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Tai-Shen Lin

Tunghai University, Taichung, Taiwan

Shichang Zhang

Tunghai University, Taichung, Taiwan

Chen-Pan Liao

Tunghai University, Taichung, Taiwan

Eileen A. Hebets

University of Nebraska-Lincoln, ehebets2@unl.edu

I-Min Tso

Tunghai University, Taichung, Taiwan, spider@thu.edu.tw

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A dual function of white coloration in a nocturnal spider *Dolomedes raptor* (Araneae: Pisauridae)

Tai-Shen Lin,¹ Shichang Zhang,¹ Chen-Pan Liao,¹ Eileen A. Hebets,² and I-Min Tso^{1,3}

¹ Department of Life Science, Tunghai University, Taichung, Taiwan

² School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE, USA

³ Center for Tropical Ecology & Biodiversity, Tunghai University, Taichung, Taiwan

Correspondence — I-Min Tso, Department of Life Science, Tunghai University,
Taichung 40704, Taichung, Taiwan; email spider@thu.edu.tw

Abstract

Nocturnal animals frequently possess seemingly conspicuous color patterns that can function in a variety of ways (e.g. prey attraction, camouflage, predator avoidance, etc.). The use of color patterns in intraspecific signaling, especially reproductive activities, in nocturnal animals has received relatively little attention. This study tested for a dual function of color in the nocturnal fishing spider, *Dolomedes raptor* (Araneae: Pisauridae), whose males develop dimorphic white stripes at sexual maturation. We tested for a role in foraging as well as mate assessment. First, quantifications of the natural variation of male stripes indicated a correlation between stripe area and male body size and weight. Subsequent diet experiments confirmed that the area of a male's white stripes are body size-dependent and thus could potentially convey information to choosy females about male quality. Field experiments used dummies resembling *D. raptor* in appearance to test a prey attraction function of the white stripes. We found that dummies with the white stripes present attracted significantly more prey than those without stripes. Finally, we used males with manipulated phenotypes in laboratory mating trials and found that males with intact white stripes were significantly more likely to be accepted by females than those with the white stripes eliminated. Together, our results document a nutrient-dependent trait that functions not only in strengthening foraging success, but also in a mating context, increasing male mating success. We suggest that the role of these male white stripes in reproduction has been facilitated by their function in foraging.

Keywords: *Dolomedes raptor*, nocturnal animal, sexual selection, visual signal, wandering spider

The elaborate coloration and intricate visual patterns found in many animal groups have inspired artists and intrigued scientists for centuries (Andersson, 1994). While aesthetically often utterly captivating, these colors and patterns can have very distinct functions. For example, aposematic coloration in some animals can be used to warn off predators (Stevens & Ruxton, 2012). The “eye spots” in the wings of some caterpillars can startle or intimidate predators (Kodandaramaiah, 2011; Stevens, 2005) or deflect attacks by predators to less vulnerable body parts (Prudic, Stoeck, Wasik, & Monteiro, 2015). Another example is aggressive mimicry, in which the color pattern closely mimics certain visual signals that can be used by some animals to lure prey (O’Hanlon, Holwell, & Herberstein, 2014; Pietsch & Grobecker, 1978). Alternatively, elaborate visual components can function in reproduction, such as for attracting mates (Gómez et al., 2009; Lim, Land, & Li, 2007). The visual signals used in mate attraction are often sexually dimorphic, with the most striking of these secondary

sexual traits typically observed in diurnally active males (Maynard Smith & Harper, 2004).

While not as immediately conspicuous or obvious to us, due, in part, to our diurnal nature, nocturnal animals also possess coloration and/or other visually conspicuous traits (Gómez et al., 2009; Penteriani, del Mar Delgado, Alonso-Alvarez, & Sergio, 2007). For example, many nocturnal animals, or those living in consistently dark environments, produce and emit bioluminescence (Broadley & Stringer, 2001; Lloyd, 1971). Bioluminescence, a phenomenon in which animals produce light by themselves rather than reflecting light from external sources, is taxonomically widespread, as it is seen in numerous marine vertebrates and invertebrates, fungi, some bacteria and fireflies (Widder, 2010; Widder, Latz, Herring, & Case, 1984). The many functions of bioluminescence include mimicry, camouflage, distraction, warning and even attracting mates (Haddock, Moline, & Case, 2010; Lloyd, 1971; Widder, 2010). In addition to bioluminescence, recent studies have

