Detritus decorations of an orb-weaving spider, *Cyclosa mulmeinensis* (Thorell): for food or camouflage?

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SUMMARY

Many species of the orb-web spider genus *Cyclosa* often adorn their webs with decorations of prey remains, egg sacs and/or plant detritus, termed 'detritus decorations'. These detritus decorations have been hypothesised to camouflage the spider from predators or prey and thus reduce predation risk or increase foraging success. In the present study, we tested these two alternative hypotheses simultaneously using two types of detritus decorations (prey remain and egg sac) built by *Cyclosa mulmeinensis* (Thorell). By monitoring the possible responses of predators to spiders on their webs with and without decorations in the field, we tested whether web decorations would reduce the mortality of spiders. Wasp predators were observed to fly in the vicinity of webs with decorations slightly more often than in the vicinity of webs without decorations but there were very few attacks on spiders by wasps. By comparing the insect interception rates of webs with and without decorations in the field, we tested whether web decorations would increase the foraging success. Webs decorated with prey remains or egg sacs intercepted more insects than those without in the field. By calculating colour contrasts of both prey-remain and egg-sac decorations against spiders viewed by bird (blue tits) and hymenopteran (e.g. wasps) predators as well as hymenopteran (bees) prey, we showed that *C. mulmeinensis* spiders on webs with egg-sac decorations were invisible to both hymenopteran prey and predators and bird predators over short and long distances. While spiders on webs with prey-remain decorations were invisible to both hymenopterans and birds over short distances, spiders on webs with prey-remain decorations were visible to both predators and prey over long distances. Our results thus suggest that decorating webs with prey remains and egg sacs in *C. mulmeinensis* may primarily function as camouflage to conceal the spider from insects rather than as prey attractants, possibly contributing to the interception of more insect prey. However, the detritus decorations exhibit varying success as camouflage against predators, depending on whether predators are jumping spiders, wasps or birds, as well as on the decoration type.

Key words: web decorations, *Cyclosa mulmeinensis*, camouflage, colour contrast.

INTRODUCTION

A conflict in signalling can exist because of different interests of the signaller and the receiver (Guilford and Dawkins, 1991; Schaefer et al., 2004). This gives rise to deceptive behaviour where the behaviour of the signaller induces the receiver to register a situation that does not occur in reality but actually benefits the signaller whereas the receiver incurs a cost (Semple and McComb, 1996). Cryptic colouration and behaviour is a form of behavioural deception and has been suggested to allow diurnally active spiders to escape the notice of predators (Cloudsley-Thompson, 1995). Crypsis can be achieved *via* physical appearance (e.g. colour patterns) but also *via* behavioural traits or both, which prevent the prey from being detected (Stevens and Merilaita, 2009).

Orb-weaving spiders are documented to incorporate a variety of materials such as silk tufts, silk ribbons, prey remains, egg sacs and plant detritus into webs (called 'web decorations') and a suite of functional hypotheses have been proposed for these web decorations (reviewed by Herberstein et al., 2000; Starks, 2002; Craig, 2003; Bruce, 2006). Web decorations are hypothesised to function as visual signals used for predator avoidance by making the spider look bigger (Schoener and Spiller, 1992), for predator defence (Blackledge and Wenzel, 1999; Blackledge and Wenzel, 2001; Eberhard, 2003; Eberhard, 2006; Jaffé et al., 2006), for web damage avoidance by advertising the presence of a web (Horton, 1980; Eisner and

Nowicki, 1983; Kerr, 1993; Blackledge, 1998; Jaffé et al., 2006) or for prey attraction by reflecting UV light (e.g. Craig and Bernard, 1990; Tso, 1996; Tso, 1998; Herberstein, 2000; Bruce et al., 2001; Bruce et al., 2004; Bruce et al., 2005; Li et al., 2004; Li, 2005). Evidence in supporting these hypotheses is contradictory, although mostly supportive. Nevertheless, the majority of the related studies have been concentrated on silk decorations built mostly by a single genus, *Argiope* (Araneidae). Other types of decorations spun by other orb-weaving spiders have received little attention.

