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A nocturnal cursorial predator attracts flying prey with a visual lure

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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.

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

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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.

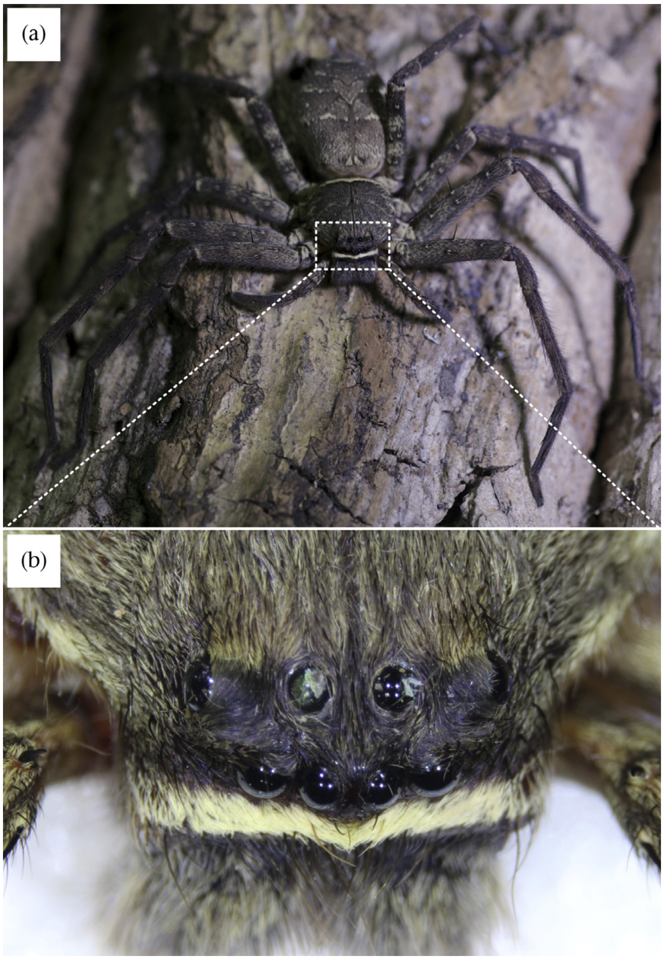

Figure 1. (a) Female brown huntsman spider, *Heteropoda venatoria*, with (b) the white stripe on the forehead region highlighted.

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:

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

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 μm); κ is the quantum efficiency