

Insect form vision as one potential shaping force of spider web decoration design

R.-C. Cheng¹, E.-C. Yang², C.-P. Lin^{1,3}, M. E. Herberstein⁴ and I.-M. Tso^{1,3,*}

¹Department of Life Science, Tunghai University, Taichung, Taiwan, ²Department of Entomology, National Taiwan University, Taipei, Taiwan, ³Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung, Taiwan and ⁴Department of Biological Sciences, Macquarie University, NSW, Australia

*Author for correspondence (spider@thu.edu.tw)

Accepted 8 November 2009

SUMMARY

Properties of prey sensory systems are important factors shaping the design of signals generated by organisms exploiting them. In this study we assessed how prey sensory preference affected the exploiter signal design by investigating the evolutionary relationship and relative attractiveness of linear and cruciate form web decorations built by *Argiope* spiders. Because insects have an innate preference for bilaterally symmetrical patterns, we hypothesized that cruciate form decorations were evolved from linear form due to their higher visual attractiveness to insects. We first reconstructed a molecular phylogeny of the Asian members of the genus *Argiope* using mitochondrial markers to infer the evolutionary relationship of two decoration forms. Results of ancestral character state reconstruction showed that the linear form was ancestral and the cruciate form derived. To evaluate the luring effectiveness of two decoration forms, we performed field experiments in which the number and orientation of decoration bands were manipulated. Decoration bands arranged in a cruciate form were significantly more attractive to insects than those arranged in a linear form, no matter whether they were composed of silks or dummies. Moreover, dummy decoration bands arranged in a cruciate form attracted significantly more insects than those arranged in a vertical/horizontal form. Such results suggest that pollinator insects' innate preference for certain bilateral or radial symmetrical patterns might be one of the driving forces shaping the arrangement pattern of spider web decorations.

Key words: web decoration, stabilimentum, *Argiope*, visual ecology, Araneidae, orb web.

INTRODUCTION

Studies investigating the evolution of signals are typically concerned with intraspecific communication, such as sexual signals. For example, the signals used in courtship displays are often examined with respect to how habitat physical characteristics (Fleishman, 1992; Marchetti, 1993; Forrest, 1994; Catchpole and Slater, 1995) or receiver preference (Proctor, 1992; Basolo, 1995; Rodd et al., 2002; Witte and Sawka, 2003) affect signal efficacy. Other studies investigate the strategic aspects of signal evolution by examining the constraints on signal intensity or signal honesty (Panhuis and Wikinson, 1999; Grether, 2000; Quillfeldt, 2002; Brandt, 2003; Hunt et al., 2004). While various modes of conspecific selection pressures could drive the evolution of communication signals, selection pressures from other species maybe equally as important. For example, several modalities of signals involved in aposematism or camouflage of certain organisms are known to be significantly shaped by the prey's major predators (Ruxton et al., 2004).

In many communication systems, the signalers and the intended receivers are not the only participants. Frequently there are unintended participants such as various forms of exploiters (Endler, 1993). For example, exploiters may follow a signal to locate the emitter or provide false signals to elicit a stereotypical response from receivers that is favorable to the exploiters (Johnstone, 1997). The latter has been termed 'code breaking' (Alcock, 2005) and has been investigated in systems such as brood parasitism (Davis et al., 1998; Kilner et al., 1999), prey courtship signal mimicking (Lloyd, 1975; Haynes et al., 2002) and prey recognition signal exploitation (Thomas et al., 2002). Currently, most relevant studies on these heterospecific sensory exploitations focus on describing the contemporary molecular, physiological or behavioral mechanisms

involved. Comparative studies using phylogenetic approaches to investigate how such signals might have evolved are still rare. Furthermore, characteristics of the exploited receiver's sensory system are likely to shape the evolution of code-breaking signals. However, empirical evidence of how prey sensory systems drive the design and evolution of exploiter signals is still rare.

In this study, we assess how prey sensory preference shape the design of luring signals generated by an exploiter by studying the web decorations built by orb-web spiders of the genus *Argiope*. Decorations are silk structures on webs built by at least 22 genera of orb-web spiders (Herberstein et al., 2000). Most members of the genera *Nephila*, *Cyclosa*, *Uloborus* and *Gea* build a linear form decoration on their webs (Fig. 1A,B). However, species of the genus *Argiope* decorate their webs with either linear or cruciate forms of decorations (Fig. 1C,D). Several hypotheses about the functions of *Argiope* decorations have been proposed (for reviews, see Herberstein et al., 2000; Bruce, 2006; Théry and Casas, 2009) but many researchers consider spider web decorations as a visual signal that influences the interactions between spiders and prey. One of the proposed functions of decorations is to visually attract prey thereby enhancing the spiders' foraging success. The prey-luring function of decorations has been demonstrated in several spider genera [*Cyclosa* (Tso, 1998a); *Octonoba* (Watanabe, 1999); *Araneus* (Bruce et al., 2004)], especially in those *Argiope* species building either discoid [early juveniles (Li et al., 2004; Li, 2005)], linear (Tso, 1996; Tso, 1998b) or cruciate form decorations (Craig and Bernard, 1990; Craig, 1991; Herberstein, 2000; Bruce et al., 2001; Cheng and Tso, 2007). Currently there are around 80 species documented in the genus *Argiope* (Platnick, 2009). For a number of *Argiope* species information regarding the decoration form was not available. However, among those with decoration form

confirmed, about 60% of them build cruciate form during adult stage while the others build linear form (Table 1). Because both forms of web decorations have been empirically demonstrated to be an effective visual lure to prey, we wonder what the evolutionary relationship and relative performance of these two types of signals in this spider genus are. Because linear form decorations are found in other spider genera and the cruciate form is only present in *Argiope*, it is likely that the cruciate form decoration is a derived trait and evolved from the linear form. But why did such evolutionary change occur in *Argiope*?

Recent neuroethological studies on insect form vision suggest that the visual effect of linear and cruciate decorations on the behavior of prey might vary. Previous studies have shown that honeybees can be trained by reward to discriminate between a pattern with vertical stripes and a pattern with horizontal stripes. Furthermore, the bees discriminate among the predominant orientation difference between different pairs of patterns that they have not previously encountered (Wehner, 1971; van Hateren et al., 1990). Recent behavioral studies by Horridge clearly indicated that honeybees did not 'see' the image but the cues of an object in front of the eyes were detected by filters, a neuron or group of neurons of the bee visual system (for a review, see Horridge, 2006). Srinivasan et al. showed that honeybees could distinguish different orientation patterns, and hypothesized that honeybees might have at least three different orientation-sensitive channels each with a preferred orientation (Srinivasan et al., 1994). This idea was supported by electrophysiological studies on hymenopteran and

dipteran insects, which reported three different types of orientation-sensitive cells each exhibiting maximum sensitivities to different orientations (Yang and Maddess, 1997; Okamura and Strausfeld, 2007). Results of these studies suggest that the linear form decoration may match the orientation-sensitive channel that is tuned to vertical orientation whereas the cruciate form decoration may elicit strong activity in the other two channels that are tuned to diagonal orientations. Therefore, cruciate decorations might be able to elicit stronger activity in the orientation-sensitive channels of insects and consequently achieve a more effective prey luring, compared with the vertically orientated linear decorations.

