

Trap barricading and decorating by a well-armored sit-and-wait predator: extra protection or prey attraction?

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Abstract Animals may build multiple structures to provide benefits to counter the costs of building. Many orb web spiders add multiple structures, e.g., barricading barrier webs and silk decorations, to their webs and these structures have been hypothesized to function to deter predators or attract prey. The heavily armored spiny spiders construct barrier webs around their orb webs and decorate them with conspicuous silk tufts. Why these organisms, already well protected by a thick cuticle and spines, make the extra investment of building barrier webs and adding conspicuous silk decorations is not known. We predicted that these structures function to both attract prey and deter predators. Field experiments were conducted in two consecutive years using orb webs built by the East Asian spiny spider *Thelacantha brevispina*. We either (1) concealed the decoration, (2) removed the barrier webs, or (3) left the decorations and barrier webs intact. We found year and treatment to interactively influence prey interception rates. In 2010, but not in 2009, we found prey interception with *T. brevispina* webs to be greater when the decorations were conspicuous than when they were concealed suggesting

that the decorations may lure prey. Prey interception was lower when the barrier webs were present without decorations compared to when they were absent without decorations. The prey-attracting function of the decorations thus may counter the reduction in prey interception incurred by adding a barrier web. Predatory wasp interactions were not influenced by any of our treatments, probably because the spiders' thick cuticle is the primary means of protection from wasps. Bird predation events, while rare, occurred only when decorations were concealed or the barrier webs were removed. It is therefore plausible that the tuft decorations both lure prey and deter birds.

Keywords Animal structure · Barrier web · Interspecific signal · Spiny spiders · Tuft decorations

Introduction

Building structures such as nests, burrows, bowers, mounds, and traps by animals may come at substantial costs (Borgia 1993; Hansell 2005; Blamires et al. 2010). These costs may be categorized as material, energetic, time, and expression costs (Eberhard 1986; Jeanne 1986; Mondy et al. 2011). Material costs are related to the production and secretion of materials from which the structures are made (Eisner 1994; Hansell 2005; Mondy et al. 2011). Energetic costs include metabolic energy expended gathering materials and building the structure (Eberhard 1986; Mondy et al. 2011). Time diverted from foraging, mating, or avoiding predators into building constitutes the time cost (Hansell 2005; Blamires et al. 2010). Expression costs are associated with a structure's appearance and are incurred over and above the costs encountered independent of the structure, e.g., increased exposure to predators, parasites, or stressful

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environments (Tolbert 1979; Petrie and Moller 1991; Bruce et al. 2001; Hansell 2005). The relative influence of these costs varies over time (Lima and Bednekoff 1999). Exposure to predators is the greatest cost that animals face so building at times that increases their exposure to predators are not likely to be favored (Ruxton et al. 2004). Conversely, building a structure that significantly reduces an animal's exposure to parasites or predators might be favored at any time provided the other costs are unchanged (Eisner 1994; Hansell 2005).

Spider orb webs are structures that come at material, energetic, time, and expression costs (Tanaka 1989; Craig 2003; Blamires et al. 2010). Exposure to predators is a potential expression cost associated with web building (Blamires et al. 2007; Manicom et al. 2008) and may explain why many spiders have returned to cursorial hunting (Blackledge et al. 2009). Many spiders have nonetheless developed strategies, e.g., building barricades, retreats, or decoys (Blackledge et al. 2003; Manicom et al. 2008; Tseng and Tso 2009), to minimize the risk of predation while on their webs. On the other hand, some spiders rely on body armory, aposematic, or disruptive body coloration to avoid predators (Théry and Casas 2009; Foelix 2011).

Many diurnal orb web spiders add structures called decorations (nomenclature following Herberstein et al. 2000) made of silk, debris, eggs, or prey remains to their webs. Since the colors of many decorations are conspicuous and attractive to both the predators and prey of orb web spiders, they appear to be a form of visual signal (Bruce et al. 2005; Cheng and Tso 2007; Blamires et al. 2008; Cheng et al. 2010). Many hypotheses have been proposed to explain their function. Both prey attraction (Craig and Bernard 1990) and predator deterrence (Blackledge 1998; Blackledge and Wenzel 1999) have been proposed, with much of the experimental evidence conflicting. A recent study showed that the prey carcass decorations and barrier webs of the orb web spider *Nephila clavata* function interactively, *i.e.*, their combined effects are disproportionately greater than the sum of their effects in isolation, to increase prey capture success (Blamires et al. 2010). Unaccounted for interactive functions between web decorations and other web components may thus, partially, explain why there has been conflicting evidence regarding decoration functions (see also Cheng et al. 2010).

Spiny spiders (*Gasteracantha* spp., *Micrathena* spp., and *Thelacantha* spp.) are colorfully conspicuous spiders that have a thick and spiny cuticle (Foelix 2011; Fig. 1a). Their cuticle coloration has been shown to attract prey (Hauber 2002). It may also attract predators, although their thick cuticle and spines offer considerable protection (Muma 1971). Many spiny spiders build a barrier web, a complex three-dimensional silk barricade, onto which some place

silken tuft decorations (Fig. 1b, c). More commonly, however, they place their tuft decorations onto the orb frame (Jaffé et al. 2006). Advertising the presence of the barrier web to bird predators has been ascribed as the most plausible primary function of spiny spider tuft decorations (Jaffé et al. 2006; Eberhard 2007; Gawryszewski and Motta 2008). Despite the tuft decorations being visible and attractive to insects (Gawryszewski and Motta 2008), they are generally assumed not to attract prey (Eberhard 2007; Gawryszewski and Motta 2008). Prey attraction has, nevertheless, only ever been indirectly assessed, e.g., from web damage, prey behavioral experiments, or correlations between capture success and decoration investment (Eberhard 2007; Gawryszewski and Motta 2008).

