東海大學生命科學系

碩士論文

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二角塵蛛所構築之食繭及卵囊型隱帶功能之探討

Testing the functions of egg sac/prey pellet decorations made by *Cyclosa mulmeinensis* (Araneae: Araneidae)

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Contents

摘要

大部份對於隱帶功能的探討大都針對金蛛科金蛛屬, 這類群的蜘蛛大部份是以絲構築成隱帶。同為金蛛科但不同屬的塵蛛，其數量及種類皆較金蛛屬多。不同於金蛛屬，塵蛛屬的蜘蛛會用卵囊或食繭來構築其隱帶。目前對於此類群隱帶之功能所進行的研究相當少，大部份的學者推測此種隱帶的功能主要是隱蔽蜘蛛、吸引獵物、增加網的穩定度或可以用來防禦捕食者；但是大部份皆沒有直接的證據。在我的研究中，設計了一系列的野外操控實驗來驗証二角塵蛛的隱帶是否可以具有上述之功能。首先藉操控卵囊或食繭的有無，以攝影機記錄不同處理組蜘蛛的被攻擊率。實驗結果顯示二角塵蜘的隱帶並不是用來隱蔽自己，而是利用網上的卵囊或食繭來誤導捕食者攻擊錯誤的目標。當捕食者在近距離以三色視覺偵察蜘蛛、卵囊以及食繭時，並不能正確的分辨出三者。雖然愈多的卵囊或食繭在隱帶上時會增加捕食者攻擊的次數，但當愈多的卵囊或食囊在隱帶上時，相對的捕食者攻擊蜘蛛的機率降低，誤擊卵囊或食繭的機率則增加。此外， 雖然隱帶的出現會吸引較多之胡蜂造訪, 但同時也吸引了較多之獵物前來而顯著提高其捕食率。最後，我將具有食繭及具有卵囊隱帶的網固定在木框中，於實驗室中測量網子之張力強度。發現在考慮網子縱、橫絲數及蜘蛛體長之情況下，有卵囊隱帶之網子其強度顯著高於只具食繭者, 顯示卵囊型的隱帶比食繭型的隱帶更能加強網子的穩固性，在強風下不易被破壞。綜合以上結果，二角塵蜘之隱帶不僅可降低蜘蛛之死亡率，更可提高其獵物捕獲率並增加其網子的強度。

ABSTRACT

Most functional studies on decorations focus on spiders of the genus *Argiope*, which build decorations composed entirely of silk. The abundance and diversity of *Cyclosa* spiders are much higher than those of *Argoipe*, however, the functions of detritus decorations build by them have received little attention. Previous studies suggest that detritus decorations may serve to camouflage the spider, attract prey, stabilize the web or as anti-predation device. However, currently most of them did not have direct evidence generated from field manipulative studies. In this study, I performed field manipulations to test whether the decorations of *Cyclosa mulmeinensis* exhibit the aforementioned functions. The results showed that the size of prey pellet correlated well with the spider body length. A comparison of color signals of spiders and decorations showed that the main predators, wasps, could not visually distinguish the body coloration of spiders from that of egg sacs and prey pellets. Thus, *C. mulmeinensis* seemed to manipulate size and color of decorations to match themselves. In a field experiment, I categorized webs into different groups according to number of prey pellet/egg sacs on webs, and attack events on these spiders were monitored using video cameras. The results showed that spiders incorporating more egg sacs or prey pellets on webs experienced more attacks. However, when there were more items on the webs, most of the wasp attacks were directed toward prey pellet or egg sacs. These results indicated that decoration might increase visibility but could dramatically decrease mortality of spiders. While webs decorated with prey pellets or egg sacs were visited by wasps more frequently,

they also intercepted higher number of prey. Moreover, the strength of webs with egg strings was significantly higher than those without, indicating that egg sac decorations could function to strengthen the webs. Therefore, decorations built by *C. mulmeinensis* not only serve as conspicuous anti-predation device, but also function to attract prey and to strengthen the webs.

INTRODUCTION

Numerous strategies are used by animals to defense themselves against predators. The strategies adopted by animals to reduce predation pressure can be divided into two categories: the primary defense and the secondary defence. Primary defense, such as crypsis, disruptive coloration or transparency, is defined as morphological or behavioral means adopted by animals to match their body with background or to change their contours to reduce their detactability to predators (Johnstone 2002, Mäthger et al. 2005). The secondary defense, such as the eyespots and false heads of butterflies, autotomy, and aposematic coloration (Goodenough et al. 2001), is defined as morphological or behavioral means adopted by animals to reduce mortality when they are detected by predators (Yachi and Higashi 1998). While animals adopting primary defense strategies usually exhibit inconspicuous body shape and coloration, those adopting secondary defense strategies are usually conspicuously colored. For example, the tail of the juvenile of *Eumeces elegans* lizards is conspicuously colored. When *E. elegans* encounters predators, tail autotomy is a common method used by them to escape (Bellairs and Bryant 1985). The conspicuous coloration and vigorous thrushing could distract predators to attack the tail and then increase the survival rate of the lizard itself (Cooper 1998).

Decorations are extra structures incorporated by orb weaving spiders on webs and web decorating behavior has been found in 16 genera of spiders in Araneidae, Uloboriae, and Tetragnathidae (Eberbard 1990). The functions of decorations have been studied for more than a centaury and most studies focus on those made entirely of silk. Silk decorations are hypothesized to function to attract preys (Tso 1996; Tso 1998; Herberstein et al. 2000; Craig et al. 2001), camouflage the spiders (Blackledge 1998a), stabilize the webs (Robinson and Robinson 1970), warn large flying animals to avoid the web (Blackledge 1998b), and to regulate spider body temperature (Humpreys 1992). Among these functional hypotheses, prey attraction and predator defense have received more empirical supports (Herberstein et al. 2000). Compared with silk decorations, those made from materials such as egg sacs or prey carcasses have received relatively little study (Eberhard 2003). Especially in the genus *Cyclosa*, their web decorations are much more diverse than those of *Argiope*, but empirical studies on them are few. Decorations of *Cyclosa* spiders can be composed of either silk (such as *C. conica*), prey carcasses (*C. confusa*), egg sac (*C. sachikoae*), or combinations of them (*C. mulmeinensis*). Tso (1998) demonstrated that the presence of silk decorations in webs of *Cycolsa conica* could increase its prey interception rate. Eberhard (2003) examined the component of debris decoration in different life stage of *Allocyclosa bifurca*. Eberhard (2003) found that the way the egg sacs were wrapped by silk resembled the appearance of spider abdomen and concluded that the decoration of *A. bifurca* might function as a camouflaging device. Recently, Chou et al. (2005) studied the functions of prey carcass decorations by both visual physiological and field manipulative approaches. Chou et al. (2005) found that wasps could not distinguish the color signal of prey carcass decoration from that of spiders. Such result might lead us to the conclusion that decorations of *C. confusa* functioned to camouflage the spider and thus was a primary defense device. Surprisingly, results of their field experiments showed that *C. confusa* on decorated webs received significantly more wasp attacks than those on undecorated webs. Such result indicated that presence of prey carcass decorations did not reduce but instead increase detectability of spiders, therefore such structures were by no means camouflaging devices. Thus, they suggested that detritus decoration of *Cyclosa* spiders may serve as a secondary anti-predation device to increase survivorship of spiders when they were detected by predators. Thus, the function of detritus decorations may be different from that concluded by the study of Eberhard (2003).