In this study, we tested the hypothesis that insect form vision was a potential shaping force of spider web decoration design by molecular phylogenetic and field experimental approaches. The phylogeny of mainly Asian *Argiope* species building linear or cruciate form decorations was reconstructed using two mitochondrial markers to infer the evolutionary relationship of the two signal forms. The relative visual luring effect of two decoration forms was evaluated in the field by using both real and dummy decorations with number and orientation of bands manipulated. We predict that the cruciate form decoration is a derived trait and is visually more attractive than the linear ones.

MATERIALS AND METHODS

Evolutionary relationship of *Argiope* signal forms

The genus *Argiope* is globally distributed, and around 80 *Argiope* species are currently documented in the catalogue of Platnick

Table 1. Decoration type of *Argiope* species with decoration information confirmed

Species	Distribution	Decoration type	Reference
<i>Argiope aemula</i>	India to Philippines	Cruciate	Bruce et al., 2005
<i>Argiope aetherea</i>	China to Australia	Cruciate	Bruce et al., 2005
<i>Argiope aetheroides</i>	China, Japan	Cruciate	Personal observation
<i>Argiope amoena</i>	China, Korea, Taiwan, Japan	Cruciate	Personal observation
<i>Argiope anasuja</i>	Pakistan to Maldives	Cruciate	Personal observation
<i>Argiope appensa</i>	Hawaii, Taiwan to New Guinea	Cruciate	Bruce et al., 2005
<i>Argiope argentata</i>	USA to Argentina	Cruciate	Bruce et al., 2005
<i>Argiope aurantia</i>	Canada to Costa Rica	Linear	Bruce et al., 2005
<i>Argiope australis</i>	Central, East, Southern Africa	Linear	Bruce, 2005
<i>Argiope boesenbergi</i>	China, Korea, Japan	Linear	Bruce, 2005
<i>Argiope bruennichi</i>	Palaearctic	Linear	Bruce et al., 2005
<i>Argiope catenulata</i>	India to Philippines, New Guinea	Tri-radiate	Herberstein, 2000
<i>Argiope doboensis</i>	Indonesia, New Guinea	Cruciate	Herberstein, 2000
<i>Argiope flavipalpis</i>	Africa, Yemen	Cruciate	Herberstein, 2000
<i>Argiope florida</i>	USA	Cruciate	Herberstein, 2000
<i>Argiope keyserlingi</i>	Queensland, New South Wales	Cruciate	Bruce et al., 2005
<i>Argiope lobata</i>	Old World	Linear	Bruce et al., 2005
<i>Argiope luzona</i>	Philippines	Cruciate	Personal observation
<i>Argiope mangal</i>	Singapore	Linear	Bruce, 2005
<i>Argiope mascordi</i>	Queensland	Discoid	Bruce, 2005
<i>Argiope minuta</i>	Bangladesh, East Asia	Cruciate	Herberstein, 2000
<i>Argiope ocula</i>	China, Taiwan, Japan	Linear	Personal observation
<i>Argiope ocyaloides</i>	Queensland	Linear	Bruce, 2005
<i>Argiope perforata</i>	China	Cruciate	Personal observation
<i>Argiope picta</i>	Moluccas to Australia	Cruciate	Bruce et al., 2005
<i>Argiope protensa</i>	New Guinea, Australia	Linear	Bruce, 2005
<i>Argiope pulchella</i>	India to China and Java	Linear	Herberstein, 2000
<i>Argiope pulchelloides</i>	China	Cruciate	Personal observation
<i>Argiope radon</i>	Northern Australia	Linear	Herberstein, 2000
<i>Argiope reinwardti</i>	Malaysia to New Guinea	Cruciate	Herberstein, 2000
<i>Argiope savignyi</i>	Mexico to Bolivia	Cruciate	Herberstein, 2000
<i>Argiope sector</i>	North Africa, Middle East	Linear	Herberstein, 2000
<i>Argiope trifasciata</i>	Cosmopolitan (except Europe)	Linear	Bruce et al., 2005
<i>Argiope versicolor</i>	China to Java	Cruciate	Bruce et al., 2005

All personal observations made by R.-C.C.

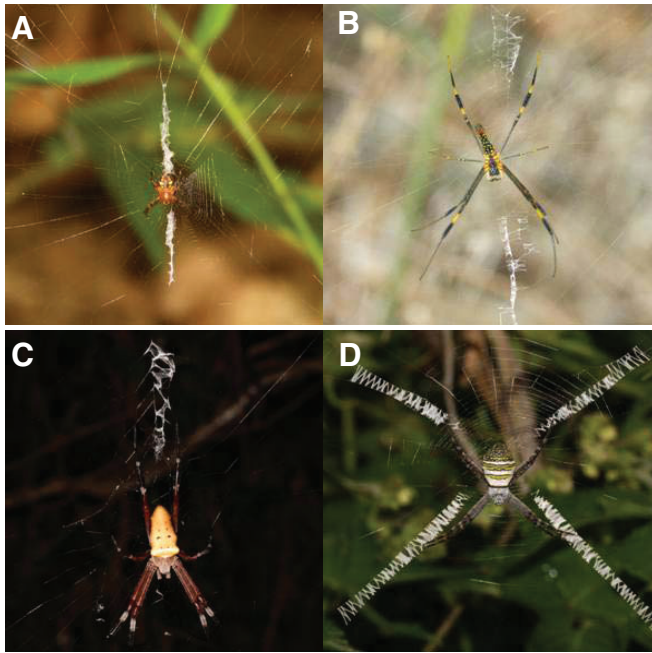


Fig. 1. Linear and cruciate silk decorations built by various genera of orb-web spiders. (A) *Gea spinies*, (B) *Nephila pilipes*, (C) *Argiope ocula*, (D) *Argiope aemula*. (A, C and D: Araneidae; B: Nephilidae.)

(Platnick, 2009). In addition to three globally distributed species, six North and South American and 10 African species, most *Argiope* species are distributed in Asian or the west Pacific regions. In this study, we investigated the evolutionary relationship of decoration forms by reconstructing a preliminary molecular phylogeny of mostly Asian *Argiope* species. A total of 23 *Argiope* species were used, including one from America, three from Africa, 17 from Asia and two worldwide species (Table 2). The nocturnal

orb-web spider genus *Neoscona*, which does not build decorations, was designated the outgroup. All specimens were preserved in 95% ethanol, and genomic DNA was extracted from leg muscle using a DNeasy tissue kit (Qiagen, Taipei, Taiwan).