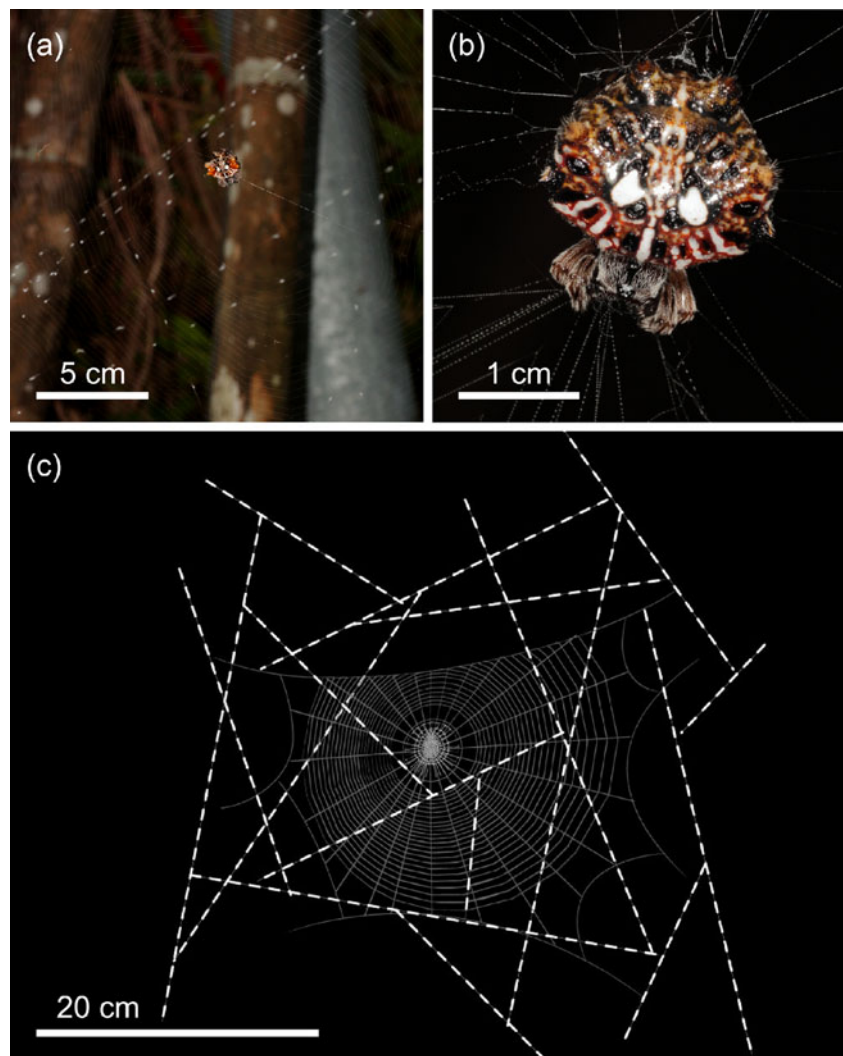
By adding tuft decorations to an already visible barrier web (Blamires et al. 2010), spiny spiders appear to undertake extra expenditure for no apparent significant gains. Since decorations and barrier webs on other spider webs may interactively attract prey (Blamires et al. 2010), we hypothesize that the tuft decorations of spiny spiders interact with the barrier web to lure and capture more prey. Hence we performed experiments using a field population of East Asian spiny spiders, *Thelacantha brevispina* to empirically determine the interactive influences of tuft decorations and barrier webs on prey interception rate by their webs. We manipulated the conspicuousness of the tuft decorations and the presence of barrier webs and monitored the webs using video cameras. We predicted that if the structures interact to lure and retain prey then prey interception rates will be lower when neither structure is present. We, additionally, identified and quantified predator attraction rates and quantified the visibility of the tuft decorations to bees and birds to assess whether a trade-off between prey attraction and predator avoidance is likely.

Materials and methods

Study site and measurements

We conducted field experiments in a secondary tropical forest beside Yung-Hsing Farm, Orchid Island, Taiwan (121°34'21.16" E, 22° 1'44.65" N) over 10 days in both July 2009 and May 2010. We repeated the experiment in two successive years to maximize the likelihood of making observations on bird approaches and attacks. We did not intend to assess annual variations in the prey attraction and predator avoidance functions of the decorations and barrier webs so no environmental variables were measured. We selected these times of year because these were times when the site was accessible. We randomly searched different proportions of the study site daily, for approximately 1 h, for webs containing adult female *T. brevispina*. As the study

Fig. 1 **a** Tuft decorations on barrier webs built by *Thelacantha brevispina*. **b** Dorsal view of the spiny spider *T. brevispina*. **c** A schematic drawing illustrating the barrier web and tuft decorations built by *T. brevispina*



site was large and the population of *T. brevispina* was large, we considered it unlikely that any spiders were re-sampled in any year. We measured the body length and width of each *T. brevispina* that we encountered using calipers. We, additionally, made the following measurements for each *T. brevispina* web that we encountered: (1) hub length and diameter, (2) web radius along four cardinal directions (up, down, left, and right), in order to estimate the web capture area excluding the hub (Herberstein and Tso 2000), (3) the total length and width of the barrier web, and (4) the number of silk tuft decorations on barrier web threads.