In my study, I used *Cyclosa mulmeinensis* to evluate if the detritus decorations serve as primary camouflage device or secondary anti-predation device. Different from *C. confusa*, *C. mulmeinensis* not only uses detritus such as prey carcasses and shaded skin but also egg sacs as decorations. In order to determine whether the detritus decoration of *Cyclosa* serve as camouflage or anti-predation device, I conducted field experiments to test whether the presence of egg sacs and prey pellets would increase attack events but increase spider survival by decreasing predation on spiders. In addition, I also calculated the color contrasts of spiders against prey pellets, egg sacs, and egg sacs without prey carcasses (undecorated egg sac) to determine how these items were viewed by wasps.

Although detritus decorations are most frequently regarded as functioning to camouflage the spider, there are other functional hypotheses such as food storage (Herberstein et al. 2000), web strengthening (Robinson and Robinson 1970; Neet 1990), food storage (Champion de Crespigny et al. 2001; Herberstein et al. 2000) and prey attraction (Bjorkman-Chiswell et al. 2004). However, empirical studies examining these hypotheses were even fewer. In my study, I conducted field experiments to test if the detritus decoration could also function to attract prey. Different from other *Cyclosa* species, *C. mulmeinensis* not only uses detritus of prey carcasses and shaded skin but also egg sacs to build decorations. In the field, a great number of *C. mulmeinensis* are found in open windy areas such as seashore. On the other hand, *Cyclosa* species exhibiting either silk or prey carcass decorations usually inhabit forest interiors (Tso 1998, Chou et al. 2005). It is possible that the decorations made of egg strings can help the webs sustain the strong wind. To test this hypothesis I compared the strength of webs decorated by egg sacs and by prey pellets to see if egg sac decorations may help to strengthen the web.

MATERIALS AND METHODS

The study site and spider

The field manipulative studies were conducted on Orchid Island, Taitung County, Taiwan (22° 03’N, 121° 32’E). Three field trips were conducted in July of 2003 and July, September and October of 2004. The area of Orchid Island is about 32 km^2, with average annual rainfall of 2600 mm, and average annual temperature of 22.4 ℃ (Chen et al. 1982). Stable populations of *Cyclosa mulmeinensis* could be found on shrubs around the shore of the island all year round. Juvenile and adult individuals of *C. mulmeinensis* would use prey carcasses to build prey pellet decorations. However, in addition to prey pellets adult females would use egg sacs to build decorations (Figure 1a, b). In the filed, the first prey pellet built by *C. mulmeinensis* would be placed either above or below the spider (?^{2} = 1.6, p > 0.05). If there were two prey pellets present on the web, spiders would position itself between the two prey pellets (?^{2} = 14.107, $p < 0.001$). When *C. mulmeinensis* built an egg sac string on the web, it would always sit on the lower edge of the egg sac string. Even *C. mulmeinensis* rebuild theirs orbs daily, they would always keep the decorations on the web. On Orchid Island, while other species of *Cyclosa* (such as *C. confusa*) inhabited forests (Chou et al. 2005), *C. mulmeinensis* were most common in open and windy shore areas (L. Tseng personal observations).

The size relationship of spiders, egg sacs, and prey pellets

In the field, I found that the size of the spiders, egg sacs and prey pellets in the same web to be quite similar. Such phenomenon made me suspected that whether *C. mulmeinensis* might manipulate the size of egg sacs and prey pellets according to their body length. To test this hypothesis a digital caliper was used to measure the size of spiders, egg sacs and prey pellets from 88 webs to the nearest mm. Linear regressions were used to analyze the relationship between spider body length and size of egg sacs and prey pellets.

Color contrast of spider, egg sac, and prey pellet

In this part of study I assessed how colorations of *C. mulmeinensis* , egg sacs and pry pellets were viewed by predators. The major predators of *Cyclosa* spiders on Orchid Island were parasitoid hymenopterans such as wasps of the genus *Vespa* (Chou et al. 2005). The spectral sensitivities of their photoreceptors are very similar to those of honeybee (Peitsch et al. 1992). The visual physiological model developed for *Vespa* (Chittka 1996) was used to calculate the color contrasts of items on the webs of *C. mulmeinensis*. To calculate color contrasts, first the color signals reflected from the surface of objects must be measured. Prey pellets, egg sacs and *C. mulmeinensis* were brought back to laboratory for color signal measurement and spiders were measured while alive. In addition to egg sacs wrapped with prey remains, the color signal of freshly made egg sacs were also measured. To collect the undecorated egg sacs, spiders were brought back to laboratory and keep them individually until the egg sacs were laid.

The reflectance spectra were measured by a spectrometer (S2000, Ocean Optics, Inc., Dunedin. Florida, U.S.A.). The illumination leg of the reflection probe was attached to a light source and the read leg to the spectrometer and than connected to the computer. The tip of the probe was placed vertically 5 mm above decorated egg sac, prey pellet, the spider's dorsum part of abdomen, and undecorated egg sac. The sample size of each item measured was 12. Color contrasts for each specimen were calculated to generate a mean value. Because the paper wasp *Vespa affinis* was the main predator in my recorded attack events, so the spectral sensitivity functions of *Vespa* was chosen to determine the photoreceptor excitation for each measured spectra (Peitsch et al. 1992). The relative amount of light absorbed by each photoreceptor type is:

$$P = R\int_{350}^{700} Is(l)S(l)D(l)dl \qquad (1)$$

where $Is\,(\lambda)$ is the reflection curve from spider or web decorations; $S(\lambda)$ is the spectral sensitivity function of the predator and $D\,(\lambda)$ is the illuminating day light spectrum from Orchid Island (Tso et al. 2004). R is the sensitivity factor determined by the equation:

$$R = 1/\int_{350}^{700} I_B(l)S(l)D(l)dl \qquad (2)$$

where $I_B\,(\lambda)$ is the spectral reflection function that receptors are adapted from the environment background. The quantum catch in the photoreceptors P (equation 1) is the input to the photoreceptors, not to the brain of insect. When the signal transported to the brain, it would operate the calculations with graded potentials generated by receptor cells. These signals are not linearly related to the logarithm of the quantum flux that forms the input to the receptor. When the maximum excitation E_{max} of the photoreceptors is set to one, the nonlinear phototransduction process is described by

$$E = P\,/\,(P+1) \qquad (3)$$

where P is the stimulus strength (equation 1), in units such that for $P = 1$, $E = 0.5$. The three excitation values in the bee's UV, blue and green receptors can be described in a three-dimensional receptor excitation space or in the color hexagon (Chittka 1996). With the three receptor excitation values plotted at angles of 120°, the x and y harmonized in the color plane would be:

$$x = \sin 60° (E_G – E_{UV}) \quad (4)$$

$$y = E_B – 0.5 (E_{UV} + E_G) \quad (5)$$

where E_G, E_{UV} and E_B are the signals from the three photoreceptors. Euclidean distance ?St, the color contrast, between stimuli are calculated as:

$$\Delta St = \sqrt{(\Delta x)^2 + (\Delta y)^2} \quad (6)$$

The color contrasts of body coloration of spiders when viewed in adjacent to prey pellet, decorated egg sacs and undecorated egg sacs were calculated and were compared with the discrimination threshold of 0.05 estimated for hymenopterans insects (Théry and Casas 2002). One-tailed t-tests were used to see whether the calculated color contrast values were significantly higher or lower than the discrimination threshold. The main predator of *C. mulmeinensis*, the *Vespa* wasps, used achromatic visual system when viewing the object from a long distance, but switched to chromatic visual system when flying near (Giurfa et al. 1997, Heiling et al. 2003). Thus both chromatic and achromatic visual system of *Vespa* were used (Peitsch et al. 1992) to determine the photoreceptor excitement for each measured spectra.

