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Signaling by decorating webs: luring prey or deterring predators?

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Many organisms convey false signals to mislead their prey or predators. Some orb-weaving spiders build conspicuous structures on webs called decorations. Web decorations and spider colorations are both suggested to be important signals involved in interactions between spiders and other organisms. There are several hypotheses about the functions of signaling by decorations, among which prey attraction had received much support, but empirical evidence regarding predator defense is controversial. In this study, we conducted field experiments to investigate the effects of spider decoration and coloration on insect interception rates of webs built by *Argiope aemula* and to evaluate whether presence of decorations may decrease predation risk of spiders. Decorated webs with spiders present had the highest prey interception rate, followed by undecorated webs with spiders, and then undecorated webs without spiders. Such results indicated that decorations of *Argiope* spiders functioned as visual lures, and so did spiders' bright body colorations. In the field, almost all wasp attack events occurred on medium-sized spiders rather than on large ones. Moreover, medium-sized *Arg. aemula* on decorated webs received far more attacks than those on undecorated webs. Results of this study thus show that the signals conveyed by decorations can visually lure prey but at the cost of an increased predation risk. *[Behav Ecol 18:1085–1091 (2007)]*

Signalers may employ various forms of signals to entice receivers to produce responses that benefit the signalers (Krebs and Davies 1997). Although various modes of selection pressures from conspecifics could cause the evolution of communication signals, those from individuals of other species are also important driving factors. In the context of interspecific interactions, although in certain cases such as pollinator–flower interactions honest signalings do occur, the responses favorable to signalers are usually detrimental to the receivers. For example, predators may convey deceptive signals to mislead the prey either visually (Broadley and Stringer 2001) or chemically (Haynes et al. 2001). Prey may also mislead their predators by exhibiting deceptive signals to achieve effects such as mimicry (Mallet and Joron 1999) or crypsis (Marshall 2000; Ruxton et al. 2004). In a communication system, in addition to the signalers and the intended receiver, frequently there are unintended participants such as various forms of exploiters (Endler 1993). For example, many animals exploit the signal transmission between other organisms and either follow the signal to locate the emitter or provide false signals to make receivers respond in a way favorable to the exploiters (Endler 1993). One type of false signals generated by invertebrates that has received much attention is spider web decoration. Many diurnal orb web spiders (from at least 17 genera, Herberstein et al. 2000) decorate their webs with various objects after they have constructed an orb. The materials various spiders used to construct decorations include prey remain, egg sacs, and detritus (Nentwig and Heimer 1987; Herberstein et al. 2000), and decorations made entirely of silk (Figure 1) have received the most attention. After McCook first described this structure in 1889, researchers have proposed several hypotheses about its functions. Although decorations have been studied for decades, their functions still remain controversial (Starks 2002).

Most researchers regard spider web decorations as some sort of visual signals involved in the interactions between spiders and other organisms (Herberstein et al. 2000; Bruce et al. 2005). Some workers proposed that the color signal of silk decorations might not be distinguishable from that of vegetation background when viewed by insects (Blackledge and Wenzel 2001; Zschokke 2002). However, recent studies showed that decorations exhibit high color contrast when viewed against vegetation background and thus are highly visible to insects (Bruce et al. 2005). Among the proposed visual signal–related functions of decorations, attracting prey and protecting the spiders against predators are the 2 most popularly accepted hypotheses (Herberstein et al. 2000). Interpreting spider web decorations as visual signals to lure prey has received much support and has been demonstrated in species such as *Argiope argentata* (Craig and Bernard 1990; Craig 1991), *Arg. trifasciata* (Tso 1996), *Arg. keyserlingi* (Herberstein 2000; Bruce et al. 2001), *Arg. versicolor* (Li et al. 2004), *Arg. aurantia* (Tso 1998a), *Cyclosa conica* (Tso 1998b), *Octonoba sybiotides* (Watanabe 1999), and *Araneus eburnus* (Bruce et al. 2004). However, there is little evidence from empirical studies supporting the antipredator hypothesis, and most of it is either indirect or conducted in artificial settings. Lubin (1975) reported that the frequencies of decorated webs built by *Argiope* spiders in Daphne and Santa Cruz islands in Galapagos were negatively correlated with the abundance of vertebrate predators. Schoener and Spiller (1992) found that among various size classes of *Arg. argentata* in Bahamas, medium-sized spiders decorated their webs most frequently. They thus suggested that the cruciate form decorations might render the medium-sized spiders look bigger and therefore could deter the lizards from attacking them. In an enclosure experiment, Horton (1980) showed that blue jays (*Cyanocilla cristata*) attacked *Argiope* spiders less frequently when spiders were on decorated webs, suggesting that these birds might have learned to avoid sticky webs by associating them with decorations. Blackledge and Wenzel (2001) showed that in enclosures, *Arg. trifasciata* on undecorated webs were more likely to be captured by predatory mud dauber wasps.

