Animal Behaviour 142 (2018) 185–190

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Vision-mediated courtship in a nocturnal arthropod

Shichang Zhang [a, b], Ho-Yin Yip [a], Ming-Yu Lee [a], Li Liu [a], Dakota Piorkowski [a], Chen-Pan Liao [a], I-Min Tso [a, c, *]

[a] Department of Life Science, Tunghai University, Taichung, Taiwan
[b] Center for Behavioral Ecology and Evolution, Hubei Collaborative Innovation Center for Green Transformation of Bio-Resources, College of Life Sciences, Hubei University, Wuhan, China
[c] Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung, Taiwan

ARTICLE INFO

Article history:
Received 17 November 2017
Initial acceptance 28 May 2018
Final acceptance 1 June 2018

MS. number: 17-00911R

Keywords:
body coloration
Heteropoda venatoria
mating
nocturnal animal
vision

Visual signals are widely used by animals in foraging, mating and predator avoidance. Body coloration plays an important role in the reproductive behavioural interactions of many diurnal animal species; however, its role in the courtship of nocturnal species has received little attention. We investigated the role of conspicuous body coloration, a white stripe on the forehead region, in the reproductive interactions of the nocturnal brown huntsman spider, *Heteropoda venatoria*. We performed a series of mating trials in which we manipulated the body coloration of males and the vision of females and determined the probabilities of mating success of males in different treatments. Results showed that males that courted females with intact vision had a significantly lower probability of mating success than males that courted females whose vision was blocked. Females with intact vision were also more likely to choose males with a white stripe than those whose stripe was removed. Therefore, we have unambiguously demonstrated for the first time that body coloration plays an important role as a visual signal in the mating of nocturnal spiders.

Animals use many kinds of communicative signals in interspecific and intraspecific interactions, such as chemical, tactile, acoustic and visual signals (Maynard Smith & Harper, 2004; Stegmann, 2013). By employing these signals individually or concomitantly, animals can more efficiently interact with other organisms or their surrounding environment and improve foraging, mating and predator avoidance (Maynard Smith & Harper, 2004; Stegmann, 2013). Visual signals are probably the most frequently used as most animals have eyes, and are used especially during mating (Cronin, Johnsen, Marshall, & Warrant, 2014; Land & Nilsson, 2012). Body coloration (i.e. visually perceptible colours and high-contrast patterns on the body of an animal) is frequently involved in reproductive interactions of many animals, such as insects, fish, birds and even mammals (Andersson, 1994). Animals with conspicuous body coloration are typically diurnal and have poor vision at night, leaving nocturnal species largely neglected in the literature (Cronin et al., 2014). However, there is growing evidence that body coloration can play an important role in female mate choice in nocturnal species, which has been mainly reported in frogs (Gómez et al., 2009; Vásquez & Pfennig, 2007) and birds (Penteriani, del Mar Delgado, Alonso-Alvarez, & Sergio, 2007). This function in nocturnal invertebrates, however, has received little attention.

Spiders use a variety of signals in their reproductive behavioural interactions (Uhl & Elias, 2011). For example, orb web spiders (araneids) use sex pheromones (Chinta et al., 2010), wolf spiders (lycosids) use seismic cues (Hebets, Elias, Mason, Miller, & Stratton, 2008; Uetz, Roberts, & Taylor, 2009) and jumping spiders (salticids) use vision (Girard, Kasumovic, & Elias, 2011; Lim, Land, & Li, 2007). However, visual cues used in female mate choice have rarely been reported in nocturnal spider species. Morphological and anatomical evidence suggests that some species, such as the tiger spider, *Cupiennius salei* (Araneae: Ctenidae), have colourful hair and good vision at night (Barth, 2002; Barth, Nakagawa, & Eguchi, 1993; Grusch, Barth, & Eguchi, 1997; Walla, Barth, & Eguchi, 1996). The eyes of *C. salei* are sensitive enough to enable the spider to see not only shortly after sundown but even under considerably dimmer conditions, such as moonlight (Barth, 2002; Barth et al., 1993).

To date, very few studies have explored the role of body coloration in the courtship of spiders at night. Lin, Zhang, Liao, Hebets, & Tso (2015) reported that the conspicuous white stripes on the cephalothorax of males in the nocturnal, semiaquatic fishing spider *Dolomedes raptor* (Araneae: Pisauridae) have an important function

* Correspondence: I.-M. Tso, Department of Life Science, Tunghai University, Taichung, 40704, Taiwan.
E-mail address: spider@thu.edu.tw (I. -M. Tso).

https://doi.org/10.1016/j.anbehav.2018.06.016
0003-3472/

in their courtship. Males with intact white stripes were significantly more likely to be accepted by females than those with the white stripes experimentally removed. Although this study experimentally demonstrated that conspicuous body parts did affect mating success, there is still no empirical evidence unambiguously demonstrating that vision plays a key role in the courtship of nocturnal arthropods. As many wandering spiders typically use multimodal signals to communicate (Stoffer & Uetz, 2017; Uetz et al., 2015; Uhl & Elias, 2011), it is difficult to determine how important vision is for the nocturnal species without manipulating visual abilities.

