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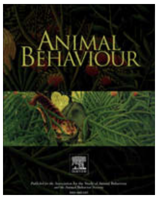

A risky defence by a spider using conspicuous decoys resembling itself in appearance

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One Darwinian puzzle is that many prey are morphologically or behaviourally conspicuous. Being conspicuous seems detrimental to prey with limited antipredator ability, because conspicuousness is likely to increase detection by predators. Theory predicts that if conspicuousness effectively redirects predator attacks and decreases hunting success, the benefits of enhanced survival can outweigh the cost of conspicuousness. We investigated a conspicuous antipredator behaviour in the orb spider, *Cyclosa mulmeinensis*, which adds decorations composed of prey pellets and eggsacs to its web. We calculated colour contrasts of spiders against prey pellets and eggsacs and recorded predators' responses to spiders on webs in the field. Webs with more decorations suffered increased numbers of wasp attacks. However because these decorations resembled spiders in size and colour, they functioned as decoys to distract predators and became the focus of predator attacks. By quantifying the costs and benefits of *Cyclosa* spiders' web-decorating behaviour in a natural setting, we found that this conspicuous antipredator display would enhance overall survival and was adaptive for this vulnerable prey.

Vulnerable animals usually have morphological and/or behavioural adaptations to avoid being detected by predators (Johnstone 2002; Mäthger et al. 2005). Organisms that are well armed or otherwise aversive are usually conspicuously coloured to enhance predator learning of prey unpalatability (Yachi & Higashi 1998; Ruxton et al. 2004). A puzzling but commonly seen phenomenon is morphological or behavioural conspicuousness in vulnerable prey. This phenomenon has been recorded in fish (MacPhail 1977), amphibians (Caldwell 1982; McCollum & Leimberger 1997), reptiles (Cooper 1998a; Hawlena et al. 2006) and insects (Robbins 1981; Wourms & Wasserman 1985). Performing conspicuous antipredator displays seems detrimental to vulnerable prey, because it makes them more likely to be detected by predators. Therefore, this phenomenon is regarded as a Darwinian puzzle (Alcock 2005). Most studies of this counterintuitive phenomenon focus on lizards with conspicuously coloured, vigorously thrashing, autotomic tails that distract attacking predators (the reactive deflective display; Cooper 1998b). Some lizards, however, consistently display conspicuous tails even when not encountering predators (the anticipatory deflective display; Cooper 2001). This paradoxical behaviour is hypothesized to enhance lizard survival by directing attacks to expendable tails and outweighs the costs of attracting the attention of predators (Cooper 1998a; Hawlena et al. 2006).

Mechanisms of how conspicuous antipredator behaviours protect vulnerable prey have attracted numerous researchers (reviewed in Ruxton et al. 2004). However, the recording of natural predation events is challenging. In the field, attack events are either rare or of short duration and this makes it difficult to quantify predation risk and the effectiveness of antipredator displays. Therefore, current evidence regarding how such displays can protect vulnerable prey is either indirect (Hawlena et al. 2006), theoretical (Hawlena et al. 2006; Cooper 1998b), gathered in artificial settings (Cooper & Vitt 1991) or does not include natural predators (Cooper 2001). Compared to prey with high mobility, organisms such as orb web spiders use a sit-and-wait foraging mode and are suitable for estimating the effects of conspicuous antipredator displays on survival. In this study, we quantified in situ the costs and benefits of conspicuous antipredator displays by a vulnerable orb spider.

Orb spiders of the genus *Cyclosa* usually incorporate decorations made of prey remains, detritus or eggsacs on their webs (Herberstein et al. 2000). Traditionally this structure is regarded as functioning to camouflage the spider but recent empirical evidence showed that *Cyclosa* decorations might render the spider webs more conspicuous (Chou et al. 2005). Web-decorating behaviour has been found in 16 genera of spiders in the Araneidae, Uloboridae and Tetragnathidae (Eberhard 1990). The functions of decorations

