Original Article

Body spot coloration of a nocturnal sit-and-wait predator visually lures prey

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Many nocturnal spiders have paired conspicuous yellow ventral spots that contrast against their black and brown abdomens. A previous experiment, manipulating the coloration of the spots of the spider *Neoscona punctigera*, suggested that the spots lure prey. We conducted a field experiment in which we placed spider dummies that either mimicked an adult female *N. punctigera* in coloration, size, and shape (standard dummies) or mimicked *N. punctigera* but with the coloration of their ventral spots manipulated onto orb webs in the field at night and monitored them with infrared video cameras. Spectrophotometry confirmed that the coloration of the dummies resembled spider bodies, with the exception of the spots of the gray spotted dummies, where chromatic and achromatic contrast differences from spider spots were found. We used entirely yellow dummies to assess whether the spots represent a compromise between prey attraction and predator avoidance. We found that the standard dummies, mimicking adult female *N. punctigera* in coloration, size, and shape, attracted more prey than the dummies with gray spots, the entirely black dummies, and webs without spiders. The entirely yellow dummies attracted fewer prey than the standard dummies. These results show that the coloration of nocturnal spider ventral spots lures prey, although whether chromatic or achromatic cues are used could not be identified. The entirely yellow dummies did not lure more prey than standard dummies, so the spots are unlikely to represent a compromise between prey attraction and predator avoidance, in contrast to the coloration of certain diurnal orb web spiders. *Key words:* color contrast, *Neoscona punctigera*, predator–prey interaction, spider, visual lure. *[Behav Ecol 23:69–74 (2012)]*

INTRODUCTION

Body coloration, used herein to represent all aspects of animal body colors such as the chromatic and achromatic properties, resolution, shape, pattern, intensity, and conspicuousness, and its perception play an important role in predator–prey dynamics (Endler 1992; Stevens and Merilaita 2009). Prey body coloration functions to conceal, startle, deter, or distract predators (Stevens et al. 2006; Dimitrova et al. 2009; Stevens and Merilaita 2009). Conversely, the coloration of predator bodies function to conceal them from their prey or to deceptively lure prey (Ortolani 1999; Tso et al. 2002, 2006, 2007; Fan et al. 2009). Recent advances in our understanding of animal visual physiology and receiver psychology have enabled the development of models explaining how animals use and perceive coloration in a diurnal context (Endler 1992; Rowe 1999; Vorobyev et al. 2001; Dyer and Chittka 2004). Generally, color vision is considered of minor importance for nocturnal animals (for review, see Warrant 2004). Nevertheless, researchers are now utilizing technology to monitor animals at night and it is becoming clear that nocturnal animals can distinguish between different colors and may exhibit color preferences (Kelber et al. 2003; Roth and Kelber 2004; Warrant 2004; Kelber and Roth 2006; Gomez et al. 2010).

Brightly colored diurnal orb web spiders, such as the golden orb web spider *Nephila pilipes*, often have a dark body with bright supine ventral and dorsal lines or spots (Tso et al. 2002, 2004; Chiao et al. 2009). The lines and spots have been shown to lure insects (Tso et al. 2002, 2004; Chiao et al. 2009; Fan et al. 2009). Furthermore, an experiment using entirely yellow spider dummies and dummies with lines and spots resembling *N. pilipes* showed that entirely yellow spiders attract predatory wasps and the lines and spots in *N. pilipes* are restricted to the supine regions as a means to avoid detection by predators (Fan et al. 2009). The body coloration of such diurnal spiders thus is shaped by a compromise between using conspicuous coloration to attract prey and disruptive coloration to avoid predators (Chuang et al. 2007; Fan et al. 2009).

Strictly nocturnal spiders are often dorsally dark. Many nocturnal orb web spiders (e.g., *Araneus* spp., *Neoscona* spp., *Eriovixia* spp., and *Nuctenea* spp.), however, have paired yellow ventral spots that contrast against their black–brown abdomens (Figure 1). Color vision and shape recognition are exceptionally poor in orb web spiders (Foelix 2011), so intraspecific signaling is not likely to be a function of the spots. In one species, *Neoscona punctigera*, the spots have been suggested to function to attract prey, principally moths (Chuang et al. 2008). Nevertheless, in that study, brown paint was used to cover the ventral spots of *N. punctigera*, so the influences of relevant nonvisual cues could not be categorically ruled out.

