# Hunting efficiency and predation risk shapes the color-associated foraging traits of a predator

Chun-Min Fan,[a] En-Cheng Yang,[b] and I-Min Tso[a,c]

[a]Department of Life Science, Tunghai University, Taichung 407, Taiwan, [b]Department of Entomology, National Taiwan University, Taipei 105, Taiwan, and [c]Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung 407, Taiwan

When animals forage or court their behaviors are often constrained by factors such as predation risk. Predator–prey interactions govern the evolution of many behavioral and morphological traits. However, animals with foraging or courtship tightly linked to morphology cannot make quick behavioral adjustments when encountering a dilemma. In this study, we investigate how opposing pressures of maximizing prey intake and minimizing predation risk shape the morphology-associated foraging traits of a sit-and-wait predator. Recently, the conspicuous body colorations of certain orb-weaving spiders have been demonstrated to be attractive to both insect prey and predators. In this study, we performed field manipulations to assess how visual luring signals of such predators trade off opposing pressures of feeding and surviving. We created dummies made of cardboard to test how changing size of conspicuous signal affected attractiveness to prey and predators. Dummies mimicked the coloration pattern and chromatic properties of giant wood spider *Nephila pilipes*. We found that dummies were similarly attractive to prey and predators as real spiders were. Uniformly yellow colored dummies attracted significantly more prey than those dummies that mimicked the color pattern of *N. pilipes*. However, such dummies also attracted far more hymenopteran predators. Our findings indicate that current morphology-associated foraging traits of certain animals do not necessarily provide the best feeding performance but reflect a trade-off between opposing pressures of foraging intake and predation risk. *Key words:* body coloration, *Nephila pilipes*, Nephilidae, orb spider, visual ecology. *[Behav Ecol 20:808–816 (2009)]*

Substantial evidence from studies on foraging and reproductive behaviors shows that animals may behave in various ways to balance opposing pressures. For example, when facing predation pressures animals may forage in inferior sites or at inferior times (Orr 1992; Romey 1995; Cowlishaw 1997), adjust foraging time or effort (Meyer and Valone 1999; Downes 2001; Walther and Gosler 2001; While and McArthur 2006; Ylonen et al. 2006; Urban 2007; Eifler et al. 2008), alter courtship intensity/vigor (Ryan et al. 1981; Sullivan and Kwiatkowski 2007), or change mate preferences (Magnhagen 1991; Koga et al. 1998; Su and Li 2006). Most studies work on animals that have high mobility and can quickly adjust their foraging or courtship behaviors (Lima and Dill 1990; Inger et al. 2006). However, in many animals, the traits involved with foraging or courtship are tightly linked to an animal's body morphology and exhibit little plasticity. Even though these animals lack quick response and plasticity, their morphology-associated foraging or courting traits are also under severe opposing selection pressures. How do opposing pressures of maximizing foraging/reproductive reward and minimizing mortality, shape traits that are tightly linked to morphology?

Many researchers explore such issues by examining body coloration involved with reproduction. For example, among guppy populations, in various habitats, the expression of bright secondary sexual traits is negatively correlated with intensity of local predation pressures (Endler 1995; Nicoletto and Kodric-Brown 1999; Kodric-Brown and Nicoletto 2005). A similar phenomenon is also observed in reptiles (Kwiatkowski 2003; Macedonia et al. 2004). Empirical studies further demonstrated that conspicuous body coloration was also associated with high predation risk (Baird et al. 1997; Stuart-Fox et al. 2003; Husak

et al. 2006). In some birds, predation pressure is also suggested to affect the survival and chromatic properties of taxa with conspicuous plumage or body parts (Jennions et al. 2001; Gregoire et al. 2004; Håstad et al. 2005; Figuerola and Senar 2007). How various selection pressures affect the evolution of secondary sexual traits that are tightly linked to morphology has received much study. However, relevant studies on foraging traits associated with morphology are still lacking. Recently, the body colorations of some animals have been found to play important roles in foraging. For example, the conspicuous body coloration of certain spider taxa has been empirically demonstrated to be a vital foraging trait, serving as visual attractants to insects (Heiling et al. 2003, 2005; Chuang et al. 2008). Although certain crab spiders can change their body coloration (Foelix 1996), in most such organisms, the chromatic properties and the arrangement pattern of their body coloration are fixed and exhibit little plasticity (Oxford and Gillespie 1998). Animals relying on body colorations as visual lures, which lack high mobility or flexibility, also face the same dilemma of feeding/surviving while foraging. However, how do opposing pressures of maximizing reward and reducing mortality shape the foraging-associated body colorations of such animals is unknown. Zuk and Kolluru (1998) proposed that many secondary sexual traits reflect compromises between attracting mates and avoiding predators. Accordingly, we hypothesized that in animals with foraging tightly linked to body color, the current coloration cannot provide the best foraging performance but represent a trade-off between opposing pressures of foraging intake and predation risk.