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have been studied for more than a century and most studies have focused on those made entirely of silk (Herberstein et al. 2000; Bruce 2006; Théry & Casas 2009). Compared with silk decorations built by *Argiope* spiders, the nonsilk decorations built by *Cyclosa* spiders (a genus more diverse than *Argiope*, Platnick 2009) have received relatively little study (reviewed in Bruce 2006). Eberhard (2003), examining the component of debris decoration in different life stages of the spider *Allocyclosa bifurca*, found that the way the eggsacs were wrapped by silk resembled the appearance of the spider's abdomen and concluded that the decoration of *A. bifurca* might function as a camouflaging device. Gonzaga & Vasconcellos-Neto (2005) used clay to make models of *Cyclosa* spiders and their detritus decorations and performed manipulations in the field. They found that spider models placed between two vertically arranged decorations had fewer bite marks than those without and thus concluded that the detritus decorations of *Cyclosa* could reduce predation risk by changing the outline image of the spiders. Chou et al. (2005) found that wasps could not distinguish the colour signal of prey carcass decoration from that of spiders.

All these results might lead us to the conclusion that nonsilk decorations function to camouflage the spider and thus are primary defence devices. Results of field experiments (Chou et al. 2005), however, showed that *C. confusa* on decorated webs received significantly more wasp attacks than those on undecorated webs. This finding suggested that, at least in certain species, the nonsilk decorations actually render the spiders more easily detected by predators, and might not function as a primary defence device to reduce detection by predators. Thus, the function and underlying mechanisms of nonsilk decorations built by *Cyclosa* and related spiders may be different from those concluded by previous studies and further empirical evidence is needed.

In this study, we used *Cyclosa mulmeinensis* to evaluate how an antipredator behaviour that is conspicuous to predators can help defend the vulnerable prey. To quantify a predator's eye view of spiders and decorations, we used a neuroethological approach that involved calculation of the colour contrasts of spiders against prey pellets and eggsacs, and we set up video cameras in the field to record predators' responses to spiders on webs with different numbers of decorations.

METHODS

Study Site and Spider

The research was conducted in July and August of 2003, 2004 and 2005 on Orchid Island (22°03′N, 121°32′E), a tropical island (area about 32 km^2) 90 km off the southeast coast of Taiwan. Stable populations of *C. mulmeinensis* were found on shrubs around the shore year-round. The webs built by these spiders are oriented vertically and spiders characteristically rest in the middle. Juveniles and adults use prey carcasses to build decorations. They are placed on the webs below and above the spiders (Fig. 1a). Adult females also use eggsacs to build decorations. Eggsacs are wrapped with prey remains and are connected in a string (Fig. 1b). Throughout the reproductive season females continue to add eggsacs to the upper half of the web and prey pellets to the lower half of the web. Even though *C. mulmeinensis* renovate their orbs daily like other orb spiders (Foelix 1996), they always keep the decorations on the webs.

Spider/Decoration Size Similarity

In the field, spiders, eggsacs and prey pellets in the same web looked approximately similar in size. We suspected that *C. mulmeinensis* made prey pellets and eggsacs into sizes matching their

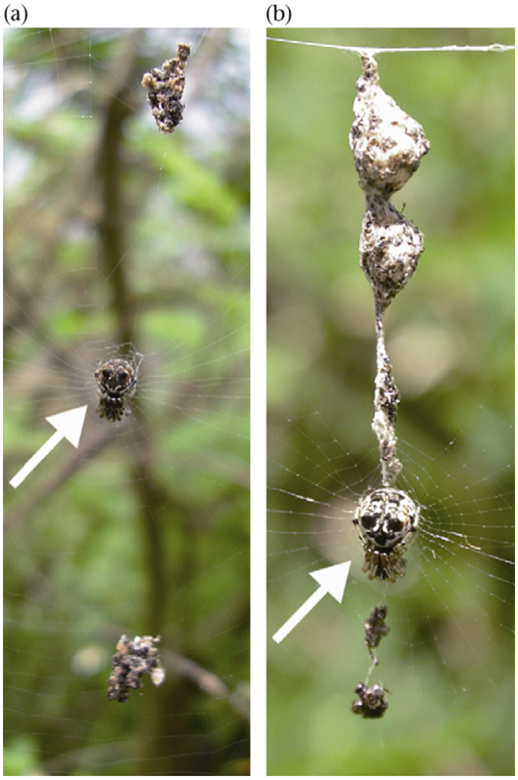

Figure 1. (a) Prey pellet and (b) eggsac decorations on webs of *Cyclosa mulmeinensis* (spiders indicated by arrows).

body length. To test this hypothesis, in the 2003 July field study we measured the body length of spiders and the greatest width of eggsacs and prey pellets (mm) from 87 webs built by females of various sizes. Linear regressions, performed in SYSTAT 9.0 (Wilkinson et al. 1992), were used to analyse the relationship between spider body length and the greatest width of prey pellets and eggsacs.