Moth photoreceptors are sensitive to light of around 600-nm wavelength (Goyret et al. 2007), the wavelength that appears as yellow to humans (Malacara 2002), so it is plausible that the spots act as a prey lure. Nonetheless, the spots seem to be too

small to be clearly resolved by nocturnal insects. Indeed, the coloration of most nocturnal displays, for example, those of insect pollinated nocturnal flowers (Lunau 2000), is generally much larger than the ventral spots of nocturnal spiders. Because the spots reflect light from the ultraviolet to the red (Chuang et al. 2008), it is possible that, in addition to prey, the spots are conspicuous to nocturnal predators (e.g., wasps and bats; Warrant 2008; Muller et al. 2009). The spots henceforth could represent a compromise between prey attraction and predator avoidance. Conjecture pertaining to the significance of the coloration of the spots of *N. punctigera*, however, remains empirically untested.

In this study, we monitored, using infrared video cameras, the prey attraction rates of *N. punctigera* dummies to determine whether the coloration of the ventral spots of these nocturnal spiders acts as a prey lure. We placed dummies that had similar sized and shaped bodies and spots as adult female *N. punctigera*, but with the coloration of the spots manipulated (yellow vs. gray), on vacant spider webs in the field at night. We used gray of a shade resembling, by eye, the shade of the yellow paper used to represent the spots in order to minimize the differences in the achromatic properties between the treatments. We used entirely yellow dummies to test the hypothesis that the spots represent a compromise between prey attraction and predator avoidance, as found for *N. pilipes* (see Fan et al. 2009). We determined, by spectrophotometry, the chromatic and achromatic contrasts of the spider and dummy spots and bodies against their natural backgrounds to ensure the manipulation of spot coloration was detectable to the spider's prey and predators. We deduced differences in prey or predator attraction in the coloration-manipulated dummies as indicative of spot coloration acting as a lure of prey or predators. A compromise between prey attraction and predator avoidance was implicated if the completely yellow dummies lured more prey or predators than the yellow-spotted dummies.

MATERIALS AND METHODS

Spider dummy construction

We made similar sized, shaped, and colored dummies as adult female *N. punctigera* (Figure 1B,F) by referring to body length and width measurements and photographs of live spiders. Four types of dummies were used in the experiments. First, a standard (SS) dummy which mimicked the ventral coloration pattern of *N. punctigera* (Figure 2A). Second, to test the importance of spot coloration in luring prey, we created a dummy with gray spots (GS) rather than yellow spots on its abdomen. Thirdly, to evaluate whether the spots represent a compromise between prey attraction and predator avoidance a completely yellow (YS) dummy (Figure 2B) was made. To control for the influence of dummy presence on the webs, we also made a completely black (BS) dummy (Figure 2C). In addition, a no dummy (NS) treatment was used to control for the movements of insects in the vicinity regardless of the influence of the dummies.

We created the dummies from brown (to represent the spider body), black (to represent the spider abdomen), and yellow and gray (to represent the coloration of unmanipulated and manipulated ventral spots, respectively) paper pasted together with odorless transparent glue. We measured the chromatic and achromatic properties of the chosen papers across a 300–700 nm spectrum using an USB4000 spectrophotometer (Ocean Optics, Dunedin, FL). The spectral properties across a 300- to 700-nm spectrum were also measured for the body, abdomen, and ventral spots of 12 live female *N. punctigera* so that comparisons between the spectral properties of the papers and the spider body parts they represent could be made.