shown that nocturnal animals may use color signals in activities such as claiming advantage in male–male combat (e.g. eagle owl, *Bubo*, Penteriani et al., 2007; frog, *Phyllomedusa boliviana*, Jansen & Köhler, 2008), defense (e.g. glow-worm, *Lampyris noctiluca*, De Cock & Matthysen, 2003; *Motyxia* millipedes, Marek, Papaj, Yeager, Molina, & Moore, 2011), prey attraction (e.g. glow-worm, *Arachnocampa luminosa*, Broadley & Stringer, 2001) and predator avoidance (e.g. leiognathid fish, McFall-Ngai & Morin, 1991). However, color signals used in the context of reproduction of nocturnal organisms have not been widely reported (Gómez et al., 2009; Lewis & Cratsley, 2008). Recently, it was reported that in the Neotropical spider *Paratrechalea ornata* (Trechaleidae) males were more attractive to females when the chelicerae of the males were painted white, implying that conspicuous visual signals can be detected and may also play roles in the mating of nocturnal arthropods (Trillo, Melo-González, & Albo, 2014).

Perhaps surprising to some, spiders are among the many taxonomic groups that possess extraordinary sexual dimorphism, with males of some species exhibiting colorful bodies and leg ornaments in addition to elaborate dynamic motion displays (Framenau & Hebets, 2007; Hebets & Uetz, 2000; Uhl & Elias, 2011). Salticids (jumping spiders), for example, can use sex-specific visually mediated displays to court females (Li et al., 2008; Lim et al., 2007; Lim, Li, & Li, 2008). Members of the diurnally active and diverse genus *Habronattus* (ca. 100 species) are well known for their elaborate male secondary sexual traits which include spectacular color patterns, morphological “ornaments” and complex courtship displays (Elias, Maddison, Peckmezian, Girard, & Mason, 2012; Girard, Kasumovic, & Elias, 2011). It has been known in sexually dimorphic animals that diet is closely related to the attractiveness of the sexual traits that are preferred by females when choosing a mate (Ferkin, Sorokin, Johnston, & Lee, 1997; Hill, 1992; McGlothlin, Duffy, Henry-Freeman, & Ketterson, 2007). Related studies in spiders, however, have rarely been reported. Hebets, Wesson, and Shamble (2008) found in *Schizocosa* wolf spiders that males receiving a high-quality diet matured more quickly and were significantly larger as adults than those receiving a low-quality diet, and high-quality diet males had larger sexual traits and were more successful in courting females than low-quality diet males. Yet, it is unknown whether, in nocturnal organisms, diet would influence physical condition and potential sexual traits.

The conspicuous body coloration of spiders not only plays roles in sexual selection, but also functions in foraging, for instance as a prey lure. For example, the brightly colored body parts of the giant wood spider, *Nephila pilipes*, have been shown to function as a visual lure for attracting both diurnal and nocturnal prey (Chuang, Yang, & Tso, 2007). The conspicuous yellow ventral spots in the garden spider, *Neoscona punctigera*, can also lure prey at night (Blamires et al., 2012). Aside from these examples, the role of conspicuous coloration in luring prey at night has not been well studied or known in nocturnal cursorial arthropods.

The fishing spider, *Dolomedes raptor* (Araneae: Pisauridae), like most members of its genus, is a nocturnal wandering species inhabiting low-altitude streams. These nocturnal predators prey on aquatic and semiaquatic invertebrates and vertebrates (Bleckmann & Lotz, 1987; Zimmermann & Spence, 1989). The species exhibits dramatic sexual color dimorphism, with mature males displaying two white stripes at the two margins of the cephalothorax (Figure 1a). Females lack these white stripes, but they do possess white spots at the tips of their legs, especially the anterior two pairs (Figure 1b). The presence of white coloration in both sexes suggests a potential function in prey attraction, while the distinct placement of coloration in males in combination with their courtship advances hints towards a role in courtship communication. Here, we hypothesized that the bright white patch on the body of male *D. raptor* plays important roles in both foraging

Figure 1. (a) Male and (b) female *Dolomedes raptor* showing their dimorphic body coloration patterns.