Spiders of the genus *Cyclosa* (Araneae: Araneidae) decorate their webs with not only silk but also prey remains, egg sacs and plant detritus so called 'detritus decorations', and usually have cryptic body colouration similar to that of the detritus decorations that they build and rest amidst (Comstock 1913; Marson, 1947; Rovner, 1976; Neet, 1990). These detritus decorations are generally thought to conceal spiders from predators (Eberhard, 1973). However, few species and forms of detritus decorations have been studied in the genus *Cyclosa*. Using field manipulative experiments and modelling visual systems of potential prey and predators, Chou and colleagues have tested the function of prey-remain decorations built by *Cyclosa confusa* from Taiwan (Chou et al., 2005). They found that prey-remain decorations do not attract insects but rather mislead predators to attack the decorations instead of the spider and/or allow time for the spider

to escape the advances of predators. Artificial webs with detritus decorations of two species of *Cyclosa* (*C. morettes* and *C. fililineata*) are also found to be unattractive to insects, and Gonzaga and Vasconcellos-Neto argued against the prey-attraction hypothesis and suggested that decorating webs with detritus may reduce predation (Gonzaga and Vasconcellos-Neto, 2005). *Cyclosa mulmeinensis* (Thorell) spans from Africa to East Asia and was previously recorded in rainforests in various parts of mainland Singapore (Koh, 1991; Tanikawa, 1992; Song at el., 2002; Platnick, 2008). *C. mulmeinensis* has a pale brown abdomen mottled with dark brown spots, and often adds prey remains in a continuous chain vertically radiating from the hub upwards to the web frame (Fig. 1A). On occasion, these prey remains also extend below the hub and downwards. *C. mulmeinensis* usually rests at the hub, in line with its web decorations (Fig. 1). Although the spiders rebuild their webs daily, most do not dispose of their collection of prey remains, keeping the frame on which the prey carcasses are attached. Often the egg sacs covered in prey remains vertically radiate from the hub upwards to the web frame in the webs of female spiders (Fig. 1B). Positioning itself at the hub, the spider appears to be part of the line of cryptic prey remains and egg sacs.

Spiders and their eggs are preyed on by a list of predators such as earwigs, wasps, lizards, birds and other spiders (Foelix, 1996; Rayor, 1996). Together with its prey remain-based web decorations, the abdomen pattern of *C. mulmeinensis* resembles detritus. As detritus is less noticeable and unpalatable, the web-decorating behaviour of *C. mulmeinensis* may be to camouflage itself from potential predators (Marson, 1947; Eberhard, 1973; Lubin, 1975; Baba, 2003; Chou et al., 2005). However, web decorations composed of prey remains may have another function – to attract prey by chemical cues released by the yeasts growing on the prey-remain decorations (Tietjen et al., 1987). The present study investigates if prey-remain and egg-sac decorations camouflage *C. mulmeinensis* from potential predators or improve foraging success. Direct tests of the predator-defence hypothesis and the prey-attraction hypothesis were performed by recording the responses of predators and prey to spiders on decorated webs in the field. To evaluate individual camouflage efficiency, chromatic and achromatic contrasts of each pair of spiders and their respective decoration were calculated. Next, the spectral sensitivities of an insectivorous avian predator and a trichromatic hymenopteran were used to evaluate the spiders' camouflage efficiency with respect to the visual systems of possible predators and prey.

MATERIALS AND METHODS
Field observations

Cyclosa mulmeinensis were found in Sungei Buloh Wetland Reserve on mainland Singapore as well as on an offshore island, Pulau Ubin. Video recordings of the webs of adult female *C. mulmeinensis* spiders were performed from 1st June 2007 to 23rd August 2007 on Pulau Ubin. Spiders were assigned to three groups: (1) undecorated webs, (2) with prey-remain decorated webs, and (3) where webs were decorated with egg sacs and prey remains (hereafter referred to as egg-sac decorations). Webs were chosen based on having similar web geometrics, resident spiders of similar sizes and web decorations of similar size for each web decoration type. Depending on the number of suitable webs available, between two and four webs were recorded a day. Video cameras (JVC Everio GZ-MG50AG HD Camcorder, Yokohama, Japan) were used to perform video recordings. We set up the video camera 1 m away and recorded in front of the hub of each web. The webs were recorded for 6 h between 09:30–17:00 h. In the course of the video recording, weather conditions such as rain or extreme strong winds often caused disruption. Video recording either resumed when conditions improved – if the disruption did not damage webs – or was aborted. At the end of each video recording session, the spiders and their webs were collected for further measurements and experiments in the laboratory.

Only when spiders had stayed on their webs for more than 4 h, were their data used in data analyses (Cheng and Tso, 2007). Data from 174 h of video recording of spiders were used to investigate the effect of decoration on the predation and prey interception rate of webs. Of which, 54 h were from nine undecorated webs, 102 h from 17 prey-remain decorated webs and 18 h from three egg-sac decorated webs. The recorded video footages were examined to retrieve data on predation and prey interception rate. Insects flying in the vicinity (i.e. within 10 cm) of the web but were not intercepted were also recorded as a measure of prey availability. Meanwhile, the number of prey intercepted and predator attack incidents were documented and the type of predator identified.