Recently, conspicuous body coloration serving as a visual lure to insect prey has been empirically demonstrated in a taxonomically wide array of orb web spiders (*Argiope* of Araneidae: Craig and Ebert 1994; Cheng and Tso 2007; Bush et al. 2008; *Gasteracantha* of Araneidae: Hauber 2002; *Leucauge* of Tetragnathidae: Tso et al. 2006, 2007; *Nephila* of Nephilidae: Tso et al. 2002, 2004; Chuang et al. 2007). These spiders all share

a similar body coloration pattern of conspicuous patches embedded in dark or green base body coloration (Yaginuma 1986). Recent neuroethological studies have shown that the bright body parts of these spiders can be chromatically distinguished from the vegetation background, but the dark/green parts cannot (Tso et al. 2004, 2006; Chuang et al. 2007; Cheng and Tso 2007). However, many visually oriented predators such as wasps use color signals to search for spiders (Richter 2000). Conspicuously colored orb spiders were found to be one major prey item of many hymenopteran predators (Coville 1987; Elgar and Jebb 1998; Richter 2000; Blackledge et al. 2003), and direct attack events were quantitatively recorded in enclosures (Blackledge and Pickett 2000; Blackledge and Wenzel 2001) and in field studies (Cheng and Tso 2007). Here we show that the body coloration pattern of a sit-and-wait predator, the giant wood spider *Nephila pilipes*, is not a best form of visual lure. However, when simultaneously considering the benefit of luring prey and the cost of increasing predator detection, the current luring signal design of *N. pilipes* reflects a trade-off between foraging benefit and predation cost.

## MATERIALS AND METHODS

### Construction of spider dummies

In this study, we used the female giant wood spider *N. pilipes* (Nephilidae; Figure 1) as the model organism. A typical female *N. pilipes* has an olive-green prosoma and a yellowish-black abdomen decorated with a transverse white band, 2 longitudinal yellow bands, and numerous yellow spots. Studies by Tso et al. (2002, 2004) showed that the insect-catching rates of *N. pilipes* exhibiting typical black-and-yellow body coloration patterns were significantly higher than that of melanic ones. Moreover, how various *N. pilipes* were viewed by their prey was quantified (Tso et al. 2004), and the luring effect of this spider's conspicuous body parts was confirmed by field manipulations (Chuang et al. 2007). Based on the results of these studies, we conducted further field experiments by using dummy spiders. The use of dummy spiders allowed us to freely manipulate the size of conspicuous visual signal. We collected various kinds of commercially available yellow and black cardboard papers. To determine which cardboards exhibit color signals most similar to those of *N. pilipes*, the color contrasts between these papers and corresponding body parts

of *N. pilipes* were calculated (Tso et al. 2004). Color contrast is the spectral difference between 2 objective areas and can only be detected by a visual system with at least 2 photoreceptor types (Chittka 1992). To calculate color contrast, we needed the illumination spectrum (the spectrum of the light source), the object's reflectance spectrum, and the spectral sensitivities of all photoreceptor types in insects' visual system (Chittka 1992). The spectral sensitivities of insect compound eye photoreceptors are more or less similar across a wide array of insect taxa (Briscoe and Chittka 2001). We used the neuroethological model developed for honeybees (on which intensive visual physiological studies have been carried out; Briscoe and Chittka 2001) to calculate the chromatic and achromatic color contrasts of cardboards and spider body parts when viewed against each other.

Reflectance spectra of cardboards were measured in the laboratory by a spectrometer (S2000, Ocean Optics, Inc., Dunedin, FL). Those of *N. pilipes* were obtained from Tso et al. (2004), which data were measured by the same methodology and equipment. The objects were illuminated with a 450 W, Xenon arc lamp. For each cardboard paper, we randomly selected 6 points to measure reflectance spectra. The tip of the probe was placed vertically 5 mm above the objects measured. Color signals were generated by multiplying the surface reflectance function and the irradiance of the habitat (Wandell 1995). The surface reflectance is the fraction of the light reflected from the surfaces of the cardboards or spiders. The irradiance was obtained from Tso et al. (2004), in which study the daylight spectrum of the forest understory illumination was measured at the study site by placing the end of the spectrometer probe 5 mm vertically above the standard white. Based on the color hexagon model (Chittka 1992, 1996, 2001) and with the color signals and the spectral sensitivity of honeybees, the color contrasts were measured in units of just identifiable distance (JND). A value greater than 0.05 was regarded as perceivably different (Théry and Casas 2002). Cardboards were chosen if the JND was smaller than or closet to 0.05 compared with the corresponding spider coloration. We used 1-tailed *t*-tests to compare color contrast values with the discrimination threshold value of 0.05 estimated for chromatic vision of hymenopteran insects (Théry and Casas 2002).