Quantification of dummies and spider body coloration

We applied a model developed to explain visual stimulus–response phenomena in the nocturnal hawkmoth *Deilephila elpenor* (Johnsen et al. 2006) to determine how the different dummies and the various spider body parts were likely to be viewed and perceived by moths under full moon illumination, the most appropriate nocturnal illumination available. The reflectance functions of the chosen brown, black, yellow, and gray cardboard ($N = 8$ measurements of each) (Figure 2D) and their corresponding spider body parts (see Chuang et al. 2008) were measured by spectrophotometry (for details, see Spider dummy construction). The parameters: 1) moth photoreceptor inclusion angle, 2) facet lens diameter, 3) cumulative photoreceptor 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 were from Johnsen et al. (2006). The mean full moonlight illumination function across the 300- to 700-nm waveband was assumed equivalent to that reported by Somanathan et al. (2008) and the background reflectance spectrum equivalent to that measured by Tso et al. (2004).
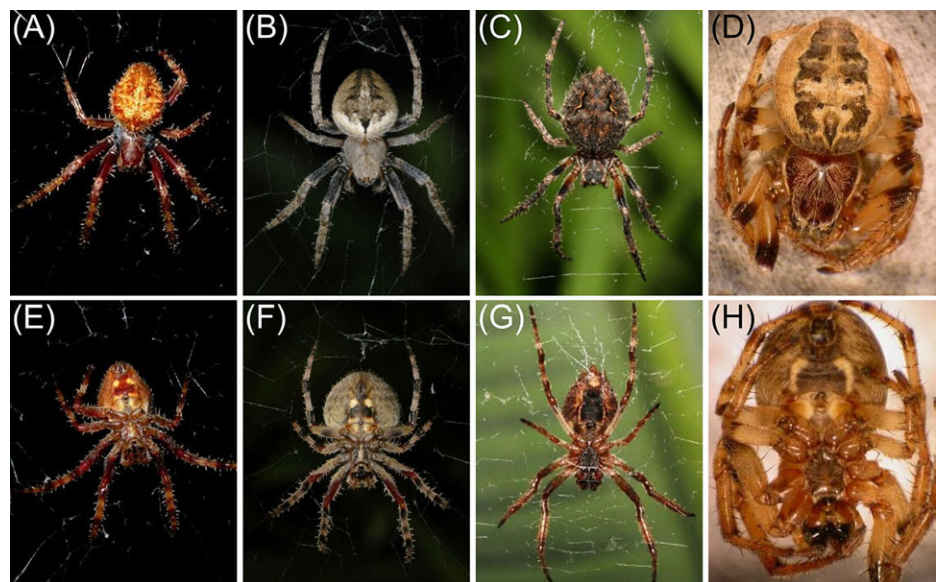

Figure 1
Body color patterns of nocturnal orb web spiders. Dorsal (A–D) and ventral (E–H) views of 4 genera of nocturnal orb spiders. (A and E) *Araneus* in East Asia. (B and F) *Neoscona* in East Asia. (C and G) *Eriovixia* in West Australia. (D and H) *Nuctenea* in North America.
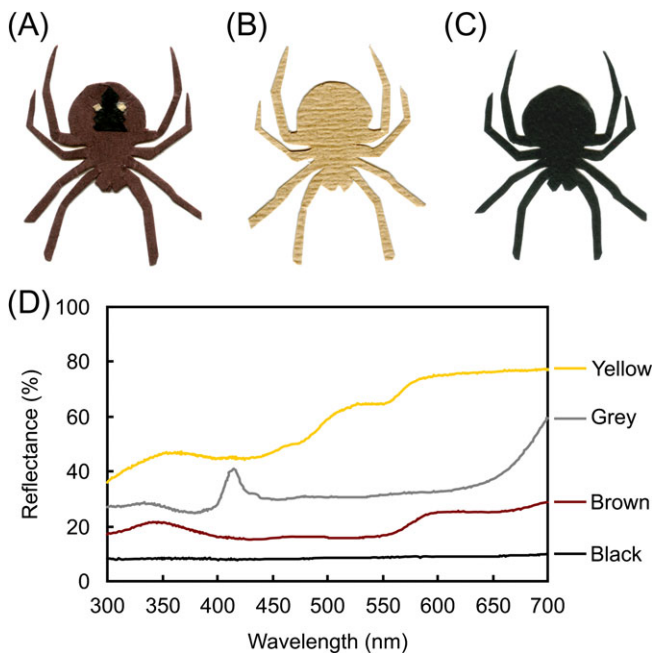
Figure 2
Dummies made from color paper used in the experiments. Treatments: (A) standard dummy (SS) mimicking the ventrum coloration pattern of *Neoscona punctigera*, (B) yellow (YS), and (C) black (BS) dummy (scale bar = 10 mm). (D) Reflectance spectra of each colored paper from which the dummies were constructed, determined by spectrophotometry. The color of the curve represents that of the paper measured.

