



Prey Luring Coloration of A Nocturnal Semi-Aquatic Predator

I-Min Tso^{*†}, Shichang Zhang^{*}, Wei-Li Tan^{*}, Po Peng^{*} & Sean J. Blamires^{*‡}

^{*} Department of Life Science, Tunghai University, Taichung, Taiwan

[†] Center for Tropical Ecology & Biodiversity, Tunghai University, Taichung, Taiwan

[‡] Evolution & Ecology Research Centre, School of Biological, Earth & Environmental Sciences, The University of New South Wales, Sydney, NSW, Australia

Correspondence

Sean J. Blamires, Evolution & Ecology
Research Centre, School of Biological, Earth
& Environmental Sciences, The University of
New South Wales, Sydney, NSW 2052,
Australia.
E-mail: s.blamires@unsw.edu.au

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Abstract

Body coloration serves a variety of purposes in animals. Diurnal and nocturnal predators such as spiders may use their body coloration to lure prey. We predicted here that the white patches on the forelegs on females of the nocturnal semi-aquatic spider *Dolomedes raptor* lure prey, explaining why they are primarily displayed when the spider forages along the water edge. To test our prediction, we developed a color vision model assessing whether the patches are visible to pygmy grasshoppers, the spider's primary prey. We conducted a field experiment using cardboard dummies that resemble *D. raptor* in size, shape, and color, but with half of them lacking leg patches, and we staged interactions between pygmy grasshoppers and *D. raptor* with and without leg patches in a greenhouse. We found the white patches to be visible to grasshoppers. The dummies with white patches attracted more grasshopper prey than the dummies without the patches. Moreover, grasshoppers were more attracted to spiders when their white patches were present. Our results supported the hypothesis that the white patches of *D. raptor* lure prey. Our findings, nevertheless, could not be explained as the spider's body coloration acting as a sensory trap but it should not be ruled out. More studies on a wider range of predators and prey will give more meaningful insights into the co-evolution of predatory lures and prey sensory modalities.

Introduction

Animals use body coloration for a variety of purposes including concealment, background matching, Batesian and Müllerian mimicry, masquerade, startle, deterrence, sexual signaling, and as visual lures (Ortolani 1999; Ruxton et al. 2004; Stevens & Merilaita 2009; Stevens 2013; White & Kemp 2015). While the vast majority of animals use body coloration to attract mates or deter, distract, or hide from predators (Ortolani 1999; Stevens et al. 2006; Stevens & Merilaita 2009; Stevens 2013), some predators use their body colors to attract prey (Ortolani 1999; Hagman et al. 2008; Wizen & Gasith 2011; Stevens 2013). As counter-selection on prey to avoid predator lures is strong (Magalhães et al. 2005; Moran et al. 2012; Stevens 2013; White & Kemp 2015), the use of body coloration by predators to attract prey would only be

sustainable if the predator exploits a visual bias of the prey, for instance displaying a color pattern that is normally associated with a food reward (Théry & Casas 2009; Wizen & Gasith 2011; Tso 2013).

A recent review of color signal theory identified a lack of a unifying framework underpinning our understanding of the evolution of visual lures (White & Kemp 2015). It was identified that this is partly because the limited taxonomic range of predators (confined primarily to carnivorous plants and spiders) and prey (primarily flying insects) examined has hampered evaluations of how predator body coloration and prey sensory modalities have co-evolved. Indeed, all studies of prey luring coloration in spiders, with the exception of two (Lin et al. 2015; Zhang et al. 2015), have involved either web building or crab spiders (Théry & Casas 2009; Tso 2013; White & Kemp 2015). These studies have shown that the bodies of

many diurnal and nocturnal web building and crab spiders contain white and/or yellow bodies, patches or stripes that exploit visual biases of insects, such as their strong attraction to UV (Heiling et al. 2003, 2005; Tso 2013; White & Kemp 2015). Spiders that forage on the ground, nevertheless, feed on a diversity of crawling insects, such as cockroaches, ants, and grasshoppers (Nentwig 1987), and these have different visual capabilities and behavioral repertoires than flying insects (Briscoe & Chittka 2001; Schmeling et al. 2014).