Mitochondrial cytochrome oxidase I (*COI*) and cytochrome oxidase II (*COII*) were used for phylogenetic analyses. Partial sequences of *COI* gene were amplified using the primer combination of *COI*-Forward26-48 (5'-GTG TCT TCW ATA GTW GAA ATR GG-3') and *COI*-Reverse570-545 (5'-ACA GAA AAY ATA TGA TGR GCY CAY AC-3') [modified from Su et al. (Su et al., 2007)]. Partial sequences of *COII* were amplified using the primer combination of *COII*-2635 (5'-TTG CCA ACG TGA GGA TCA-3') and *COII*-3131 (5'-CCT AAA GAG GGA ATA GTT CA-3'). The PCR conditions were as follows: initial denaturation for 3 min at 95°C, followed by 35 cycles of 60 s at 9°C, 90 s at 5°C (*COI*) or 4°C (*COII*), 60 s at 7°C, and then a final extension of 10 min at 72°C. The PCR products were assayed on a 1.2% agarose gel and were visualized under a UV light after ethidium bromide staining. The PCR products were purified with a Gel/PCR DNA fragment extraction kit (Geneaid, Taipei, Taiwan) and were sequenced with an automatic sequencer ABI 3730 (Applied Biosystems, Foster City, CA, USA).

The DNA sequences and their chromatograms were first manually checked for correct reading. Multiple alignments were subsequently performed by BioEdit version 7.0.4.1 (Hall, 1999), and sequences were converted to the FASTA format. We conducted maximum parsimony (MP) analyses in PAUP* [version 4 (Swofford, 2001)] and Bayesian estimation in MrBayes [v3.0b4 (Huelsenbeck and Ronquist, 2001)]. The nucleotide substitution models, the parameters associated with base composition and the numbers of substitutional classes were evaluated using the MODELTEST [version 3.06, Posada and Crandall (Posada and Crandall, 1998)]. Equal-weighted parsimony analyses were first performed with a heuristic search, the starting trees were obtained by random sequence addition and the trees searched using tree-bisection-reconnection (TBR) branch swapping, with gaps treated as missing data. Only minimal-length

Table 2. Spider taxa used in the molecular phylogenetic analyses with distribution range, web decoration form and collection localities specified

Taxa	Distribution	Decoration	Collection locality
<i>Argiope aemula</i> (Walckenaer 1842)	East/Southeast Asia	Cruciate	Taiwan
<i>A. sp1</i>	Philippines	Cruciate	Philippines
<i>Argiope ocula</i> (Fox 1938)	East Asia	Linear	Taiwan
<i>Argiope anajusa</i> (Thorell 1887)	Southeast Asia	Cruciate	Philippines
<i>Argiope aetheroides</i> (Yin et al., 1989)	East Asia	Cruciate	India
<i>Argiope pulchelloides</i> (Yin et al., 1989)	East Asia	Cruciate	China
<i>Argiope pulchella</i> (Thorell 1881)	Southeast Asia	Cruciate	Sumatra
<i>Argiope macrochoera</i> (Thorell 1891)	East Asia	Cruciate	China
<i>Argiope versicolor</i> (Dolleschall 1859)	East/Southeast Asia	Cruciate	Singapore
<i>Argiope appensa</i> (Walckenaer 1842)	Southeast Asia	Cruciate	Sumatra
<i>A. sp2</i>	Philippines	Cruciate	Philippines
<i>Argiope minuta</i> (Karsch 1879)	East Asia	Cruciate	China
<i>Argiope perforata</i> (L. Koch 1878)	East Asia	Cruciate	Taiwan
<i>Argiope mangal</i> (Koh 1991)	Southeast Asia	Linear	Singapore
<i>Argiope amoena</i> (L. Koch 1878)	East Asia	Cruciate	Philippines
<i>Argiope luzona</i> (Walckenaer 1842)	Southeast Asia	Cruciate	Philippines
<i>Argiope aetherea</i> (Walckenaer 1842)	East/Southeast Asia	Cruciate	Taiwan
<i>Argiope australis</i> (Walckenaer 1805)	Africa	Linear	Africa
<i>Argiope flavipalpis</i> (Lucas 1858)	Africa	Cruciate	Africa
<i>Argiope levii</i> (Björn 1997)	Africa	Linear	Africa
<i>Argiope bruennichi</i> (Scopoli 1772)	Eurasia	Linear	Japan
<i>Argiope aurantia</i> (Lucas 1833)	North America	Linear	USA
<i>Argiope trifasciata</i> (Forskål 1775)	Eurasia, Africa, America	Linear	Africa
<i>Neoscona punctigera</i> (Dolleschall 1857)	East Asia	No decoration	Taiwan

trees were saved in each iteration and zero-length branches were collapsed. The consensus tree was constructed using a 50% major rule. In MP analyses, we used 1000 bootstrap replications (Felsenstein, 1985). Bayesian analyses were performed using the model selected by MODELTEST. We ran four Markov chains simultaneously with random starting trees, and the MCMC process was run for 1,500,000 generations, with a sampling frequency of 100 and a burn-in of 1000 generations.

The parsimony reconstruction of ancestral character states was performed using MacClade version 4.06 (Maddison and Maddison, 2003). Bayesian methods were also applied to estimate the probable ancestral states on the phylogeny using BayesMultiState in BayesTraits version 1.0 (Pagel and Meade, 2006). Maximum likelihood tree topologies with branch lengths from the Bayesian phylogenetic analyses were used for the analysis to account for phylogenetic uncertainty. We used a uniform prior on the models, and an exponential distributed (0, 10) reverse jump hyperprior for rate coefficients. The rate deviation was set as 10. The Reverse Jump Markov chain Monte Carlo (RJ-MCMC) was run for 5×10^6 iterations with a 50,000 burn in. The Bayes Factor test was used to test whether there was support for one state over the other by constraining the node into one state and calculating the difference of harmonic means between alternative models.

Evaluating attractiveness of signal forms using real decorations

To assess whether different forms of decorations varied in their attractiveness to insects, we conducted a field manipulative study by using naturally produced webs mounted on wooden rings. This field study was conducted in 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. *radiata* and giant false sensitive plant *Mimosa diplotricha*. Female oval St Andrew's cross spiders, *Argiope aemula* Walckenaer 1841 (Araneae: Araneidae) (Fig. 1D) were used in this study. *Argiope aemula* are widely distributed in grasslands or forest edge understory vegetation in tropical and subtropical Asia and build vertical orb webs (Yin et al., 1997).

Female *A. aemula* were first collected from the study site in LHCRC and kept in an empty laboratory at Tunghai University, Taichung, Taiwan, where individuals were allowed to roam freely to build webs. They were given two mealworms or one cricket every two or three days. The photoperiod was controlled as 12h:12h light:dark. Circular frames (made of 2mm thick wood) with a diameter of 30 cm were used to collect decorated webs. We applied glue on one side of the wooden ring and gently pressed the ring against the webs with decorations positioned in the center. We then removed silk around the margin of the ring using a stick of burning incense. The web ring was mounted with another wooden ring of the same size to enhance the structural stability of the web. A total of 56 webs with cruciate form silk bands were collected from about 20 female spiders. In half of the cruciate form decorated webs, we used a stick of burning incense to remove decoration bands (without breaking the web radii) in a way that two diagonally positioned decoration bands were left. In the field experiment these linear form web rings were turned into a vertical position. To control for the effects of the removal treatment we also burned two holes on cruciate form webs without removing any decoration bands. Because the visibility of webs has been known to affect the prey interception rate of webs (Craig, 1986; Craig and Freeman, 1991), we quantified

web visibility by measuring the number of radial silk threads within each web ring.