(i.e. prey attraction) and sexual selection (i.e. a sexual character in female mate assessment). To test these two hypotheses, we first quantified the natural variation in color patterns of males that were collected from the field. We next conducted diet experiments in the laboratory to test whether the color pattern was nutrition dependent and thus potentially capable of conveying information about a male's past foraging history. Then, we conducted field observations using different dummies that resembled male *D. raptor* in size and color. Finally, we conducted mating trials using manipulated males. We predicted that dummies with the color pattern would attract more prey and males with the color pattern would be more successful in mating.

Methods

Natural Variation in Male Coloration

The white stripes on the males are composed of tiny white hairs. To determine the natural variation in the area of these white stripes, we collected males ($N = 32$) at low-altitude streams near Dongshi Forest Recreation Area in Dongshi, Taichung city, Taiwan ($120^{\circ} 52' 03.96''$ E, $24^{\circ} 17' 06.78''$ N) and brought them back to the laboratory in Tunghai University. To measure the area of white stripes on the carapace, we first anaesthetized the spiders with carbon dioxide and then used a digital camera (Olympus m1030 SW) to take images of the spiders. We used GIMP2 software (www.gimp.org) to measure the foreleg length, carapace length, carapace width and the area of the white stripe on the cephalothorax. The body weights were also measured. We then calculated the standard scores (i.e. [variable – mean variable]/standard deviation of variable) for these variables. To check the relationship between white stripe area and body condition (i.e. body size and weight), we first applied a principal component analysis (PCA) based on the standard scores of four body characteristics (carapace length, carapace width, foreleg length and

spider weight). Then, we calculated the score of 'body size and weight' by extracting the first principal components of the PCA analysis. Finally, we fitted the white stripe area with the 'body size and weight score' using a simple linear regression. Using the same method, we also calculated the score of 'body size' using variables such as carapace length, carapace width and foreleg length. We then fitted the white stripe area with 'body size score' using a quadratic regression to calculate the residuals. Finally, we fitted the white stripe area with these residuals by using a simple linear regression.

To investigate whether the brightness of the white stripe correlated with spider body size and weight, we first measured the reflectance spectra of 32 mature males using the following equation:

$$\text{white stripe brightness} = \int_{300 \text{ nm}}^{700 \text{ nm}} S \, d\lambda$$

where S is the reflectance spectra (%) of the white stripe and λ is wavelength (nm). We fitted the white stripe brightness with "body size and weight score" as well as "residual of spider weight against body size score" by using simple linear regressions. The normality of the residuals of the linear regression was checked by the Shapiro–Wilk normality test, while the homoscedasticity of the variance of the residuals was checked by the White's test.

Nutrition Dependence of Male Coloration

Sexual traits are often closely associated with body condition of mate-searching individuals (Andersson, 1994) and our aim here was to determine whether the white stripes on male *D. raptor* were nutrition dependent. To achieve this, subadult males were subjected to different levels of nutrient intake to see whether such treatments would affect the area of white stripes when the spiders matured. We collected juvenile males from the study site in Dongshi, Taichung city, Taiwan and raised them individually to the subadult stage by giving them one cricket (*Acheta bimaculata*; body length ca. 10 mm) once a week. Before the nutrition manipulation, we measured the body weight and white stripe area of subadults and randomly assigned them to high-nutrition (fed one cricket every 2 days; $N = 19$) and low-nutrition (fed one cricket every 7 days; $N = 12$) treatments. When the spiders matured, we measured the body weight, white stripe area and number of days taken to reach maturity. The white stripe area of males in the two treatment groups was compared by a general linear model in which the nutrition treatment, spiders' pre-treatment white stripe area and the interaction term were considered. The homogeneity assumption of the model was checked by a Bartlett's test, and we found that the variances among the four treatments were not (but very close to) significantly different. Shapiro–Wilk normality tests showed that the variables in the two groups were normally distributed, so we used a Welch two-sample t test to compare the number of days taken to reach maturity of males in the two treatment groups.

Prey Attraction Function of Male Coloration

To investigate the function of the white stripes on males' bodies, we first tested the hypothesis that white stripes may function in prey attraction. We conducted field observations using dummies that resemble male *D. raptor* in size and color. We measured the chromatic properties of selected brown and white dummy construction paper across a 300–700 nm spectrum using a USB4000 spectrophotometer (Ocean Optics, Dunedin, FL, U.S.A.; Chuang, Yang, & Tso, 2008). The spectral properties across a 300–700 nm

spectrum were also measured for the body (legs, palps, carapace and abdomen) and the white stripe of live adult male *D. raptor* collected from Dongshi ($N = 5$) so as to compare spectral properties between corresponding dummy and live spider body parts.