Experiments

We systematically assigned all webs to one of three treatment groups, manipulated so that: (1) barrier webs (BW) were present but decorations (D) absent (designated as BW+/D-), (2) both barrier webs and decorations were absent (designated as BW-/D-), and (3) both barrier webs and decorations were present (designated as BW+/D+). For

the BW+/D- treatment, we painted the tuft decorations using a watercolor brush and paint (Poster color no. 64, Pentel, Inc., Tokyo, Japan) that was pre-selected based on its color match with the background (see below for details of the determination of background color) to visually conceal the decorations from predators and prey. For the BW-/D- treatment, we removed the barrier webs using a stick of burning incense. For the BW+/D+ treatment webs, the barrier webs and decorations were both left intact. To account for a possible influence of paint odor, we painted leaves near the orb webs of the BW-/D- and BW+/D+ treatments using the same amount of paint that was used to paint the decorations. We did not use a “positive control”, e.g., painting the tufts with white paint, as we could not accurately match the spectral properties of any commercially available white paint with the decorations.

We used video monitoring to assess the interactions between spiders and their predators and prey. We simultaneously monitored five webs from each of the treatments ($N=15$ overall) each day between 0800 hours and 1600 hours.

We placed the video cameras (TRV 118 Hi-8 and 10 HDD, Sony, Tokyo, Japan) 1 m from each web at approximately 45° to perpendicular. We used the same 15 video cameras over the entire 10 days of monitoring in each year.

Because the tuft decorations are placed on the barrier web threads therefore we could not create a BW-/D+ treatment. Thus we could not directly assess the function of the decorations in isolation of the barrier webs (Blamires et al. 2010). Given this constraint we systematically tested five hypotheses: (1) decorations alone influence the interactions between *T. brevispina* and its prey or predators (implicit if BW+/D- = BW-/D- ≠ BW+/D+), (2) barrier webs alone influence the interactions between *T. brevispina* and its prey or predators (if BW+/D- = BW+/D+ ≠ BW-/D-), (3) decorations in the presence of the barrier web influence the interactions between *T. brevispina* and its prey or predators (if BW-/D- = BW+/D+ ≠ BW+/D-), (4) both structures independently influence the interactions between *T. brevispina* and its prey or predators (if BW+/D- ≠ BW-/D- ≠ BW+/D+), or (5) neither structure influences the interactions between *T. brevispina* and its prey or predators (if BW+/D- = BW-/D- = BW+/D+).

Predator and prey vision modeling

We cut ten tufts from ten different spiny spider webs ($N=100$ in total) from the study site and returned them to the laboratory at Tunghai University, Taichung, to generate reflectance functions, using an S4000 spectrometer (Ocean Optics, Inc., Dunedin, Florida, USA) of the decorations and the paint used to conceal them. The reflectance functions of the background onto which the decorations were viewed by predators and prey were determined by spectrometry of live leaves, dead leaves, bark, and rocks collected from the study site (see Tso et al. 2004, 2006; Théry et al. 2005).

We were interested in determining how hymenopterans and insectivorous birds perceived the decorations as they represented the likely predators (wasps and birds) and prey (bees) of spiny spiders. We therefore used a photoreceptor sensitivity model derived for honeybees (Stavenga et al. 1993), to represent the visual sensitivity of hymenopterans, and blue tits (Hart 2001), to represent the visual sensitivity of insectivorous birds, to calculate the chromatic and achromatic contrasts of the decorations. We used the honeybee and blue tit models because, at present, they are the best representatives of the predator and prey groups of interest to us for which there are sufficient data across the visible spectrum to confidently calculate photoreceptor excitation values. Additionally, these models have been previously used to elucidate the signaling function of spider web decorations (Bruce et al. 2005).

We calculated the excitation values (E_i) of bee and blue tit UV, blue and green photoreceptors when exposed to decorations or concealing paint using the equations (Defrize et al. 2010):

$$Q_i = \int_{300}^{700} S(\lambda)D(\lambda)I_s(\lambda)d\lambda$$

and

$$E_i = Q_i/(Q_i + 1)$$

Where Q_i is the “quantum catch” of the receptor under investigation (i). $S(\lambda)$ is the sensitivity function of the receptor under investigation. $D(\lambda)$ is the daytime illumination function, a measure of the ambient reflectance spectra in the area under normal daylight illumination, which was determined at the study site by Tso et al. (2004), and $I_s(\lambda)$ is the signal (decorations or paint) reflectance function.

We calculated the chromatic contrasts as the excitation sensitivity of all photoreceptor types to the background subtracted from the excitation sensitivity of the photoreceptor to the decorations or paint. We calculated the achromatic contrasts as the sensitivity of the bee green receptor or blue tit double cone receptors to the decorations or paint divided by that of the background (Vorobyev and Osorio 1998). All chromatic and achromatic contrasts were each calculated using Avicol[®] software (Gomez 2006). For honeybees the visual discrimination threshold under achromatic and chromatic conditions is 1 U of just noticeable difference (JND), a statistical measure based on the probability of observers noticing differences in a gradually differing image (Lubin 1995). For birds, the visual discrimination threshold under achromatic conditions is 1 JND while that under chromatic conditions is 5 JND (Defrize et al. 2010).