To make dummies, first a black cardboard was cut into the shape of a spider with 8 legs extended and then color strips
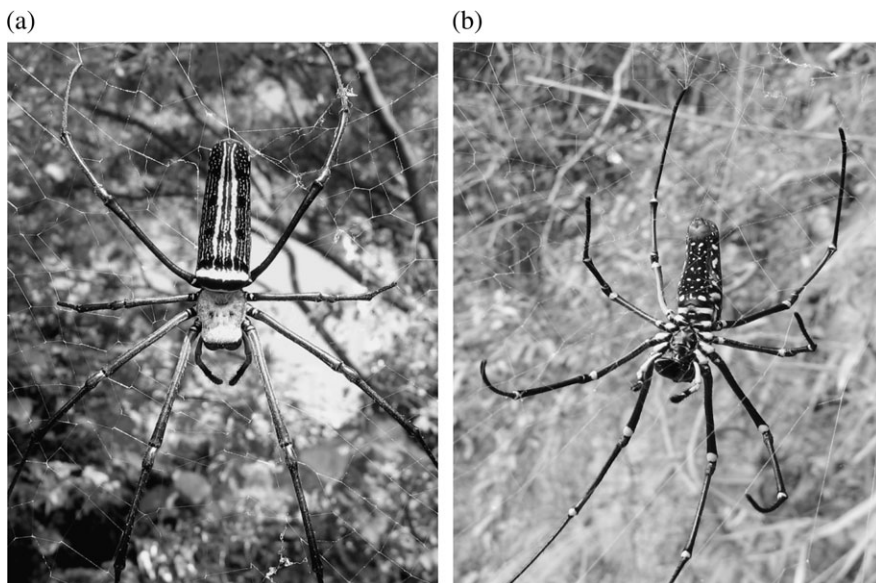


**Figure 1**
The dorsal (a) and ventral (b) views of an adult female giant wood spider *Nephila pilipes*.
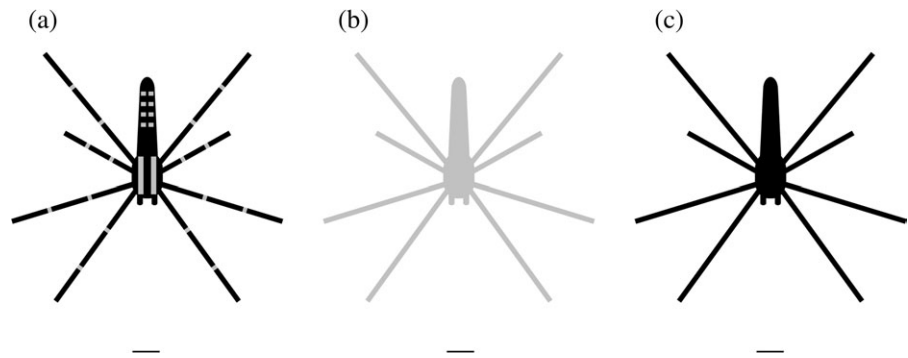
**Figure 2**
Coloration patterns of dummies used in the field manipulation. The basic coloration pattern mimicked that of the ventral side of the giant wood spider *Nephila pilipes*. (a) SS treatment, (b) YS treatment, and (c) DS treatment. Scale bar: 1 cm.

and spots were stuck on it by water-soluble glue (Transparent School Glue, En-Yuan Chemical Co., Tainen, Taiwan). The advantage of using spider dummies made of colored cardboards is that any observed phenomenon could be attributed to color signals alone. The potential confounding effects such as chemical cues that might be produced by live spiders (LS) can be well controlled. Moreover, if we greatly change the body coloration pattern of real spiders by using a large quantity of paint, the spiders might die or exhibit abnormal behaviors due to such chemicals. During the field experiments, the dummies used for each day of data collection were made in the previous day. Each dummy was used only once to avoid the chromatic property changes of cardboards due to sunlight or other environmental factors. From preliminary surveys, we found that most *N. pilipes* built webs on understory shrubs with their dorsal side facing dense foliage and ventral side facing the open space. Results of a previous field experiment conducted in the same study site monitoring *N. pilipes* prey catching with video cameras also showed that most intercepted insects came from the open space (Chuang CY, personal communication). Therefore, for all the dummies used in this study, their coloration patterns followed those of the ventrum of *N. pilipes* (Figure 1b).

**Study site and field manipulation**

The field experiment was conducted in Huoyan Mountain (24°06′42.2″N, 121°11′51.1″E), Sanyi Township, Miaoli County, Taiwan, in July and August of 2007. The study site was located on a trail winding through a secondary forest. The main tree species in the study site included the tung oil tree (*Aleurites fordii* and *Aleurites montana*) and Formosa acacia (*Acacia confusa*). During late spring and summer, *N. pilipes* were quite abundant in the study site (about 1–2 females every 10 m along the trail). We used video cameras to record the responses of prey and predator insects to dummies, and the recordings were made 8 h a day (from 0800 to 1600). Before the recording, we removed the spider from the web, randomly chose one type of dummy spider, and placed it on the hub. Dummies could be easily fixed on spider webs, and there was no need to use glue. Video cameras (Sony DCR-TRV series and Sony DCR-SR series) were placed 1–2 m away from the spider webs, depending on the vegetation nearby. Before video recording, the hub radius, web radius, and number of spirals and radii of the 4 cardinal directions of the webs were measured. These variables were used to estimate the capture area of the spider web by the formula given in Herberstein and Tso (2000). Dummy spiders used in the control group (the standard spider [SS] treatment) mimicked the ventral body coloration pattern of female *N. pilipes* (Figure 2a). We then manipulated the size of attractive signal by using dummies made entirely of yellow or black cardboards to test whether such treatments would affect insect attractiveness.