Effects of number of web decorations on attack success:

To find out how predators of *C. mulmeinensis* respond to presence of decorations on webs, TRV 118 Sony Hi-8 video cameras were set up in the study site to monitor the spiders. The recordings were conducted from 0800 to 1600 daily. Webs built by *C. mulmeinensis* were categorized into five groups: (A) undecorated webs (N = 16), (B) webs with one egg sac (N = 15), (C) webs with one prey pellet (N = 16), (D) web with more than two prey pellets (N = 14), and (E) webs with more than two egg sacs (N = 16). Each day during the study period, two spiders in each group were randomly selected from the study site and two video cameras were placed 1 m in front of the spiders. The monitoring was conducted for a total of 590 hours. When the field study was completed the video tapes were brought back to the laboratory and analyzed. While the video tapes were viewed in the laboratory, the number of attacks on *C. mulmeinensis*, pry pellets and egg sacs were recorded respectively. Chi-square tests were used to compare attack frequency on *C. mulmeinensis* and egg sac/prey pellets in each treatment group by SYSTAT 9 (Wilkinson et al. 1992).

Effects of manipulating color signals of egg sacs:

To test whether prey carcass wrapping of egg sacs could effectively decreases predators' attack success, pregnant *C. mulmeinensis* were captured and individually kept them in vials until they laid egg sacs. The egg sacs were immediately removed from the vial to obtain undecorated egg sacs. Three undecorated egg sacs were stuck on a transparent acetate film (the size of transparent acetate film was 3×40 mm) and were attached on freshly-built webs of *C. mulmeinensis* (N = 22). Another 23 webs with three egg sacs (wrapped with prey carcasses) were randomly chosen as the control group. To control for the effect of transparent acetate film, in the control group, in the back of the egg sacs string transparent acetate films were also attached. TRV 118 Sony Hi-8 video cameras were used to record the attack events on both groups. Chi-square test was used to test for the differences of predation events between experimental and control groups by SYSTAT 9 (Wilkinson et al. 1992).

Effects of decorations on foraging success:

When the aforementioned video tapes were viewed the number of prey intercepted by webs of *C. mulmeinensis* were also recorded. During the field study each day before video recordings were started, the hub diameter and the web radius of each web were measured. These variables were used to calculate their capture area using the formulae of Herberstein and Tso (2000). The average prey interception rate (number of intercepted prey per web per hour of monitoring) was calculated for each web from video tapes. The prey interception data fitted well with the Poisson distribution (Person ?^{2} test, $p > 0.05$). Thus, Poisson regression was used to compare prey interception rate of different groups while considering the web area. Web area was ranked into seven groups: <50, 50-100, 100-150, 150-200, 200-250, 250-300, >300 cm^2. The Poisson model was:

$$\log m_N = \log N(X_i) + X_i b$$

where m is the expected value, X represents variables of web groups and web area, ß is the probability and N is total number of individuals (Steel et al. 1997).

Comparison of strength between different web types:

In this part of study I evaluated whether webs of *C. mulmeinensis* decorated with egg sacs would have higher strength than those simply incorporated with prey pellets. Two types of webs were collected by carefully attaching a wooden frame coated with adhesives on the web and freed the frame from the web with a burning incense. These webs were brought back to the laboratory and then the web strength was measured. The wood frame was placed horizontally and the center of the web was attached with a hook connected to a microbalance. The microbalance was attached to a dissecting microscope. To measure the relative strength of two types of webs, the web was lift up for 3 cm by turning the control wheel of the dissecting microscope then recorded the reading of the microbalance. The values showed on the microbalance were used to represent the strength of the webs. An ANCOVA (analysis of covariance) test was used to analyze the strength between webs with egg sacs (N = 14) and with only prey pellets (N = 16). The covariances were the spider body length, captured area, web radii number, and the number of spirals.

RESULT

The size relationship of spiders, egg sacs, and prey pellets

There was a significantly positive relationship between the body length and the size of prey pellet (F = 77.651, P < 0.001, R^2 = 0.4773) (Figure 2a). The ratio of body length and the size of prey pellet almost equaled to 1 (the slop = 0.81). Although the there was a positive relationship between body length and the size of egg sacs, the relationship was not statistically significant (F = 0.764, P = 0.764, R^2=0.1196) (Figure 2b). Such results showed that the spider would make the prey pellets as big as itself, no matter in juvenile or adult stage. As they mature, female spiders would make egg sacs according to their body size.

Color contrast of spider, egg sac, and prey pellet

Twelve samples of *C. mulmeinensis* spiders, egg sacs wrapped with prey carcasses, undecorated egg sacs, and prey pellets were collected from the study site respectively. The reflectance spectra of different items were shown in figure 3. The reflectance spectra of the spider, prey pellet and decorated egg sac were very similar (Figure 3a, b, c). The spectrum of undecorated egg sac exhibited a high reflection across wavelength ranges between 450 and 700 nm (Figure 3d). The color contrasts of spiders against different items on the web viewed by the wasp were shown in figure 4. The results of one tailed t-tests comparing the color contrasts against different items were given in table 2. The results showed that no matter wasps used achromatic or chromatic visions, they could not distinguish the spider from prey pellets or egg sacs wrapped with prey carcasses (Figure 4). Once the spider did not decorate the egg sac, predators could easily distinguish the color signals of that from the spiders, decorated egg sacs or prey pellet.

Effects of number of web decorations on attack success:

The details of attack events in different treatment groups were shown in table 1. Only two attacks were recorded from undecorated web group. Not surprisingly, both attack events were directed straightly on the spider. In the rest of treatment groups, webs decorated with more items received higher number of attacks. *C. mulmeinensis* in treatment B group (one spider and one egg sac) received only two attack events, one on the spider and the other on the egg sac. Similar to this 50-50 trend, among the five attacks experienced by *C. mulmeinensis* in C treatment group (one spider and one prey pellet), three were on spider and two on prey pellets. In D and E treatment groups there were more than three items on webs (including the spider), and these groups received 13 attacks. However, only two of them were directed on spider.

Since previous results showed that the size and color of spiders, prey pellets and egg sacs were similar, I divided webs in the five treatment groups into two categories to have a large sample size to facilitate statistical analysis. I divided those webs into those exhibiting less than three items (treatments B and C) and those with more than three items (treatments D and E) (Figure 5). Chi-square tests were used to compare the number of attacks on spiders and egg sac/prey pellets in each categories respectively. In the less-than-three category the number of attacks between spiders and egg sac/prey pellets did not differ significantly ($?^2 = 0.143$, $p = 0.705$). However, in the more-than-three item category, significantly more attacks were directed on egg sac/prey pellet than on spiders ($?^2 = 6.429$, $p = 0.013$).

Effects of manipulating color signals of egg sacs:

The results of field study showed that the total number of attacks was higher in decorated egg sac group (N = 9) than undecorated one (N = 3) (Figure 6). Chi-square test showed no significant difference in attack frequencies between spiders and decorations in both groups ($?^2 = 0.111$, $p = 0.739$ in decorated egg sac group; $?^2 =$

2.96, *p* = 0.083 in undecorated egg sac group), due to a small sample size. However, in the undecorated group all attacks were directed accurately on the spiders. While in the decorated group, more than half of the attacks were directed to egg sacs.