Measurement of environmental parameters

Various environmental parameters were measured to examine whether they affected the prey capture rate or predator attack rate in the different groups of spiders. For the present study, the web height, the shrub density and the canopy cover for each web were recorded. The web height was measured using a meter tape measure from ground level to the hub of the web. The shrub density was
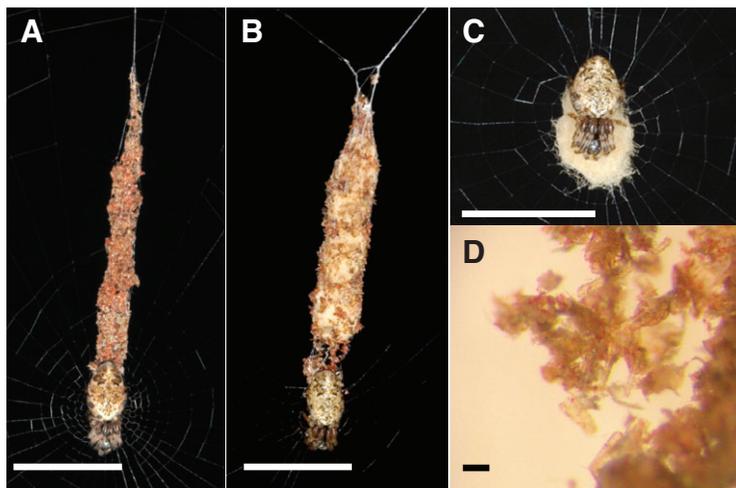

Fig. 1. *Cyclosa mulmeinensis* and its web decorations. (A) *C. mulmeinensis* adult with prey-remain web decoration. (B) *C. mulmeinensis* adult incorporating egg sacs covered in prey remains. (C) *C. mulmeinensis* adult resting on egg sacs yet to be covered with prey remains. (D) Close-up photograph of prey remains teased apart from a web decoration. Scale bar represents 10 mm for A, B and C but represents 1 mm for D.

estimated by picturing the web in the centre of 1 m×1 m quadrat. The canopy cover was measured using a spherical concave densiometer (Model C, Robert E. Lemmon, Bartlesville, OK, USA). Other environmental parameters such as temperature, relative humidity and light intensity at each web were taken hourly. Temperature and relative humidity were measured by a thermo-hygrometer (Traceable® Humidity/Temperature Pen, Control Company, Friendswood, TX, USA) whereas light intensity was measured by a LI-250A Light Meter (LI-COR, Lincoln, NE, USA). The readings were obtained by placing the respective probes approximately 50 mm in front of the hub of each web.

All data were checked for normality using the Kolmogorov–Smirnov test before further analysis. The environmental parameters were examined for differences between the differently decorated groups using one-way analysis of variance (ANOVA) whereas the prey interception rate of differently decorated webs were compared using one-sample t-test.

Web geometry measurements

It is known that the type and numbers of prey intercepted can be directly affected by web geometry. For instance, a larger web can increase the rate of prey interception (Chacón and Eberhard, 1980) whereas the density of the spirals of a web can affect the web visibility and thus the rate of prey interception (Rypstra, 1982; Craig, 2003). To evaluate the web parameters of *Cyclosa* in the field and the laboratory, web geometric characteristics were measured to calculate the following: the capture area (Tso, 1996), the mean mesh height (Tso, 1996; Herberstein and Tso, 2000), and the capture thread length (Venner et al., 2001). All web geometric characteristics were measured using a metre rule. The web geometry measurements were then examined for differences among the differently-decorated groups using an one-way ANOVA, followed by *post hoc* LSD multiple paired-comparisons between prey-remain and egg-sac decorated webs.

Calculation of colour contrasts
Spectral reflectance measurements

To investigate the colouration and brightness of *C. mulmeinensis* and their web decorations, we evaluated the efficiency of using the web decorations as camouflage by quantifying the colour contrasts of the spiders against their decorations when viewed by hymenopteran prey and predators as well as bird predators. We measured the spectral reflectance of *C. mulmeinensis* and decorations using following standard protocols (Cuthill et al., 1999; Lim and Li, 2006) and only the essential details are given here. To collect the spectral reflectance data, we used an Ocean Optic USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA) with a DH-2000 deuterium and tungsten halogen light source (Ocean Optics). The reflectance reading (300–700 nm) was recorded from a circular spot (diameter 3 mm) on the sample (spider or decoration), perpendicular to and 5 mm above the sample. Five readings were taken for each spider while 5–10 readings were taken for each web decoration, depending on the size of the decoration. A larger web decoration had a greater number of reflectance measurements so as to obtain a better representation of the entire web decoration. Due to the relatively small size of the spiders, only the reflectance spectra of the dorsal abdomen were measured. A total of 32 *C. mulmeinensis* spiders and their respective webs were collected and transported back to the laboratory for measurements. Eight spiders were with undecorated webs, 18 spiders with prey-remain decorations and six spiders with their egg-sac decorations. A total of 180 readings of the prey-remain decorations and 60 readings of the egg-sac

decorations were recorded whereas 160 readings were taken for the abdomen of *C. mulmeinensis* spiders. In addition, we measured the spectral reflectance of foliage background for each webs surveyed in the field. Twenty readings were taken at a distance of 5 mm away from the web, around the spider and the decorations. The mean spectral reflectance of these readings was used in the calculation of colour contrasts of spider body and web decorations (see below).