Although the results of the aforementioned studies are congruent with the hypothesis that decorations serve as signals to

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Figure 1
Female oval St Andrew's cross spider *Arg. aemula* with silk decorations on its web.

deter predators, results of others show that silk decorations actually attract predators to spiders. Bruce et al. (2001) found that when praying mantids were placed in a Y-maze, they were more likely to choose decorated webs than undecorated ones no matter whether there were spiders on webs or not. Similarly, jumping spider predators also use silk decorations to locate the position of *Argiope* prey (Seah and Li 2001). In a laboratory experiment, Li and Lee (2004) showed that in the presence of jumping spider predators, *Argiope* spiders decreased not only the building frequency but also the size of decorations. In conclusion, currently there is still no direct evidence from field manipulative studies to evaluate whether signaling by web decorations may protect spiders from predators and existing evidence is contradictory to each other. The major reason for the lack of direct evidence is that it is very difficult to record the ephemeral and unpredictable predation events on *Argiope* spiders in the field (Bruce 2006). So far, empirical evidence from the field is still not available to demonstrate what organisms are the major predators of *Argiope* spiders.

In addition to web decorations, spider body colorations have also been proposed as important visual signals (Oxford and Gilliespie 1998). The conspicuous coloration patterns of certain spiders have been proposed to function to attract prey to orient toward these sit-and-wait predators (Hauber 2002). Conspicuous body coloration as effective visual attractant to prey has been demonstrated in crab spiders *Thomisus spectabilis* (Heiling et al. 2003), giant wood spiders *Nephila pilipes* (Tso et al. 2002, 2004), spiny spiders *Gasteracantha fornicate* (Hauber 2002), and orchid spiders *Leucauge magnifica* (Tso et al. 2006) as well as *Arg. argentata* (Craig and Ebert 1994). However, recently some researchers argued that the coloration of *Argiope* spider might not attract prey but functioned to camouflage the spiders. Václav and Prokop (2006) found that the number of prey intercepted by artificial webs with dead *Arg. bruennichi* was not higher than that trapped in webs without spiders. Hoese et al. (2006) found that some insects kept in a Y-maze showed no preference to webs with or without *Arg. keyserlingi* and concluded that the conspicuous coloration pattern serves to camouflage the spiders. Therefore, it is still not clear whether body colorations of *Argiope* spiders function as visual lures to attract prey or serve to conceal the spiders. Nor do we understand how web decorations and spider colorations interplay in the interactions between spiders and other organisms.

In this study, we investigate the functions of 2 conspicuous signals of *Argiope* spiders, web decoration and body coloration, by field manipulative studies. We performed a direct test of the predator defense hypothesis by using video cameras to monitor spiders of different size classes with or without decorations in the field, to identify the predators, and to catch the rare and ephemeral predation events on *Argiope* spiders. We also manipulated the presence of decorations and spiders to determine how these 2 signals interact in influencing the hunting success of spiders.