The four-day field monitoring (10 to 13 September 2006) was conducted in a forest edge meadow in LHCRC. In the study site we used bamboo sticks and strings to establish seven web stations and the distance between each of them was about 8 m. In each web station, a linear and a cruciate form web ring were placed side by side, separated by 10 cm. Each day in each web station two fresh web rings were used, and we swapped the left or right position of linear and cruciate decorations daily. The distance between the centers of the web rings to the ground was about 60 cm, which was similar to the web height of *A. aemula* in the study site (R.-C.C., unpublished data). During the study each web station was monitored by two Sony TRV 118 Hi-8 or HDD video cameras, Tokyo, Japan (one for each web ring) from 07:00h to 15:00h (a total of 14 video cameras used each day). The video cameras were placed about 1 m away from the web rings. We adjusted the focus of the video cameras to allow the whole web ring 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 any disturbances generated by researchers could be reduced to minimum. A total of 56 web rings (28 cruciate and 28 linear form) were monitored from these seven web stations (7 stations $\times$ 2 webs $\times$ 4 days).

After the field experiments, while viewing the videotapes in the laboratory, we recorded the number and taxonomic orders of intercepted prey. The exact timing of each prey interception event was specified to avoid double counting. The prey interception rate (designated as the mean number of insects intercepted by a web ring per hour of monitoring) did not meet the normality assumption (Lilliefors test, $P < 0.05$). Therefore, we used a Wilcoxon signed-rank test to perform pairwise comparisons on prey interception rates of 28 pairs of web rings. By using pairwise statistical tests to compare prey interception rates of web rings placed side-by-side, the effects of spatial and temporal insect abundance variations was controlled. A paired *t*-test was used to compare the number of web radii between web rings to see whether web silk densities differed between two treatments.

Evaluating attractiveness of signal forms using dummy decorations

One potential problem of using real decorations to evaluate attractiveness of two signal forms is that the quantity of silk could have varied between treatments. Experimental webs generated by removing decoration bands tended to have less silk and thus potentially had lower signal intensity. To unambiguously test the effect of orientation alone, the quantity of silk should be the same between two decoration forms. Because under natural conditions it was extremely difficult to obtain linear and cruciate silk decorations containing similar amount of silks, we decided to use realistic dummies made of cardboards. The advantage of using dummy decorations is that we can easily manipulate their orientation pattern and band number while controlling the overall quantity of material used. In this part of our study, the insect attractiveness of four cruciate dummy bands (each 4 cm in length and 0.5 cm in width) and that of two linear bands (each 8 cm in length and 0.5 cm in width) was compared. We first color matched the cardboard used for dummy decorations with real silk decorations by measuring the color reflectance of both (S2000, Ocean Optics, Inc., Dunedin, FL, USA, with a 450 W, Xenon arc lamp). We then calculated the chromatic color contrast following established methods [(Chittka, 1992; Chittka, 1996; Chittka, 2001) with illumination and vegetation reflectance spectra from Tso et al. (Tso et al., 2004)]. The methods were originally

developed for honeybees, upon which intensive physiological studies had been carried out (Briscoe and Chittka, 2001). The cardboard paper used had chromatic color contrast values lower than 0.05 when compared with the silk decorations of *A. aemula*. At such low levels of contrast, insect prey such as hymenopterans are unlikely to be able to detect a color difference (Théry and Casas, 2002).

The field experiment was conducted in March 2009 in LHCRC. Eighteen pairs of wooden poles (90 cm in length) were set up, and each pair was separated by at least 5 m. In each pair the distance between poles was 60 cm and was connected by 10 fine green strings (diameter 0.2 mm, spacing between them 15 mm) onto which dummy decorations were attached using water-soluble glue (Transparent School Glue, En-Yuan Chemical Co., Kaohsiung, Taiwan). The visibility of these green strings to honeybees against the vegetation background was quantified by measuring reflectance spectra and calculating color contrasts. The distance between the dummy decorations and the ground was about 60 cm. On each monitoring day in nine of the 18 pairs stick-string sets we placed four 4×0.5 cm dummy decoration bands arranged in a cruciate form. In the other nine pairs we placed two 8×0.5 cm bands and arranged them in a vertical linear form. On the next monitoring day the arrangement pattern of bands was swapped. The dummies used in any given monitoring day were made the previous day and each dummy was used only once to avoid the chromatic property changes of cardboards due to sunlight or other environmental factors. Each decoration form was monitored by a Sony TRV 118 Hi-8 or HDD video cameras from 08:00 h to 15:00 h (a total of 18 cameras used each day). The field experiment was conducted for three days (11 to 13 March 2009), and a total of 54 decoration sets (27 cruciate and 27 linear forms) were monitored. After the field experiments, while viewing the videotapes in the laboratory, we recorded the number and taxonomic orders of prey attracted to the dummy decorations. The prey attraction rate followed a Poisson distribution (Pearson chi-square goodness-of-fit test, $\chi^2_{0.05,1}=1.4405$, $P=0.491$). Therefore, a Poisson regression was used to compare the prey attraction rates (number of prey attracted per hour of observation) between two decoration forms while considering the day effect to

control for the temporal variation of insect abundance. A χ^2 test of homogeneity was used to compare taxonomic compositions of prey attracted by the two decoration forms.

Evaluating the effect of decoration band orientation

If the cruciate-arrangement pattern of decoration bands functions to elicit responses of diagonal orientation-sensitive channels of insects, then changing the orientation of decoration bands should reduce their attractiveness to insects. The main problem of comparing linear and cruciate decorations is that even though they have same quantity of silk, the former contains a maximum of two bands while the latter can contain up to four bands. In this part of the study, we evaluated the effect of changing band orientation on insect attractiveness while controlling for the number of bands. Again dummy decorations made of cardboard (4 cm in length and 0.5 cm in width) were used because we could easily manipulate their orientation patterns and number. We compared the insect attractiveness of four dummy bands arranged in a typical cruciate pattern (designated as cruciate form) and those arranged in a form of two vertical plus two horizontal bands (designated as vertical/horizontal form). The field experiment was conducted between 11 and 13 September 2008 in LHCRC. The experimental settings, field monitoring and data retrieval followed those described in the previous experiment comparing attractiveness of cruciate and linear dummy decorations. From three days of field experiment a total of 37 dummy decoration sets (19 cruciate and 18 vertical/horizontal forms) were monitored. The prey attraction rate of this experiment was nearly congruent with a Poisson distribution (Pearson chi-square goodness-of-fit test, $\chi^2_{0.05,1}=6.2976$, $P=0.049$). Therefore, the analyses of prey attraction rate and prey composition followed the procedures described in the previous experiment.