Modelling visual systems and colour contrasts

Colour contrast is referred to as the contrast caused by the spectral difference between two objective areas, which can only be detected by a visual system with at least two types of photoreceptors. In order to evaluate how spider body and web decoration colourations were viewed by insects, the models developed from honeybees were used for computation. The visual physiology and neuroethology of Hymenoptera has been extensively studied amongst the various insect taxa (Briscoe and Chittka, 2001; Land and Nilsson, 2002) The visual sensitivity of Hymenoptera would be useful to interpret the perception of web decorations by insect prey as well as by predatory or parasitic wasps of spiders. In addition, wasps were the potential predators appearing in the vicinity of the webs and in two of three recorded attacks (see below). Using the spectral sensitivity functions of standard photoreceptors for trichromatic Hymenoptera, photoreceptor excitations for each measured spectra was determined and the colour contrasts of decorations and spiders against foliage background viewed by hymenopteran prey and predators were calculated following standard protocols (Goldsmith, 1990; Peitsch et al., 1992; Chittka et al., 1994; Kelber et al., 2003; Théry et al., 2005).

The computed colour contrasts were compared with the optimal discrimination thresholds of bird predators and Hymenoptera prey in their particular colour space. Chromatic contrasts were utilised for short-range detections. In the blue tit colour tetrahedron, the minimal Euclidean distance of colour contrast discrimination was the minimal distance generated between two normal spectra separated by 4 nm, a contrast threshold of 0.06 (Théry et al., 2005). Meanwhile, the contrast threshold for Hymenoptera was 0.05 (Théry and Casas, 2002). The colour contrast for each pair of spiders and decoration was then compared with the hymenopteran prey and bird predator discrimination thresholds using one-sampled t-tests to obtain a measure of individual colour mimicry in the separate visual systems.

Honeybees and birds have been documented to use achromatic contrast at long range or to detect small objects (Osorio et al., 1999a; Osorio et al., 1999b; Spaethe et al., 2001). For detection at longer distances, bees use green receptors whereas birds use double-cones that combine the absorbance spectra of the medium and long wavelength-sensitive photoreceptors (Giurfa et al., 1997; Giurfa and Vorobyev, 1998; Hart el al., 2000; Spaethe et al., 2001). Achromatic contrasts were calculated using the value of green or double-cone photoreceptor signals when excited by spiders divided by the corresponding values for the web decorations (Théry et al., 2005). By comparing with the value of 1.0 as predicted for equal brightness using one-sampled t tests, the achromatic contrast of the spiders with respect to their web decorations was evaluated. All statistical analyses were performed with SPSS version 11.0 for Macintosh (SPSS Inc., Chicago, IL, USA).

RESULTS
Field observations

Of 81 webs observed, 90% of *C. mulmeinensis* in the field had either prey remains decorating their webs (Fig. 1A) or undecorated webs

(not shown). Ten percent of adult females had egg sacs covered with prey remains incorporated in their webs (Fig. 1B), with between five and eight egg sacs used in each decoration.

The web geometries of the different types of decorated webs had no significant differences in the mean (±s.e.m.) capture area (undecorated, 60±18 mm^2; prey-remain, 118±72 mm^2; egg-sac, 150±32 mm^2; $F_{2,26}$=2.462, P=0.110) and mean (±s.e.m.) mesh height (undecorated, 1.27±0.09 mm; prey-remain, 1.41±0.13 mm; egg-sac, 1.47±0.28 mm; $F_{2,26}$=0.252, P=0.779). However, there were significant differences in the mean (±s.e.m.) capture thread length (undecorated, 420±80 mm; prey-remain, 880±110 mm; egg-sac, 1000±270 mm; $F_{2,26}$=3.507, P=0.049). The undecorated webs had significantly shorter capture thread lengths compared with the prey-remains and egg-sac decorated webs (*post hoc* LSD, P=0.024 and P=0.047, respectively). There were no significant differences in the environmental parameters of the different groups of web decorations (Table 1).