MATERIALS AND METHODS

The study site and the spider

Field manipulative experiments were conducted in August and September 2006 at a forest edge meadow in Lien-Hwa-Chih Research Center (LHCRC) operated by the Taiwan Forest Research Institute situated in Yu-Chi, Nantou County, Taiwan (120°52′36″E, 23°55′13″N). The dominant vegetation species in the study site were big bidens *Bidens pilosa* var. *radiate* and giant false sensitive plant *Mimosa diplotricha*. We used female oval St Andrew's cross spiders, *Arg. aemula* Walckenaer1841 (Figure 1) (Araneae: Araneidae) in all experiments. On the dorsum of the abdomen were numerous silver, yellow, and black wavelike transverse stripes, and the ventrum was black but with 2 yellow bands running longitudinally (Figure 2a).

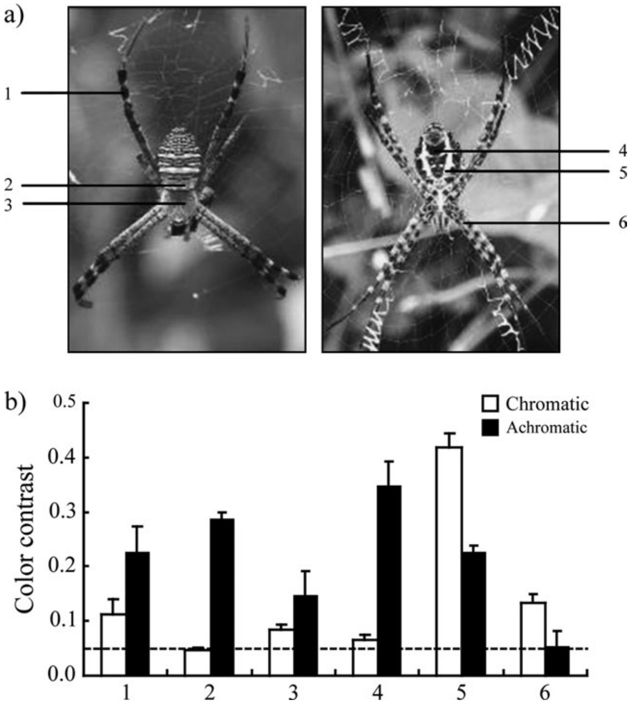

Figure 2
(a) Dorsal and ventral view of adult female *Arg. aemula*. Color contrasts were calculated from the area specified. (b) Mean (± standard error) color contrast values of different parts of *Arg. aemula*. Numbers correspond to areas specified in (a). Dashed line indicates the discrimination threshold for color contrast detection estimated for hymenopteran insects.

Similar to other *Argiope* spiders, only female *Arg. aemula* have conspicuous body coloration and males are small (<10% of the females' weight) and inconspicuously colored (Sasaki and Iwahashi 1995). *Argiope aemula* in the study site build discoid decorations on webs when their body size is smaller than 0.3 cm and cruciate decorations when they grow bigger (Cheng RC, unpublished data).

Ontogenetic variations of *Arg. aemula* decoration types

Results of preliminary surveys showed that the types of decorations built by *Arg. aemula* ranged from no silk band at all to a perfect cross. To determine whether the proportion of different decoration types changed along with the development stages of spiders, we surveyed the *Arg. aemula* population in LHCRC. Each *Arg. aemula* individual was marked by fastening a color tape on vegetation nearby, and the body length and decoration type were recorded. We divided the decoration types into the following categories: the complete cruciate form, three-quarter form, half form, one-quarter form, discoid form, and empty webs. We divided the spiders into 3 size categories: larger than 1.7 cm (large-sized), between 1.0 and 1.7 cm (medium-sized), and smaller than 1.0 cm (small-sized). The reason for such grouping was that when female *Arg. aemula* mature, their body length usually exceeds 1.7 cm, and spiders smaller than 1.0 cm usually build webs deep inside the vegetation (Chang RC, personal communication). We compared the proportion of decoration types between these 3 groups by chi-square tests of homogeneity.