The dummies were divided into two groups: control group (with white stripes, $N = 35$) and experimental group (without the white stripes, $N = 46$). In the control group, stripes made from white paper were pasted onto the cephalothorax region, while in the experimental group, only the glue that was used to paste the white stripes was applied on that region (Appendix Figure A1). Field experiments were conducted between 28 August and 1 September in 2009 and between 17 and 24 July in 2010 at the study site where we collected *D. raptor*. The habitat is characterized by the presence of many rocks (20–40 cm in diameter) along the banks of calm streams with slow water flow and relatively closed canopy. In the field, male *D. raptor* were frequently observed perching on the rocks. Therefore, we randomly chose rocks of similar size and placed two types of dummies on them alternately. Video cameras with infrared night view scopes (Sony SR-100 and SR-62, Tokyo, Japan) were placed approximately 1 m from each dummy to monitor them from 2000 to 0400 hours each night. The video footages were viewed in the laboratory in Tunghai University to check for events such as prey attraction and predator attraction. An "attraction" event was defined as an insect approaching directly within 5 cm of a dummy. We defined prey attraction rate as the number of prey approaching events per hour of footage. A negative binomial regression was used to compare the prey attraction rates of two types of dummies.

Reproductive Function of Male Coloration

Finally, we tested the hypothesis that the white stripes of males were involved in reproductive behavior and thus would affect a male's courting success. We collected subadult males and females from the study site in Dongshi, Taichung city, Taiwan and each spider was individually raised in a Plexiglas container (30 × 15 cm and 18 cm high). The bottom of the container was submerged in 2 cm of water (water changed once a week) and a sponge was placed for the spider to perch on. Opaque plastic sheets were placed between containers to prevent visual contact between individual spiders. We fed spiders one cricket (*A. bimaculata*, body length ca. 10 mm) once a week until they reached maturity. The age of spiders used in the experiment was no more than 1 month after sexual maturity.

We randomly assigned mature males into two groups. Males in the experimental group were manipulated by covering the white stripes with brown paint with a reflectance spectrum similar to that of the spiders' brown body color (Appendix Figure A2). For males in the control group, we applied the same amount of brown paint on the brown part of the cephalothorax. All the spiders were used only once to exclude the potential influence of prior experience. A glass terrarium (30 × 30 cm and 15 cm high) with a cylindrical stage and plastic board at the bottom was used as the arena for mate choice trials. The arena was covered by a piece of glass to prevent the spiders from escaping during the experiments. In each trial, a female was first introduced to the arena for 1 h to let it adapt to the environment and produce dragline silks, which may contain sex pheromones, and then a male was introduced to the arena. The behaviors and interactions of the spiders were recorded by infrared video cameras. Preliminary experiments showed that the courtship of a male *D. raptor* includes the following four steps: (1) following female's dragline; (2) waving forelegs; (3) tapping female's legs; and (4) climbing onto female's back. It has been reported that vibratory signals (transmitted by water surface wave) play roles in the courtship of *Dolomedes* spiders (Arnqvist, 1992; Bleckmann & Bender, 1987;

Roland & Rovner, 1983). Thus, to differentiate the role of the visual signal, we did not provide water in the arena for the spider to generate vibratory signals. We considered courtship successful when a male was able to climb onto a female's dorsum without being kicked off or cannibalized. A permutation Pearson chi-square test of homogeneity was used to compare the courtship success of male *D. raptor* receiving different treatments. All statistical tests were carried out in the R programming environment version 3.1.2 (R Core Team, 2014). A general linear mixed model was fitted by using an R package lmerTest version 2.0-20 (Kuznetsova, Brockhoff, & Christensen, 2014).

Ethical Note

To minimize adverse impacts on their welfare, we treated the spiders gently during the experiment and released them afterwards to their original habitat. The experimental procedures strictly adhered to the "research ethics and animal treatment" legal requirements of Tunghai University.