The range of affected prey examined has generally been confined to flying insects such as bees and moths (e.g., Chittka 1992; Johnsen et al. 2006). One reason why a limited taxonomic range of prey has been assessed is that currently there are only a few visual models available and these may be only suitably applied to certain prey (Kemp et al. 2015). For instance, there are well-developed visual discrimination models for honeybees (Chittka 1992), moths (Johnsen et al. 2006) and birds (Hart 2001), and these have facilitated robust assessments of the influence of predatory lures on the behavior of many hymenopteran, lepidopteran or avian predators and prey. Nevertheless, as identified by White & Kemp (2015), there is an urgent need to expand the range of predator and prey assessed to facilitate the development of more inclusive theories. The receptor-noise limited model is a model which assesses whether any animal viewer can distinguish between two differently colored objects without requiring *a priori* knowledge of its receptor opponent mechanisms and discriminatory thresholds (Vorobyev & Osorio 1998). This model nevertheless requires that the researcher knows or can estimate: (1) the wavebands at which the photoreceptors are maximally sensitive, (2) ambient illumination levels at which the objects are viewed, (3) the spectra reflected off the objects of interest, and (4) the spectra reflected off the background, prior to application (Vorobyev & Osorio 1998; Vorobyev et al. 2001).

Color vision and shape recognition are thought to be poorer in nocturnal insects than diurnal insects because the compound eyes of nocturnal insects draw photons from several adjacent ommatidia to elicit neural propagation, whereas neural propagation is directly associated with individual ommatidia in diurnal insects (Kelber et al. 2003; Warrant 2004; Klaus & Warrant 2009; Honkanen et al. 2014). Nevertheless, recent research has shown that a variety of different body colors, including silver, yellow, and white, from a variety of nocturnal spiders can lure nocturnal insects (Chuang et al. 2007, 2008; Blamires et al.

2012, 2014; Peng et al. 2013; Zhang et al. 2015). These results, and recent experiments showing the receptors of nocturnal insects responding to single photon sources (Kelber et al. 2002; Honkanen et al. 2014), suggest that the visual capabilities of nocturnal insects are greater than we thought.

While the bodies of most ground foraging nocturnal spiders are drab in color, they may have colorful patches and/or stripes on their abdomen, legs, or fore-head (Oxford & Gillespie 1998; Zhang et al. 2015). For example, the brown huntsman, *Heteropoda venatoria*, has a white “moustache-like” stripe along the front of its prosoma, which functions to lure prey at night (Zhang et al. 2015). However, we do not know whether the conspicuous body colors of other nocturnal ground foraging spiders likewise attract prey.

Fishing spiders (*Dolomedes* spp.) are largely nocturnal ground foraging spiders of the family Pisauridae; a diverse family that includes drab and colorful ground foraging and web building species (Bradley 2012; Proctor et al. 2014). *Dolomedes raptor* is an example of a ground foraging, nocturnal pisaurid that inhabits low altitude streams of undisturbed primary forests and urban environments throughout East Asia (Zhang et al. 2004; Platnik 2014). Adult females of this species have distinct patches of white hairs, approximately 2 mm in length, on the dorsal surface of forelegs I and II, and smaller, less distinct patches on legs III and IV (Zhang et al. 2004) (Fig. 1). The leg patches are absent in adult males and juveniles (see Fig. 1 in Lin et al. 2015). While *Dolomedes* spp. have good vision (Bleckmann & Barth 1984; Bleckmann & Bender 1987), meticulous observations of the mating behavior of *D. raptor* (Lin et al. 2015) have never witnessed females using their white leg patches as a visual signal to attract males.

Adult and sub-adult female *D. raptor* forage at the edges of slow-flowing waterways for semi-aquatic insects, such as pygmy grasshoppers *Eucrotettix ocellatus* (which wade or swim in shallow water at night foraging on algae), and small fish and amphibians (Nyffeler & Pusey 2014). They posture themselves on rocks or soil, remaining motionless for hours at a time with their legs often splayed and placed on the water surface or edge (Zhang, personal observation). Such posturing renders the white patches on legs I and II highly conspicuous (Fig. 1). The tips of legs I and II may be, but not necessarily, in contact with water to sense waves caused by the movements of semi-aquatic insects (Bleckmann & Lotz 1987; Arnqvist 1992). Male and juvenile *D. raptor*, on the other hand, forage actively and never exhibit such posturing. Males, nonetheless, have conspicuous white stripes on their