Spider/Decoration Colour Similarity

While many diurnal orb spiders are brightly coloured (Yaginuma 1986) and visually attract prey with conspicuous body parts (Craig & Ebert 1994; Hauber 2002; Tso et al. 2002, 2006, 2007; Cheng & Tso 2007; Chuang et al. 2007, 2008; Bush et al. 2008; Théry & Casas 2009), the body colouration of *C. mulmeinensis* resembles that of their prey remains (at least to humans; Fig. 1a). To test whether *C. mulmeinensis* used materials of a colour similar to that of their body for decoys to mislead predators, we quantified whether wasp predators could discriminate the colours of *C. mulmeinensis*, eggsacs and prey pellets. In addition, we also evaluated whether the spiders and web decorations were conspicuous to predators by quantifying how their colours were viewed against the vegetation background. To do this, we calculated colour contrast, which is the spectral difference between two objective areas and can only be detected by a visual system with at least two photoreceptor types (Chittka 1996). To calculate colour contrast, we needed the illumination spectrum (the spectrum of the light source), the object's reflectance spectrum and the spectral sensitivities of all photoreceptor types in the predators' visual system (Chittka 1992). The main predators of *Cyclosa* spiders on Orchid Island were parasitoid hymenopterans of the genus *Vespa* (Chou et al. 2005). The spectral sensitivities of *Vespa*'s photoreceptors are similar to those of a whole array of insect taxa including the honeybee, *Apis mellifera*, upon which intensive visual physiological studies have been carried out (Briscoe & Chittka 2001). Therefore, we used the neuroethological model developed for honeybees to calculate the colour contrasts of live spiders, prey pellets and eggsacs when viewed against each other and when viewed against the vegetation background.

Reflectance spectra of spiders, eggsacs and prey pellets were measured in the laboratory ($N = 12$, respectively). We also measured the reflectance spectra of freshly made undecorated eggsacs ($N = 12$). Before the eggsacs were wrapped with prey remains by spiders, they were pinkish in colour. A comparison of colour signals of spiders, decorated and undecorated eggsacs could show whether wrapping eggsacs with prey remains could change them into decoys matching the spiders' body colouration. To obtain undecorated eggsacs, we brought gravid spiders back to the laboratory and kept them individually in containers. As soon as the eggsacs were produced they were removed from the containers for measurement. Reflectance spectra were measured by a spectrometer (S2000, Ocean Optics, Inc., Dunedin, Florida, U.S.A.) and the operation was performed in a dark room. A standard white reflectance card was used as the reference surface. The illumination leg of the reflection probe was attached to a light source (450 W, Xenon arc lamp). The read leg was attached to the spectrometer and then connected to the computer. The tip of the probe was placed vertically 5 mm above the objects measured. Colour signals were generated by multiplying the surface reflectance function and the illumination function of the habitat (Wandell 1995). The surface reflectance function is the fraction of the light reflected from the surfaces of the spiders and various decorations. The daylight illumination function and vegetation background reflectance spectra were obtained from a previous study (Tso et al. 2004).

The calculations of colour contrasts followed the method provided by Chittka et al. (1994). In this method, for a given chromatic stimulus the relative amount of light absorbed by each photoreceptor type (green, blue and ultraviolet, UV) was first estimated. These variables were used to calculate the relative neural excitation values of three photoreceptor types, which in turn were described in a colour hexagon (Chittka 1992). The colour contrast was the Euclidean distance between two chromatic stimuli in this hexagon (Chittka et al. 1994). One-tailed *t* tests were used to evaluate whether the colour contrast values were significantly greater than the discrimination threshold value of 0.05 estimated for the chromatic vision of hymenopteran insects (Théry & Casas 2002). Previous studies showed that hymenopterans adopt achromatic vision by using a green receptor signal alone when viewing an object from a long distance (i.e. with a subtending area between 5 and 15°), and chromatic vision by using green, blue and UV receptor signals when viewing the object from a short distance (i.e. with a subtending area greater than 15°; Giurfa et al. 1997; Spaethe et al. 2001; Heiling et al. 2003). In this study, the colour contrasts were calculated under these two conditions to examine how predators see the colours of spiders and decorations under different chromatic systems.

