that flying insects may have been attracted by the achromatic contrast at a distance. Actually, moths can use both achromatic and chromatic cues in their foraging at night, and most flowers pollinated by nocturnal moths are white, which thus exhibit a high and reliable achromatic contrast to the dark background (Kelber, 2005). It has been reported that when forced to discriminate stimuli at specific distances, bees, *Apis mellifera*, use achromatic cues at long distances and chromatic cues at short ones (Giurfa, Vorobyev, Brandt, Posner, & Menzel, 1997). So flying insects may also use achromatic or chromatic cues of the white stripe in *H. venatoria* at different distances. However, we have not measured the actual number of photons that are reflected by the white patch at night. Thus, we do not know the distance range that could be detected by flying insects. Therefore, we suggest that comparative studies be conducted to investigate evolutionary relationships of colour-mediated prey luring in Araneae lineages. Currently, the function of conspicuous body parts in nocturnal spiders, especially that of the RTA clade (a clade of entelegyne Araneomorphae, which have a particular knob, the retrolateral tibial apophysis, on their palps) and basal lineages such as Mygalomorphae (Bond et al., 2014; Fernández, Hormiga, & Giribet, 2014), are poorly understood. We suggest behavioural studies be conducted on taxa such as these to uncover the potential functions of the conspicuous body parts and comparative studies be performed to reveal the evolutionary patterns of these traits. These studies will help demonstrate how the visual signals evolved and are involved in the interactions between spiders, the major nocturnal arthropod predators in terrestrial ecosystems, and their prey.

Mechanisms controlling how nocturnal cursorial spiders sense approaching flying insects have been well studied (Barth, 2002). However, no study has examined how sedentary predators encounter flying insects at the initial stage of the predation process. Most relevant studies have focused on the sensory biology of spider body hairs (Barth, 2002), while largely ignoring the function of their coloration. In addition to the brown huntsman spider, many nocturnal cursorial spiders such as fishing spiders *Dolomedes* (Pisauridae), wandering spiders *Cupiennius* (Ctenidae) and even tarantulas (Theraphosidae) also exhibit conspicuous body parts (Barth, 2002; Foelix, 2011; Tanikawa & Miyashita, 2008). Also, many taxa of nocturnal terrestrial cursorial arthropod predators (such as certain species in Dermaptera and predatory Hemiptera) also have conspicuous coloration on certain body parts (Abbott & Favreau, 1971; Briscoe & Chittka, 2001; Duffey & Scudder, 1972). These terrestrial cursorial predators are believed to forage exclusively for crawling prey as their major food resource. However, results of our study suggest that colour-mediated prey luring might be a common foraging strategy adopted by many nocturnal cursorial predators. We suggest that studies be conducted on other conspicuously coloured nocturnal cursorial predators to reveal the role visual signals play in their interactions with conspecifics, predators and prey.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.12.028>.

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