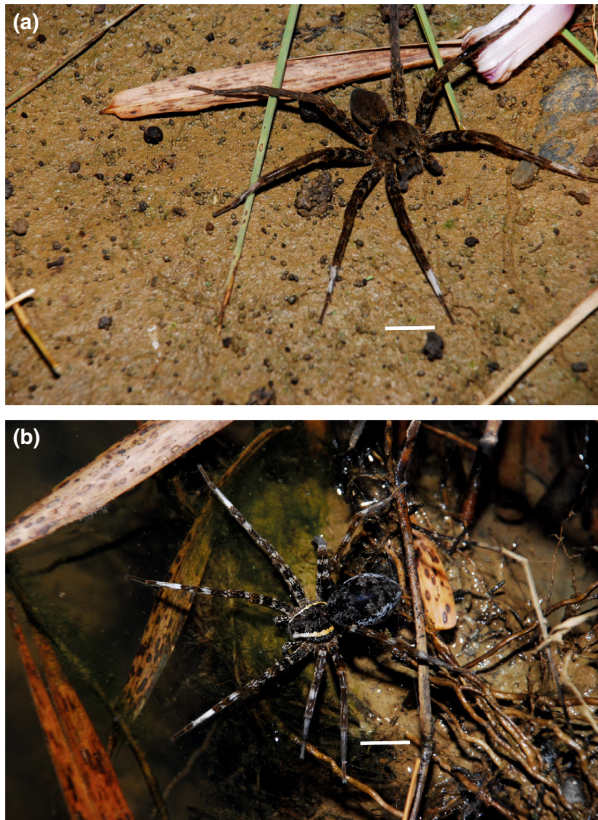


Fig. 1: Photographs of female *Dolomedes raptor* in a foraging posture with legs I and II (a) touching the ground and (b) in contact with water. Both photographs show the conspicuous white patches on legs I and II and that the marks on legs III and IV are less distinctive. The bars represent 10 mm. For a comparison with the legs and bodies of males, see Lin et al. (2015).

cephalothorax which appear to lure prey (Lin et al. 2015).

Female *D. raptor* grow larger than males (females: 15–25 mm in length, males: 9–16 mm in length), presumably to maximize fecundity. We therefore expect females to consume more prey. We hypothesized that female *D. raptor* achieve greater prey capture success by displaying their leg patches to lure prey. Hence, we performed experiments to accomplish two objectives. First, we ascertained whether the leg patches on *D. raptor* are visually discriminable to their most common prey, pygmy grasshoppers, by developing a provisional trichromatic color space model (Vorobyev & Osorio 1998) of orthopteran vision using documented photoreceptor sensitivities of a cricket and reflectance spectra measured from *D. raptor* leg patches and bodies. We then performed field and greenhouse experiments using dummies and live spiders to assess whether the leg patches of female *D. raptor* attract pygmy grasshoppers.

Materials and Methods

Determination of *D. Raptor* leg Patch Visibility To Pygmy Grasshoppers

We wanted to determine whether pygmy grasshoppers (i.e., an animal other than a bee, moth or bird) can distinguish between *D. raptor* white leg patches and the brown spider bodies and dark rocks, but no visual discriminability modeling has been done for orthopterans. According to Kemp et al. (2015), the most suitable model for this kind of analysis is the receptor-noise limited model of Vorobyev & Osorio (1998). Spectral analyses (e.g., Endler 1990; Grill & Rush 2000) are unsuitable since we were not interested in color perception, color-based decisions or the types of receptors stimulated by different colored objects (Kemp et al. 2015).

Studies report λ_{\max} of cricket (*Gallus* sp.) and locust (*Schistocerca* sp.) photoreceptors lie within the UV (~330 nm), green (~445 nm), and blue (~515 nm) wavebands (Zufall et al. 1989; Briscoe & Chittka 2001; Henze et al. 2012; Frolov et al. 2014). Accordingly, we constructed a model assuming that pygmy grasshoppers: (1) have trichromatic vision that can be represented by a UV-blue-green Maxwell triangle, (2) have superposition-type photoreceptors (Schmeling et al. 2014) and can discriminate colors under scotopic illuminations down to 0.0001 cd m² (Kelber et al. 2002), and (3) noise within the photoreceptor types is independent of background illumination (Vorobyev & Osorio 1998). Photoreceptor noise will undoubtedly be greatest in dim light since the number of photons arriving at the eye from external stimuli is low but nocturnal animals can physiologically adapt to such limitations (Warrant 2004; Osorio & Vorobyev 2005).

Spiders were anesthetized with carbon dioxide and their legs extended flat on a workbench. We then measured the spectra reflected off the white leg patches of ten *D. raptor* as well as their brown bodies and ten rocks collected from our study site using a spectrophotometer (USB-4000, Ocean Optics, Inc., Dunedin, FL, USA) equipped with a Y-shaped reflection probe (QR200-7UV-VIS), six illumination fibers, a reading fiber, and a halogen light source (DH 2000). The probe was held against the legs above and below the white patches in a direction perpendicular to them during scanning. Labsphere certified white and black reflectance standards were used to calibrate the spectrometer to 100% and 0% reflectance, respectively. The area captured for all body parts and the standards was 2 mm², and the integration time was

150 ms. Multiple scans from each sample were taken and averaged to account for any sampling error (Maia et al. 2013). All scans were performed in a darkroom against a black cardboard background.