Predator Responses

We recorded predator responses to spiders and decorations in two field studies conducted in 2004 and 2005. In the study site on Orchid Island, we set up 10 Sony TRV 118 Hi-8 video cameras and recorded daily from 0800 to 1600 hours. The populations of *C. mulmeinensis* on Orchid Island reproduce all year round (I. M. Tso, personal observations) and in the study site most adult females would place various numbers of prey pellets and eggsacs on webs. In addition, when females are forced to relocate their web sites because of web damage from biotic (such as large animals) or abiotic (such as fallen leaves or winds) causes, the first few webs they build are undecorated. We took advantage of this natural variation to monitor predators' responses to webs with various numbers of decorations. The webs were placed in two catogories according to the number of their decorations. We used these variables as an indication of how conspicuous this antipredator behaviour was. The first category included webs without decoration or with one eggsac or prey pellet. The second category included webs with more than two eggsacs or prey pellets.

The field monitoring was conducted in two periods, the first between 25 July and 3 August 2004, the second between 9 July and 14 July of 2005. Each day for each category five webs (with spiders on them) were randomly selected for monitoring and video cameras were placed 1 m in front of the webs. In 2004, we monitored 47 first- and 30 second-category webs and in 2005 22 first- and 23 second-category webs. Special attention was paid to ensuring that spiders used in the monitoring were similar in size (around 4 mm body length), to control for the potential confounding effect of predators' preference for small or large spiders. In addition to decorations, the area of webs might also affect the visibility of spiders to predators. Therefore, before video monitoring we measured the radii of webs (from four cardinal directions) to calculate the orb area following the formulae of Herberstein & Tso (2000). A nonparametric Kruskal–Wallis test was used to compare the web areas of both categories.

After the completion of field recordings we scanned the videotapes for the number of attacks that occurred in each web monitored and specified whether the attack was directed towards the

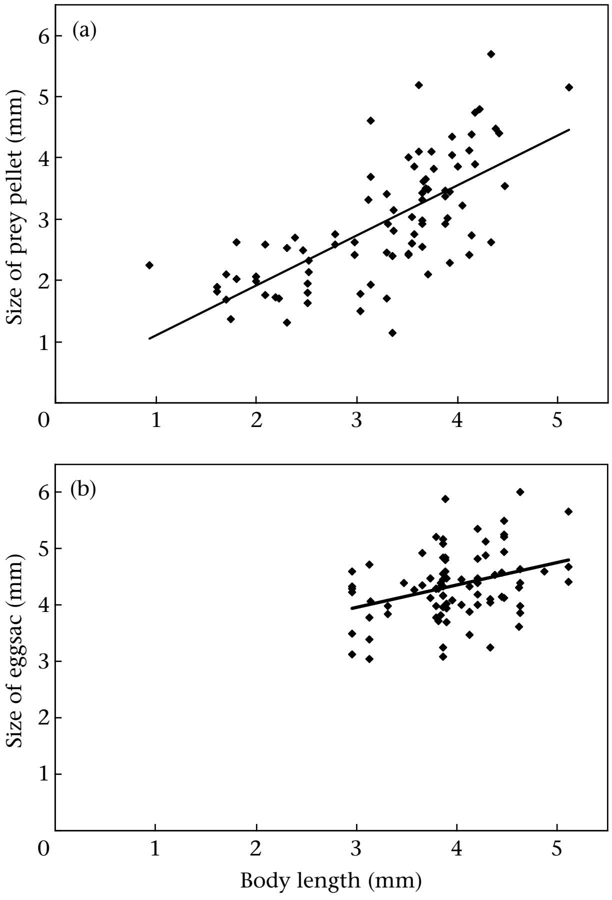

Figure 2. Relationship between body length of *C. mulmeinensis* and size of (a) prey pellets and (b) eggsacs. Linear regression lines are shown.

spider or decorations. Because predator attack data were binomial, we used a stepwise binomial regression (McCullagh & Nelder 1989) to compare attack rates of spider webs with few or many decorations. In the initial model decoration level, year and interaction term were all included. Then a reduced model was used by removing nonsignificant factors in a stepwise way. Finally, a chi-square test of homogeneity was used to compare the number of predator attack events on spiders and decoys recorded from both categories. The result of this test was used to evaluate whether having more decoys on webs could effectively switch attacks away from spiders.