Dummy spiders created by cutting yellow cardboards into the shape of a spider were designated as yellow spider (YS) treatment (Figure 2b). Dummy spiders created by cutting black cardboards into the shape of a spider were designated as dark spider (DS) treatment (Figure 2c). *Nephila pilipes* webs with LS present (the LS treatment) or removed (the no spider [NS] treatment) were also monitored, and data from such treatment were used as a control to test for the effectiveness of SS dummies in attracting insects. During the field manipulation, around 15 spider webs were used each day. Webs used for monitoring were randomly selected from the *N. pilipes* population in the study site. Data used in the analyses were obtained from 585 h of video monitoring. Among them, 145 were from LS treatments ($n = 23$), 96 from NS treatments ($n = 18$), 108 from SS treatments ($n = 19$), 117 from YS treatments ($n = 19$), and 119 from DS treatments ($n = 18$).

**Quantifying attractiveness of dummies**

After the completion of field manipulations, while viewing the videotapes, we searched for events such as prey flying around the dummy spiders, contacting the dummy spiders, or being intercepted by the webs. The body length of prey attracted by dummy spiders (determined by referring to the size of dummies) and their taxonomic order were also recorded. For each individual dummy used, the number of such events was totaled and divided by the number of monitoring hours to calculate the prey attraction rate (number of prey attracted per hour). In addition to prey attraction events, while viewing videotapes, we also searched for predator attack events. A predator attack event was defined as a predator (mostly wasps) directly attacking or hovering around the dummies. For each individual

**Table 1**

**The results of Poisson regressions comparing the prey attraction rate of SS dummy (SS treatment) and webs without spider (NS treatment) while considering web areas[a,b]**

| Parameter | Group | DF | Estimate of $\beta$ | SE | $\chi^2$ | $P$ |
|---|---|---|---|---|---|---|
| Intercept | | 1 | −5.1974 | 0.2870 | 327.85 | <0.0001 |
| Web area | 150–510 | 1 | −1.5894 | 0.6408 | 6.15 | 0.0131 |
| Web area | 510–750 | 1 | −0.3881 | 0.4211 | 0.85 | 0.3567 |
| Web area | >750 | 0 | 0 | 0 | — | — |
| Treatment | NS | 1 | −1.5411 | 0.5442 | 8.02 | 0.0046 |
| Treatment | SS | 0 | 0 | 0 | — | — |

Web areas (cm²) were divided into 3 size categories to facilitate statistical analyses.

[a] The $\beta$ of the SS group and the web area >750 size category was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

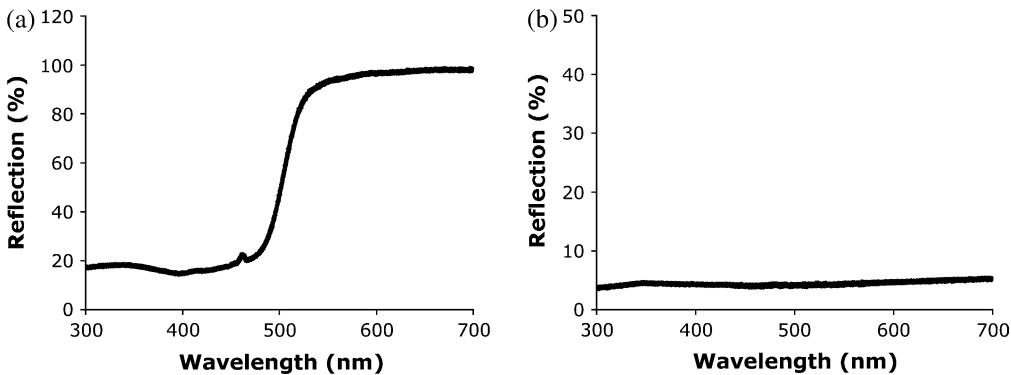[b] The ratio between probabilities of 2 certain events is $e^{\beta}$.

**Figure 3**
Reflectance spectra of yellow (a) and black (b) cardboards used for making dummies.

dummy spider used, the number of such events was totaled and divided by the number of monitoring hours to calculate predator attack rates (number of attacks per hour).

### Statistical analyses

All the data obtained from field manipulations were first tested for the normality assumption. If the data fitted the normal distribution, then parametric tests such as *t*-tests or 1-way analysis of variance (ANOVA) were used. If the data were corresponded with a Poisson distribution, then Poisson regressions were used (Tso et al. 2004). Before analyzing data by Poisson regression, in each replication, the web capture area variable was categorized into 3 size classes to facilitate the analyses (for range of each size class, see Tables 1 and 3). For those data that did not follow any distribution, nonparametric tests such as Kruskal–Wallis and Mann–Whitney $U$ tests were used. To determine whether the prey composition among treatments was similar, the prey compositions were classified by taxonomic orders and were analyzed by $\chi^2$ tests of homogeneity. All the aforementioned statistical tests were performed by SYSTAT 9.0 (Wilkinson et al. 1992).