Results

Natural Variation in Male Coloration

In the field, body size, body weight and white stripe area of mature males varied considerably. The white stripe area was significantly and positively correlated with body size and weight score (Figure 2a, Appendix Table A1). This result indicated that the white stripe area can be used as an indicator of spider body size and weight. Spider weight was highly correlated with spider size ($R^2 = 0.954$, $P < 0.0001$; Figure 2b, Appendix Table A1). However, the white stripe area was not significantly correlated with the residual of spider weight against body size score (Figure 2c, Appendix Table A1). This result indicated that, after we controlled for the spider body size, the spider body weight cannot predict the white stripe area. The residuals of the simple linear regression were all normally distributed, and the variances of these residuals were all homogeneous.

Neither the "body size and weight score" nor the 'residual of spider weight against body size score' was significantly correlated with white stripe brightness (Appendix Figure A3, Table A2). These results showed that the white stripe brightness cannot be predicted by raw/standardized spider size.

Nutrition Dependence of Male Coloration

We found no significant difference in the stripe area of the two groups of spiders before the nutrition manipulation (Figure 3, Appendix Table A3). However, the stripe area of spiders in the two groups varied greatly after the treatments. Males receiving the high-nutrition treatment ($N = 19$) molted faster ($t_{14} = -6.36$, $P < 0.001$; Appendix Figure A4) and had larger white stripe areas than those receiving the low-nutrition treatment ($N = 12$; Figure 3, Appendix Table A3). These results indicate that the white stripe area can reflect the feeding history of adult males.

Prey Attraction Function of Male Coloration

From field experiments conducted in 2009 and 2010, more than 600 h of video footage were obtained. A preliminary analysis showed no significant difference between results obtained from the 2 years, so we pooled the 2009 and 2010 data. A Pearson goodness-of-fit chi-square test showed that the prey attraction data fitted well with a negative binomial model ($\chi^2_{79} = 86.15$, $P = 0.273$). Results of a negative binomial regression showed that dummies with white stripes attracted significantly more prey than those without (Figure 4a, Appendix Table A4).

Figure 2. Relationships between (a) white stripe area and body size and weight score, (b) spider weight and spider body size score, and (c) white stripe area and residual of spider weight against body size score of adult males collected from the field.

Reproductive Function of Male Coloration

In the laboratory, 29 mating trials were performed ($N = 14$ for males without white stripes and $N = 15$ for males with white stripes). Males in the two groups did not differ significantly in their body weight (t test: $t_{27} = 0.366$, $P = 0.718$). Males with white

Figure 3. White stripe area of male *D. raptor* before (pretest) and after (post-test) receiving low-nutrition ($N = 12$) and high-nutrition ($N = 19$) treatments. $**P < 0.01$.

Figure 4. (a) Mean $\pm$ SE prey attraction rates (number of prey attracted per hour of monitoring) of dummies in experimental (white stripe removed, $N = 46$) and control (white stripe present, $N = 35$) groups. *** $P < 0.001$. (b) Courting success rates of male *D. raptor* in the experimental (white stripes covered by paint, $N = 14$) and control (paint on brown part, $N = 15$) groups. * $P < 0.05$.

stripes were more likely to be accepted by females (control group: 13 of 15) than those in which the white stripes were covered up (experimental group: 6 of 14; $\chi^2_1 = 6.152$, simulated $P = 0.021$, based on 5 000 000 replications; Figure 4b). Males without white stripes had a high probability of being rejected or attacked by females (8 of 14, 57%).

Discussion

This study empirically shows that color signals in the nocturnal predatory spider *D. raptor* have a dual function, foraging and reproduction. The nutrition-dependent white stripes on male *D. raptor* appear to function in both courtship success and prey attraction. The increased prey attraction of spider dummies with versus without white stripes suggests their role in prey attraction while the finding that males with white stripes were more likely to be accepted by females indicates that this conspicuous body color probably serves as a visual-based sexual signal, a rarely documented phenomenon in animals active at night. In this paper, we used the term “conspicuous” to describe the color pattern of the body of the spiders, because the reflectance of the white part (above 40%) is much higher than that of other parts of the body (around 5%; Appendix Figure A2). However, the visual systems of humans and arthropods are very different (Endler, 1990), so the conspicuousness of color patterns under the two systems may be different as well, especially in dim light conditions. However, the results of our dummy experiments showed that the sharp contrast between the white and brown body parts did attract the attention of prey insects. Therefore, we may safely state in this case that the color pattern is highly visible to these organisms.