RESULTS

Spider/Decoration Size Similarity

The size of spiders and prey pellets on the same webs followed a significantly positive relationship ($F_1 = 77.651$, $R^2 = 0.4773$, $P < 0.001$; Fig. 2a). Because prey pellets were built by both juvenile and adult spiders and the range of body length was relatively large (1–5 mm), the R^2 value was high in this comparison. The slope of the regression line ($Y = 0.815X + 0.250$) was nearly 1 and the *Y* intercept was not significantly different from zero ($P = 0.345$), also indicating a strong similarity in spider body length and greatest width of prey pellets. There was also a positive relationship between body length and greatest width of eggsacs ($Y = 0.399X + 2.759$) and the relationship was statistically significant ($F_1 = 11.53$, $R^2 = 0.1196$, $P = 0.001$; Fig. 2b). Compared with the size range of prey pellets, that of eggsacs was relatively small. The size of eggsacs seemed to be constrained by a lower size limit of around 3 mm, which could be indicated by a *Y* axis intercept of nearly 3 ($P < 0.0001$).

Spider/Decoration Colour Similarity

The reflectance spectra of spiders, prey pellets and eggsacs were similar, with low reflection across all wavelengths measured (Fig. 3a–c). The achromatic and chromatic colour contrasts of spiders compared to prey pellets and decorated eggsacs were low. None were significantly higher than the discrimination threshold of chromatic vision estimated for hymenopteran insects (Fig. 4, Table 1). Such results indicated that when predators viewed these objects, it was very likely that they were not able to distinguish their colour. Undecorated eggsacs were pinkish with a high reflection across the wavelength range 450–700 nm (Fig. 3d). The colour contrast of the pinkish undecorated eggsacs when compared with spiders or prey pellets was significantly higher than the discrimination threshold (Table 1). However, when the eggsacs were wrapped with prey remains their reflectance (Fig. 3c) was similar to those of spiders (Fig. 3a) and prey pellets (Fig. 3b). Such results indicated that decorating eggsacs with prey remains effectively changed them into decoys chromatically similar to the spiders. Colour contrast values of spiders and various decorations when viewed against the vegetation background were rather high (Fig. 4b) and were all significantly higher than 0.05 (Table 1), whether under chromatic or achromatic vision. Such results indicate that the colours of spiders and web decorations differed considerably from the background vegetation and therefore should be visually conspicuous to hymenopteran predators.

Predator Responses

The wasp attack rate (number of wasp attacks per 8 h of monitoring) on webs with two or more decorations was twice that