Video processing

When the field experiments were completed we viewed the video footage in the laboratory at Tunghai University. We recorded all insects that were intercepted by *T. brevispina* webs and identified them to order and estimated their length by reference to length of the spider. We defined predator interaction events as a wasp or bird predator moving close to the spider and hovering with or without launching an attack. Any individual web with < 4h of available footage was not included in the analyses. As all of the footage was watched at low speed by the same person (HJT) and every prey and predator approach/attack event was repeatedly watched, and the tape time recorded, to ensure the prey/predator was positively identified and could all be double-checked, we were confident that the results attained were accurate.

Statistical analyses

We used one-sample *t* tests (one-tailed) to determine whether the chromatic and achromatic contrast values of conspicuous and concealed tuft decoration against the mean background were below honeybee or blue tit visual discrimination threshold values. Threshold JND under achromatic/chromatic conditions is 1/1 for honeybees and 1/5 for blue tits.

All prey interception and wasp approach data failed tests for normality and homogeneity of variances (Kolmogorov–Smirnov and Levene’s tests; $P < 0.05$) thus parametric procedures such as ANOVA/ANCOVA were not appropriate (Zar 2010). We therefore used a likelihood-ratio test to ascertain the effects of treatment, year, and their interaction on prey interception rates. We dropped the two independent variables sequentially from a full model to develop a reduced model and we calculated the differences of deviance between the full model and the reduced model using a likelihood-ratio test following a χ^2 distribution. As the prey interception rates for both 2009 (Pearson $\chi^2 = 8.865$, $P = 0.306$) and 2010 (Pearson $\chi^2 = 8.702$, $P = 0.698$) fitted well with the negative binomial model, we used a series of pairwise (assigned based on our hypotheses outline in the “experiments” section) negative binomial regressions to compare the prey interception rates (number of prey intercepted per hour per square meter of web capture area) of *T. brevispina* webs across treatments in 2009 and 2010. In 2009 and 2010, mean body length of spiny spiders used was 0.496 (± 0.010) cm, mean body width was 0.492 (± 0.013) cm, the mean orb area was 306.06 (± 18.81) cm², the mean barrier web volume was 0.226 (± 0.035) m³, and the average number of tuft decorations on barrier webs were 139.256 (± 7.207). We used Mann–Whitney *U* tests to test for differences between years and between-treatment groups. The body size of spiny spiders in our experiments ($N = 158$) were similar between years ($U = 3018$, $P = 0.82$) and treatments ($U = 3313$, $P = 0.96$). There were, likewise, no significant yearly or between-treatment differences in web area (yearly comparisons: $U = 1,051$, $P = 0.21$; treatment comparisons: $U = 949$, $P = 0.27$) or number of decorations added to barrier webs (yearly comparisons: $U = 599$, $P = 0.10$; treatment comparisons: $U = 417$, $P = 0.06$). Bird and wasp approach and attack rates in either year were too low to analyze the affects of treatment, year, and their interactions. We therefore used a χ^2 tests for homogeneity to compare the prey composition between treatments in each year. Wasp approach rates in both years fitted well with negative binomial model (Pearson $\chi^2 = 12.113$, $P = 0.800$) so we used pairwise binomial regressions to compare the wasp approach rates across treatments in 2009 and 2010. We observed only six bird interactions in both years combined ($N = 4$ in 2009 and $N = 2$ in 2010), so these could not be analyzed.

Results

We found the achromatic and chromatic contrasts of the tuft decorations were significantly higher than the bee visual discrimination threshold of 1 JND, but those of the paint did not exceed this threshold (Table 1 (honeybees)). The achromatic and chromatic contrasts of tuft decorations were significantly higher than the blue tit visual threshold values (1 and 5 JND, respectively), but those of the paint used to conceal the decorations did not exceed these thresholds (Table 1 (birds (blue tits))). Hence the decorations were visible to the prey and predators of *T. brevispina* but the paint was not.

We observed a total of 1,066 h video footage (538 h from 2009 and 528 h from 2010). For the BW+/D− group, a total of 338 h (181 h, 27 individuals in 2009 and 157 h, 27 individuals in 2010) was observed, while a total of 405 h (204 h, 28 individuals in 2009 and 201 h, 28 individuals in 2010) and 323 h (153 h, 23 individuals in 2009 and 170 h, 25 individuals in 2010) were observed for the BW−/D− and BW+/D+ group, respectively. We found that the year and the year–treatment interaction affected the prey interception rate of *T. brevispina* webs (Table 2). Our negative binomial regressions found that prey interception rates did not significantly differ among treatments in 2009 (Online Resource 1, Fig. 2a). However, in 2010 the BW+/D− group had a significantly lower prey interception rate than that of the other two groups (Online Resource 1, Fig. 2b), agreeing with our pre-nominal hypothesis 3 that decorations influ-

Table 1 Mean (\pm SE) achromatic and chromatic contrast values of tuft decorations built by *Thelacantha brevispina* and paint used to conceal the decorations when viewed against the vegetation background by honeybees and birds (blue tits), showing results of one-sample *t* tests comparing the values with discrimination thresholds