In many nocturnal animals, intraspecific communication under dim light conditions relies on pheromones (e.g. moths and rodents, Wyatt, 2014), acoustic signals (e.g. crickets and frogs, Searcy & Andersson, 1986), ultrasound (e.g. bats, Pfalzer & Kusch, 2003) or bioluminescence (e.g. fireflies, Lewis & Cratsley, 2008). Nocturnal spiders have been previously reported to employ mainly acoustic signals (e.g. percussion and stridulation in wolf spiders; Hebets & Uetz, 2000) and pheromones (Gaskett, 2007) in intraspecific communication. The documented dual function of male white stripes in *D. raptor* suggests that this prey attraction signal might have been co-opted for a communicative function in reproductive behavior.

The potential role of visual signals in the courtship of nocturnal animals has not been extensively explored, except in fireflies (Lewis & Cratsley, 2008). In addition to a prior study on a tree frog (Gómez et al., 2009), our present study on the fishing spider *D. raptor* suggests that color signals may be more broadly employed in the courtship of nocturnal animals than previously appreciated. Numerous nocturnal animals have good color vision and color cues have been demonstrated to be important in nonreproductive aspects of their lives, such as foraging (Kelber, Balke, & Warrant, 2002), navigation (Warrant & Dacke, 2011) and mutualistic interaction (Peng, Blamires, Agnarsson, Lin, & Tso, 2013). However, so far it is unknown whether in nocturnal animals a conspicuous body color can serve as disruptive coloration under dim night conditions. In theory, the contrasting colors can enhance the disruptive effect (Cuthill et al., 2005), which may enable these nocturnal species to avoid attack from their predators. Therefore, we expect that, as more effort is invested in studying the roles of body color of nocturnal animals, the findings may dramatically change our perspective regarding the nature of interspecific and intraspecific interactions at night.

The results of our study suggest that the conspicuous white stripes in male *D. raptor* may represent a reliable visual indicator of feeding history and body size/weight, and may be a visual signal used by females during mate assessment. Exaggerated sexual traits of males may be favored by females because they may reflect the survival or competitive capacities of the owner (Emlen, 2008; Emlen, Warren, Johns, Dworkin, & Lavine, 2012). In diurnal animals, the physical form of traits that may convey increased survival or competitive capacities are very diverse, with visual signals employed in many organisms (Andersson, 1994). In contrast to diurnal animals, previously documented sexually selected traits associated with male quality in nocturnal animals have typically been acoustic or chemical in nature (Fisher, Swaisgood, & Fitch-Snyder, 2003; Márquez, Bosch, & Eekhout, 2008). Our study, however, documented a clear example in which the white stripe area of male *D. raptor* in the field varied considerably, yet was closely associated with body size/weight. Indeed, our manipulations showed that nutrition could influence a male's time to maturation as well as the area of his white stripes, with high nutrition males displaying larger white stripe areas than low nutrition males. It is currently unknown whether females are inclined to choose males with larger white stripes when they are given multiple options and research examining the preference of females for males with different sizes of white stripe is needed.

Our field experiment using dummies showed that the white stripes on male *D. raptor* can attract prey, implying that this conspicuous color signal has a foraging function. Conspicuous body coloration has recently been reported to function as a prey lure in nocturnal web-building spiders, such as *N. pilipes* (Chuang et al., 2007) and *N. punctigera* (Blamires et al., 2012). In these spiders, coloration can apparently increase foraging success (i.e. increase the interception rate of the web) by attracting prey such as moths (Blamires et al., 2012; Chuang et al., 2008). The conspicuous body color of these nocturnal web-building spi-

ders, however, is unlikely to also have a sexual function because males of these species are very myopic and dull in color (Land, 1985). Therefore, the role of conspicuous body coloration in orb-weaver spiders seems restricted to prey attraction.

In Araneae, the true spiders, species using conspicuous body color in sexual activities have been mostly reported in the RTA (retrolateral tibial apophysis) clade, such as spiders in the family Lycosidae (Hebets & Uetz, 1999) and Salticidae (Lim et al., 2007), taxonomic groups that also have good vision. We suspect that in Pisauridae fishing spiders (also an RTA taxon), the prey-attracting conspicuous body color may be endowed with a sexual function in accordance with the evolution of good nocturnal visual ability in these spiders, a hypothesis that requires additional testing. Regardless, the sexually dimorphic white stripes on mature males appear to function in mate attraction, suggesting that females at least have the perceptual capacity to assess this trait. While comparative work would be necessary to test this, we propose that the white coloration on female and male *D. raptor* evolved initially in a prey attraction context and then this coloration was co-opted for a role in male courtship and female assessment. Examples such as this of dual-function signals can help us understand the evolutionary history and current functions of animal displays.