Effects of decorations on foraging success:

Because the preys of *C. mulmeinensis* were very small when viewed from video tapes, thus I did not measure the size of preys but simply counted the number of prey intercepted. Prey interception rate was calculated by dividing the total number of prey intercepted by one spider web by the number of monitoring hours. The prey interception rate of undecorated webs (group A) was significantly lower than those of other four treatment groups (group B-E) (Figure 7, Table 3). There was no significant difference in prey interception rates between treatment groups with various number of web items (Table 3).

Comparison of strength between different web groups

Webs brought back to the laboratory were abandoned if they were broken during the transpiration or measuring. Complete data was available from 14 webs with egg sac string and 16 webs with prey pellets. The results of ANCOVA analysis showed that webs with egg sac string exhibited significantly higher strength than webs with prey pellet (Table 4). The other covariances did not differ significantly between two types of webs. However, the variable of body length of spider (an indication of spider's weight) was marginally statistically significant (Table 4).

DISCUSSION

Results of this study demonstrated that the sit-and-wait predator *C. mulmeinensis* could make decoys according to its size. The size of prey pellets correlated well with the body length of the spiders. Eberhard (2003) suggested that the spider *Allocyclosa bifurca* would use different materials to construct their decoration in different life stages. Similar to *A. bifurca,* juveniles of *C. mulmeinensis* used prey carcasses or shaded cuticles to make prey pellets as decorations. Many *Cyclosa* spiders, such as *C. confusa,* uses all of the prey carcasses they obtained to construct decorations on the web (Chou et al. 2005). However, *C. mulmeinensis* did not utilize all the prey remains available but manipulate the size of prey pellet according to their body length. The mechanisms how *C. mulmeinensis* determine the size of prey pellet they made are still unknown. Since prey pellets were built by both juvenile and adult spiders and the range of body length was relatively large (1 mm to 5 mm), therefore the R^2-value was high in this comparison. When the spider grew up to the mature stage, especially in females they used egg sacs to construct decoration. Since the size ranges of mature females and egg sacs were relatively small (3-5 mm in both), thus the R^2-value was small and positive relationship was not significant in this set of comparison. Although the size correlation between spiders and egg sacs is not as perfect as that between the spiders and prey pellets, from the eyes of the hymenopterans predators different items on the same web should looked similar in size. Hymenopteran insects have compound eye and when they are flying the images formed are not sharp but relatively blurred (Wehner 1997). Although the size correlation between *C. mulmeinensis* and egg sacs was not very high, it should be very difficult for wasps to distinguish them simply by the size differences.

Results of this study also demonstrated that *C. mulmeinensis* makes decoys according to its color. The reflectance spectra of spider, prey pellet, and decorated egg sac were quite similar to each other. Results of color contrasts also demonstrated that hymenopteran predators were not able to visually distinguish these items. Since the spiders, egg sacs and prey pellets were similar in both size and color, when they were both present on the same web they looked like a string of nearly identical oval objects to the predators. Therefore, it becomes more difficult for the predator to correctly identify the real target, the spiders, if there are more items on the same web. In undecorated webs, since there was noting but only spider on the web, so when they were detected by wasps all the attacks were directed toward the spiders. When there was either one prey pellet or egg sac on the web, from the eyes of the predators there would be two identical oval objects (including the spider). Since *C. mulmeinensis* would placed these items either above or beneath itself, when the wasps detected a two-item-web it was not certain whether the lower or the upper one was the real target. Therefore, theoretically there would be a 50 to 50 chance that the predators chose the real target. As there were more than three egg sacs/prey pellets on webs, the chances of correct hit would be reduced further. From video tapes I found that there were 13 attack events in D and E treatment groups, in 12 of them the wasp attacked the item on the edge ($?^2$ = 9.308, p = 0.003). Congruent with such inferences were the recorded predation events from the field. This explains why *C. mulmeinensis* would always place as many items as possible on their webs and positioned them both above and below the spiders. In *Argiope*, the presence and shape of silk decoration of individual spiders vary considerably from day to day (Tso 2004). In *C. mulmeinensis*, however, individual spiders would always keep their prey pellets or egg sacs and the number of items of webs would keep increasing unless the webs of the spiders are completely destroyed (L. Tseng, personal observations).

In this study, I used visual physiological modeling and field video monitoring to directly assess the functions of detritus decorations and underlying mechanisms. However, results of this study were not congruent with some conclusions of previous studies. For example, Eberhard (2003) suggested that the decoration of *Allocyclosa bifuraca* is a camouflage device, and Gonzaga and Vasconcellos-Neto (2005) suggested that the detritus stabilimenta of *C. fililineata* and *C. morretes* were more conspicuous than spiders. If the decoration of *Cyclosa* really serves as camouflage device, in my recording the predation events should be the lowest in the groups exhibiting the highest number of items on the webs. Results of field monitoring in this study, however, showed that as there were more items on the webs the number of wasp attacks also increased. Therefore, decorations made by *C. mulmeinensis* are by no means camouflaging device functions to reduce detecability of the spiders. On the other hand, if the decorations were visually more conspicuous than the spiders, when there were only two items on the webs the decorations should receive more attack than the spiders. However, results of this study showed that when there were two items on the webs the number of attacks they received were equally. Moreover, results of this present study showed that the color signal of spider and the decorations were indistinguishable to predators. Therefore, decorations built by *C. mulmeinensis* do not seem to enhance the survivorship of spiders via a primary defense mechanism, as were proposed by numberous previous studies.

Gonzaga and Vasconcellos-Neto (2005) also suggested that the detritus stabilimenta of *Cyclosa* spiders may not serve to attract insects. However, from video recording data I found that although webs containing decorations received more attacks, they also intercepted higher number of prey. Therefore, although building decorations attracts the attention of hymenopteran predators, such behavior also attracts prey to the web. While the predator-defense function of detritus decoration is achieved primarily by visual means, through what modality is prey attraction achieved is still not clear. The major predator of *Cyclosa*, the *Vespa* wasps, did not seem to rely heavily on olfactory cues to locate their prey (Chou et al. 2005). Therefore, olfactory signals of the spiders and decorations should not be the major determinant of the observed results of this study. However, the prey of *C. mulmeinensis* is taxonomically more diverse than their predators. Judged from identifiable prey catching events in video recording and prey carcasses of the decoration, the prey of *C. mulmeinensis* was composed of small sized Hymenoptera, Diptera, Lepidoptera, or Homopera. Within this diverse array of insects different taxa might utilize different signals to detect decorations. The use of olfactory signals to attract prey had been reported in the social spider *Mallos gregalis* (Tietjen et al. 1987). *Mallos gregalis* deliberately deposited consumed prey in their webs and the scents produced by yeasts were attractive to numerous dipteran insects (Tietjen et al. 1987). Perhaps the newly-deposited prey remains in the decorations of *C. mulmeinensis* would also attract those insects using olfactory cue to locate food resource. More studies are needed to realize the mechanisms responsible for the attractiveness of *C. mulmeinensis*'s decorations to prey.