Field manipulative studies on functions of decorations

In the field manipulative studies, spiders with body length larger than 1.0 cm were used. Before the experiment, we randomly divided the spiders and webs into the following groups: decorated webs with spiders, undecorated webs with spiders, and undecorated webs without spiders. Here, we defined the decorated webs as the webs with either complete or three-quarter cruciate form decorations. Undecorated webs were generated by using a burning incense stick to remove the silk bands. In order to control for the influence of removing decorations, we also used a burning incense stick to generate a small hole on decorated webs nearby the decorations. Elgar and Jebb (1998) showed that mud dauber wasps, the potential predator of *Argiope* spiders, would choose spiders of a specific size range as food for their larvae. Hence, to determine whether *Arg. aemula* of different body size had different level of predation risk, we compared the number of predator attacks received by large spiders. In our study site, the abundance of the medium-sized spiders was relatively low, so only large spiders were used in the undecorated web without spider treatment. Each day, a total of 16 Sony TRV 118 Hi-8 and Sony HDD video cameras were set up in front of the webs to monitor the prey interception rates of webs and predator attack events on spiders. The video cameras were placed 1–2 m away from the spider webs, depending on the vegetation nearby. The recordings were conducted from 8:00 AM to 3:00 PM (8 h a day) between 27 August and 6 September 2006. We adjusted the focus of the video cameras to allow the whole web to be videotaped. During the monitoring, the insects intercepted by webs were not removed. By using video cameras, we could monitor the webs continuously and the disturbances to spiders could be reduced to minimum. After the field experiments, while viewing the videotapes in the laboratory, we recorded the number and taxonomic orders of intercepted prey and number of attack events by predators on *Arg. aemula*. The exact timing of each prey interception event was specified to avoid double counting. Prey interception rate was defined as the number of prey bumping into the web per hour of video recording. Previous studies showed that the prey interception rate of orb webs was also affected by the capture area (Higgins and Buskirk 1992; Sherman 1994) and visibility of the webs (Craig 1986, 1988; Craig and Freeman 1991). Therefore, for each web to be monitored, we measured the spider body length, hub height, hub diameter and radius, and number of sticky spirals from 4 cardinal directions to estimate capture area and mesh height. The capture area and mesh height of the orbs were calculated according to the formulae given in Herberstein and Tso (2000).

To investigate whether decorations functioned to attract prey, we compared prey interception rates and mesh heights of webs with or without decorations. Because prey interception rate fitted neither normal nor Poisson distributions, we could not use multivariate statistical methods, such as analysis of covariance or Poisson regressions. Instead, we divided prey interception rate by capture area to generate unit area prey interception rate (UAPIR). Because in our study site the smallest recorded capture area of webs was around 200 cm^2, we used that as a unit area to make the values more realistic and to avoid overestimating the actual values. UAPIRs of webs with and without decoration were compared with Mann–Whitney *U* tests. In addition, we also simultaneously assessed the effects of decorations and spider body colorations on prey attraction. Prey interception rates of decorated webs with spiders, undecorated webs with spiders, and undecorated webs without spiders were compared by a Kruskal–Wallis analysis. In this analysis, only data from large spiders were used. Because of the relatively low abundance of medium-sized spiders, we did not designate them to the undecorated web without spider treatment. To control for the confounding effects of unequal sample size and heterogeneity in spider body size and web area among the 3 treatments, we made an a priori decision to use data from spiders of large size class to perform the Kruskal–Wallis analysis. To compare the number of attacks by predators between spiders in large and medium-sized classes and between spiders on decorated and undecorated webs of each size class, log-likelihood ratio tests (*G*-test) were used.