	Chromatic	Achromatic
Honeybees		
Tuft decorations	1.876 \pm 0.082	7.451 \pm 0.575
<i>t</i> ₁₉	11.870	11.867
<i>P</i>	<0.0001	<0.0001
Paint	0.783 \pm 0.018	0.775 \pm 0.271
<i>t</i> ₄	−11.872	−0.829
<i>P</i>	0.999	0.773
Birds (blue tits)		
Tuft decorations	7.370 \pm 0.332	18.873 \pm 1.048
<i>t</i> ₁₉	7.140	16.764
<i>P</i>	<0.0001	<0.0001
Paint	2.974 \pm 0.031	1.879 \pm 0.495
<i>t</i> ₄	−66.404	1.776
<i>P</i>	1	0.075

Table 2 Results of likelihood-ratio test comparing the reduced model to the full model

Dropped variable	Deviance	Δdf	Likelihood-ratio χ^2	<i>P</i> value
Full model	185.17	–	–	
Treatment	185.91	2	0.7457	0.6888
Year	193.45	1	8.2821	0.0004
Treatment \times year	195.77	2	10.5991	0.0005

The significance level of deviance between the full model and the reduced model is used as an indication of the effect of dropped variable

ences the interactions between *T. brevispina* and its prey but this is dependent on the presence of the barrier web. We found the prey interception rates in 2009 for all treatments to be significantly higher than those in 2010 (BW+/D–: $U=89$, $P<0.001$; BW–/D– $U=176$, $P=0.01$; and BW+/D+: $U=194$, $P=0.02$; Fig. 2). The prey composition nonetheless did not differ among treatments in 2009 ($\chi_1^2=9.71$, $P=0.28$) or 2010 ($\chi_1^2=4.47$, $P=0.61$), with Hemiptera, Diptera, and Hymenoptera predominantly intercepted at all times. The body length of prey in all treatment groups in 2009 (BW+/D+= 1.69 ± 0.13 mm, BW+/D–= 1.32 ± 0.06 mm, and BW–/D–= 1.41 ± 0.07 mm) and 2010 (BW+/D+= 1.48 ± 0.12 mm, BW+/D–= 1.79 ± 0.65 mm, and BW–/D–= 1.19 ± 0.11 mm) was also similar.

The wasp predators we principally observed approaching *T. brevispina* webs were *Batozonellus* sp. and *Eumenes* sp. Wasp interactions did not differ significantly between 2009 and 2010 ($U=3376$, $P=0.96$) so we pooled the data. Wasp interaction rates did not differ among treatment groups (Fig. 3; Online Resource 2) and most approaches (nine out of 11) did not involve an attack. From 2 years of video monitoring, we observed only six bird interaction events. Bird approach events only occurred in the control group ($N=2$), in which the birds looked at the webs without launching an attack. We witnessed four bird attack events,

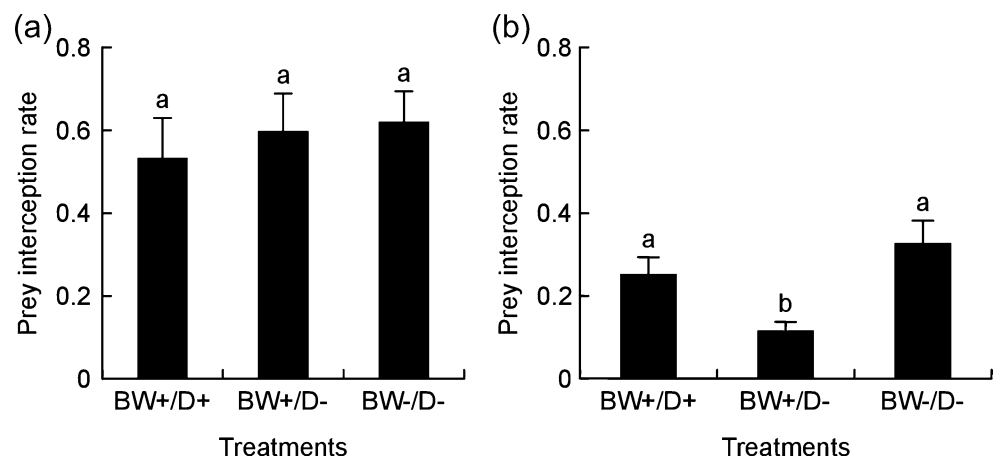
three of which occurred on the BW–/D– group and one on the BW+/D– group. In all four cases the spiders were consumed by the birds.

Discussion

Our study empirically shows that the tuft decorations of the spiny spider *T. brevispina* are visible to insects and it is the first to suggest that they may function to improve prey interception under certain circumstances. We could not directly assess whether the tuft decorations and the barrier webs interact to attract prey (e.g., as in Blamires et al. 2010) as the prey-attracting properties of the tuft decorations without the barrier webs could not be assessed. Nonetheless, our pairwise statistical analyses suggested that the prey-attracting influence of the decorations is dependent on the presence of the barrier web. Moreover, in 2010 the webs in the BW–/D– treatment group caught more prey than the webs in the BW+/D– group, suggesting that the presence of the barrier web alone has a negative influence on prey capture success. Our results therefore provide indirect evidence that adding tuft decorations and barrier webs increases prey capture success in *T. brevispina* webs via interactions between the structures.