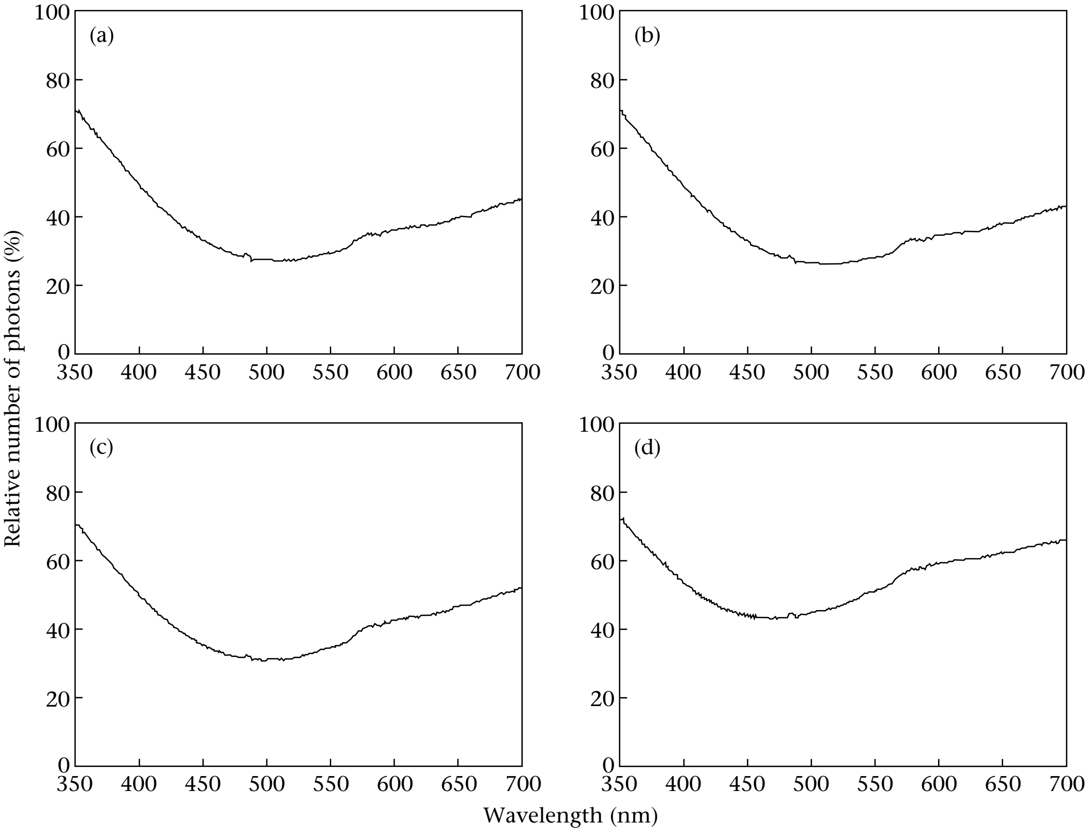

Figure 3. Reflectance spectra of (a) live *Cyclosa mulmeinensis*, (b) prey pellets, (c) decorated eggsacs and (d) undecorated eggsacs. In each spectrum curve the data represent the mean of 12 replications.

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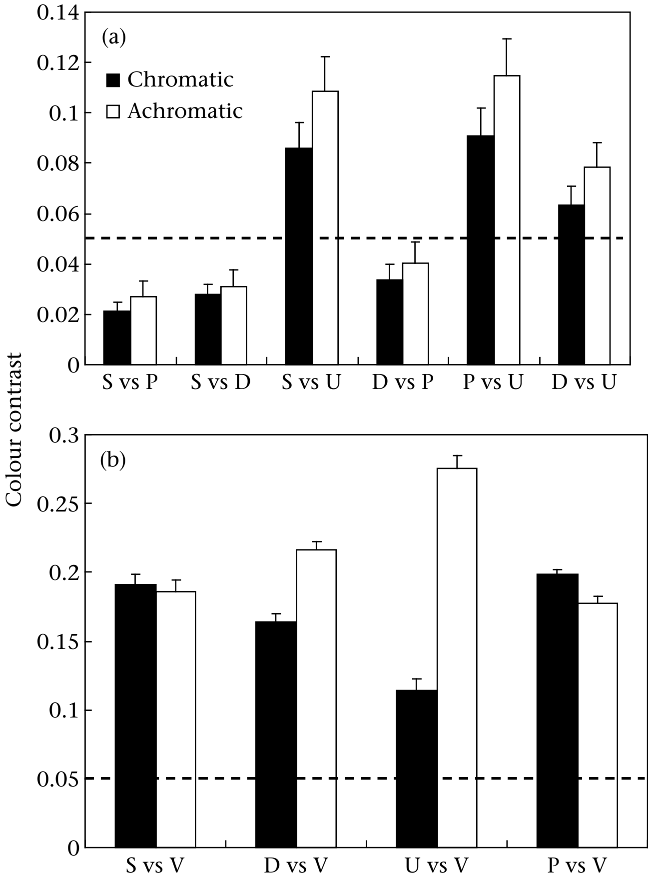

Figure 4. Colour contrast values ($\overline{X} \pm \mathrm{SE}$) viewed by hymenopteran insects under chromatic and achromatic vision. (a) *Cyclosa mulmeinensis* (S), prey pellets (P), decorated (D) and undecorated (U) eggsacs. (b) Values of these objects when viewed against a vegetation background (V). Dashed line represents the chromatic vision discrimination threshold estimated for hymenopteran insects.