Calculation of color contrasts

In order to determine how spider body coloration was viewed by insects, the color contrasts of various body parts of *Arg. aemula* were calculated. Because among various insect taxa, the visual physiology and neuroethology of Hymenoptera have received the most intensive study (Briscoe and Chittka 2001), we used the models developed from honeybees to perform the calculation. Color contrast quantifies the color signal differences between the object and background (Chittka 1992). In order to calculate the color contrasts, we measured the reflectance spectra of various body parts of 5 *Arg. aemula* collected from the study site by a spectrometer (S2000, Ocean Optics Inc, Dunedin, FL) in the laboratory. We measured reflectance spectra from the carapace, the silver bands on the dorsum abdomen, the yellow and black stripes on the ventrum abdomen, and the gray and black color rings on the legs (Figure 2a). The reflectance spectra of different parts were measured by placing the probe vertically 5 mm above the objects. We followed the color hexagon model of Chittka (1992) to calculate color contrast values. The background vegetation reflectance spectra and daylight illumination were those used in Tso et al. (2004). The color contrast values of different spider body parts were compared with the discriminating threshold of 0.05 estimated for honeybees (Théry and Casas 2002) by one-tailed *t*-tests.

Table 1

Result of field survey of the proportion of decoration forms in 3 size classes of *Arg. aemula* (a) and results of chi-square test of homogeneity (b)

(a)

Body length (cm)	Complete cruciate	Three-quarter cruciate	One-half cruciate	One-quarter cruciate
<1.0 (S)	17	5	6	2
1.0–1.7 (M)	10	5	2	1
1.8–2.5 (L)	5	3	8	0

(b)

Comparisons	χ^2	P
S versus M	0.1216	0.7273
S versus L	1.9051	0.1675
M versus L	2.6388	0.1024

S, small spiders; M, medium-sized spiders; L: large spiders.

Table 2

Result of Mann–Whitney *U* tests comparing UAPIR and mesh height of decorated ($n = 56$) and undecorated ($n = 59$) webs built by medium- and large-sized *Arg. aemula* (a) and those of decorated webs with spiders (DS, $n = 28$), undecorated webs with spider (US, $n = 31$), and undecorated webs without spiders (UN, $n = 20$) built by large *Arg. aemula* (b)

		UAPIR		Mesh height	
	Comparisons	*U* value	*P*	*U* value	*P*
(a)	DS versus US	2086.000	0.015	1489.500	0.363
(b)	Overall	20.385	<0.001	2.650	0.266
	DS versus US	606.000	0.009	383.000	0.429
	DS versus UN	484.000	<0.001	203.000	0.066
	US versus UN	436.000	0.013	270.000	0.310

RESULTS

Ontogenetic variations of *Arg. aemula* decoration types

Regardless of the body size, 82% of *Arg. aemula* individuals built decorated webs (64 out of 78 spiders recorded). The discoid form could only be found from individuals whose body length was smaller than 0.3 cm. When the spiders' body length exceeded 0.3 cm, they changed decoration form into cruciate. We recorded the decoration form of 64 individuals in the field, and the result showed that there was no significant difference in the proportion of decoration types between 3 size groups (Table 1a). In small and medium-sized spiders, more than half of the individuals recorded built complete cruciate decorations. In large spiders, only about one-third of individuals recorded built complete cruciate decorations. However, there was no statistical difference in the percentage of decoration types among the 3 size classes (Table 1b).

Field manipulative studies on the function of decorations

In this part of the study, only when the spiders stayed on the webs for more than 4 hours were their data used in the statistical analyses. Data from 710 h of video recording were used to investigate the effect of decoration on the prey interception rate of webs. Among them, 344 h were from the decorated group ($n = 56$ spiders) and 366 h were from the undecorated group ($n = 59$ spiders). The prey interception rates of decorated and undecorated groups fitted neither normal nor Poisson distributions, so we used the nonparametric Mann–Whitney *U* test to compare the UAPIRs between different treatment groups. The UAPIRs (number of prey intercepted per hour of recording per 200 cm^2 capture area) were significantly different between decorated and undecorated groups (Table 2a, Figure 3a). The decorated webs intercepted 60% more insects than undecorated webs. Among the prey intercepted by decorated webs, Hymenoptera comprised the highest proportion (61%), followed by Diptera (28%), and Orthoptera (7%). In undecorated webs, the dominance pattern of intercepted prey was similar (Hymenoptera: 53%, Diptera: 28%, Orthoptera: 10%). There were no significant differences in mesh height between the 2 groups (decorated webs = 4.12 ± 0.18 mm, undecorated webs = 4.43 ± 0.23 mm, Table 2a).