RESULTS

Evolutionary relationship of two *Argiope* signal forms

Partial sequences of mitochondrial *COI* and *COII* genes were successfully obtained from 23 *Argiope* species and the outgroup (Table 3). Among a total of 893 bps, 301 were variable sites and 241 of them were parsimoniously informative. An equal-weighted

Table 3. The accession numbers of sequences used in this study

Taxa	GenBank access. no. (<i>COI</i>)	GenBank access. no. (<i>COII</i>)
<i>Argiope aemula</i> (Walckenaer 1842)	GU353191	GU353215
<i>A. sp1</i>	GU353192	GU353216
<i>Argiope ocula</i> (Fox 1938)	GU353193	GU353217
<i>Argiope anajusa</i> (Thorell 1887)	GU353194	GU353218
<i>Argiope aetheroides</i> (Yin et al., 1989)	GU353195	GU353219
<i>Argiope pulchelloides</i> (Yin et al., 1989)	GU353196	GU353220
<i>Argiope pulchella</i> (Thorell 1881)	GU353197	GU353221
<i>Argiope macrochoera</i> (Thorell 1891)	GU353198	GU353222
<i>Argiope versicolor</i> (Dolleschall 1859)	GU353199	GU353223
<i>Argiope appensa</i> (Walckenaer 1842)	GU353200	GU353224
<i>A. sp2</i>	GU353201	GU353225
<i>Argiope minuta</i> (Karsch 1879)	GU353202	GU353226
<i>Argiope perforata</i> (L. Koch 1878)	GU353203	GU353227
<i>Argiope mangal</i> (Koh 1991)	GU353204	GU353228
<i>Argiope amoena</i> (L. Koch 1878)	GU353205	GU353229
<i>Argiope luzona</i> (Walckenaer 1842)	GU353206	GU353230
<i>Argiope trifasciata</i> (Forskål 1775)	GU353207	GU353231
<i>Argiope australis</i> (Walckenaer 1805)	GU353208	GU353232
<i>Argiope flavipalpis</i> (Lucas 1858)	GU353209	GU353233
<i>Argiope levii</i> (Björn 1997)	GU353210	GU353234
<i>Argiope bruennichi</i> (Scopoli 1772)	GU353211	GU353235
<i>Argiope aurantia</i> (Lucas 1833)	GU353212	GU353236
<i>Argiope aetherea</i> (Walckenaer 1842)	GU353213	GU353237
<i>Neoscona punctigera</i> (Dolleschall 1857)	GU353214	GU353238

parsimonious analysis of the data set yielded a single most parsimonious tree. Results of model selection showed that the GTR+G+I model best explained the nucleotide substitution pattern. The empirical base frequencies (A, 0.3048; C, 0.0585; G, 0.1515; T, 0.4851), gamma distribution shape parameter (0.3503), proportion of invariable sites (0.5195) and substitution rates ($\text{rate}_{\text{A-C}}$, 1.3803; $\text{rate}_{\text{A-G}}$, 18.9197; $\text{rate}_{\text{A-T}}$, 1.9080; $\text{rate}_{\text{C-G}}$, 1.6954; $\text{rate}_{\text{C-T}}$, 42.0894; and $\text{rate}_{\text{G-T}}$, 1.0000) derived from the test were used for Bayesian analyses. The tree topologies resulting from MP and Bayesian analyses were similar (Fig. 2). The reconstructed phylogeny suggested that all Asian *Argiope* species formed a monophyletic group and evolved from a basal lineage containing African, Eurasian and North American species (MP bootstrap and Bayesian posterior probability were 96 and 100, respectively). The sister taxa of this Asian *Argiope* lineage was *Argiope trifasciata*, which is widely distributed in Eurasia, Africa and North America. Results of ancestral state reconstruction suggested that the linear form was the ancestral state occurring frequently among basal lineages (Fig. 2). The cruciate form decoration was a derived trait within the genus and evolved independently at least twice, one within the basal African lineage (Fig. 2, node 1) and another in the split of the Asian lineage and *A. trifasciata* (Fig. 2, node 2).

Luring effectiveness of cruciate and linear silk decorations

In this field experiment a total of 362 h of video recordings was made, half from cruciate and half from linear decorations. In each treatment group recordings were obtained from 28 web rings, and each ring were monitored for about 6–7 h daily. Web rings with cruciate decorations intercepted significantly more (around 1.6 times) insects than those with linear ones (Wilcoxon Signed Ranks Test: $Z=96$, $N=28$, $P=0.041$) (Fig. 3A). The insects intercepted by both types of webs were all flying insects, and most of them were dipterans. Prey taxonomic composition did not differ significantly between webs containing linear and cruciate decorations (Chi-square test of homogeneity, $\chi^2=0.000$, $P=0.99$). The number of radii between these two groups were not significantly different (paired t -test, $t=0.314$, $P=0.756$) (Fig. 3B), indicating that these two types of web rings did not differ in web silk density and hence visibility.

Luring effectiveness of cruciate and linear dummy decorations

Under chromatic vision, the color contrast between the cardboard used for dummies and silk decoration of *A. aemula* was not significantly higher than the discrimination threshold of 0.05 estimated for hymenopteran insects (chromatic contrast=0.044,