In our experiments year interacted with treatment, influencing the experimental outcomes in the 2 years. This was manifested in our finding of a significant decrease in prey interception rate in the webs of the BW+/D– treatment in 2010 but not in 2009. This finding was nonetheless incidental as we repeated the experiment in 2010 to gather further information on bird predation. We had no *a priori* basis to devise a testable hypothesis about the influence of annually varying parameters (Polis et al. 1998), so we did not measure any annually varying environmental factors that could be influencing the prey attraction or predator avoidance properties of *T. brevispina* barrier webs or tuft decorations. Spider body size, orb web size, barrier web volume, and the

Fig. 2 Mean (\pm SE) prey interaction rates (number of prey intercepted per hour per 100 square centimeter of capture area) of *T. brevispina* on webs with either tuft decorations concealed (BW+/D–), barrier webs removed (BW–/D–) or decorations and barrier webs left intact (BW+/D+) recorded in 2009 (a) and 2010 (b) field studies. Letters ($a > b$) represent results of negative binomial regressions



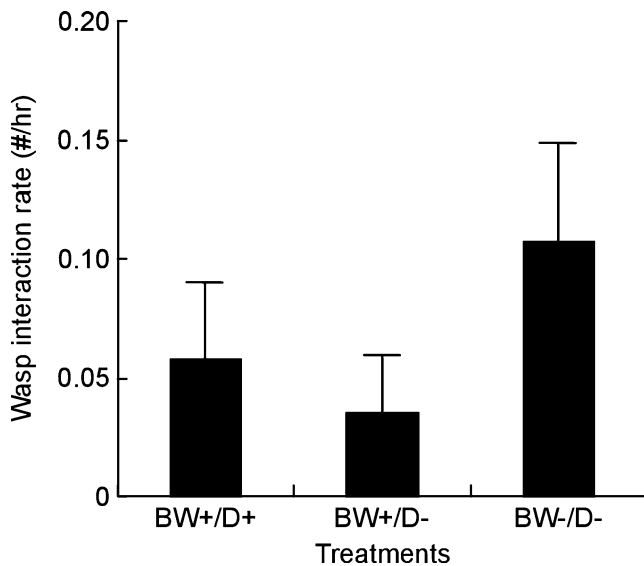


Fig. 3 Mean (\pm SE) wasp interaction rates (number of wasps interacted with spider per hour of monitoring) of *T. brevispina* webs with either tuft decorations concealed (BW+/D-), barrier webs removed (BW-/D-) or decorations and barrier webs left intact (BW+/D+)

number of decorations used per barrier web thread and prey ordinal composition or size did not vary between years, so these were not factors influencing between year variations in prey interception. A multitude of ecological factors, e. g., temperature, weather, light conditions, may have varied between the 2 years at our site (see Huang 2006). We, however, are not convinced that the yearly differences in prey interception are driven by any of them. Less prey, overall, interacted with webs in 2010 so our finding may be a random anomaly generated by greater noise encountered at lower prey abundances. Whatever the proximal reasons for the annual variations, our results suggest that the tuft decorations may affect prey interception rates differently at different times. We, accordingly, suggest that future investigations of the functions of spider web decorations account for possible temporal influences.

As there was no difference in the number of tufts placed on barrier web threads between years, despite there being large differences in the amount of prey interacting with webs, satiation levels did not appear to influence decoration building in *T. brevispina*. Prey attraction, thus, appears not to be the principal function of *T. brevispina* tuft decorations. Indeed, since they are associated with the barrier web and the barrier web is principally built as a barricade to protect the spider from predators (Blackledge and Wenzel 2001; Blackledge et al. 2003; Manicom et al. 2008), advertising the barrier web to predator appears to be their main function, as found for the tuft decorations placed on web frames in *Gasteracantha cancriformis* (Eberhard 2007; Gawryszewski and Motta 2008).

The tuft decorations of *T. brevispina* strongly reflect UV and blue light. Birds and bees have UV and blue photoreceptors and are phototactic toward UV and blue light (Briscoe and Chittka 2001; Bennett and Cuthill 1994). For this reason, reflection of light at these wavelengths has been used to argue that the silk decorations of orb web spiders of the genus *Argiope* are signals perceived by, and attractive to, hymenopteran and avian prey and predators (Bruce et al. 2005; Blamires et al. 2008; Cheng et al. 2010). The shape of *Argiope* decorations conform to insect form-vision (Cheng et al. 2010), strengthening the argument that they principally function to lure prey. Spiny spider tuft decorations are visible to hymenopteran and avian prey and predators, however, they do not conform to any insect or bird form-vision model, nor do they appear to mimic any resource. Nonetheless, imperfect mimics may still be attractive to a receiver (Gilbert 2005). The tuft decorations of *T. brevispina* may, hence, be an imperfect mimic that is inadvertently attractive to insects despite prey attraction not being their principal function.