We used the photoreceptor absorbance function for *Gryllus bimaculatus* UV, green and blue photoreceptors ($R_i(\lambda)$) derived from Zufall et al. (1989) and the reflectance spectra of the spider white leg patches, spider bodies, or rocks ($I(\lambda)$) to calculate quantum catches for each photoreceptor (q_i) using the following equations (Vorobyev & Osorio 1998):

$$q_i = k_i \int_{\lambda} R_i(\lambda) I(\lambda) d\lambda \quad (1)$$

where k_i is an arbitrary scaling factor derived by:

$$k_i = 1 / \int_{\lambda} R_i(\lambda) I(\lambda) d\lambda \quad (2)$$

We then calculated color contrast thresholds (ΔS^t), the value at which correct color choices are made by honeybees approximately 75% of the time, using the equation (Vorobyev & Osorio 1998):

$$\Delta S^t = \frac{e_1^2(\Delta q_3 - \Delta q_2)^2 + e_2^2(\Delta q_3 - \Delta q_1)^2 + e_3^2(\Delta q_1 - \Delta q_2)^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2} \quad (3)$$

Values of e_i were derived from the standard deviations of the spectral sensitivities of *G. bimaculatus* UV, green, and blue photoreceptors taken from Henze et al. (2012). We converted the ΔS^t values to units of just noticeable differences (JND), where values >1 were considered discriminable, by comparing the Euclidean distances between the ΔS^t values within color space for the leg patches and rocks and spider bodies and rocks (Siddiqi et al. 2004).

Since the achromatic (brightness) contrast of objects is an important component of nocturnal vision (Menzel 1981; Kelber & Roth 2006), we used a variant of the receptor-noise limited model (see Equations (5) and (7) of Siddiqi et al. 2004) to ascertain the achromatic values of spider white leg patches and spider bodies when viewed by pygmy grasshoppers against rocks. The brightness (ΔS) contrast values we calculated were converted to JND with values >1 considered discriminable (Siddiqi et al. 2004). We repeated the above procedures for the white paper and brown paper used to construct the dummies for the proceeding experiment. All calculations and modeling were done using the program pavo (Maia et al. 2013).

Field Experiment

The field experiment was performed beside a slow-flowing stream in Dongshi Forest Recreation Area,

Taichung City, Taiwan (E120°52'03", N24°17'06") over five consecutive nights. The temperature ($20.0 \pm 0.3^\circ\text{C}$) and relative humidity ($86.0 \pm 0.9\%$) remained relatively constant during the experimental period. The area has many small to medium-sized rocks lining the slow flowing stream banks.

Prior to the experiment, we made 78 dummies that resembled female *D. raptor* in size, color, and shape using brown (corresponding to the spider's body) and white (corresponding to the white patches) paper card. We measured the length of the: (1) body, (2) legs, and (3) white foreleg patches, of ten randomly selected female *D. raptor*, so we could make dummies that matched *D. raptor* in size and shape. We pasted patches of white paper cut to match the size of the white patches of live spiders onto the tips of the first and second legs of 39 of the dummies. To the remaining dummies, we pasted similar sized patches made from the brown paper used to make the dummy bodies. All patches were attached using the same odorless, transparent waterproof glue (SC317-03, Kronyo, Taipei). To ensure that the coloration of the dummies resembled that of *D. raptor*, we measured the reflectance spectra of the brown and white parts of ten *D. raptor* bodies and 100 sheets of brown and white paper, respectively, using a spectrometer as described above.

In the field, female *D. raptor* were frequently seen sitting on rocks in close proximity to a stream within our study area. We therefore used a water resistant, odorless, silicon-based adhesive (502 Adhesive, Fortuna, Taipei) to stick dummies onto rocks of similar size to those used by *D. raptor* at haphazardly chosen locations. Hence, the two types of dummies (i.e., dummies with and without white patches) were haphazardly distributed throughout the study area. The same adhesives were used to construct all of the dummies and stick all dummies onto rocks. Sixteen infrared video cameras (Sony SR-100 and SR-62, frame speed = 24 frames/s) were used to monitor the dummies nightly between 2000 and 0400 h. Each video camera was placed perpendicular to the dummies at a distance of approximately 1 m so an area of ~0.25 m² could be recorded by each camera, enabling all the dummies to be monitored simultaneously. At the completion of the experiment, the footage was viewed at Tunghai University, Taichung. Prey attraction was identified when a pygmy grasshopper moved to within ~1 cm of a dummy. This was adequate as a measure of foraging gain as we had previously observed that whenever an insect moved to within ~1 cm of a real spider, it was inevitably caught and consumed. Furthermore, we estimated that the

probability of including an insect that is wandering past and not responding to the white leg patches significantly increases at distances >1 cm from a dummy. We calculated prey attraction rate as the number of prey attracted per hour of video footage to account for occasional camera positional adjustments, battery failure, or other technical issues.