To simultaneously investigate the effects of web decorations and spider body coloration on prey interception rates, we used the data from large spiders. Data from a total of 490 h of video recording were used in this part of the analyses. Among them, 178 h were from a decorated web with spider group ($n = 28$), 198 h from the undecorated web with spider group ($n = 31$), and 114 h from the undecorated web without spider group ($n = 20$). Unit area prey interception data of these groups were analyzed by a nonparametric Kruskal–Wallis test and pairwise Mann–Whitney *U* tests. The UAPIRs differed significantly among the 3 groups (Table 2b). Decorated webs with spiders intercepted significantly more insects than the other 2 groups (Figure 3b). Although the UAPIR of undecorated webs with spiders was lower than that of the decorated webs with spider group, it was 2 times that of the undecorated web without spider group (Figure 3b). There was no significant difference in mesh height between the 3 treatment groups (decorated webs with spider = 4.73 ± 0.21 mm, undecorated webs with spiders = 5.21 ± 0.33 mm, and undecorated webs without spider = 3.56 ± 0.30 mm, Table 2b).

The 710 h of video recording used in evaluating the effect of decoration on prey interception was also used in assessing decoration's effects in defending the spiders. Among them 376 h were from large and 334 h were from medium-sized spiders. Within each size class, decorated and undecorated webs were monitored for equal amounts of time. A total of 18 predator attack events were recorded from 710 h of video recording, and the predators were wasps with body length about 2.0–3.5 cm. Although large and medium-sized *Arg. aemula* were monitored for a similar amount of time, only one predation event was recorded from the former and the rest were all recorded from the latter (*G*-test, $G_{0.05,1} = 29.45$, $P < 0.001$). Among the 17 predation events recorded from

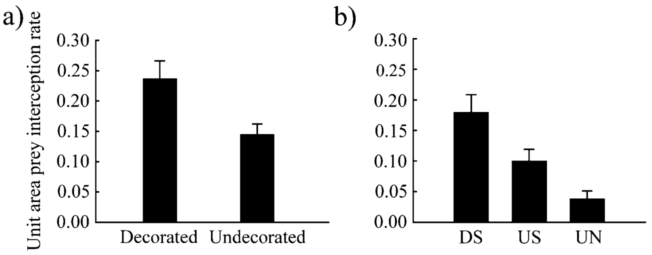

Figure 3
Mean (± standard error) prey interception rate (number of prey intercepted per hour of monitoring per 200 cm^2 orb area) of decorated and undecorated webs built by medium- and large-sized *Arg. aemula* (a) and that of decorated web with spider (DS), undecorated web with spider (US), and undecorated web without spider (UN) treatment groups built by large spiders (b).

Table 3

Results of one-tailed *t*-tests comparing the achromatic and chromatic color contrast of different body parts of *Arg. aemula* with the discrimination threshold value of 0.05 estimated for hymenopteran insects

	Areas examined					
Color contrast	1	2	3	4	5	6
Achromatic						
t	3.748	19.144	2.200	6.623	14.684	0.175
P	0.010	0.000	0.047	0.002	0.000	0.435
Chromatic						
t	2.213	−0.635	3.684	1.475	14.828	5.02
P	0.005	0.265	0.011	0.107	0.000	0.004

Numbers correspond to areas specified in Figure 2a. Areas with positive *t* values and with *P* values smaller than 0.05 indicate that their color contrast values are higher than the discrimination threshold of 0.05.

medium-sized *Arg. aemula*, 12 were from spiders on decorated webs and 5 from spiders on undecorated webs. Although spiders in the decorated group experienced twice as many attacks compared with those in the undecorated group, the result of the log-likelihood ratio test (*G*-test) was marginally significant (*G*-test, $G_{0.05,\ 1} = 3.158$, $P = 0.076$).