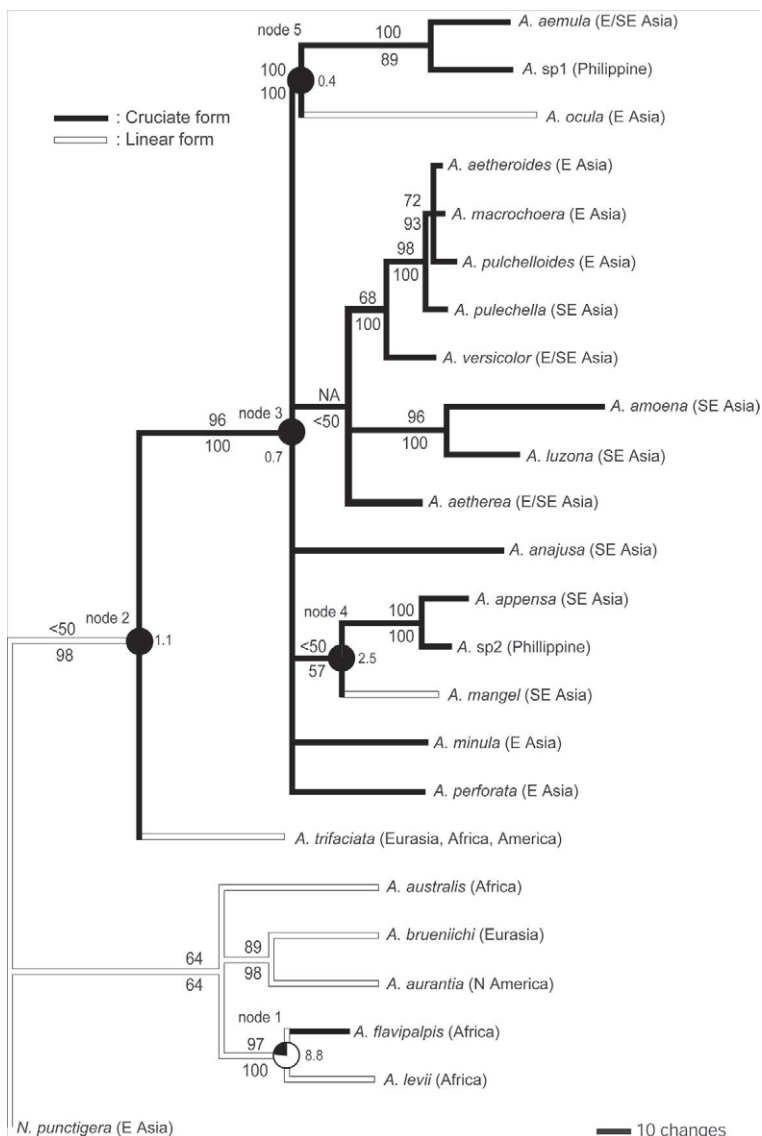


Fig. 2. Phylogenetic relationships of the Genus *Argiope* based on combined *COI* and *COII* gene partial sequences. Numbers above and below branches are parsimony bootstrap values and Bayesian posterior probabilities, respectively. Parsimony reconstructions of ancestral states are labeled on the branches. The percentages of the internal nodes indicate the posterior probabilities of Bayesian estimation of ancestral states. Numbers to the right of internal nodes are Bayes factors of alternative models of character evolution.

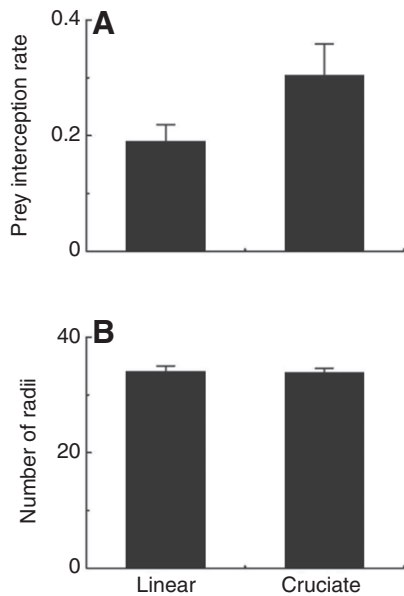


Fig. 3. Mean ($\pm$ s.e.) prey interception rates (number of prey intercepted per hour of recording) (A) and number of radii (B) of web rings with linear or cruciate decorations.

$t_{=0.05(1),23}=-2.9407$, $P=0.996$). The chromatic color contrast between green strings (used to fix dummy decorations) and vegetation was also not significantly higher than the discrimination threshold (chromatic contrast=0.019, $t_{=0.05(1),7}=-2.9407$, $P=0.999$). These results indicated that considering the visual system of hymenopterans, the color signals of dummy decoration bands fixed on green strings were indistinguishable from those of real silk decorations.

A total of 327 h of video recordings was made, 158 on cruciate and 169 on linear dummy decorations. The results of Poisson

regression showed that even though cruciate and linear forms contained same quantity of material, the former attracted significantly more insects than the latter (Table 4A, Fig. 4A). The insects attracted by both types of dummy decorations were all hymenopterans, dipterans and lepidopterans. Results of a Chi-square test of homogeneity showed that the prey taxonomic composition did not differ significantly between cruciate and linear dummy decorations ($\chi^2_{0.05,3}=2.596$, $P=0.458$).

The effect of decoration band orientation

A total of 193 h of video recordings was made, 98 on cruciate and 95 on vertical/horizontal decorations. A comparison of insect attraction rates derived from these recordings showed that altering the orientation pattern of dummy decoration bands, whilst keeping the number of bands constant, significantly affected their attractiveness to insects. Those dummy decorations arranged in a cruciate form attracted significantly more insects (per hour of monitoring) than those arranged in a vertical/horizontal form (Table 4B, Fig. 4B). The insects attracted by both types of dummy decorations were all hymenopterans, dipterans and lepidopterans. Results of a Chi-square test of homogeneity showed that the prey taxonomic composition did not differ between cruciate and vertical/horizontal decoration forms ($\chi^2_{0.05,3}=1.026$, $P=0.795$).

DISCUSSION

Our results suggest that linear decorations are an ancestral state character in *Argiope* spiders, and the cruciate form evolved independently at least twice within the genus. The majority of the Asian species formed a strongly supported monophyletic lineage and the decoration form of almost all of them was cruciate. The molecular phylogeny also shows that the cruciate form has reversals back to the linear form. According to the morphological phylogeny of the family Araneidae (Scharff, 1997), decoration building evolved independently several times among various genera. Most genera of spiders build linear decorations, and the cruciate form decorations can only be found in certain subadult and adult *Argiope* spiders

Table 4. Results of Poisson regressions comparing the prey attraction rates of dummy decorations used in various treatments

Parameters	d.f.	Estimate of β	s.e.	χ^2	P
(A)					
Intercept	1	1.861	0.306	36.880	<0.0001
Vertical/horizontal	1	-0.818	0.310	6.970	0.008
Cruciate	0	0.000	0.000	—	—
Day 1	1	-0.847	0.398	4.520	0.033
Day 2	1	-0.100	0.317	0.100	0.752
Day 3	0	0.000	0.000	—	—
Scale	1	0.000	1.000	—	—
(B)					
Intercept	1	-0.5136	0.1620	10.04	0.0015
Linear	1	-0.8735	0.2011	18.86	<0.001
Cruciate	0	0.000	0.0000	—	—
Day 1	1	-0.5136	0.2564	47.63	0.0057
Day 2	1	0.0428	0.2086	0.04	0.8373
Day 3	0	0.000	0.000	—	—
Scale	1	1.000	0.000	—	—

(A) Cruciate vs linear form dummies. (B) Cruciate vs vertical/horizontal form dummies. The effect of which day the field experiment was conducted was considered in both analyses*†.

s.e., standard error.

*The β of the cruciate form group and the day 3 group was arbitrarily designated as 0 to facilitate comparison of probabilities of different events.

†The ratio of probabilities of two certain events is designated as e^{β} .

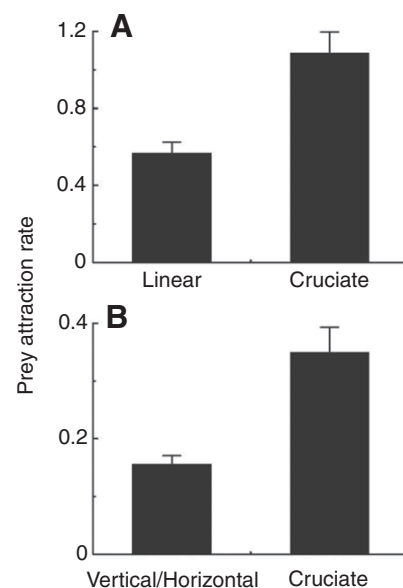


Fig. 4. Mean ($\pm$ s.e.) prey attraction rates (number of prey approaching per hour of recording) of linear and cruciate form (A) and cruciate and vertical/horizontal form (B) dummy decorations.