Greenhouse Experiment

We conducted the following greenhouse experiment at the Taiwan Endemic Species Research Institute, Low Altitude Research Station, Wu-Shy-Keng, Taichung City, Taiwan (N24°16'25.15", E120°56'53.51") over 11 nights. The temperature, relative humidity (mean temperature = $19.6 \pm 0.2^\circ\text{C}$, relative humidity = $86.9 \pm 0.6\%$), and light levels during the greenhouse experiment closely resembled that of the field study.

Into each of the $30 \times 30 \times 60$ cm fiber glass aquaria, we placed: (1) 200 g of small pebbles, (2) one rock (~20 cm in diameter), (3) 2 l of stream water, and (4) one adult female *D. raptor* ($n = 25$ spiders used overall) collected from our field site. The spiders were given 48 h to acclimate to the aquaria before two pygmy grasshoppers ($N = 50$, length = 10–16 mm) were also added to each aquarium. The grasshoppers were collected from our field site prior to the commencement of the greenhouse experiment and acclimated within a separate aquarium for 48 h. We placed infrared video cameras (Sony SR 100, Tokyo, Japan) ~1 m above each aquarium to monitor the predatory behavior of *D. raptor* over 4 h (from 2000 to 000 h), after which this part of the experiment was terminated. The white patches on all of the spider's legs were clearly visible when the footage was viewed at the completion of the experiment.

Upon termination of the first part of the experiment, we removed the spiders and anesthetized them using carbon dioxide. The white hairs from legs I and II of each spider were then carefully removed using a razor blade. The entire experiment was then repeated 48 h later using 50 different laboratory-acclimated grasshoppers, collected anew from our field site. We waited 48 h to minimize any possible influence that anesthetization and handling might have on the experimental outcome. The experiment was staged using the same individual spiders rather than using different spiders at the same time because we estimated that in order to account for inter-individual variation in *D. raptor* behaviors, at least 25 individuals per treatment needed to be examined at once to get meaningful results and we did not have the facilities

or enough video cameras to run such a large-scale experiment. Nevertheless, conditions (e.g., light levels, temperature, relative humidity) were identical during the two experiments and we noticed no substantial (albeit unmeasured) differences in the behavior of individual spiders or their grasshopper prey when the experiment was repeated. Accordingly, time-induced changes in spider or grasshopper behavior between the first and second experiment did not confound our results.

We identified prey attraction in the greenhouse experiment in precisely the same way as we did for the field experiment, i.e., as a grasshopper moving to within ~1 cm of *D. raptor*. Since all grasshoppers that moved to within ~1 cm of a spider were caught and consumed, a maximum of two prey attraction events were observed per spider and the same grasshopper never approached a spider twice. Once an individual spider had eaten both grasshoppers in its aquarium, no more video footage was watched. To account for the different times that the individual spiders were watched across treatments, and occasional camera positional adjustments, battery failure, or other technical issues, prey attraction rate was calculated as the number of prey attracted per hour of video footage.

Statistical Analyses

A generalized mixed model specifying a Poisson response distribution and natural logarithm link function best fitted the field experiment data (Pearson goodness of fit test, $\chi^2 = 79.73$, $df = 68$, $p = 0.564$). We therefore used this model to compare prey attraction between dummies with and without white patches. On each day, 6–8 dummies without white patches and 6–7 dummies with white patches were tested. In total, 38 (of 39) dummies without white patches and 33 (of 39) dummies with white patches were tested on five consecutive days. The coefficient of treatment was specified as the log of the ratio of prey approach rate when white patches were present against that when white patches were absent. The five different days were considered a categorical random factor to cope with between-day heterogeneity and the log of the hours of footage was considered as an offset for each experiment. A generalized mixed model, specifying the response distribution as Poisson and the link function as a natural logarithm likewise fitted the greenhouse experiment data (Pearson goodness of fit test, $\chi^2 = 52.34$, $df = 55$, $p = 0.577$). This model was therefore used to compare the prey attraction rates between *D. raptor* with white patches and *D. raptor* with their patches removed. The coefficient

of the treatment was specified as the log of the ratio of the prey approach rate when the white patches were present against that when white patches were absent. Individual spiders were considered a categorical random factor and therefore designated as a block in the model. For each of the above Poisson mixed models, we calculated the marginal R^2 and conditional R^2 according to Nakagawa & Schielzeth (2013).