Calculation of color contrasts

Colorations of various body parts of *Arg. aemula* were not equally distinguishable from the vegetation background when viewed by hymenopteran insects. Under chromatic vision, the color contrasts of silver prosoma (area 2 in Table 3 and Figure 2) and black body parts (area 4 in Table 3 and Figure 2) of *Arg. aemula* were not significantly higher than the discrimination threshold of 0.05 estimated for hymenopteran insects (Théry and Casas 2002). The chromatic color contrasts of the other parts of spiders were significantly higher than the discrimination threshold. Under the achromatic vision of hymenopteran insects, most body parts of the spiders were easily distinguishable from the vegetation background, besides the grey color rings on the legs (area 6 in Table 3 and Figure 2).

DISCUSSION

Results of this study indicate that signaling by decorating webs can lure prey to webs but at the cost of increasing predation risk. Some researchers proposed that decoration might increase the apparent size of medium-sized spiders and thus could deter certain predators (Schoener and Spiller 1992). According to this hypothesis, medium-sized *Argiope* spiders on decorated webs are expected to experience fewer predator attacks than those on undecorated webs. However, our results show that medium-sized *Arg. aemula* on decorated webs were more likely to be attacked by predatory wasps, and therefore, the predator defense hypothesis is not supported. Our study is the first to provide direct field data to demonstrate that web decorations attract more predators to the spiders. In this study, the use of a large quantity of video cameras enabled us to monitor a number of spiders continuously and to record the unpredictable and ephemeral attack events on spiders, which was extremely difficult to observe and quantify by traditional methods. The higher number of attack events experienced by spiders on decorated webs indicates that the predatory wasps may use the cruciate form decorations to locate the position of the spiders, a result which is congruent with those of recent studies using Y-mazes in the laboratory (Bruce et al. 2001; Seah and Li 2001). However, our results are not congruent with those reported by Blackledge and Wenzel (2001), who showed that in artificial enclosures *Arg. trifasciata* on undecorated webs were more likely to be captured by mud dauber wasps than those on decorated webs. A possible explanation for such incongruence might be that the *Argiope* spiders used in different studies exhibited different decoration forms. The decorations of *Arg. keyserlingi* (Bruce et al. 2001), *Arg. versicolor* (Seah and Li 2001), and *Arg. aemula* (this study) are all cruciate form, but the decorations of *Arg. trifasciata* (Blackledge and Wenzel 2001) are linear. Bruce and Herberstein (2005) showed that bees seemed to respond differently to linear and cruciate-from decorations, and more field studies are needed to further investigate whether different forms of decorations represent different signals to predators thus function differently.

In this study, almost all *Arg. aemula* that were attacked by predators were smaller than 1.7 cm, which indicates that the predation pressure of medium-sized *Arg. aemula* spiders is much higher than that of large individuals. When *Arg. aemula* spiders are very small, they build webs deep within the vegetations. Previous studies showed that the predatory wasps were not generalist predators but searched for prey of a specific size range (Elgar and Jebb 1998). So, the observed higher magnitude of attacks on medium-sized *Arg. aemula* indicates that spiders of this size class are preferred prey of wasps in our study site. Our field census showed that all size classes of *Arg. aemula* exhibited a similar building frequency of decorated webs. Because decorating the webs greatly increases the prey intake of spiders, the high frequency of decoration building in medium-sized *Arg. aemula* might reflect their strategy to maximize prey intake to speed up the growth rate, even at the cost of increased predation risk. Because large *Arg. aemula* are rarely attacked by wasps, if juvenile spiders develop quickly and grow into a certain size as soon as possible, they could shorten the vulnerable period.