Figure 5. Mean ± SE wasp attack rates (number of attacks per 8 h of monitoring) on webs with one or no decoration ($N = 69$) and those with more than two decorations ($N = 53$).

on webs with one or no decoration (Fig. 5). Results of binomial regression using the initial model showed that year and the interaction term were not significant, and they were therefore omitted from the model (Table 2). The final model showed that wasp attack rates differed significantly between the two categories of webs (Table 2). The deviance of the final model was 3.116 ($df = 2$), which was not significantly different from that of the initial model (deviance $= 0$; $df = 0$; chi-square test: $\chi^2_1 = 5.992$, $P = 0.211$). It was unlikely that the variation in probability of detection by predators resulted from web size differences, because recorded webs in the two categories had similar areas (first ($N = 69$) versus second category ($N = 53$) $= 162.1 \pm 51.41$ cm^2 versus 183.22 ± 45.60 cm^2; Kruskal–Wallis test: $\chi^2_1 = 0.519$, $P = 0.471$). In about 950 h of videos from both field trips we recorded 34 wasp attacks. Among the 12 attacks recorded from webs with one or no decorations, nine were directed towards the spiders. A total of 22 attacks were recorded from webs with more than two decorations and only seven were directed towards the spiders. Results of a chi-square test of independence showed that the relative number of attacks on spiders and decorations differed significantly between the two categories of webs ($\chi^2_1 = 5.79$, $P = 0.016$). Such results indicated that incorporating more decoration items on webs could effectively redirect the wasp attacks away from spiders. From video recordings we found that among the 22 attacks in web groups with more than two eggsacs/prey pellets, 17 were directed towards the upper or lower edge of the string of objects (chi-square test: $\chi^2_1 = 5.55$, $P = 0.016$; most of the 17 attacks were on decorations and some on spiders).

DISCUSSION

Our results show that this vulnerable spider protects itself from predator attacks by constructing decoys that increase the conspicuousness of the web and resemble its own appearance in

Table 1
Results of one-tailed *t* tests comparing colour contrast values with the discrimination threshold of 0.05 under chromatic and achromatic vision

Comparisons	Chromatic		Achromatic	
	t	*P*	*t*	*P*
Between objects				
S versus D	−5.408	0.0001	−2.787	0.009
S versus P	−7.495	<0.0001	−3.794	0.002
S versus U	3.649	0.002	4.351	0.001
P versus D	−2.663	0.011	−1.179	0.132
P versus U	3.648	0.002	4.483	0.001
D versus U	1.889	0.043	2.959	0.007
Between objects and background				
S versus V	19.343	<0.0001	15.325	<0.0001
D versus V	21.039	<0.0001	26.418	<0.0001
U versus V	7.960	<0.0001	23.508	<0.0001
P versus V	35.353	<0.0001	25.653	<0.0001

Comparisons were between different pairs of objects on *Cyclosa mulmeinensis* webs and between objects and a vegetation background. S: spider; P: prey pellet; D: decorated eggsac; U: undecorated eggsac; V: vegetation background. $N = 12$ and $df = 11$ for all tests. Pairwise comparisons with t values > 0 and P values < 0.05 indicate colour contrasts significantly greater than the discrimination threshold.

Table 2
Results of binomial regressions comparing wasp attack rates of *Cyclosa mulmeinensis* webs with different level of decorations

Parameter	*df*	Estimate	SE	Wald χ^2	*P*
Initial model[*]					
Intercept	1	1.2088	0.2391	25.562	<0.0001
Year	1	0.2027	0.3617	0.314	0.575
Decoration level	1	0.4342	0.2391	3.299	0.069
Interaction term	1	0.3036	0.4782	0.403	0.526
Stepwise reduced model					
Intercept	1	1.1116	0.2151	26.714	<0.0001
Decoration level	1	0.4466	0.2151	4.312	0.038

[*] Initial model includes year and interaction term.

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size and colour. The size of prey pellets correlated well with the body length of the spiders. Many *Cyclosa* spiders, such as *C. confusa*, simply arrange all the prey carcasses into a vertical line and the spider keeps adding material to it (Chou et al. 2005). However, *C. mulmeinensis* do not mix all the prey remains together but distribute them into separate pellets. As the spiders grow larger, the size of prey pellets and eggsacs on webs also increases. The compound eyes of most insects have limited resolution ability (Wehner 1997; Land & Nilsson 2002) and so it should be relatively difficult for wasps to discriminate visually the subtle size difference between *C. mulmeinensis* and their web decorations because the two are closely correlated in size. Furthermore, we found that hymenopteran predators are not able to distinguish the colours of spiders, prey pellets and decorated eggsacs. When both spiders and web decorations are present on the same web, they look like a string of nearly identical oval objects to the predators. Web decorations clearly act as decoys that closely correlate in size and coloration with those of the spiders. Therefore, it becomes more difficult for the predator to identify the real target, the spiders, correctly if there are more items on the same web. In undecorated webs, all wasp attacks were directed towards the spiders because they were the sole available target.