Results

D. raptor leg Patch Visibility to Pygmy Grasshoppers

The reflectance spectra measured from spider legs and bodies and the experimental dummies showed similar reflectance curves (Fig. 2a). Our color contrast calculations found that the mean color contrast values for the white leg patches of *D. raptor* were chromatically

and achromatically discriminable by pygmy grasshoppers against their body, but the body of *D. raptor* against rocks was not. Moreover, the white paper used for construction of the dummies were chromatically and achromatically discriminable by pygmy grasshoppers against the brown paper used to construct the dummies, but the brown paper against rocks was not (Table 1). Accordingly, we deduced that both the spider white leg patches and the white paper component of the dummies were visible and perceived as being of similar color by the grasshoppers.

Experiments

Our generalized mixed model showed that the dummies with white patches had greater prey attraction rates than those without white patches (Table 2; Fig. 3a). Some small insects, spiders, and harvestman were attracted to the dummies, but pygmy grasshoppers comprised the majority (~90%) of the attracted prey.

The greenhouse experiment corroborated with the field experiment, as we found that pygmy grasshopper attraction rates significantly decreased (Table 3; Fig. 3b) upon removal of the spider's white leg patches. The spiders always consumed any grasshopper that approached to within ~1 cm. The results of our experiment and our receptor-noise limited model thus substantiated our prediction that female *D. raptor* display their white leg patches to lure prey.

Discussion

The results of our experiments and visual modeling suggested that the white leg patches of the nocturnal cursorial spider *Dolomedes raptor* are visible to pygmy grasshoppers and lure them as prey. Thus showing

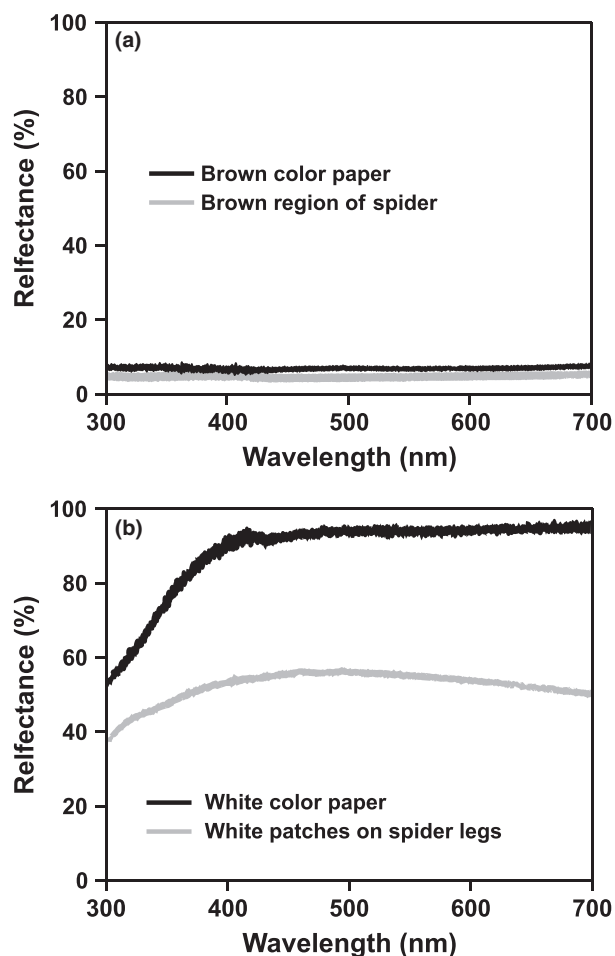


Fig. 2: The reflectance spectra of (a) the brown bodies of *Dolomedes raptor* and the brown paper used to construct dummies, and (b) the white leg patches of *D. raptor* and the white paper.

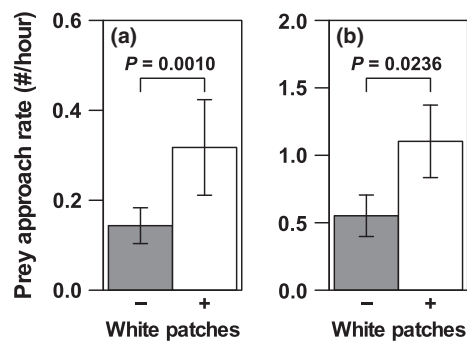
Table 1: Chromatic and achromatic (as just noticeable differences; JND) discriminability values for (1) the white leg patches of *Dolomedes raptor* against their body, (2) the body of *D. raptor* against rocks, (3) the dummy white paper against the dummy brown paper, and (4) the dummy brown paper against rocks

Comparison	Chromatic contrast (JND)	Achromatic contrast (JND)
<i>D. raptor</i> leg patch v <i>D. raptor</i> body	4.373 ± 1.089 ^a	1.409 ± 0.282 ^a
<i>D. raptor</i> body v rock	0.439 ± 0.076	0.110 ± 0.001
Dummy white paper v dummy brown paper	14.725 ± 0.395 ^a	2.886 ± 1.151 ^a
Dummy brown paper v rock	0.488 ± 0.069	0.740 ± 0.043

^aIndicates that the value is above the discriminability threshold.