The quantum catch values for the brown, yellow, gray, and black paper and their representative spider body parts were plotted onto a hawkmoth UV–blue–green visual triangle (Johnsen et al. 2006) and their Euclidean positions were used to calculate their chromatic contrast values. We also calculated the achromatic contrasts of the brown, yellow, gray, and black paper and their representative spider body parts when viewed against the vegetation background using the equation (Malacara 2002):

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

where N_x is the green photoreceptor quantum catch for the target (colored paper or *N. puncigera* body parts) and N_{green} is the green photoreceptor quantum catch for the vegetation background.

Field experiments

Field experiments were performed in a secondary forest, dominated by mulberry and elephant's ear shrubs, at Ape Hill (22°38′19″N, 120°15′54″E) near National Sun Yat-Sen University, Kaohsiung City, Taiwan, more than 13 consecutive nights in August–September 2008. Each night, we randomly selected 20 *N. punctigera* webs (N = 4 for each treatment) of similar size, removed all of the spiders from each web, and selected 1 of 5 dummies to place on the hub. For the first web encountered, we placed no dummy (NS treatment), for the second web, we encountered, we placed a standard dummy, for the third web a dummy with gray spots, for the fourth, an all yellow dummy, and for the fifth, an all black dummy, repeating this sequence 3 more times. We walked haphazardly through the area, thus the locations of the webs containing each of the dummies were randomly distributed. All dummies were constructed on the previous day of use and discarded immediately after use.

We placed video cameras with infrared night view scopes (Sony DCR-TRV and DCR-SR series, Tokyo, Japan), perpendicular to each web at a distance of ~1 m. Monitoring the responses of insects to various dummies by infrared video cameras minimized the disturbances caused by the experimenters. On each night each web was recorded more or less simultaneously for 8 h (from 2000 to 0400 h, stopping recording only in the event of inclement weather) and therefore potential confounding factors such as temporal changes in insect abundance over the course of night should have uniform effect on all types of dummies. So, any differences in performance between dummy types should result from the manipulated properties. The video footage was monitored at Tunghai University, Taichung, Taiwan. Whenever possible, insects were identified to taxonomic order. "Attraction" was recorded as an insect moving within 10 cm of a dummy. Due to poor resolution, inadvertent adjustments to the camera position, battery failure, or other technical issues, there were unequal hours of nightly footage available for each of the dummies, thus biasing any determination of how much prey were attracted to each dummy per night. To account for this bias, we determined the "attraction rate" for each dummy as the number of prey or predators attracted per hour of footage. Any individual web with <4 h of available footage was not included in the subsequent analyses.

Statistical analyses

Two-tailed Student's *t*-tests were used to compare the chromatic and achromatic contrast values of the brown and black papers against the vegetation backgrounds, as viewed by moths calculated using the above model, with those of the corresponding spider body parts. As the spots are contrasted against black and brown in the ventrum of *N. punctigera* (Figures 1F and 2A), we calculated the chromatic contrast values of yellow and gray paper against black and brown paper, separately. Chromatic contrast values were also calculated separately for the spider's ventral spots against a black and brown spider body background. Analysis of variance (ANOVA) tests and Games–Howell post hoc comparisons were used to sequentially compare the derived values. In addition, the achromatic contrast values of yellow and gray paper when viewed against the vegetation background were compared by 2-tailed Student's *t*-tests. Because all of the field data failed Kologorov–Smirnov tests for normality ($P < 0.05$), parametric procedures such as ANOVA/analysis of covariance models were inappropriate (Zar 2010). Specifically, prey attraction data were skewed leftward owing to a high proportion of 0 values. We therefore used a Poisson regression model (Agresti 2002) to compare the prey attraction of the no dummy, dummy with gray spots, all yellow dummy, and all black dummy against the standard dummy treatments. In this model, the prey attraction rates of black dummy and no dummy treatments were also compared to ensure that adding dummies to the webs alone did not alter nocturnal insect behaviors. Date of experiment was included in the model to account for differences in insect abundances or illumination intensities that may have occurred each night. The deviance in the goodness of fit test reflects the fit of the data to a Poisson regression model ($P > 0.05$). A likelihood-ratio test was used to evaluate the overall effect of treatment and date on prey attraction rates. There was only one predator attraction event so no statistical analyses were done for predator attraction. A series of χ^2 homogeneity tests were used to compare the ordinal composition of prey attracted by the no dummy, dummy with gray spots, dummy with yellow spots, and all black dummy against the standard dummy treatments. The goodness of fit