Prey interception

There was no significant difference in the amount of available prey [defined as the mean (±s.e.m.) number of insects flying in the vicinity of the web per hour but not recorded] between the undecorated webs (3.5±1.0), prey-remain decorated webs (6.4±1.1) and the egg-sac decorated webs (9.0±2.1) ($F_{2,26}$=2.525, P=0.100). However, undecorated webs had significantly lower rates of prey interception [defined as the mean (±s.e.m.) number of insects intercepted per hour per web] compared with prey-remain decorated webs and egg-sac decorated webs (undecorated, 0.80±0.21; prey-remain, 1.97±0.34; egg-sac, 2.63±0.53; $F_{2,26}$=3.750, P=0.037). There were no significant differences in the prey interception rate of decorated webs (prey-remain *versus* egg-sac; *post hoc* LSD: P=0.392).

Predation incidents

Potential predators were observed in the vicinity of the webs of *C. mulmeinensis* and there was a tendency for slightly more predators to be found near the decorated webs than near the undecorated webs (undecorated webs, 4; prey-remain decorated webs, 11; χ^2=3.267, d.f.=1, P=0.071). However, only three attacks were recorded by video on *C. mulmeinensis* individuals. Two attacks were made by wasps, one on a spider with a prey-remain decorated web and other on a spider with an egg-sac decorated web. A third attack was observed by a salticid on a spider with a prey-remain decoration.

In the video recordings, the wasps flew erratically around the web but oriented mainly towards the spider on its hub. However, as the wasp attack was from the reverse side of the web (i.e. the web is between the wasp and the spider), the web might have prevented the wasp from contact with the spider. The spiders dropped off the webs almost instantaneously. As the wasps were not captured, they were not identifiable. In a separate collection of spiders, three *C. mulmeinensis* individuals that had been attacked

by the Ichneumon wasp, were found when they were in their third- and fourth-instars. At these stages the wasp is still much larger and thus would not have been in much danger.

During the predation incident, only the ventral side of the salticid was observed and thus we were unable to identify the species. However, based on its morphology, it is likely to be *Telemonia festiva*, a sun-loving spider also commonly observed in the back mangroves where *C. mulmeinensis* was studied (E.J.T. and D.L., personal observation). The *C. mulmeinensis* individual dropped off the web less than a second before the salticid landed on the hub.

Colour contrasts

The prey-remain and egg-sac decorations of *C. mulmeinensis* did not reflect light in the UV and blue range but rather in the yellow and orange range (570–620 nm) (Fig. 2A). The spiders from different groups of web decorations had almost identical spectra (Fig. 2B) and this was also observed for the background of *C. mulmeinensis*, where reflectance spectra began at about 450 nm, rising to a peak at about 550 nm and then dipping shortly after (Fig. 2C).

Bird predators would not be able to discriminate *C. mulmeinensis* from both prey-remain and egg-sac decorations at close proximity because the chromatic contrast values were not significantly higher than the detection thresholds of birds (Fig. 3A; Table 2). However, at a distance, spiders are significantly brighter than their prey-remain decorations to bird predators. Although spiders are darker than their egg-sac decorations to bird predators over long distances, the difference was not statistically significant due to a small sample size (power=0.253, where N=6, effect size, d=0.052) (Fig. 3B; Table 2).

Insects would not be able to distinguish *C. mulmeinensis* from its prey-remain and egg-sac decorations at close proximity as the chromatic contrast values are below the detection threshold of Hymenoptera (Fig. 3A; Table 2). On the contrary, from a distance (based on achromatic contrast), to insect prey spiders are brighter than their prey-remain decorations but the contrast between spiders and their egg-sac decorations was not statistically significant due to a small sample size (Fig. 3B; Table 2).

DISCUSSION
Effect of web decorations on prey
Our results show that the addition of prey remains and/or egg sacs to webs can improve the spider's foraging success by intercepting more insects in *C. mulmeinensis* from Singapore. Prey attraction by reflecting UV light or other colours of web decoration (Craig and Bernard, 1990; Tso, 1996; Herberstein, 2000; Bruce et al., 2001; Li et al., 2004) is unlikely to be the explanation for the higher insect interception rates, because our spectrophotometric analysis shows that both prey-remain and egg-sac decorations built by *C. mulmeinensis* do not reflect light in the UV range (Fig. 2A), and that *C. mulmeinensis* spiders could not be discriminated by insects

Table 1. Comparisons of environmental parameters (means ± s.e.m.) between undecorated, prey-remain decorated and egg-sac decorated webs of *C. mulmeinensis* using one-way ANOVA