Table 2: Results of a generalized mixed model comparing prey attraction rate (number attracted per hour of video footage) to dummies resembling female *Dolomedes raptor* in size, shape, and color with those lacking patches. Marginal $R^2 = 2.65\%$ and conditional $R^2 = 22.05\%$

Variables	Estimate of β	SE	Z	P	Bootstrap 95% CI
Intercept	-2.5958	0.5415	-4.794	<0.0001	[-3.9316, -1.6362]
Treatment	0.9162	0.2776	3.300	0.0010	[0.3236, 1.6809]
Date	$\sigma = 1.036$	—	—	—	[0.0001, 1.7949]

**Fig. 3:** (a) Mean (\pm SE) grasshopper attraction rates (number attracted per hour of video footage) of *D. raptor* dummies with and without white patch on their legs. (b) Mean (\pm SE) grasshopper attraction rates (number attracted per hour of video footage) of female *D. raptor* with white patches on their legs and with the white patches on their legs removed. Shows the results (p-values) of a generalized mixed model comparing the prey attraction rates between *D. raptor* with white patches and *D. raptor* with their patches removed.

that leg patches on a semi-aquatic predator can be used to attract prey at night. It is the second such study (following Zhang et al. 2015) to report a ground hunting nocturnal spider using a visual lure to attract prey. More importantly, it expands the taxonomic range of predators reported using colorful prey lures, the diversity of prey affected, and the ecotypes in which prey luring is documented. The findings are thus conducive to improving our evaluations about how predator body coloration and prey sensory modalities have co-evolved (Kemp et al. 2015; White & Kemp 2015).

Recently, White & Kemp (2015) argued that there is a need for a unifying theory underpinning our understanding of the evolution of visual lures. They advocated the sensory trap hypothesis (Christy 1995)

as a possible explanation of visual lure evolution. Two important criteria for a lure to be considered a sensory trap are that the lure must: (1) exploit a visual bias of the receiver and (2) appear at a lower frequency than the object it is perceived as being (Christy 1995; White & Kemp 2015). Here, we found that *D. raptor* lured pygmy grasshoppers using small, bright, white leg patches in an otherwise drab environment. While the behavior of the grasshoppers suggested that a visual bias was exploited, it is not conceivable from an inspection of the environment what *D. raptor*'s legs patches might mimic. Pygmy grasshoppers wade or swim in shallow water, foraging primarily on dark-colored algae. The sensory trap hypothesis, therefore, does not seem explanatory in this instance. Nevertheless, the grasshoppers could be attracted to white structures that resemble the spider's leg patches in some other context, so the sensory trap hypothesis should not be ruled out.

The spiders appeared to sense the presence of the grasshoppers using ripples in the water and other, e.g., olfactory, cues and moved swiftly (faster than could be captured by filming at 24 frames per second) to capture and consume them once they move close enough. During our observations, no grasshoppers escaped an attack by a spider. It thus seems that there is little or no chance for the grasshoppers to learn to avoid the spider's leg patches. Intriguingly, no other species of *Dolomedes* that we are aware of has these leg patches, yet a similarly sized Pisaurid from Argentina, *Thaumasia* spp., which forages along the water edge in a similar fashion to *D. raptor*, does (Blamires, personal observation). It, accordingly, seems that the effectiveness of using leg patches as a visual lure depends largely upon the prey targeted and/or the specific ecological circumstances.

Table 3: Results of a generalized mixed model comparing prey attraction rates (number attracted per hour of video footage) to female *Dolomedes raptor* with white patches on their legs compared with those with the white patches on their legs removed. Both marginal and conditional $R^2 = 7.47\%$.