test, Poisson regression and likelihood-ratio tests were performed using the program R (version 2.12.2, Zeileis et al. 2008).

RESULTS

The chromatic contrast values of the chosen brown and black papers against vegetation background did not differ significantly from those of the *N. punctigera* body parts to which they correspond, but the achromatic values differed significantly (Table 1). The chromatic contrast values of the yellow paper when viewed against black paper were different from those of the spider spots against a black background ($F_{2,25} = 3.5412$, $P = 0.0443$). Nonetheless, there was no difference in the chromatic contrasts between the yellow paper and spider spots when viewed against a brown background (Table 2). The chromatic contrasts of the chosen gray paper when viewed against brown or black papers were all significantly different from those of the yellow paper and corresponding spider spots ($F_{2,25} = 16.04$, $P < 0.0001$) (Table 2). The achromatic contrast values of yellow paper against vegetation background differed significantly from those of the gray paper (yellow vs. gray = 0.6580 ± 0.0060 vs. 0.4300 ± 0.0068, $t_{13} = 25.308$, $P < 0.0001$). Because both chromatic and achromatic color contrasts of gray paper differed from those of yellow papers and yellow spider spots, using gray paper as the ventral spots of the dummies effectively manipulate the chromatic properties of spider ventral spots.

At the completion of the field experiment, we viewed the no dummy, standard dummy, dummy with gray spots, all yellow dummy, and black dummy treatments 25, 29, 27, 27, and 27 times, respectively, representing a total of 911 h of video footage (166, 188, 180, 183, and 184 h for the no dummy, standard dummy, dummy with gray spots, all yellow dummy, and black dummy treatments, respectively). The overall effect of treatment was significant but that of the date of experiment was not (Table 3a). The dummies alone could not account for any difference in prey attraction rates in any treatment because the black dummy did not differ from the no dummy treatment (Table 3b). The standard dummy treatment had significantly greater (approximately double) prey attraction rates than the no dummy, dummy with gray spots, and black dummy treatments, that is, the dummies containing no yellow coloration (Table 3b and Figure 3). This result suggests that the yellow coloration of nocturnal spider ventral spots lures prey. The prey attraction rate of the all yellow dummies was lower than the standard dummies ($P = 0.0593$; Figure 3). Only one predator attack (a toad attacking a standard dummy) was observed in the entire experiment. These results are contrary to our prediction of a compromise between prey attraction and predator avoidance as an explanation of the functional significance of the spots. The ordinal composition of insects attracted to the dummies did not differ between treatments (Supplementary Table S1). Lepidopterans, principally moths, were the predominant

insect group attracted to all treatments (>80% in all instances), with hymenopterans, dipterans, and unidentified insects attracted less often.

DISCUSSION

We effectively manipulated the coloration of a nocturnal spiders' ventral spots using dummies and infrared video footage to show that the coloration of the spots functions to lure prey; supporting the conclusions of Chuang et al. (2008). Nonetheless, we could not manipulate the chromatic contrasts of the spots without also manipulating achromatic contrasts. Thus, whether chromatic or achromatic cues are the actual lure could not be resolved here. We suspect that chromatic contrasts play a greater role because results of a previous study showed that chromatic cues are more important than achromatic cues for hawkmoths to locate food sources (Kelber et al. 2002). Nonetheless, it is possible that both chromatic and achromatic contrasts are used by the insects to identify and move toward the spots, as chromatic and achromatic cues stimulate moth photoreceptors differently according to the distance and angle of the signal (Kelber and Roth 2006). There was no difference in the type of insects attracted to the different dummies, with moths principally attracted in all instances, so it seems that there were no groups of insects that were any more or less attracted to the spots. We also showed that, in contrast to diurnal spiders (Tso et al. 2004, 2006, 2007; Hoese et al. 2006; Bush et al. 2008; Fan et al. 2009), the spots do not appear to represent a compromise between prey attraction and predator avoidance. However, as few predator attacks were observed, we cannot be certain that nocturnal predators will attack all yellow spiders in the same way as do diurnal predators.