(Bruce and Herberstein, 2005; Cheng and Tso, 2007). The inter-genus evolutionary relationship of decoration forms within the family Araneidae is congruent with the intra-genus evolutionary relationship of decoration forms in *Argiope* spiders. Both indicate that the linear form is ancestral and the cruciate form is derived. However, what were the driving forces that shaped the design of web decorations in *Argiope*? A comparison of luring performance of linear and cruciate decorations indicates that a higher prey attractiveness of the latter might be one of the candidates.

Currently, no study has simultaneously compared the insect attractiveness of webs decorated with linear and cruciate decorations in the field. Results of our field manipulations showed that web rings with natural cruciate decorations attracted significantly more insects than webs with linear decorations. We also demonstrated that decorations composed of four short dummy bands arranged in a cruciate pattern were significantly more attractive than those composed of two long bands arranged linearly. Because in the second experiment the overall size of decorations was identical, it was not the overall quantity of material but the number and/or arrangement of bands that influences insect attractiveness of decorations. Empirical evidence currently available indicated that decoration band number was an important attribute of this luring signal. Herberstein showed that *Argiope keyserlingi* webs containing more decoration bands captured more insects than those with fewer bands (Herberstein, 2000). Accordingly, the greater attractiveness of cruciate form decorations built by *A. aemula* in this present study might be achieved by a larger number of silk bands on webs (four vs two bands) even if the total size of the signal is the same. A larger number of silk bands on webs could generate a visual signal of greater intensity and therefore become more attractive to insects. However, if cruciate decorations represent a way to increase the overall number of silk bands and thus signal intensity, why are these bands arranged diagonally rather than in the form of two vertical plus two horizontal bands? While such decoration form can be relatively easily generated by incorporating two additional horizontal silk bands to the pre-existing vertically arranged bands, more evolutionary steps had to be involved to generate the cruciate decoration form. Therefore, from an evolutionary viewpoint, arranging four silk bands in a vertical/horizontal pattern is more parsimonious than putting them into a cruciate form. However, we know of no species of spider exhibiting such decoration form.

Results of our field experiments manipulating band arrangement pattern by dummy decorations show that the orientation of the decoration bands also contributes to the overall effectiveness of the signal. When the arrangement of decoration bands was changed into a vertical/horizontal form, insect attraction was reduced by half compared with the same number and size of bands arranged in a diagonal pattern. It is now well established that flying insects exhibit an innate preference for patterns arranged diagonally. For example, various insects have an innate preference for certain bilateral or radial symmetrical patterns (Lehrer et al., 1995; Enquist and Johnstone, 1997; Neal et al., 1998; Giurfa et al., 1999; Lehrer, 1999; Rodríguez et al., 2004; Wignall et al., 2006), and their resources frequently exhibit radial stripes, dark centers and peripheral dots (Biesmeijer et al., 2005). Therefore, the bilateral symmetrical arrangement pattern of cruciate form decorations might match the innate orientation preference of flying insects. Results of Bruce and Herberstein also showed that hymenopteran insects responded differently to the orientation of decoration bands (Bruce and Herberstein, 2005). They used a Y-maze approach to examine the response of stingless bees to webs of *A. keyserlingi* with two decoration bands either orientated vertically (linear pattern) or

inclined at 30 deg. (cruciate pattern). Although stingless bees showed no preference for either pattern, they did respond significantly more quickly to the inclined decorations. Therefore, results from Bruce and Herberstein (Bruce and Herberstein, 2005) and this present study both suggest that the orientation pattern of bands significantly affect the attractiveness of *Argiope* decorations.

Although signaling by cruciate decorations can enhance prey attraction, the cost is an increased predation risk. Cheng and Tso provided direct field evidence that *A. aemula* on webs with cruciate decorations experienced significantly more wasp attacks than those on undecorated webs (Cheng and Tso, 2007). These results (Cheng and Tso, 2007) and those of laboratory studies using Y-mazes (Bruce et al., 2001; Seah and Li, 2001) showed that predators may use cruciate form decorations to locate the spiders. However, responses of wasps to *Argiope* spiders on webs with linear decorations seem to differ. Blackledge and Wenzel showed that in artificial enclosures *A. trifasciata* with linear form decorations on webs were less likely to be captured by mud-dauber wasps than those on undecorated webs (Blackledge and Wenzel, 2001). Together, these results suggest that while cruciate form decorations increase foraging success, linear form decorations might enhance the survival of spiders. The trade-off between prey luring and predator attraction might be one potential reason why certain Asian *Argiope* species regained the ancestral linear form. Ancestors of these species might inhabit environments with very high predation pressures and therefore a reversal to less attractive but more protective linear decoration form was favored. However, although *Argiope* spiders with linear decorations may have lower foraging success, this could be buffered by the attractive properties of their bright body coloration. Recent studies showed that bright coloration of various taxa of orb-web spiders, including *Argiope*, in itself is attractive to insects (Craig and Ebert, 1994; Hauber, 2002; Tso et al., 2002; Tso et al., 2004; Tso et al., 2006; Cheng and Tso, 2007; Bush et al., 2008). We suggest that the evolution of spider web decorations was shaped by a complex array of interacted selection pressures (such as foraging performance vs predation pressure) and might have co-evolved with other traits (such as body coloration).

Although the results of this present study are congruent with the predictions of the hypothesis that insect form vision serves as one driving force of decoration form, is it possible that other factors are also involved? In addition to functioning as a visual signal, several other functions for web decorations have been proposed. For example, silk decorations might be used by spiders to adjust the tension of webs (for a review, see Herberstein et al., 2000). However, because the decoration silks are loosely placed on webs rather than tightly uniting two adjacent radial silks (Foelix, 1996), it is unlikely that decorations function to adjust web tension. Other researchers showed that the discoid form decorations can help regulate the body temperature of spiders by serving as a shade for sunlight (Humphreys, 1992). Perhaps cruciate form decorations can achieve a better temperature regulation than the linear form and therefore the polymorphism reflected responses to variations in ambient temperatures. However, Nentwig and Rogg (Nentwig and Rogg, 1988) compared *Argiope* webs with and without decorations and found no significant difference in spider body temperatures. Recently, several researchers demonstrated that silk decoration building might function to regulate aciniform silk gland activity (Tso, 2004; Walter et al., 2008a). Because aciniform gland silks are used for prey wrapping and decoration building, the silk reserve of this gland might be quite variable according to various environmental conditions. Therefore, the polymorphism might reflect a variation in spiders' silk gland physiological conditions mediated by factors

such as frequency of prey-wrapping events (Tso, 2004) or moulting (Walter et al., 2008b). Although this hypothesis can well explain the inconsistent occurrence and polymorphic nature of *Argiope* silk decorations, it cannot explain why spiders arrange the silk bands in a cruciate way. If placing more silk bands on webs can enable spiders larger capacity to regulate silk gland activities, why are these bands arranged in a cruciate rather than the more parsimonious vertical/horizontal form?