Because decorations are visible to insects (Bruce et al. 2005) and some hymenopteran predators use them to locate the spiders, it is possible that prey of spiders also learn to associate decorations with dangers. Although the color signals and shape of decorations might be similar to the general pattern of pollinator insects' food resources (Prokopy and Owens 1983; Biesmeijer et al. 2005), insects that are attracted and trapped by decorated webs would learn to associate them with danger if insects successfully escape (Craig 1994). Although to the prey of *Argiope* spiders the luring signals of decorations and the spiders may represent either food resource or danger, because the density of *Argiope* spiders is much lower than flowers, in most circumstances insects will gain positive feedbacks by flying toward such a pattern (Craig 1994). The preference of pollinator insects for an ultraviolet-bright radiating pattern, and low frequency of negative feedbacks associated with such stimuli due to relatively low density of spiders, renders signaling by decorating the webs a form of sensory exploitation on the innate preference of pollinator insects.

In addition to web decorations, the spiders themselves also served as a form of prey attractant. Many insects such as honeybees have innate preference for symmetric and disruptive patterns (Rodríguez et al. 2004). In this study, we quantified how different body parts of *Arg. aemula* were viewed by hymenopteran insects against the vegetation background and found a cooccurrence of high- and low-contrast body colorations. The arrangement of body color patches and their differential visual distinctiveness to insects may make *Arg. aemula* resemble innate preference of pollinator insects such as symmetric and disruptive patterns (Figure 2a). While both web decorations and spider colorations are attractive to insects, we suggest that they are 2 vital components of the overall lure signal of *Argiope* spiders. Our results showed that when both signals (decorations and the spiders) were present, the prey luring effect was the highest. Biesmeijer et al. (2005) found that the floral guides, stingless bee nest entrances, and insectivorous pitchers all similarly exhibit a dark center, radiating stripes, and peripheral dots. The cooccurrence of *Argiope* spiders (potentially representing a dark center and disruptive pattern) and decorations (potentially representing radiating stripes) might have rendered the overall signal more highly resembling the aforementioned general visual attributes of pollinators' resources. More studies are needed to determine how decorations and spider body colorations are involved in constituting effective visual luring signals to exploit innate preferences of pollinator insects.

A very controversial attribute of *Argiope* spiders' web decorations is this structure's inconsistent occurrence and shape polymorphism on the individual level (Starks 2002). Not being able to appropriately address such attribute has rendered many functional hypotheses not well supported (Nentwig and Rogg 1988). If web decorations function as signals to lure prey, why do *Argiope* spiders build them so inconsistently and why is their form so polymorphic? In this field study, we successfully identified the benefit and cost of signaling by decorating webs, and based on such results (and those of previous ones) we can now address such signaling polymorphism. Results of our study demonstrate that luring prey by decorating webs goes with a cost of increased predation risk, at least during certain developmental stages. Therefore, there will be a selection pressure to prevent the spiders from consistently decorating their webs. Moreover, another pressure in the context of risk learning of prey also selects against consistent building of decorations of a fixed form. Therefore, from ultimate perspectives the inconsistent building and shape polymorphism of decorations can be regarded as products of trade offs between opposing selection pressures. Proximately, these attributes might be generated by both spiders' genetic makeup and physiological status. Works by Edmunds (1986) and Craig et al. (2001) showed that heredity played a substantial role in determining the building frequencies of decorations in *Argiope* spiders. Tso (2004) showed that stochastic prey abundance and capture success might influence the amount of silk reserve in the aciniform silk glands and thus affect the size of decorations in subsequent webs. On the other hand, although *Argiope* spiders might receive less prey intake when they build undecorated webs, their bright body coloration can still provide them with substantial luring effects. Therefore, *Argiope* spiders can afford to build undecorated webs for a certain period of time to balance hunting success and predation risk. In conclusion, we suggest that silk decorations primarily function as luring signals to visually attract prey. However, cooccurrence of opposing selective pressures mediated by cognitive behaviors of prey and predators, and the complicated interactions between genetic makeup, stochastic prey abundance, and aciniform gland silk reserve result in the observed inconsistent occurrence and signal polymorphism. We suggest that the relative strengths of these selection pressures and proximate factors are responsible for the observed variation in extent of signaling inconsistency in different *Argiope* species.

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