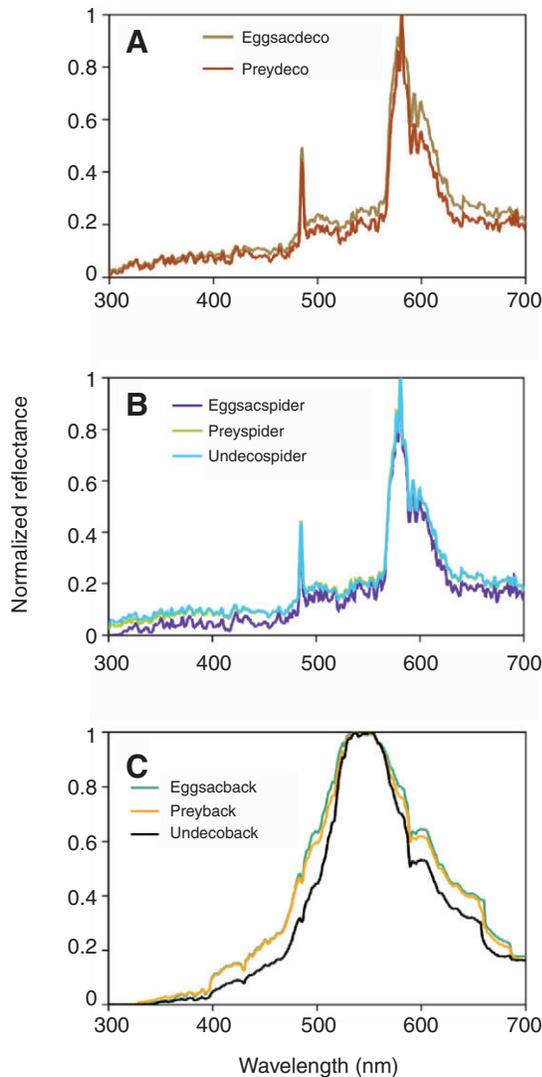|	Undecorated webs (N=9)	Prey-remain decorated webs (N=17)	Egg-sac decorated webs (N=3)	$F_{2,26}$	P
Temperature (°C)	36.14±0.84	36.40±0.53	35.61±0.65	0.170	0.844
Relative humidity (%)	58.18±1.55	57.53±1.24	57.01±3.67	0.077	0.926
Light intensity (μmol)	178.07±24.64	195.81±25.27	221.78±73.55	0.241	0.788
Canopy cover (%)	17.26±2.39	25.99±3.20	17.49±9.65	1.829	0.181
Understorey cover (%)	47.78±8.13	52.64±8.50	18.33±7.26	1.579	0.225
Height (mm)	1000±390	940±440	620±600	0.859	0.225

Fig. 2. Normalised reflectance spectra of *Cyclosa mulmeinensis* decorations, spider abdomen and background. (A) Reflectance spectra of prey-remain (N=18) and egg-sac decorations (N=6). (B) Reflectance spectra of spiders (spider with undecorated web, N=8; with prey-remain decorations, N=18; with egg-sac decorations, N=6). (C) Reflectance spectra of backgrounds (spider with undecorated web, N=8; with prey-remain decorations, N=18; with egg-sac decorations, N=6). The abbreviations refer to the following: Preydeco – prey-remain decoration; Eggsacdeco – egg-sac decoration; Undecospider – spider with undecorated web; Preyspider – spider with prey-remain decoration; Eggsacspider – spider with egg-sac decoration; Undecoback – background of undecorated web; Preyback – background of web with prey-remain decoration. Eggsacback – background of web with egg-sac decoration. Spectra displayed are means. Error bars (±s.e.m.) were calculated but omitted for clarity.

Fig. 3. (A) The mean (±s.e.m.) chromatic contrast of *Cyclosa* spiders against prey-remain (N=18) and egg-sac (N=6) decorations. The broken lines represent the minimum discrimination threshold for hymenopteran (0.05) and bird (0.06) predators. Hymenopteran (prey and predators) and bird predators are unable to distinguish the spider from its prey-remain and egg-sac decorations at close proximity. (B) The mean (±s.e.m.) achromatic contrast of *Cyclosa* spiders against prey-remain (N=18) and egg-sac (N=6) decorations. The broken lines represent the point of equal brightness (1.00). The spider can be discriminated from its prey-remain decorations but not from its egg-sac decorations at a distance by both hymenopteran (prey and predators) and bird predators.