How does the conspicuous anti-predation devise evolve in *C. mulmeinensis*? In the past, we usually thought that the spider used decorations to camouflage itself. Results of this study showed that the more items on the web more predators were attracted. So, the decoration is a conspicuous signal to wasps. It is the resemblance of spiders and egg sacs/prey pellets that enables *C. mulmeinensis* to escape direct attacks. Therefore, how could a trait renders an organism more deteactable to predator but in the same time enhances survivorship? Actually, such seemingly controversial scenario commonly occurs among animals. Cooper and Vitt (1991) suggested a model for the evolution of such conspicuous anti-predation devices. This model has two components: the probabilities of being detected and those of prey escaping the attack. According to Cooper and Vitt (1991), if Pd is the probability that cryptically colored prey is detected by a predator, and Pe is the probability that after being detected the prey successfully escapes, then a prey's probability of being captured by a predator is:

$$Pd\,(1 - Pe) \tag{1}$$

Therefore, this relationship could be regarded as the expected mortality of an inconspicuous prey exhibiting no anti-predation device. Suppose that a conspicuous anti-predation device evolves in prey and such trait could increase the probability of escaping the attack by an amount β, but increase the probability of being detected by an amount of α, Then, the probability that a prey exhibiting a conspicuous ant-predation device is detected and successfully attacked by predator could be denoted as:

$$(Pd + \alpha)(1 - Pe - \beta) \qquad (2)$$

The conspicuous anti-predation device would be selected for if the probability in equation (2) is smaller in that in equation (1):

$$Pd\,(1 - Pe) > (Pd + \alpha)(1 - Pe - \beta)$$

In other words, although exhibiting certain anti-predation devices would render the prey easier to be detected by predators, if such device could dramatically decrease the attack success of predator, then the cost of increased detectability would be more than compensated by the benefit of safe escapes. The model developed by Cooper and Vitt (1991) could be applied to *C. mulmeinensis* to explain why the conspicuous decorations made of prey pellets or egg sacs could evolve. The undecorated webs of *C. mulmeinensis* could be regarded as the inconspicuous prey type. Acording to the predation events recorded from web group A, the $Pd\,(1 - Pe)$ value was 0.125 (Table 5). The decorated webs built by *C. mulmeinensis* could be regarded as prey exhibiting conspicuous anti-predation device. When there were two items on the webs (including the spiders), the value of $Pd\ (1 - Pe)$ estimated from predation events recorded from web groups B and C was 0.129. This result suggested that although the addition of one egg sac or prey pellet may reduce the attack success on spiders by half, such benefit could not offset the cost of increased detectability. However, when there were more than three items on webs (including the spiders), the value of $Pd\ (1 - Pe)$ estimated from web groups D and E was 0.067 (Table 5). This value is much lower than that estimated from the undecorated web group. This result indicated that only when *C. mulmeinensis* incorporated many items on webs would the benefit of reduced mortality offset the cost of increased conspicuousness. This result also explains why *C. mulmeinensis* would always keep adding prey pellets/egg sacs to their webs. In Orchid Island some female *C. mulmeinensis* incorporated as many as 11 egg sacs on the web (L. Tseng personally observation). In the field, however, three to four egg sacs were the most common number on the web (77 of 151 webs contained three to four egg sacs on the web, L. Tseng unpublished data). If there were too many egg sacs on the web, the web may crash down due to overweighting.

Results of this study also showed that egg sac decorations function to strengthen the web. When incorporating prey pellets, *C. mulmeinensis* simply weaved them onto the webs without adding extra structure. However, when they placed incorporated egg sacs they would first make a thick horizontal thread composed of numerous silk threads on the upper margin of the web. Between the hub and the midpoint of horizontal thread *C. mulmeinensis* would build a thick vertical thread and add egg sacs one by one onto it. A comparison of webs with and without egg sacs showed that the strength of the former was significantly higher than the latter, indicating that the thick threads could effectively fortify the web. This result may explain why *C. mulmeinensis* could be commonly found in the open and windy shore areas of Orchid Island. However, why most of the *C. mulmeinensis* populations are distributed in shore areas rather than in forest interior in which habitats the disturbances are much lower? While *C. mulmeinensis* is most commonly seen in open shore areas, the dominant *Cyclosa* spiders in the forest on Orchid Island is *C. confusa* (Chou et al. 2005). Why *C. mulmeinensis* exhibiting decorated webs which are more resistant to physical disturbances do not extend their ranges into the forest? One major reason might be that although the presence of egg sacs and associated thick silk threads could reinforce the web, these objects also make *C. mulmeinensis* difficult to switch web sites. For orb-weaving spiders, web site relocation is a common way to maximize their foraging intake or to escape unsuitable environment (Nakata and Ushimaru 1998). The forest-dwelling *C. confusa* also construct decorations made of pry carcasses. They were frequently seen to leave the old web site, take with them the decorations and place the old decoration on the new web site (I. C. Chou personal observations). For *C. mulmeinensis*, the egg sac strings and the associated thick silk threads had to be reused repeatedly and were very difficult to be transferred from place to place. Therefore, the inflexibility in web site relocation and consequently poor ability in responding to spatial variations in prey abundance might make *C. mulmeinensis* less competitive than *C. confusa* in forest habitats.

However, even though *C. mulmeinensis* exhibiting webs decorated with egg sacs could inhabit high disturbance areas than other *Cyclosa* spiders, they still have the disadvantage of quite inflexible web site relocation. One way *C. mulmeinensis* used to cope with this problem might be to aggregate together. Aggregating behavior has been seen in numerous web spiders such as *Metepeira*, *Cyrtophora*, and *Nephila* (Lubin 1974, Uetz 1989). One of the major advantages of aggregation in web spiders is to increase foraging success of individuals via ways such as ricochet effect (Uetz 1989). In Orchid Island, *C. mulmeinensis* are usually found in aggregations of several dozens to hundreds of individuals. Aggregation of *C. mulmeinensis* might be able to increase the foraging success of individuals to offset the cost of a strong but immovable orb web. Moreover, aggregation may further reduce the predation risk by mechanisms such as dilution effect (Uetz et al. 2002). However, further studies are needed to see whether aggregating behavior of *C. mulmeinensis* can increase their foraging success.

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TABLES

Table 1. Attack events recorded in different web groups with number of attacks in different web items specified. (A: undecorated webs, B: webs with one egg sac, C: webs with one prey pellet, D: web with more than two prey pellets, and E: webs with more than two egg sacs with prey pellet.)

Web groups	N	Attack on Spider	 Prey pellet	 Egg sac	Total
A	16	2	-	-	2
B	15	1	-	1	2
C	16	3	2	-	5
D	14	1	4	-	5
E	16	1	4	3	8

Table 2. Results of one tailed t-test comparing the color contrast against different items viewed by chromatic and achromatic vision of *Vespa* with the discrimination threshold of 0.05.

	Chromatic		Achromatic	
Comparison	*t*	*p*	*t*	*p*
U vs D	1.889	0.085	2.959	0.013
U vs P	3.648	0.004	4.483	0.001
U vs S	3.649	0.004	4.351	0.001
D vs P	2.663	0.022	1.179	0.262
D vs S	5.408	0.000	2.787	0.018
P vs S	7.495	0.000	3.794	0.003

(U: undecorated egg sac, D: decorated egg sac, P: prey pellet, S: spider)

Table 3. Result of Poisson regression comparing prey interception rates between different web groups while considering the effect of web area. (A: undecorated webs, B: webs with one egg sac, C: webs with one prey pellet, D: web with more than two prey pellets, and E: webs with more than two egg sacs with prey pellet.)