We found that the presence of neither the barrier web nor decorations influenced wasp approach rates. Thus a trade-off between prey attraction and wasp predator avoidance does not appear to be implicit in their use. The wasp approach rates were marginally, but insignificantly, lower for the BW+/D- treatment compared to the BW-/D- treatment. Henceforth, the barrier web seems not to function to protect spiny spiders from wasp predators, contrary to the predictions for other spiders (Blackledge and Wenzel 2001; Blackledge et al. 2003). Spiny spiders, however, invest in a thick, spiny cuticle that, presumably, deters wasp predators (Elgar and Jebb 1999). Wasps, accordingly, do not represent a significant threat to spiny spiders. Indeed, we found that few of the wasps that approached the spiny spiders ever attacked them. It is therefore unlikely that the barrier web is built primarily to protect the spider from wasps. More likely, the barrier web is built as a barricade against birds (Jaffé et al. 2006; Eberhard 2007). Our spectral modeling found that the decorations are conspicuous to birds. Nevertheless, we witnessed few bird attacks despite viewing immense video footage (1,066 h). Lethal events, however, can affect fitness in animals even if they are exceptionally rare (Lima and Bednekoff 1999; Lind and Cresswell 2005). It is therefore conceivable that spiny spiders will invest time and energy into building barrier webs because the benefits (protection from bird attacks) bestow survivorship impacts. In addition to barricading the spider from predators, barrier webs have been implicated as reducers of the number of prey caught in spider webs (Blackledge and Wenzel 2001; Blamires et al. 2010). Indeed, we found that when the barrier webs had their decorations concealed prey interception was lower than when decorations were present. Tuft decorations may thus be placed on the barrier

web as a means to counter the negative influence on prey capture rate induced by the barrier web in addition to web advertising.

The principal function previously assumed for spiny spider tuft decorations is advertising the barrier web to ensure bird predators do not approach (Jaffé et al. 2006; Eberhard 2007; Gawryszewski and Motta 2008). We could not directly assess whether this holds for *T. brevispina* barrier webs containing tuft decorations because we observed too few bird approach events. Nonetheless, we did note that birds never approached spiders when both barrier webs and decorations were present. The empirical results and visual models developed in this study and others (e.g., Gawryszewski and Motta 2008) suggest that it is plausible that the barrier webs and tuft decorations of spiny spiders provide both antipredatory and prey attraction benefits. Perhaps such combined benefits provide an explanation for the extra investment in both structures by *T. brevispina* despite already investing in a thick cuticle and spines for defense (Foelix 2011).

In summary, our field studies and vision models show that the tuft decorations on *T. brevispina* barrier webs may increase prey interception rates and that this attraction is dependent on the barrier web's presence. As the barrier web alone appears to reduce prey interception rates, the barrier web and the decorations interact to induce this effect but the influence of the decorations alone could not be assessed. This is the first time this function has been shown for any spiny spider silk decorations. We found that the prey-attracting influence of the decorations may vary yearly. Barrier webs are built by these already well-armed sit-and-wait predators as a barricade from birds and the tuft decorations may advertise its presence (Jaffé et al. 2006; Eberhard 2007; Gawryszewski and Motta 2008). Since building multiple structures is associated with material, energetic, time, and expression costs for animals (Jeanne 1986; Craig 2003; Hansell 2005; Blamires et al. 2010; Mondy et al. 2011), the survivorship benefits experienced by building multiple structures must outweigh the costs. If birds represent rare but lethal predators to *T. brevispina*, building multiple structures to vigilantly prevent bird attacks while maintaining foraging gains may bestow fitness advantages that significantly outweigh the associated costs.

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References

- Bennett ATD, Cuthill IC (1994) Ultraviolet vision in birds: what is its function? *Vis Res* 34:1471–1478
- Blackledge TA (1998) Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *J Zool* 246:21–27
- Blackledge TA, Wenzel JW (1999) Do stabilimenta in orb webs attract prey or defend spiders? *Behav Ecol* 10:372–376
- Blackledge TA, Wenzel JW (2001) Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* 138:155–171
- Blackledge TA, Coddington JA, Gillespie RG (2003) Are three-dimensional spider webs defensive adaptations? *Ecol Lett* 6:13–18
- Blackledge TA, Scharff N, Coddington JA, Szuts T, Wenzel JW, Hayashi CY, Agnarsson I (2009) Reconstructing web evolution and spider diversification in the molecular era. *Proc Natl Acad Sci U S A* 106:5229–5234
- Blamires SJ, Thompson MB, Hochuli DF (2007) Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecol* 32:551–563
- Blamires SJ, Hochuli DF, Thompson MB (2008) Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web. *Biol J Linn Soc* 94:221–229
- Blamires SJ, Lee YH, Chang CM, Lin IT, Chen JA, Lin TY, Tso IM (2010) Multiple structures interactively influence prey capture efficiency in spider orb webs. *Anim Behav* 80:947–953
- Borgia G (1993) The cost of display in the non resource-based mating system of the satin bowerbird. *Am Nat* 141:729–743
- Briscoe AD, Chittka L (2001) The evolution of color vision in insects. *Ann Rev Entomol* 46:471–510
- Bruce MJ, Herberstein ME, Elgar MA (2001) Signalling conflict between prey and predator attraction. *J Evol Biol* 14:786–794
- Bruce MJ, Heiling AM, Herberstein ME (2005) Spider signals: are web decorations visible to birds and bees? *Biol Lett* 1:299–302
- Cheng RC, Tso IM (2007) Signaling by decorating webs: luring prey or deterring predators? *Behav Ecol* 18:1085–1091
- Cheng RC, Yang EC, Lin CP, Herberstein ME, Tso IM (2010) Insect form vision as one potential shaping force of spider web decoration design. *J Exp Biol* 213:759–768
- Craig CL (2003) Spiderwebs and silks: tracing evolution from molecules to genes to phenotypes. Oxford University Press, Oxford
- Craig CL, Bernard GD (1990) Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* 71:616–624
- Defrize J, Thery M, Casas J (2010) Background colour matching by a crab spider in the field: a community sensory ecology perspective. *J Exp Biol* 213:1425–1435
- Eberhard WG (1986) Effects of orb-web geometry on prey interception and retention. In: Shear WA (ed) *Spiders: webs, behavior and evolution*. Stanford University Press, Stanford, pp 70–100
- Eberhard WG (2007) Stabilimenta of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): evidence against a prey attractant function. *Biotropica* 39:216–220
- Eisner T (1994) Integumental slime and wax secretion: defensive adaptations of sawfly larvae. *J Chem Ecol* 20:2743–2749
- Elgar MA, Jebb M (1999) Nest provisioning in the mud-dauber wasp *Sceliphron laetum* (F. Smith): body mass and taxa specific prey selection. *Behaviour* 136:147–159
- Foelix RF (2011) *Biology of Spiders*, 3rd edn. Oxford University Press, Oxford
- Gawryszewski FM, Motta C (2008) The silk tuft web decorations of the orb-weaver *Gasteracantha cancriformis*: testing the prey attraction and the web advertisement hypotheses. *Behaviour* 145:277–295
- Gilbert F (2005) The evolution of imperfect mimicry. In: Fellowes MDE, Holloway GJ, Rolff J (eds) *Insect evolutionary ecology*. CABI, Wallingford, pp 231–288
- Gomez D (2006) AVICOL, a program to analyse spectrometric data. Available free at <http://sites.google.com/site/avicolprogram/>