from their prey-remain and egg-sac decorations at close proximity (i.e. chromatic contrast) (Fig. 3A; Table 2). This instead suggests that decorating webs with prey remains or egg sacs by *C. mulmeinensis* may reduce the detection of the web or the spider by prey, consequently intercepting more prey. Our data contradict Baba (Baba, 2003), Chou et al. (Chou et al., 2005) and Gonzaga and Vasconcellos-Neto (Gonzaga and Vasconcellos-Neto, 2005), who showed that undecorated webs built by *Cyclosa* species either intercept more insects than decorated ones or intercept as many as decorated webs do. Chou and colleagues (Chou et al., 2005) argued
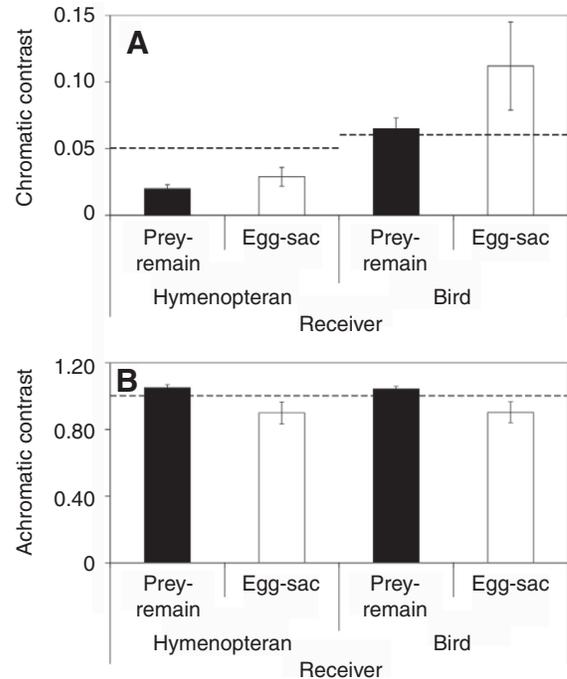
that the rather low reflectance spectrum and relatively small size (less than 10 mm long) of prey carcass decorations, thus lacking both visual and olfactory attractiveness (Tietjen et al., 1987), may be responsible for the lower rate of prey interception. Our data on spectral reflectance and colour contrasts provide little support for the former idea because both the intensity and peak wavelengths of spectral reflectance of both prey-remain and egg-sac decorations of *C. mulmeinensis* were also rather low across a wide range of wavelengths (i.e. 300–550 nm in Fig. 2A).

Environmental factors may not affect insect interception rates of decorated webs because there were no significant differences in any environmental variable measured between decorated and undecorated webs (Table 1). Given that it is in any prey's interest to avoid predation, impeding prey detection of the web and/or spider by adding prey remains and/or egg sacs to webs of *C. mulmeinensis* would hence best explain the improved foraging success of spiders.

However, an alternative explanation for the higher insect interception rate of decorated webs is that yeasts may be growing on the prey carcasses of the decorations of *C. mulmeinensis*, functioning to attract insect prey, as previous studies on prey remains on spider webs by Tietjen and colleagues show (Tietjen et al., 1987). Although the spiders are brighter than their prey-remain decorations from a distance, once lured by the olfactory cues from yeast, insect prey that fly in the vicinity of the web may not be alerted to the presence of the spider and thus face greater possibility of being intercepted by the web. Egg-sac decorations may function in a similar manner,

Table 2. Summary of one-sample *t*-tests of chromatic and achromatic contrasts of *Cyclosa* spiders on their respective decorations

	Decoration type	*t*	d.f.	*P*
Hymenoptera vision				
Chromatic contrast	Prey-remain	−9.767	17	<0.0001
	Egg-sac	−2.906	5	0.034
Achromatic contrast	Prey-remain	2.647	17	0.017
	Egg-sac	−1.529	5	>0.05
Bird vision				
Chromatic contrast	Prey-remain	0.600	17	>0.05
	Egg-sac	1.575	5	>0.05
Achromatic contrast	Prey-remain	2.623	17	0.018
	Egg-sac	−1.539	5	>0.05

The discrimination threshold for Hymenoptera is 0.05 whereas it is 0.06 for birds. Achromatic contrasts were compared with the value of 1.0.

attracting insect prey *via* olfactory cues. However, spiders with egg-sac decorations remain cryptic to insect prey from a distance (Fig. 3B; Table 2). This could be to compensate for the smaller amounts of yeast growing on the egg sacs because there is only a layer of prey remains over the egg sacs (Fig. 1C,D), as compared with entire pellets of prey carcasses for the prey-remain decorations. These findings support what was observed in the field, as the decorated webs attracted more prey than undecorated webs (*P*=0.037). However, in this study, the prey remains of decorated webs built by *C. mulmeinensis* were not examined for the presence of yeasts. Even though yeasts were found on the prey remains of webs, further studies are needed to determine whether yeasts or decaying organic material (Bjorkman-Chriswell et al., 2004) on prey remains can release these odours and whether the odours can attract insects.

The type and number of prey intercepted can be directly affected by variations in web geometrics. For instance, a larger web can increase the rate of prey interception (Chacón and Eberhard, 1980) whereas the mesh height (i.e. the density of the spirals) of a web is also known to affect the web visibility and thus the rate of prey interception (Rypstra, 1982; Craig, 2003). However, this is not the case in our field observations because we found no significant differences in the capture area and the mean mesh height between decorated and undecorated webs built by *C. mulmeinensis*. It is possible that the longer capture thread length of decorated webs in our study may be the possible explanation for the higher rate of prey interception of decorated webs found in the field. However, when all of the web geometrics were well controlled in the laboratory experiments, decorated webs, particularly with prey remains, attracted more fruit flies than undecorated webs (E.J.T. and D.L., unpublished data). Thus, shorter capture thread length of undecorated webs alone may not be responsible for the low rate of insect interception in our study.