Nocturnal spiders, such as *N. punctigera*, retreat during the day with their ventral side against a tree or other substrate (Chuang et al. 2008). The dark dorsal coloration of nocturnal orb web spiders thus most likely conceals them against bark,

Table 2

Mean (±SE) chromatic contrast values of yellow and gray paper and spider body coloration against black and brown backgrounds and results of ANOVA test (df = 2, 25) least-significant difference post hoc comparisons

Comparisons	Color contrast values
Yellow paper versus brown paper	0.0992 ± 0.0011[a]
Gray paper versus brown paper	0.0600 ± 0.0013[b]
Spider yellow versus spider brown	0.1438 ± 0.0303[a]
Yellow paper versus black paper	0.0689 ± 0.0014[a]
Gray paper versus black paper	0.0198 ± 0.0013[b]
Spider yellow versus spider black	0.1968 ± 0.0315[c]

Letters represent results of post hoc comparisons.

Table 1

Mean (±SE) chromatic and achromatic contrast values of the black and brown paper and black and brown spider body parts when viewed by a moth against a vegetation background and results of 2-sample *t*-tests (2 tailed)

Comparisons	Contrast values	*t*	df	*P*
Brown paper versus spider brown				
Chromatic	0.1456 ± 0.0007 versus 0.1581 ± 0.0445	0.2821	7.0003	0.7860
Achromatic	0.1858 ± 0.0613 versus -0.2986 ± 0.0132	7.7263	7.6530	<0.0001
Black paper versus spider black				
Chromatic	0.1188 ± 0.0014 versus 0.1193 ± 0.0225	0.0201	11.082	0.9843
Achromatic	-0.1896 ± 0.0211 versus -0.4567 ± 0.0520	4.7562	14.307	0.0003

SE, standard error; df, degrees of freedom.

Table 3

Results of (a) a likelihood-ratio test evaluating the overall effect of treatment and date of experiment on prey attraction rates and (b) Poisson regressions comparing the prey attraction rates of various dummies while considering the effect of date

(a)

Factor	df	Deviance	Likelihood-ratio χ^2	P
Treatment	4	150.53	11.176	0.0247
Date	9	150.78	11.430	0.2474

(b)

Comparisons	$\log_e$ (attraction rate ratio)	SE	Z	P
NS versus SS	−0.9124	0.3597	−2.537	0.0112
GS versus SS	−0.7825	0.3411	−2.294	0.0218
BS versus SS	−0.9608	0.3614	−2.659	0.0078
YS versus SS	−0.5910	0.3134	−1.886	0.0593
BS versus NS	−0.0484	0.4273	−0.113	0.9098

Only the most relevant pairwise comparison results are shown. SE: standard error, SS: standard dummy, GS: dummy with gray spots, YS: all yellow dummy, BS: all black dummy, NS: no dummy treatment.

dirt, or rock in their daytime retreats (Oxford and Gillespie 1998; Chuang et al. 2008). The functional importance of the coloration of their ventral spots has, however, received little attention. Although Chuang et al. (2008) covered the ventral spots of N. punctigera to show that the spots attract prey, nonvisual influences could not be ruled out using these methods. As we used dummies made of paper of predetermined colors that match N. punctigera body parts, we were able to manipulate spot coloration while keeping olfactory, auditory, chemical cues, and other variables (e.g., spider body size, shape, and coloration and spot size and shape) controlled. Our results therefore reliably show that it is the coloration of nocturnal spider ventral spots that lures insects.