Parameter	Estimate	SE	$?^2$	*P*
Intercept	1.7157	0.2031	71.36	<.0001
Treatment group				
Group A	-0.3736	0.0948	15.52	<.0001
Group B	0.0351	0.0807	0.19	0.6634
Group C	0.1034	0.0789	1.72	0.1902
Group D	-0.1165	0.0847	1.89	0.1692
Group E	0.0000	0.0000		
Web area				
<50	-0.6017	0.2256	7.11	0.0077
50-100	-0.8269	0.2011	16.90	<.0001
100-150	-0.7798	0.1967	15.71	<.0001
150-200	-0.5956	0.1997	8.90	0.0029
200-250	-0.5680	0.2043	7.73	0.0054
250-300	-0.7216	0.2314	9.72	0.0018
>300	0.0000	0.0000		

Table 4. Mean (± SE) web strength, web area, radii number, spiral number and body size of webs with egg sacs and prey pellets built by *Cyclosa mulmeinensis* and result of ANCOVA test.

Variables	Web with egg sac	Web with prey pellet	*F*	*P*
Web strength (g)	0.064 ± 0.005	0.042 ± 0.003	4.808	0.037
Web area (cm^2)	188.378 ± 10.917	204.792 ± 8.952	2.169	0.153
Radii number	48.500 ± 3.234	55.500 ± 2.041	0.021	0.886
Spiral number	27.839 ± 2.029	28.328 ± 0.966	0.265	0.611
Body length (mm)	5.000 ± 0.001	4.389 ± 0.122	3.756	0.064

Table 5. Relative probabilities of *Cyclosa mulmeinensis* being detected and being captured estimated from field video monitoring of different web groups. *Pd*: the probability that cryptically colored prey is detected by a predator. *Pe*: the probability that after being detected the prey successfully escapes.

Relative probablities[1.2]	Undecorated webs	Webs with 2 items	Webs with 3 items
Pd	1/16 = 0.125	7/31 = 0.226	13/30 = 0.433
1 - Pe	1 - 0 = 1	1 – 3/7 = 0.571	1 – 11/13 = 0.154
Pd (1 – Pe)	0.125	0.129	0.066

1. Assuming that *C. mulmeinensis*' probability of being captured when detected is proportional to probability of direct attacks on spiders.
2. Probabilities of being detected is defined as probability of being detected per spider per day (or per eight hours of observation).

FIGURES

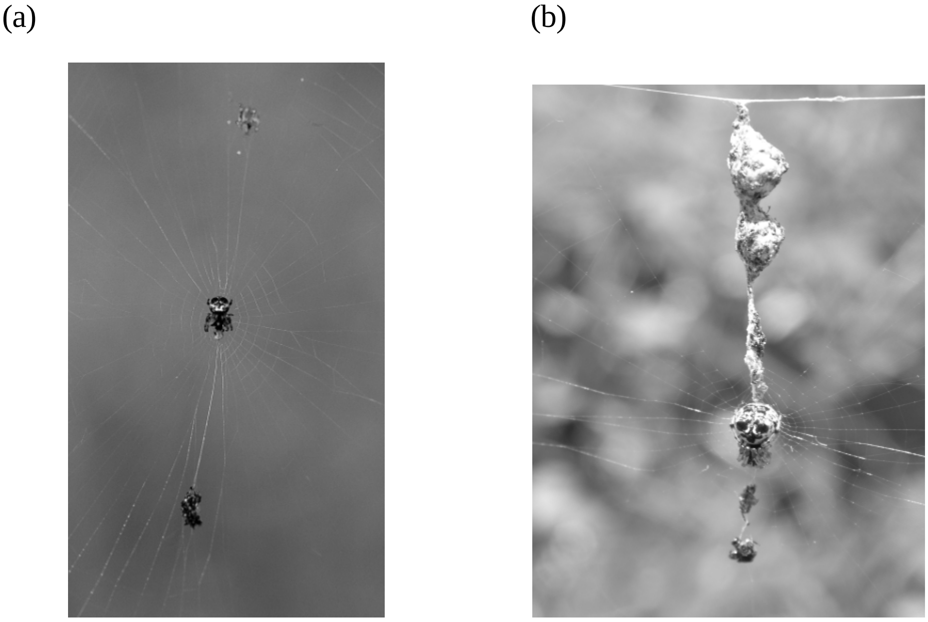
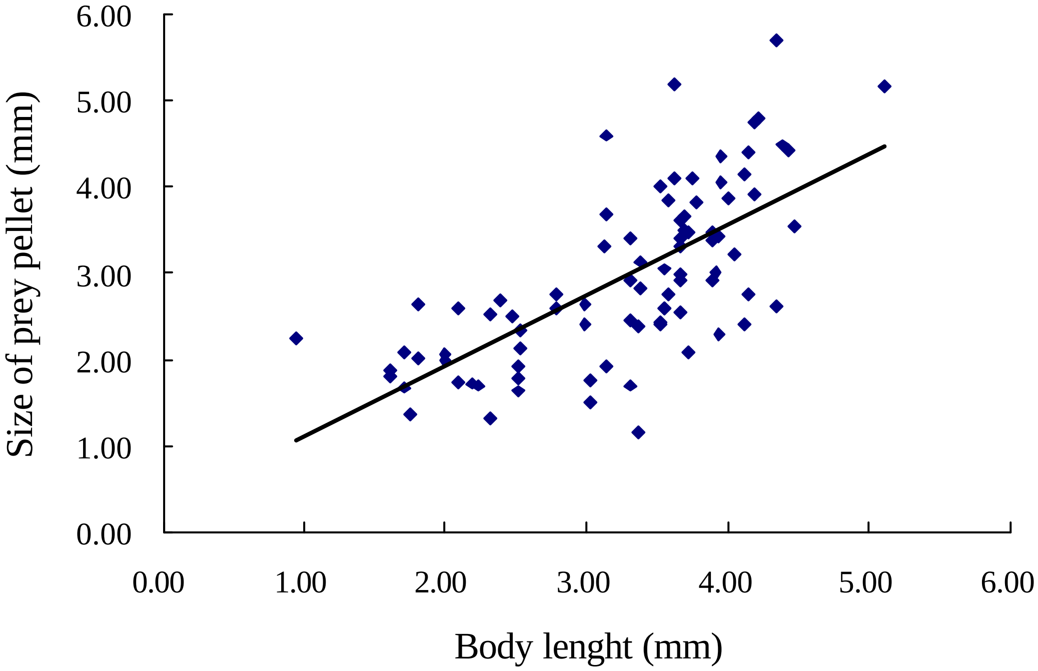


Figure 1. The prey pellet (a) and egg sac (b) decorations on the web of *Cyclosa mulmeinensis*.