### RESULTS

#### Chromatic properties of dummies

The reflectance spectra of yellow cardboards from various commercial sources varied considerably. The color contrast values of all 8 types of yellow cardboards measured when viewed against YS body parts were greater than 0.05. Therefore, we chose the one with a reflectance spectrum most similar to that of *N. pilipes* yellow body parts (Figure 3a) and exhibiting the smallest color contrast values (mean ± standard error [SE] = 0.134 ± 0.001 for chromatic and 0.453 ± 0.030 for achromatic contrast) to use as yellow parts of dummies. The chromatic color contrast of yellow cardboard when viewed

against the vegetation background was 0.152 ± 0.05, whereas the achromatic contrast was 0.338 ± 0.001. All black cardboards examined had similar reflectance spectrum patterns (Figure 3b), and we chose the one with the smallest color contrast value (mean ± SE = 0.054 ± 0.004 for chromatic and 0.126 ± 0.006 for achromatic contrast) when compared with the black body parts of *N. pilipes*. The chromatic color contrast of black cardboard when viewed against the vegetation background was 0.106 ± 0.002, whereas the achromatic contrast was 0.292 ± 0.006. The chromatic contrasts between yellow and black cardboard used for dummies (mean ± SE = 0.25 ± 0.004) were not significantly different from that between spider yellow and black body parts (mean ± SE = 0.19 ± 0.04; Tso et al. 2004; $t_{9.18} = 1.460$, $P = 0.177$), although the achromatic contrasts differed significantly (mean ± SE = 0.303 ± 0.054 for spiders and 0.631 ± 0.002 for cardboards, $t_{9.03} = 6.060$, $P = 0.0002$).

#### Prey's responses to various dummies

During the field experiments sometimes, there were heavy rains in the afternoon and the video monitoring had to terminate. Therefore, for some of the dummies, the overall recording time was shorter than 4 h, and such data were not included in the analyses. The capture area (cm$^2$) of webs used in various treatments did not differ significantly (ANOVA test, $F_{0.05,3} = 0.43$, $P = 0.7$). The prey attraction rate of webs with LS (LS treatment) was significantly higher than that of SS treatment (Mann–Whitney $U$ test, $U = 329.000$, $P = 0.005$, Figure 4a). However, results of Poisson regressions showed that dummies resembling the ventral coloration pattern of *N. pilipes* (SS treatment) attracted more prey insects than those without dummies (NS treatment; Table 1, Figure 4a). Such results indicated that the SS dummies were attractive to prey insects and the color signal alone was sufficient in luring prey. Altering the size of yellow spots significantly influenced
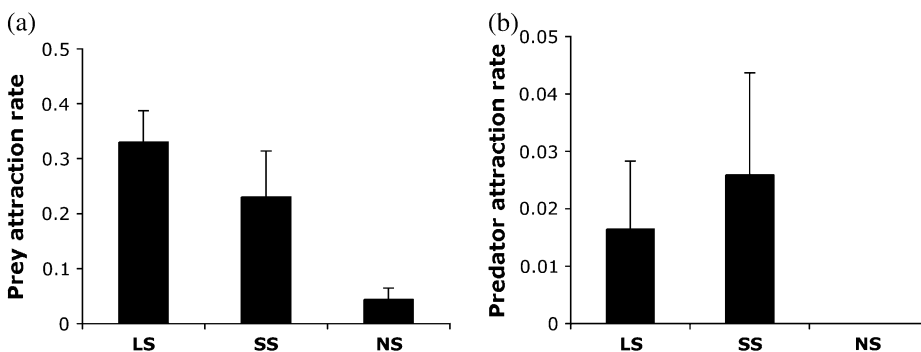


**Figure 4**
Mean (+SE) prey attraction rate (number of prey attracted/hour/dummy) (a) and predator attraction rate (number of predator attacks/hour/dummy) (b) of LS (the LS treatment), SS dummies (the SS treatment) and webs without spiders (the NS treatment) recorded in the field.

**Table 2**

**The results of Kruskal–Wallis (*K-W*) and Mann–Whitney *U* tests comparing the prey attraction rate (a) and predator attack rate (b) of YS (YS treatment), SS (SS treatment), and DS (DS treatment) dummies**

|     | Comparisons | *K-W/U* | *P* |
|-----|-------------|---------|-----|
| (a) | All | 16.823 | <0.001 |
|     | YS versus SS | 89.500 | 0.006 |
|     | YS versus DS | 56.500 | <0.001 |
|     | SS versus DS | 115.000 | 0.041 |
| (b) | All | 8.897 | 0.012 |
|     | YS versus SS | 114.000 | 0.015 |
|     | YS versus DS | 110.000 | 0.022 |
|     | SS versus DS | 172.000 | 0.955 |

the attractiveness of dummies to insect prey. Results of Kruskal–Wallis tests showed that prey attraction rates differed significantly between dummies made entirely of yellow paper (YS dummies), SS dummies, and those made entirely of black paper (DS dummies; Table 2a). YS dummies attracted significantly more prey insects than SS dummies, which in turn were significantly more attractive than DS dummies (Table 2a, Figure 5a). Such results indicated that the larger the size of the yellow signal, the more attractive the dummies. The prey insects attracted by dummies mostly consisted of insects of the orders Hymenoptera, Lepidoptera, Diptera, and Coleoptera. The results of pairwise $\chi^2$ tests of homogeneity showed that the prey compositions were not significantly different between these treatments (YS vs. DS: $\chi^2 = 0.879$, $P > 0.05$; SS vs. DS: $\chi^2_9 = 2.074$, $P > 0.05$), except those of YS and SS dummies ($\chi^2 = 8.548$, $P < 0.05$).