Comparisons between the yellow-spotted dummies and the entirely yellow dummies and the extremely low number of observed predation events suggest that, unlike diurnal spiders, the ventral spots of nocturnal spiders do not represent a compromise between prey attraction and predator avoidance. Henceforth, the questions remaining to be resolved are why do nocturnal spiders use spots to lure their prey and not yellow bodies or some other colorful bodily arrangement? What is limiting the size of the spot? Is the shape of the spot and its contrast with the other body colors important in luring
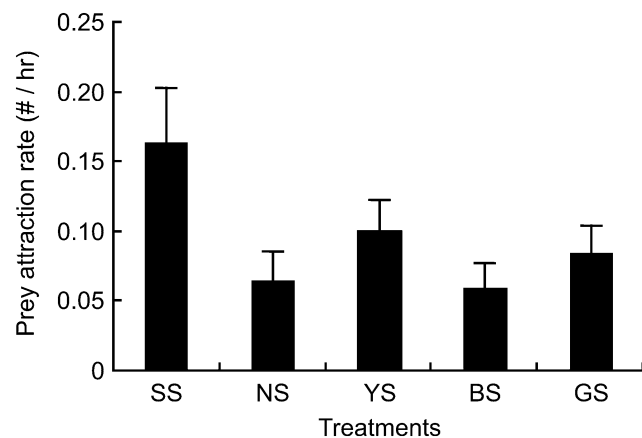

Figure 3
Prey attraction rates (mean ± standard error) for the 4 types of dummies and the no spider treatment. Prey attraction rate = insects attracted per hour of video footage. SS = standard dummy; YS = yellow dummy; BS = black dummy; GS = dummy with gray spots; and NS = no spider treatment.

prey, as has been suggested for the prey luring function of spider web decorations (Cheng et al. 2010)?

Insect visual models suggest that, depending on the spatial resolution of any particular insect, spider ventral spots are likely to be poorly resolved unless an insect is very close to the spider (Land and Osorio 2003; Kelber et al. 2006). Nonetheless, recent studies suggest that spatial resolutions by insects may be better than previously thought (Somanathan et al. 2008; Goyret 2010). It, however, remains to be tested whether resolution in any nocturnal insect is good enough to detect spider ventral spots at long distances. Perhaps high resolution is not necessarily required for the spots to lure prey. Perhaps the spots are exploiting a key, as yet unidentified chromatic or achromatic visual cue used by foraging or navigating insects. The symmetry of the spots may be implicit in the luring of insects as they may resemble pattern symmetries that insects use to identify flower parts (Dafni and Kevan 1996), although this suggestion remains speculative at present.

The finding of similar body coloration patterns in numerous taxonomically distant nocturnal orb web spiders suggests that the selective pressure for the development of these spots is strong. It might be expected that, contrary to the diurnal system where the risk of predator attraction influences on the behavioral repertoire of animals (Ruxton et al. 2004), the low predation pressure experienced by nocturnal spiders allows them sovereignty to invest more in offensive traits. The ecological significance of the shape and symmetry of the spots nonetheless remains unresolved. More investigations are needed to determine if the yellow spots of other nocturnal spiders function similarly as prey lures. They may, for example, resemble nectar guides used by insects to locate food. Alternatively, they may be the most energy efficient way, given the available resources, for nocturnal spiders to invest in prey enticing coloration (Kelsh et al. 2009) or is an evolutionary or ontogenetic remnant that is costly to discard and happens to lure prey (Wittkopp et al. 2003; Kemp et al. 2005). Time and resource constraints, unfortunately, meant it was not possible to perform experiments to test the significance of spot size, shape, and position herein, but these should be considered in follow up studies.

In summary, we found that the coloration of the paired ventral spots of the nocturnal spider N. punctigera act as a prey lure through chromatic and/or achromatic components. Because spider dummies of an entirely yellow body attracted fewer prey than spider dummies with yellow spots, we concluded that the spots do not represent a compromise between prey attraction and predator avoidance. If the spots do not mimic a visual cue

relied on by insects there must be other selective explanations for their repeated emergence. Identification and information on the coloration of other potentially acting nocturnal insect cues, for example, nectar guides, and spectral comparisons between these cues and the spider ventral spots is required to elucidate their evolutionary and ecological significance.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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