Variables	Estimate of β	SE	Z	P	Bootstrap 95% CI
Intercept	-0.7152	0.2845	-2.514	0.0119	[-1.3977, -0.2318]
Treatment	0.6931	0.3062	2.264	0.0236	[0.1054, 1.3863]
Spider individual	$\sigma = 0.4897$	—	—	—	[0.0000, 0.8487]

Among spiders prey luring, body coloration has been most commonly documented for diurnal web building spiders and crab spiders, who use their colorful bodies to exploit visual biases, such as a strong UV attraction, in flying insects (Heiling et al. 2005; Hoese et al. 2006; Tso et al. 2006; Chuang et al. 2007; Bush et al. 2008; Fan et al. 2009; Tso 2013). There are, nevertheless, a growing number of documented examples of exploitation of prey visual biases by nocturnal spiders (Blamires et al. 2012, 2014; Peng et al. 2013; Zhang et al. 2015). When nocturnal spiders visually lure prey, they generally use yellow, silver or white bodies, stripes or patches, most likely because these colors contrast strongly against a dark background under nighttime illumination (Tso et al. 2007; Chuang et al. 2008; Blamires et al. 2012, 2014; Peng et al. 2013; Zhang et al. 2015). Nocturnal insects thus seem to have visual biases toward certain colors, suggesting their color discriminability is reasonably good. Indeed, the attraction to specific colors by nocturnal insects is exploited in pest control systems (Shimoda & Honda 2013). Our results concur that by contrasting strongly against the spider's body under nighttime illumination levels, the white leg patches on female *D. raptor* are attractive to nocturnally foraging pygmy grasshoppers.

Considering most orthopterans exhibit typical trichromacy and have dense, highly sensitive receptors that are adaptable to diurnal and nocturnal vision (Zufall et al. 1989; Schmeling et al. 2014), it seems reasonable to suspect that the receptor-noise limited model can be used, as was done here, to explain visual discriminability in grasshoppers at night. We assumed high signal to noise ratio and that the pygmy grasshoppers had 'typical' trichromatic sensitivity. We concede, however, that the receptor-noise limited model is less powerful at predicting insect receptor responses and thresholds under nighttime than daytime illuminations (Vorobyev & Osorio 1998). We accordingly cannot be sure that the discriminability of the leg patches by pygmy grasshoppers was as strong as our model suggested. More experiments determining the physiological and behavioral responses of nocturnal orthopterans to light stimulations across the 300–700 nm waveband are needed to ascertain how strongly the spider leg patches or similar signals are discriminable from spider bodies or similar dark backgrounds by pygmy grasshoppers at night.

Our reflectance spectra for the spider legs and bodies and the corresponding colored paper used to construct the dummies were similarly shaped, so we concluded that grasshoppers perceived the dummies as being similar in color as *D. raptor*. The white paper

used to represent *D. raptor*'s white patches, nevertheless, had greater reflectance than the spider's white leg patches across all wavebands. The paper approached 100% reflectance across the entire spectra, so it reflected all colors at nearly the same intensity as the white standard used to calibrate the spectrometer. Nonetheless, the achromatic contrasts of both the spider's leg patches and the white paper exceeded the discriminability threshold. We thus cannot be sure whether the greater reflectance of the white paper rendered them brighter than the spider's leg patches in the eyes of pygmy grasshoppers. Under the assumption that the grasshoppers rely largely on achromatic cues for nocturnal vision, the white paper should be detectably brighter than the spider leg patches. However, our finding that the pygmy grasshoppers behaved similarly (i.e., always moving toward the white patches) upon exposure to the dummies and spiders with and without white leg patches suggested that they did not respond to any difference in brightness during our experiments.

Since we never witnessed females using their white leg patches to signal to males, we do not think that the patches are likely to be used in intra-specific communication. However, alternative explanations, such as antipredator or other non-sexual intra-specific signaling, need to be independently assessed before they can completely eliminated as additional functions of the leg patches (Hebets & Papaj 2005). We are not entirely sure why only adult and sub-adult females contain the white leg patches, as males and juveniles might also benefit from luring prey in this way. We hypothesized elsewhere (Lin et al. 2015) that males can catch enough prey by foraging actively to sustain their growth. Furthermore, an additional white stripe on the male body (see Lin et al. 2015) serves to lure prey.

In summary, we modeled pygmy grasshopper visual discriminability and generated a hypothesis that the white patches on female *D. raptor* lure pygmy grasshoppers at night. We then found initial experimental evidence to support this hypothesis. Nevertheless, our observations do not appear to be consistent with the spider's body coloration acting as a sensory trap. We, however, need more information about the type of objects that pygmy grasshoppers encounter throughout their life and their behaviors toward different objects before ruling it out. To further test the hypothesis that the white patches of *D. raptor* lure pygmy grasshoppers, we suggest more experiments be done to test: (1) the influence of diet on female and male coloration, (2) whether other behaviors, body colors, or signals associated with female spiders interact with the white leg patches, and (3) the behavioral

responses of grasshoppers to the simultaneous presence of female and male *D. raptor*.

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