In this study, we used neuroethological modelling and field video monitoring to assess directly the functions of nonsilk decorations and the underlying mechanisms. Our results show that such behaviour does not function via a primary defence mechanism to reduce detection by predators. One reason for the incongruence of our conclusion and those of previous studies regarding underlying mechanisms of *Cyclosa* decorations might be the different methodologies used in different studies. For example, Gonzaga & Vasconcellos-Neto (2005) used models made of clay to quantify attack rates by evaluating damage to model spiders. One major disadvantage of such an approach is that one cannot be sure whether such bite marks are caused by predators of *Cyclosa* spiders or other organisms. Alternatively, the incongruence of conclusions might reflect diversity in the function of nonsilk decorations among various spider species, as has been proposed for silk decorations (Starks 2002). Relevant studies on the function of nonsilk decorations have used spiders of different species and genera. Given the great species and decoration diversity of *Cyclosa* spiders (Bruce 2006; Platnick 2009), it is possible that in certain species the nonsilk decorations serve as a device to reduce detection of the web but in others as a device to divert attacks. We suggest that a more direct methodology of quantifying predation risk be used and more spider taxa examined to generate a more comprehensive view of the functions of nonsilk decorations.

Our results show that *Cyclosa* spiders' decoys make the spiders more likely to be detected by visually oriented predators and thus represent a risky defence. It is the resemblance of spiders and decoys that enables the spider to escape direct attacks. How could a risky behaviour rendering an organism more easily detected by predators enhance survivorship? Such a seemingly controversial scenario commonly occurs among animals. Cooper & Vitt (1991) modelled the way survivorship is enhanced by traits rendering an organism more likely to be detected by predators. This model has two components: the probability of being detected and the probability of escaping an attack. When a display effectively decreases predator success, it can then compensate for the cost of increased detection. Quantitative data for probabilities of prey being detected and escaping attack are difficult to obtain under natural conditions involving real prey and predators. Some researchers have used lizard replicas with conspicuously coloured tails (Castilla et al. 1999) to evaluate whether such a trait would redirect the predator attack. Others placed prey and predators in small enclosures to estimate relevant variables (Cooper & Vitt 1991). In our study, the results obtained from monitoring predator attacks experienced by a relatively immobile vulnerable prey are congruent with the model of Cooper & Vitt (1991). *Cyclosa mulmeinensis* on decorated webs can be seen as performing a conspicuous antipredator behaviour. When there were few decoys on the web, the probability of being detected was low but that of direct attack was high. When there were many decoys on webs, although the probability of being detected was high, that of predator attack success was considerably reduced. This result may explain why *C. mulmeinensis* always keep adding prey pellets/eggsacs to their webs. On Orchid Island female *C. mulmeinensis* on average incorporated three to four eggsacs on the webs, and some even placed as many as 11 (L. Tseng, unpublished data). Because all *Cyclosa* spiders incorporate decoys on webs, it seems that, in the course of natural selection, the benefit of reduced attack success has outweighed the cost of increased predator detection.

Superficially it seems maladaptive for vulnerable prey to perform conspicuous antipredator displays. To date, few studies have quantified the costs and benefits of such behaviours in the field under completely natural conditions. In this study, by using video cameras in the field to monitor a vulnerable prey with a sit-and-wait foraging mode, we were able to estimate the probabilities of being detected and of escaping attacks. We have provided quantitative data on how *Cyclosa* nonsilk web decorations increase both the spiders' probability of being detected and the probability of successful escape from wasp predators. By demonstrating the costs of increased predator attacks and benefits of enhanced escape efficiencies, we have offered an explanation for the Darwinian puzzle of why many vulnerable prey perform conspicuous antipredator displays. Our study measured the costs and benefits of building conspicuous antipredator devices by a relatively stationary web spider. By contrast, many conspicuous but vulnerable prey are highly mobile. Quantifying the consequences of conspicuousness in these prey under completely natural conditions will be challenging. Once this task is achieved, we expect the mechanisms of how conspicuousness protects mobile prey to be similar to what we have demonstrated here for sit-and-wait prey.

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