(a)



(b)

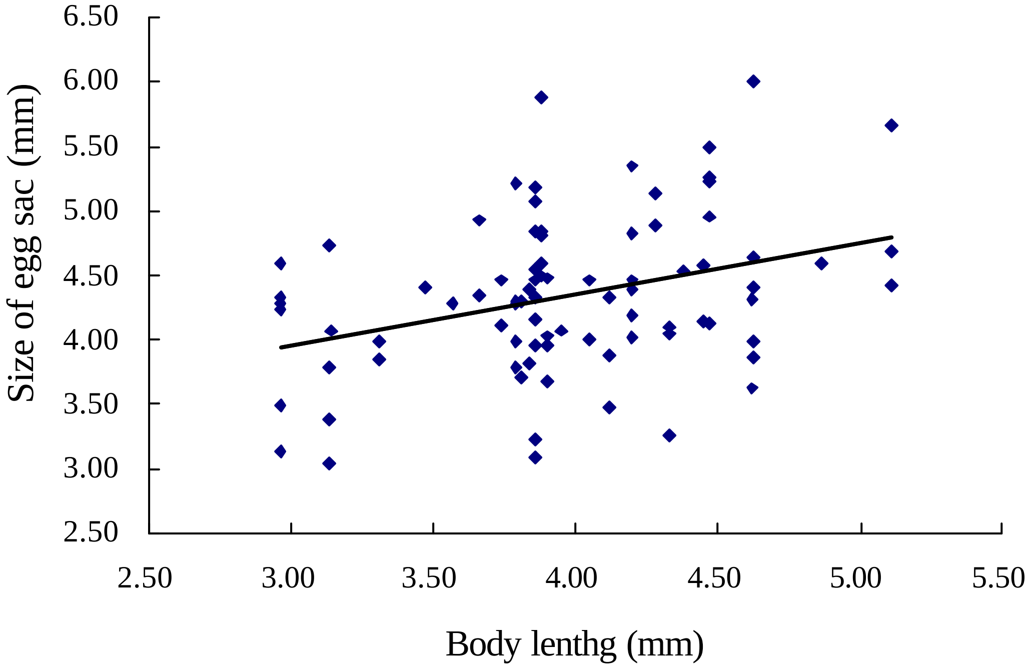


Figure 2. Relationship between body length of *Cyclosa mulmeinensis* and size of prey pellet (a) and egg sacs (b).

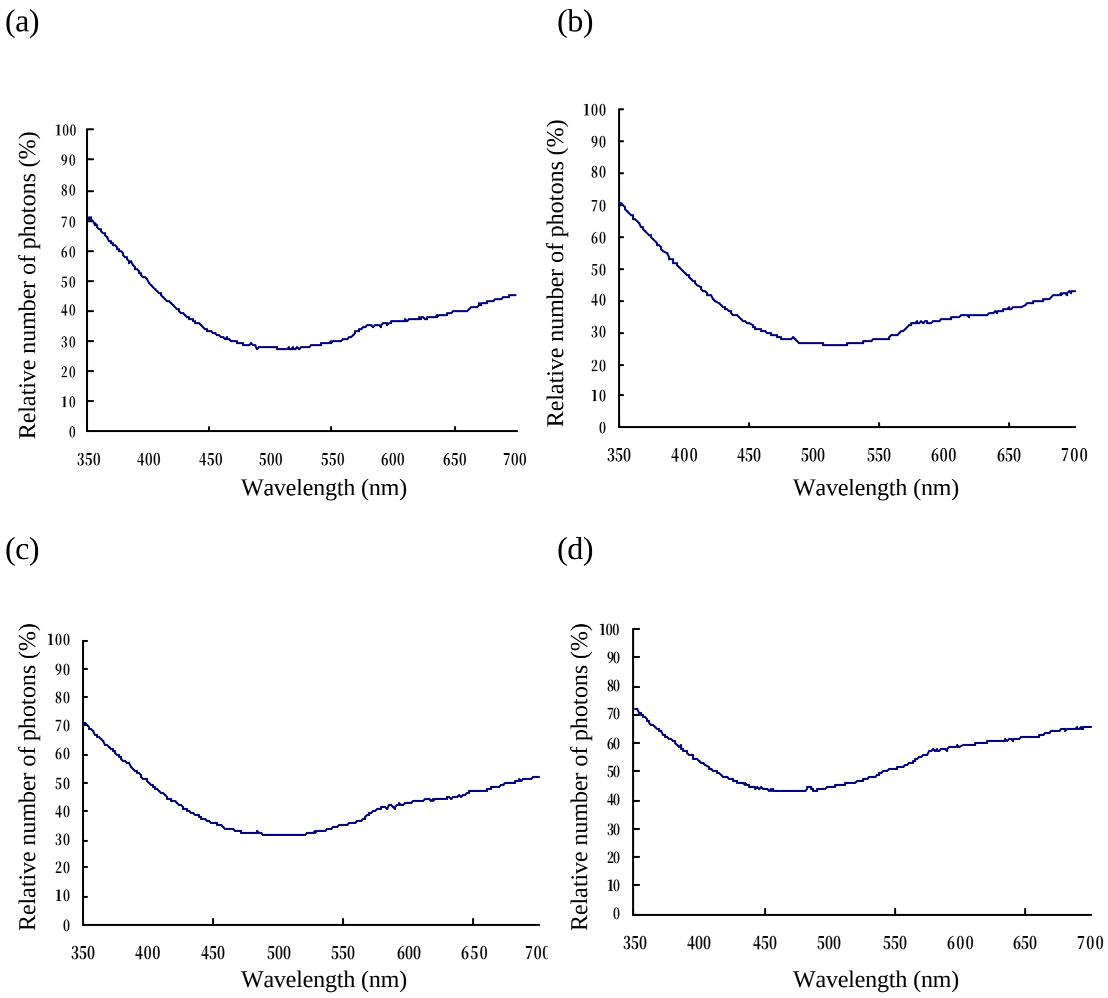


Figure 3. The reflectance spectra of the body coloration of *Cyclosa mulmeinensis* (a), prey pellet (b), egg sacs wrapped with prey carcasses (c), and the undecorated egg sacs (d).

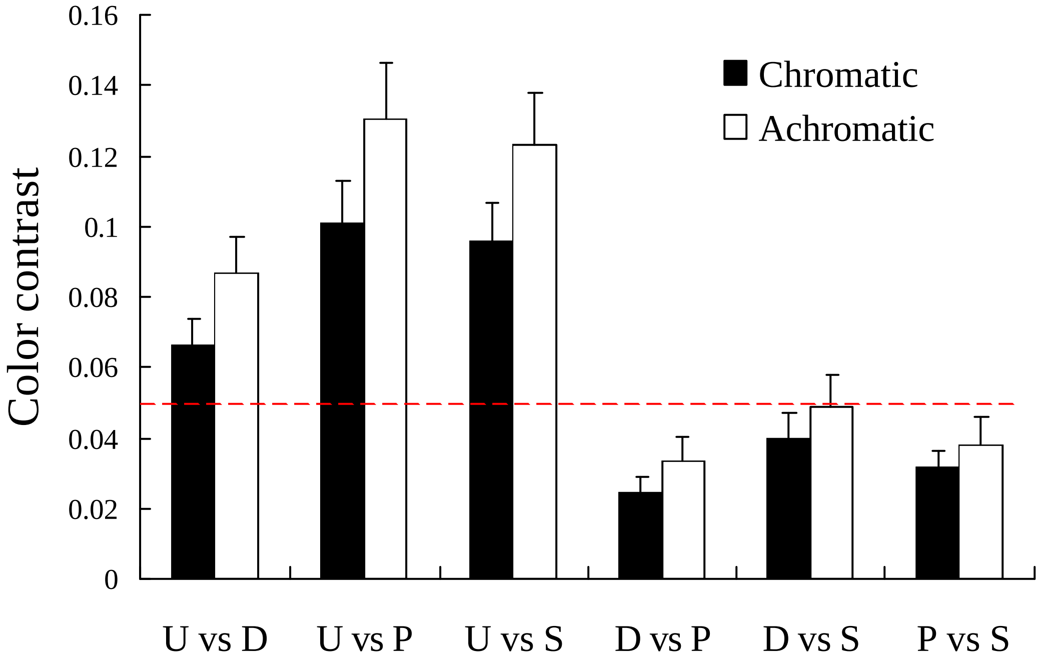
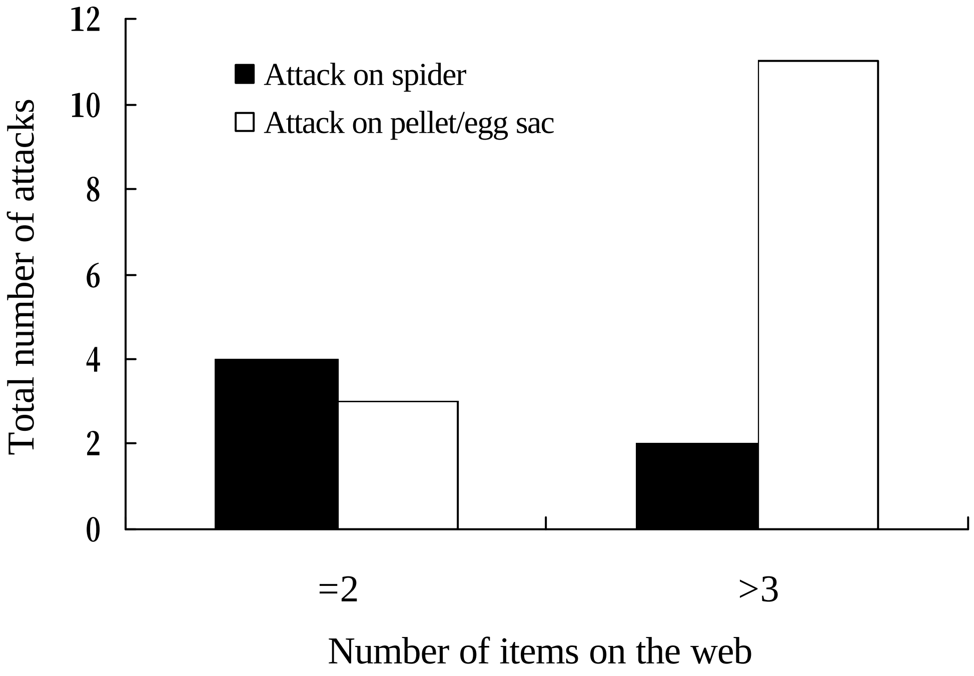