## Predators' responses to dummies

Webs without spiders or dummies (the NS treatment) received no predator attack at all, and the predator attraction rate of webs with LS (LS treatment) was similar to that of SS treatment (Table 3, Figure 4b). Altering the size of yellow signals of dummies also significantly altered the responses of predatory insects. Predators attracted by various dummies were all Hymenoptera insects such as wasps. Predator attraction rates (number of predators attracted per hour of monitoring) differed significantly between various types of dummies. Although dummies made entirely of yellow papers (YS dummies) were attractive to prey insects, they were also highly attractive to predatory insects (Table 2b, Figure 5b). The predator attraction rate of YS dummies was 6 times that of SS dummies. Although dummies made of black cardboards (DS dummies) were less attractive to prey, their predator attraction rates were similar to those of SS dummies (Table 2b, Figure 5b).

## DISCUSSION

Our manipulative study is the first to unambiguously show that a spiders' color signal alone is sufficient to lure prey in the natural condition and that the current body coloration pattern does not achieve the best luring performance. Many relevant studies used real spiders while evaluating spiders' visual attractiveness. However, whether or not spiders' olfactory, or other cues, were involved in attracting prey in these studies cannot be ruled out. In this study, although SS dummies were 2-dimensional and their chromatic properties did not perfectly match those of true spiders, their prey attraction rate was still significantly higher than that of webs containing NS. A comparison between prey attractiveness of SS dummies and real spiders showed that the latter attracted significantly more prey. One reason for such a difference was that the presence of spiders could help us detect small prey while estimating the prey attraction rate. While viewing the videotapes, the very small prey that we could not discriminate from pollen or debris can be confidently recognized because real spiders usually moved to attack them. However, while viewing the video recordings of SS dummies only relatively larger prey (body length > 3 mm) could be unambiguously identified. If we excluded prey smaller than 3 mm from the LS data set, then the prey attraction rates of SS and LS treatments were no longer significantly different (Tso IM, unpublished data). So, a higher probability of detecting smaller prey might be responsible for a higher prey attraction rate of LS treatment. Even though we potentially underestimated the prey attraction rate of dummies, the recorded attractiveness of YS dummies was still much higher than that recorded from SS dummies. One reason for the better attraction performance of YS dummies is that the intensity of a visual signal may affect the maximum distance at which such a signal could be perceived. Although multimodal signals are used in the interactions between angiosperms and pollinator insects, visual signals are most effective in long distance signaling (Schaefer et al. 2004). Many flowering plants exhibit showy petals or bracts to attract pollinator insects from a long distance (Proctor et al. 1996; Lunau 2000, 2001; Borges et al. 2003). Such long-range signaling is achieved by both the large size and spectral reflectance differences between petal/bract and green leaves (Borges et al. 2003). Accordingly, a much higher visibility and thus maximum distance of detection may be why YS dummies in this study attracted more insects than SS dummies. Previous studies showed that insects such as hymenopterans adopt achromatic vision by using green receptor signal alone when viewing an object from a long distance (i.e., with an subtending area between 5° and 15°). When hymenopterans view objects from a relatively short distance (i.e., with an subtending area greater than 15°) will they adopt chromatic vision by using green, blue, and UV receptor signals (Giurfa et al. 1997; Spaethe et al. 2001; Heiling et al. 2003). Because YS dummies contained large-sized yellow signals and
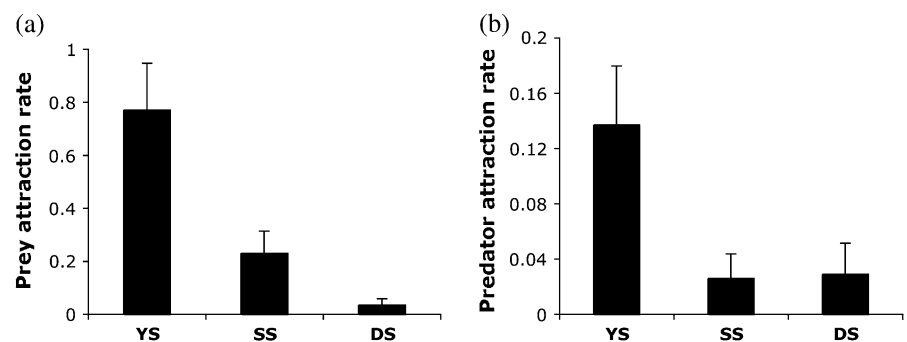
**Figure 5**
Mean (+SE) prey attraction rate (number of prey attracted/hour/dummy) (a) and predator attraction rate (number of predator attacks/hour/dummy) (b) of various treatments recorded in the field (YS treatment, SS treatment, and DS treatment).