- Hansell M (2005) *Animal Architectures*. Oxford University Press, Oxford
- Hart NS (2001) The visual ecology of avian photoreceptors. *Prog Ret Eye Res* 20:675–703
- Hauber ME (2002) Conspicuous coloration attracts prey to a stationary predator. *Ecol Entomol* 27:686–691
- Herberstein ME, Tso IM (2000) Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneioidea, Araneae). *J Arachnol* 28:180–184
- Herberstein ME, Craig CL, Coddington JA, Elgar MA (2000) The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biol Rev* 75:649–669
- Huang WS (2006) Ecological characteristics of the skink, *Maybuya longicauda*, on a tropical East Asian island. *Copeia* 2006:293–300
- Jaffè R, Eberhard WG, De Angelo C, Eusse D, Gutierrez A, Quijas S, Rodríguez A, Rodríguez M (2006) Caution, webs in the way! Possible functions of silk stabilimenta in *Gasteracantha cancriformis* (Araneae, Araneidae). *J Arachnol* 34:448–455
- Jeanne RL (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav Ecol Sociobiol* 19:333–341
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659
- Lind J, Cresswell W (2005) Determining the fitness consequences of anti-predation behaviour. *Behav Ecol* 16:945–956
- Lubin J (1995) A visual system discrimination model for imaging system design and evaluation. In: Peli E (ed) *Visual models for target detection and recognition*. World Scientific Publishers, River Edge, pp 245–283
- Manicom C, Schwartzkopf L, Alford RA, Schoener TW (2008) Self-made shelters protect spiders from predation. *Proc Natl Acad Sci* 105:14903–14907
- Mondy N, Cathalan E, Hemmer C, Voituron Y (2011) The energetic costs of case construction in the caddisfly *Limnephilus rhombicus*: direct impacts on larvae and delayed impacts on adults. *J Ins Physiol* 57:197–202
- Muma MH (1971) Biological and behavioral notes on *Gasteracantha cancriformis* (Arachnida: Araneidae). *Fla Entomol* 54:345–351
- Petrie M, Moller AP (1991) Laying eggs in others' nests: intraspecific brood parasitism in birds. *Trends Ecol Evol* 6:315–320
- Polis GA, Wise D, Hurd SD, Sanchez-Pinero F, Wagner JD, Jackson TD, Barnes JD (1998) The interplay between natural history and field experimentation. In: Reserits WJ, Bernado J (eds) *Experimental ecology: issues and perspectives*. Oxford University Press, Oxford, pp 254–280
- Ruxton GD, Sherratt TN, Speed MP (2004) *Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry*. University Press, Oxford
- Stavenga DG, Smits RP, Hoenders BJ (1993) Simple exponential functions describing the absorbance bands of visual pigment spectra. *Vis Res* 33:1011–1017
- Tanaka K (1989) Energetic costs of web construction and its effects on web relocation in the web building spider *Agelena limbata*. *Oecologia* 81:459–464
- Théry M, Casas J (2009) The multiple disguises of spiders: web colour and decorations, body colour and movement. *Phil Trans Roy Soc B* 364:471–480
- Théry M, Debut M, Gomez D, Casas J (2005) Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behav Ecol* 16:25–29
- Tolbert WW (1979) Thermal stress of the orb-weaving spider *Argiope trifasciata*. *Oikos* 32:386–390
- Tseng L, Tso IM (2009) A risky defense by a spider using conspicuous decoys resembling itself in appearance. *Anim Behav* 78:425–431
- Tso IM, Lin CW, Yang EC (2004) Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes. *J Exp Biol* 207:2631–2637
- Tso IM, Liao CP, Huang RP, Yang EC (2006) Function of being colorful in web spiders: attracting prey or camouflaging oneself? *Behav Ecol* 17:606–613
- Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. *Proc Roy Soc Lond B* 265:351–358
- Zar JH (2010) *Biostatistical analysis*, 5th edn. Pearson, Upper Saddle River