Figure 4. Chromatic and achromatic color contrasts of *Cyclosa mulmeinensis*, prey pellets, decorated and undecorated egg sacs when viewed against each other. The dash line represents the 0.05 discrimination estimated for hymenopteran insects. (U: undecorated egg sac, D: decorated egg sac, P: prey pellet, S: spider) (N = 12 for each items)



Figrue 5. Number of attacks by *Vespa* wasps on *Cyclosa mulmeinensis* on webs with two items and on those with more than three items.

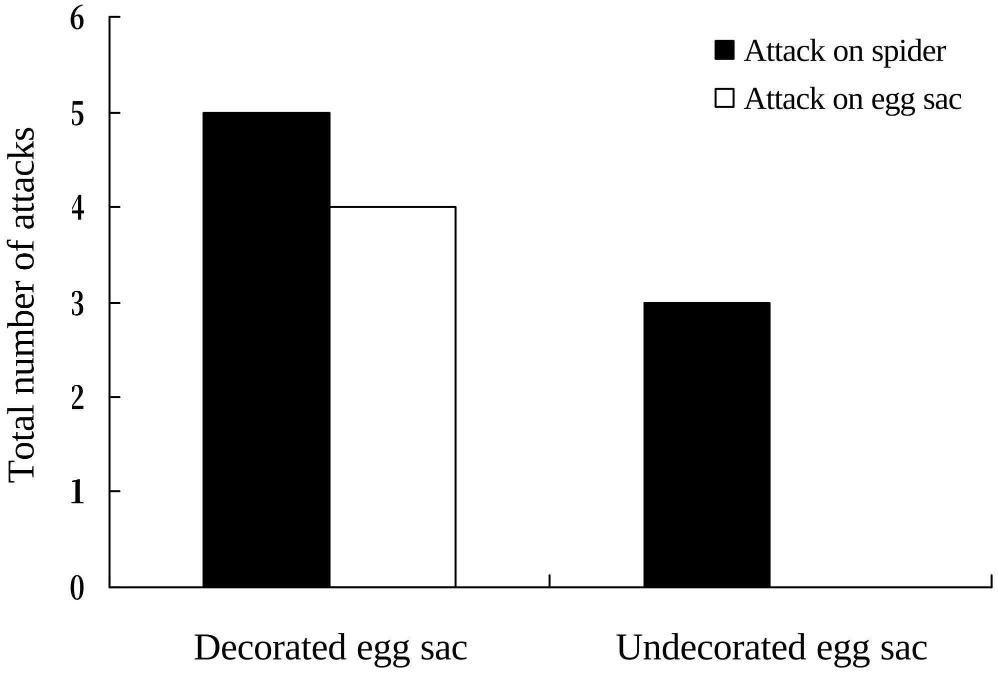


Figure 6. Number of attacks by wasps on *Cyclosa mulmeinensis* on webs with decorated egg sacs and undecorated egg sacs.

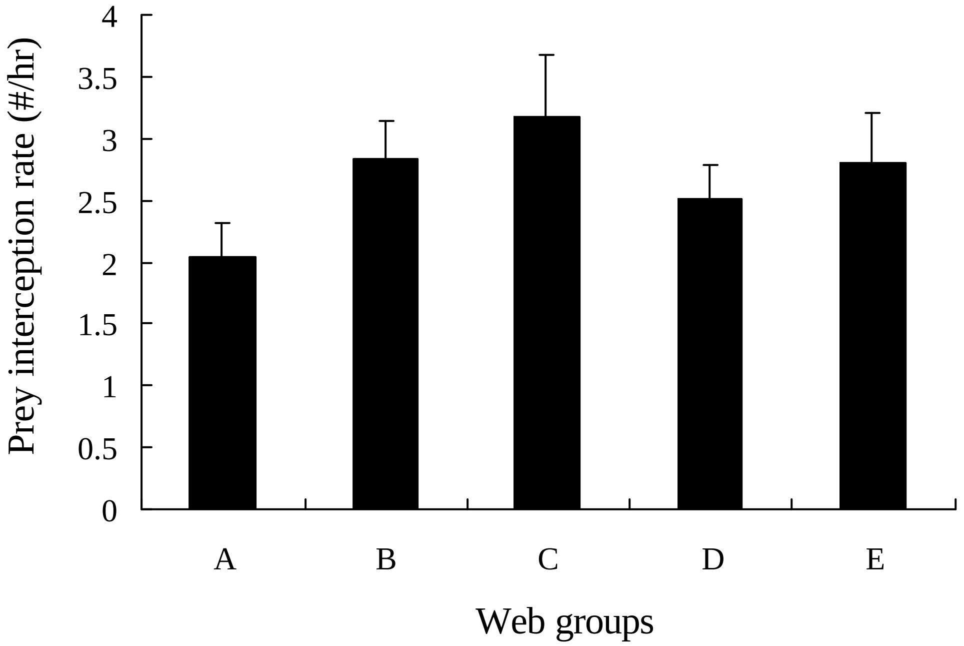


Figure 7. Mean (± SE) prey interception rates of webs in different web groups. (A: undecorated webs, N = 16; B: webs with one egg sac N = 15; C: webs with one prey pellet, N = 16; D: web with more than two prey pellets, N = 16; E: webs with more than two egg sacs, N = 14)