The nocturnal brown huntsman spider, *Heteropoda venatoria* (Araneae: Heteropodidae), has a conspicuous moustache-like white stripe on its forehead (i.e. the clypeus, Fig. 1a and b). This spider can perceive its surroundings over a very large visual angle (almost 360°), as studies have shown that its multiple eyes have different fields of view (Lorenz, 2012). It forages on tree trunks, rocks and the walls of human houses, with mating usually occurring under dim light conditions on exposed surfaces (S. Zhang, personal observation). Although Zhang et al. (2015) demonstrated that conspicuous body parts served as a visual lure to attract nocturnal prey, it remains speculative whether these traits are also used in courtship. In pilot experiments, we observed that when a male *H. venatoria* courted a female, he closely approached her and displayed his conspicuous white stripe. We hypothesized that the conspicuous coloration on the 'face' area of *H. venatoria* is a 'sexy' character that influences mate choice in females. To test this hypothesis, we conducted behavioural assays in the laboratory. We manipulated the presence of the male's white stripe as well as the visual abilities of females. We monitored reproductive behavioural interactions of manipulated and control individuals to investigate the role of female vision and male body coloration in the courtship of this nocturnal arthropod.

METHODS

Spiders and Maintenance

The *H. venatoria* individuals used in our experiments were collected as subadults from the Tunghai University campus (120°9′56″E, 24°18′00″N) and 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). They were kept in the laboratory until maturity. We housed them individually in plastic containers (ca. 2 litres) fitted with mesh covers. They were watered and fed with one cockroach (body length ca. 1.5 cm) daily. All spiders were kept in the laboratory under controlled environmental conditions (temperature: 25 ± 1 °C; relative humidity: 80 ± 10%; photoperiod: 12:12 h light:dark with lights on between 0800 and 2000 hours). All the spiders used in the experiments were virgin, and they were used only once. Body length and body weight of each spider were measured before the experiment. The female–male body length ratio and female–male body weight ratio of each pair were also calculated.

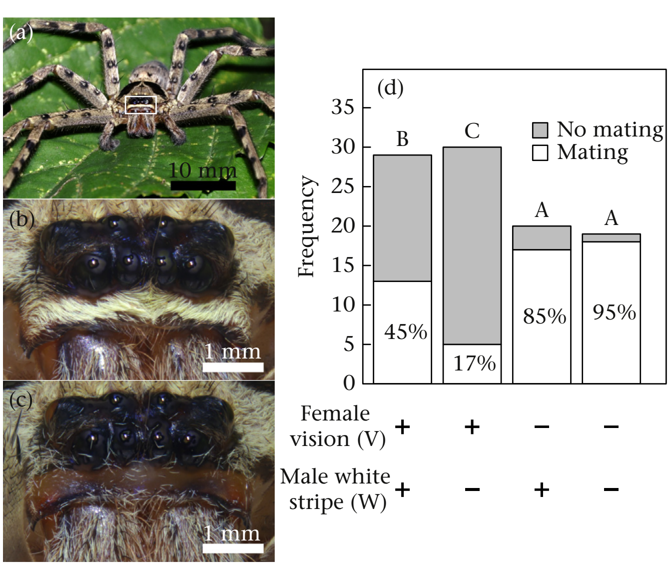

Figure 1. (a) Male brown huntsman spider, *Heteropoda venatoria* (the white stripe is highlighted). (b) Male spider with white stripe. (c) Male spider with white stripe removed. (d) Mating success of males in different groups. Uppercase letters indicate the rank (from A to C) of probability of mating success, which is determined by multiple comparisons with the *P* value corrected by the Holm–Bonferroni method.

Mating Trials

To examine the importance of the conspicuous white stripe during mating, we performed mating trials using manipulated males and females, which were conducted at night in dim light in the laboratory. We randomly divided the spiders into an experimental and a control group. Males in the experimental group were anaesthetized with CO_2 and placed on a foam platform where their white stripes were carefully removed with a razor blade under a dissecting microscope (Zhang et al., 2015). Males in the control group were also anaesthetized with CO_2 and their white stripes were carefully scraped with the blunt side of the blade so as not to harm the spiders (Zhang et al., 2015; Fig. 1c). Females in the experimental group were anaesthetized with CO_2 and their eyes were covered with black paint. For the control group, we applied water to the females' eyes, in an equal quantity to the paint used in the experimental group, and black paint on their cephalothorax to control for the potential effect of paint odour. Four groups were set up: (1) females with vision blocked (V-) and males with an intact white stripe (W+) ($N = 20$); (2) females with vision blocked (V-) and males with white stripe removed (W-) ($N = 19$); (3) females with intact vision (V+) and males with white stripes (W+) ($N = 29$); (4) females with intact vision (V+) and males with their white stripe removed (W-) ($N = 30$). Manipulated spiders were put back in their containers and allowed to acclimate for half an hour prior to mating trials. If a spider was hurt during manipulation, and haemolymph bled out, it displayed behaviours indicative of physiological stress such as constant motion, biting anything presented or even death. When a manipulation was successful, the spider remained calm, but still displayed normal avoidance behaviours when disturbed with a fine brush. Only individuals that did not display stress-related behaviours were used in the experiment.

We used a large glass tank (100 × 50 cm and 50 cm high) as the mating arena. To reduce potential seismic cues that the courting males may send to females, we covered the inner wall of the container with soft foam panels, 2 cm thick, made of soft sponge. Females and males were matched only when their body length ratio was between 0.9 and 1.5. However, a few exceptions ($N = 10$) to this criterion were made as not enough matching spiders were available. During mating trials, we positioned a female in a corner of the arena and, 15 min later, we introduced a male into the arena 20 cm away from her. The arena was covered with plastic wrap to prevent the spiders from escaping. All the events occurring in the arena were recorded by an infrared video camera (Sony HDR-CX720V, Tokyo, Japan) placed ca. 1 m from the arena with the observer standing ca. 2 m away to avoid disturbing the spiders. We measured the light intensity of the natural mating habitat of the spiders to be about 2 lm at full moonlight and less than 1 lm at other moon phases. We set up the light intensity of mating trials in