**Table 3**

**The results of Poisson regressions comparing the predator attraction rate of SS dummies (SS treatment) and LS (LS treatment) while considering web area[a,b]**

| Parameter | Group | DF | Estimate of β | SE | $\chi^2$ | $P$ |
|---|---|---|---|---|---|---|
| Intercept | | 1 | −7.4901 | 0.9103 | 67.71 | <0.0001 |
| Web area | 150–540 | 1 | −26.3482 | 418170.3 | 0 | 0.9999 |
| Web area | 540–825 | 1 | −0.2803 | 1.0094 | 0.08 | 0.7813 |
| Web area | >825 | 0 | 0 | 0 | — | — |
| Treatment | LS | 1 | −0.6113 | 1.0094 | 0.37 | 0.5448 |
| Treatment | SS | 0 | 0 | 0 | — | — |

Web areas (cm$^2$) were divided into 3 size categories to facilitate statistical analyses. LS, live spider.

[a] The β of the SS group and the web area >825 size category was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

[b] The ratio between probabilities of 2 certain events is $e^{\beta}$.

thus had greater subtending area, they could be chromatically detected from a longer distance and consequently became more attractive.

Visual signals of various floral parts play important roles in the interactions between angiosperms and pollinator insects (Lunau 1995; Schaefer et al. 2004), and some orb spiders seem to exploit such interaction. In the field, yellow pigments are quite common in pollens of angiosperms (Lunau 1995). Lunau (2000) reviewed research about the color pattern of floral parts and concluded that yellow centers or yellow pollens were com-

mon attributes. Because pollens represent important resources for insects, the inner parts of many flowers resemble the color of pollens, and pollinators such as bumblebees exhibit an innate preference for such visual cue (Heuschen et al. 2005). In addition, there was empirical evidence that yellow anthers played an important role in attracting and guiding the landing of pollinator insects on flowers (Ushimaru et al. 2007). On the other hand, in the field of applied entomology, many researchers evaluated the effectiveness of different chromatic cues to trap pest insects. Results of many such studies showed that the yellow sticky papers are effective visual lures to dipteran and hymenopteran insects (Vargas et al. 1991; Cornelius et al. 1999; Alyokhin et al. 2000; Wu et al. 2007). Results from both empirical and applied studies demonstrate that a yellow cue plays an important role in the signal communication between pollinator insects and flowers. Coincidently, many taxa of orb spiders exhibit various forms of yellow markings on their bodies. Such trait can be found in numerous orb spider genera in Asia (Yaginuma 1986), and its role as a visual lure had been empirically demonstrated in 3 families (Araneidae, Tetragnathidae, and Nephilidae). We suggest that the effectiveness of yellow signals in luring pollinator prey might be one major reason for the convergent possession of such a trait in spiders of divergent phylogenetic relationships.

For the first time, we show that the current bright-and-dark coloration pattern of orb spiders is not a best form of visual lure but can reduce the cost of predator attacks. In previous studies, researchers manipulated spider color signals by either removing the spiders or reducing the spiders' conspicuousness. However, these experimental designs could only test for the benefit, and it was not able to empirically demonstrate whether spider colorations exhibit any cost. In this present study, however, we used a novel approach by using dummies to quantify the
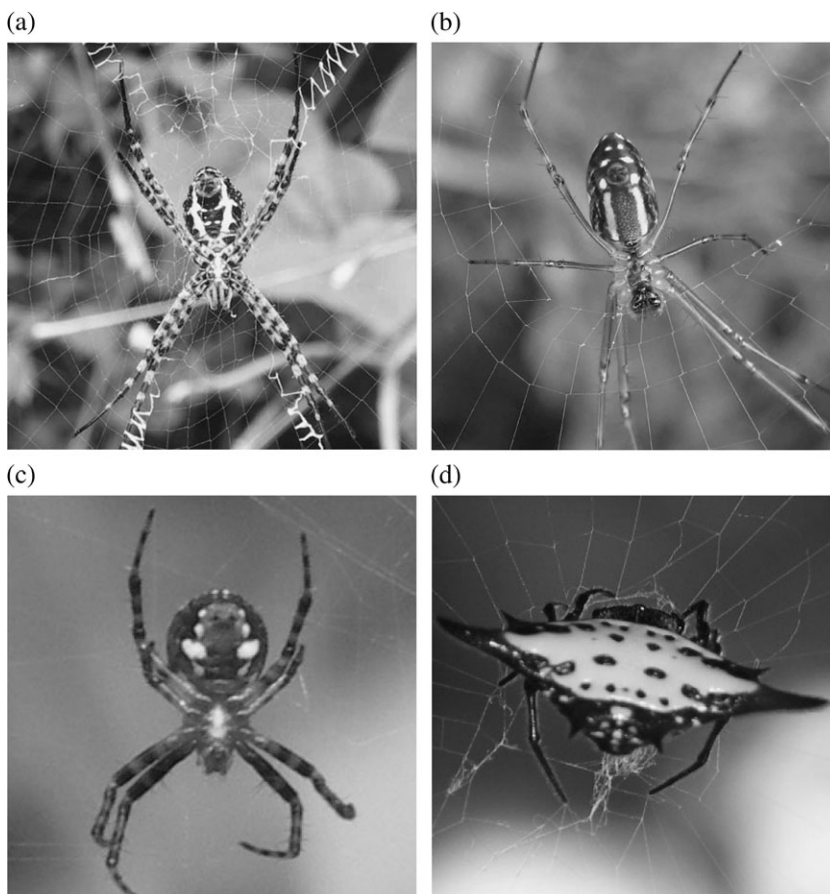