Although the conspicuous visual signal of white stripes appears important for courting males, nothing is yet known of any costs they might incur. Bright signals, even in nocturnal animals, can be exploited by potential predators and parasitoids (Zuk & Kolluru, 1998). For example, the aquatic wasp, *Anoplius depressipes*, can actively search for *Dolomedes* spiders that hide inside the curled-up leaves of water lilies (Roble, 1985) and vertebrate predators with relatively good low-light vision such as fishes and frogs also pose a large threat to fishing spiders (Suter, 2003). In this particular system, these trade-offs would be especially complex as the presence/absence of white stripes influences foraging success, which in turn influences the size of the white stripes, which then influences a male's mating success. Studies exploring the evolutionary and functional interplay between all of these interactions would be illuminating.

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Appendix

Table A1. Results of simple linear regression (SLR) between different spider body parameters

SLR analysis	Coefficient	Estimate	SE	<i>t</i>	<i>df</i>	<i>P</i>
White stripe area against body size and weight score	DV: white stripe area (cm ²)					
	Intercept	0.0778	0.0012	65.04	30	< 0.0001
	Body size and weight score	0.0120	0.0006	19.74	30	< 0.0001
Spider weight against body size score	DV: spider weight (g)					
	Intercept	0.2227	0.0063	35.276	29	< 0.0001
	Body size score	0.0599	0.0025	23.930	29	< 0.0001
	(Body size score) ²	0.0041	0.0016	2.592	29	0.015
White stripe area against residual of spider weight against body size score	DV: white stripe area (cm ²)					
	Intercept	0.0778	0.0045	17.420	30	< 0.0001
	Residual of spider weight against body size score	0.0609	0.1945	0.313	30	0.756

Table A2. Results of simple linear regression (SLR) between the brightness of the white stripe area and the body size or the residual of spider weight against body size score

SLR analysis	Coefficient	Estimate	SE	<i>t</i>	<i>df</i>	<i>P</i>
White stripe brightness against body size and weight score	DV: white stripe brightness					
	Intercept	24,949.4	552.3	45.175	30	< 0.0001
	Body size and weight score	236.8	279.9	0.846	30	0.404
White stripe brightness against residual of spider weight against body size score	DV: white stripe brightness					
	Intercept	24,949.4	540.6	46.150	30	< 0.0001
	Residual of spider weight against body size score	33,757.9	23,540.9	1.434	30	0.162

Table A3. Results of a general linear mixed model comparing the white stripe area of males receiving different nutrition treatments

Coefficient	Estimate	SE	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	0.06680	0.004018	16.627	< 0.0001	< 0.0001
β_1 [posthigh vs postlow]	0.02331	0.008377	33.96	2.783	0.009
β_2 [prehigh vs prelow]	-0.001273	0.008377	33.96	-0.152	0.880
β_3 [(prehigh + prelow)/2 vs (posthigh + postlow)/2]	-0.04477	0.002367	28.63	-18.91	< 0.0001

The nutrition treatment, spiders' pretreatment white stripe area and the interaction term were considered in this model.

Table A4. Results of negative binomial regression comparing the prey attraction rates of dummies of the experimental (white stripes removed) and control group (white stripes intact)

Coefficient	Estimate of β	SE	<i>Z</i>	<i>P</i>
Intercept	-0.9913	0.1795	-5.522	< 0.0001
Treatment* (Experiment vs control)	-1.0592	0.2691	-3.9368	< 0.0001

* The ratio between probabilities of two certain events was e^β .

Figure A1. A schematic drawing of dummies used in (a) control (white stripes present) and (b) experimental (white stripes absent) groups.

Figure A3. Relationships between the white stripe brightness and (a) “body size and weight score” and (b) “residual of spider weight against body size score.”

Figure A2. (a) The reflectance spectra of the brown region of male *D. raptor*, the brown paper used to construct dummies and the brown paint used to alter the color signal of white stripes. (b) The reflectance spectra of the white stripes of male *D. raptor* and the white paper used to construct white stripes on dummies.

Figure A4. Mean + SE number of days taken to reach maturity of subadult males receiving high-nutrition ($N = 19$) and low-nutrition ($N = 14$) treatments. *** $P < 0.001$.