Effect of web decorations on predators
Our present study shows that although the addition of prey remains and/or egg sacs to webs of *C. mulmeinensis* may primarily increase the foraging success of spiders, these web decorations also exhibit varying success as camouflage against predators, depending on whether predators are wasps or birds. From the field observations, both prey-remain and egg-sac decorations of *C. mulmeinensis* are not effective as predator defences against salticids. In contrast to the prediction of the predator-defence hypothesis, undecorated webs did not attract more predators than decorated ones although only three spiders on decorated webs were attacked by wasps and salticids. Given the predation on spiders' eggs (Foelix, 1996), it appears to be counter-intuitive to display egg sacs prominently on the orb-web. However, thick cocoons may be effective in protecting the eggs from earwigs, while cocoon crypsis has been suggested to protect against lizards and birds (Cloudsley-Thompson, 1995).

Spectrophotometric analysis using Hymenoptera spectral sensitivities suggests that *C. mulmeinensis* spiders cannot be discriminated from their prey-remain decorations at close proximity by wasps but can be discriminated at a distance. This would be sufficient for predatory wasps to home in onto *C. mulmeinensis* during hunting and wasps may then use other cues, such as olfactory cues, to locate *C. mulmeinensis* (Richter, 2000). This is corroborated by field observations where wasps were observed attacking spiders on webs with prey remains and egg sacs. A predator of *C. mulmeinensis,* Ichneumon female wasps generally would attack the spider while it is at the hub of the orb-web and sting it. While the spider is paralysed from the sting, the wasp lays an egg on the spider's abdomen and the spider then resumes regular activity, building normal orb-webs for 1–2 weeks to capture prey (Eberhard, 2000b). This window period of normal orb-weaving activity was observed in the laboratory from field-collected spiders, in line with earlier findings by Eberhard (Eberhard, 2000a; Eberhard, 2000b). Prior to killing its orb-weaving spider host, the larva of ichneumonid wasps induced the spider to build a 'cocoon web' especially to support the wasp larva's cocoon. Next, the larva killed the spider and spun its pupal cocoon hanging by a line from the cocoon web. After approximately four days, the larva pupated and emerged as an adult wasp a week later. However, our results differ from those of Chou and colleagues (Chou et al., 2005), who showed that the prey-remain decorations of *C. confusa* did not attract insects but instead may function to redirect another group of predatory wasps, the paper wasp *Vespa affinis* (Vespidae), into attacking the wrong target (i.e. decorations), thus enhancing the survival rate of the spiders. Such a difference may reflect the different predatory behaviour or sensory systems of different wasp species living in different habitats. *V. affinis* are predators that kill prey whereas ichneumonid wasps are parasitoids, which do not kill the host but instead lay their eggs inside their host.

Several common birds spotted in the site could be potential predators on *C. mulmeinensis* – the yellow-vented bulbul, *Pycnonotus goiavier*, copper-throated sunbird, *Nectarinia calcostetha* and the ashy tailorbird, *Orthotomus ruficeps*. All three are known to feed on arthropods in the foliage as insectivores or to supplement their diets (Fogden, 1972; Greig-Smith, 1980; Lambert, 1992; Roxburgh and Pinshow, 2000). Despite being of different families, these birds belong to the order Passeriformes, same as that for blue tits. Using the spectral sensitivities of blue tits, the birds cannot differentiate the spider from its prey-remain decorations at close proximity but from a distance they can (Table 2). Meanwhile egg-sac decorations remain highly camouflaged even from predators

like birds, as birds cannot discriminate *C. mulmeinensis* from its egg-sac decorations from a distance or at close proximity (Fig. 3A; Table 2). This would be effective in reducing predation by these predatory birds.

Conclusions

The results from field observations and visual system modelling suggest that prey-remain and egg-sac decorations of *C. mulmeinensis* may function primarily to reduce the rate of detection by insects, at least at close proximity, thus increasing the rate of insect interception. However, prey-remain and egg-sac decorations exhibit varying success as camouflage against predators, depending on the types of predators. These decorations seem to be effective as predator defences against bird predators but not against wasps. The trade-off between improving foraging success and reducing predation risks possibly contributes to the observed inconsistent incidence and signal polymorphism of web decorations in this species. Finally, continuous monitoring of the webs by video recording developed by Chou and colleagues (Chou et al., 2005) is useful in testing a few hypotheses for web decorations simultaneously and thus future studies on function of web decorations and even other behaviour of sit-and-wait predators, such as orb-weaving spiders, should consider using video recording.

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