**Figure 6**
Ventral (a–c) or dorsal views (d) of several conspicuously-colored orb web spiders in Taiwan: (a) *Argiope aemula*, (b) *Leucauge magnifica*, (c) *Gea spinipes*, and (d) *Gasteracantha sauteri*.

consequences of enhancing the intensity of attractive signals. It is by such a design that we can quantify the cost associated with the conspicuous color signals and uncover the constraints on this trait. In addition to *N. pilipes*, many orb spiders from a diverse array of families also exhibit similar body coloration patterns (Figure 6). We hypothesize that the contrasting conspicuous and inconspicuous parts may generate a contour-breaking disruptive coloration pattern (Cuthill et al. 2005) to reduce detection by predators (Zschokke 2002; Hoese et al. 2006; Václav and Prokop 2006) and lower the cost of this morphology-associated foraging trait. Such commonly seen coloration pattern might reflect orb spiders' adaptation in response to high predation pressure from predators such as wasps. Blackledge et al. (2003) proposed that the presence of parasitoid hymenopterans was a major driving force for the high diversity of Orbiculariae lineages building 3-dimensional webs because such adaptation could effectively protect the spiders. It was possible that those lineages of Orbiculariae retaining the ancestral 2 dimensional orb webs evolved a broken body coloration pattern to simultaneously attract prey and reduce predator detection. It will be interesting to conduct field experiments to test whether broken coloration pattern can break the outline and consequently camouflage the spiders. Comparative studies should also be carried out to evaluate whether predation pressures from hymenopteran predators were one driving force of the broken coloration pattern in Orbiculariae.

Trading off the benefits and costs linked to conspicuous prey-luring signals seems to exert a great pressure on foraging-associated behavioral and morphological traits of numerous orb spiders. In certain taxa of orb-weaving spiders, in addition to bright body parts, they also construct conspicuous silk bands called decorations on their webs (Eberhard 1990). Functions of web decorations made entirely of silk has received much study and numerous hypotheses have been proposed (Herberstein et al. 2000; Bruce 2006). Recently, results of numerous empirical studies show that one of the functions of silk decorations is to visually lure prey by reflecting certain chromatic properties (Herberstein et al. 2000; Bruce 2006; Cheng and Tso 2007). However, a very controversial attribute of *Argiope* spiders' web decorations is this structure's inconsistent occurrence and shape polymorphism on the individual level (Nentwig and Rogg 1988; Starks 2002). If web decorations function as signals to lure prey, why do *Argiope* spiders build them so inconsistently and why is their form so polymorphic? Cheng and Tso (2007) demonstrate that luring prey by decorating webs comes with a cost of increased predation risk by wasps, and therefore, there seems to be a selection pressure preventing the spiders from consistently decorating their webs. So the inconsistent building and shape polymorphism of decorations can be regarded as a behavioral plasticity to trade off opposing selection pressures. However, for spiders relying on conspicuous body coloration to lure prey, even though they do not have such behavioral plasticity as do decoration builders they also face the same dilemma of attraction/detection. Results of this present study demonstrate how spiders relying on fixed body coloration to forage respond to such dilemma. Costs and benefits associated with the luring signal might have generated a coloration pattern not that effective in attracting prey but could reduce predation cost. Therefore, it seems that these 2 foraging traits (one behavioral and the other morphological) were shaped by similar selection pressures and both exhibited properties reflecting trade-offs of costs and benefits associated with conspicuous visual lures.

Our results demonstrate that a receiver exploiter's signal design reflects a compromise between efficaciously increasing foraging benefit and strategically reducing predation cost. Behavioral ecologists propose that the evolution of animal communication signals exhibits both efficiency and strategy aspects (Endler 1993); our results showed that properties of orb spider body coloration seemed to be shaped by these 2 aspects. From the efficiency aspects, the spider's body coloration possesses chromatic properties similar to those of yellow pollens, so they can visually attract insects. From the strategic aspect, high predation pressures might have prevented orb spiders from exhibiting a large area of conspicuous colorations. The luring signals of conspicuously colored orb spiders seem to be shaped by the color vision of both insect prey and predators. Although selection pressures in the efficiency context might act to maximize the bright part of spider coloration, pressures in the strategy context might act toward the opposite direction. Here we show that opposing selection pressures not only affect sexually selective morphological traits but also shape the properties of foraging-associated morphological traits.

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