Concluding from the above review, non-visual signal functional hypotheses failed to explain the evolution of decoration forms. However, recent empirical evidence regarding benefits and costs of the visual signal function of decorations can well explain the evolution as well as the inconsistency and polymorphic nature of decoration form. Results of this present study showed that compared with linear form decorations, cruciate silk bands can better attract the attention of insects so can serve as a better visual lure. However, results of several recent studies demonstrate that luring prey by decorating webs with cruciate decorations goes with a cost of increased predation risk (Seah and Li, 2001; Bruce et al., 2001; Cheng and Tso, 2007), and there will be a selection pressure to prevent the spiders from consistently decorating their webs (Li and Lee, 2004). Moreover, another pressure in the context of risk learning of prey also selects against consistent building of decorations of a fixed form (Craig, 1994). Therefore, the inconsistent building and shape polymorphism of decorations can be regarded as products of trade-offs between opposing selection pressures associated with this structure's visual signal function.

Our study showed that the visual signal design of a code breaker seemed to be shaped by the sensory properties of their target organisms. The evolution of floral guide characters (such as form and color) is tightly associated with sensory characteristics (especially visual systems) of pollinator insects (for reviews, see Neal et al., 1998; Lunau, 2004; Schaefer et al., 2004). However, in addition to flowers and pollinator insects, orb-web spiders such as *Argiope* also participate in this communication system and exploit the insect/plant communication. We suggest that the visual sensory system of insects not only drives the evolution of angiosperm floral guides but also shapes the design of spider web decorations. Shifting the focus from the context of signaler and intended receiver might discover that exploiters breaking the code are more common than we currently understand.

ACKNOWLEDGEMENTS

We thank C. P. Liao, R. A. Chen, Y. C. Chen, Y. T. Lin, P. S. Hwang, S. C. Hwang, J. Hou, W. T. Sheu, C. M. Fan and W. C. Lin for field assistance; and the Lien-Hwa-Chih Research Center, Taiwan Forest Research Institute for providing research facilities and the field study site. A. S. Dippenaar-Schoeman, D. Li, H. Ono and M. S. Zhu kindly provided *Argiope* specimens. This study was supported by grants from the National Science Council, Taiwan (NSC-96-2311-B-029-001, NSC-97-2311-B-029-002-MY3) to I.-M. T.

REFERENCES

- Alcock, J. (2005). *Animal Behavior, An Evolutionary Approach*, 8th edition. Sunderland, Massachusetts: Sinauer.
- Basolo, A. L. (1995). Phylogenetic evidence for the role of pre-existing bias in sexual selection. *Proc. R. Soc. Lond. B* **259**, 307-311.
- Biesmeijer, J. C., Giurfa, M., Koedam, D., Potts, S. G., Joel, D. M. and Dafni, A. (2005). Convergent evolution: floral guides, stingless bee nest entrances, and insectivorous pitchers. *Naturwissenschaften* **92**, 444-450.
- Blackledge, T. A. and Wenzel, J. W. (2001). Silk mediated defense by an orb web spider against predatory mud-dauber wasps. *Behaviour* **138**, 155-171.
- Brandt, Y. (2003). Lizard threat display handicaps endurance. *Proc. R. Soc. Lond. B* **270**, 1061-1068.
- Briscoe, A. D. and Chittka, L. (2001). The evolution of color vision in insects. *Annu. Rev. Entomol.* **46**, 471-510.
- Bruce, M. J. (2005). The function and phylogeny of web decorations in orb-web spiders. PhD thesis, Macquarie University, Australia.
- Bruce, M. J. (2006). Silk decorations: controversy and consensus. *J. Zool.* **269**, 89-97.
- Bruce, M. J. and Herberstein, M. E. (2005). Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. *J. Nat. Hist.* **39**, 3833-3845.
- Bruce, M. J., Herberstein, M. E. and Elgar, M. A. (2001). Signaling conflict between predator and prey attraction. *J. Evol. Biol.* **14**, 786-794.
- Bruce, M. J., Heiling, A. M. and Herberstein, M. E. (2004). Web decorations and foraging success in '*Araneus*' *eburnus* (Araneae: Araneidae). *Ann. Zool. Fennici.* **41**, 563-575.
- Bruce, M. J., Heiling, A. M. and Herberstein, M. E. (2005). Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. *J. Nat. Hist.* **44**, 3833-3845.
- Bush, A. A., Yu, D. W. and Herberstein, M. E. (2008). Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae). *Proc. R. Soc. Lond. B* **275**, 1337-1342.
- Catchpole, C. K. and Slater, P. J. B. (1995). *Bird Songs, Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Cheng, R. C. and Tso, I. M. (2007). Signaling by decorating webs: luring prey or deterring predators? *Behav. Ecol.* **18**, 1085-1091.
- Chittka, L. (1992). The color hexagon: a chromaticity diagram based on photoreceptor excitation as a generalized representation of color opponency. *J. Comp. Physiol. A* **170**, 533-543.
- Chittka, L. (1996). Optimal sets of color receptors and color opponent systems for coding of natural objects on insect vision. *J. Theor. Biol.* **181**, 179-196.
- Chittka, L. (2001). Camouflage of predatory crab spiders on flowers and the colour perception of bees (Arana: Thomisidae/Hymenoptera: Apidae). *Entomol. Gen.* **25**, 181-187.
- Craig, C. L. (1986). Orb-web visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs within the Araneioidea. *Anim. Behav.* **34**, 54-68.
- Craig, C. L. (1991). Physical constraints on group foraging and social evolution: observations on web-spinning spiders. *Funct. Ecol.* **5**, 659-654.
- Craig, C. L. (1994). Limits to learning: effects of predator pattern and colour on perception and avoidance-learning by prey. *Anim. Behav.* **47**, 1087-1099.
- Craig, C. L. and Bernard, G. D. (1990). Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71**, 616-623.
- Craig, C. L. and Ebert, K. (1994). Color and pattern in predator-prey interactions-the bright body colors and patterns of a tropical orb spinning spider attract flower-seeking prey. *Funct. Ecol.* **8**, 616-620.
- Craig, C. L. and Freeman, C. R. (1991). Effects of predator visibility on prey encounter: a case study on aerial web weaving spiders. *Behav. Ecol. Sociobiol.* **29**, 249-254.
- Davis, N. B., Kilner, R. M. and Noble, D. G. (1998). Nestling cuckoos *Cuculus canorus* exploit hosts with begging calls that mimic brood. *Proc. R. Soc. Lond. B* **265**, 673-678.
- Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R. Soc. Lond. B* **340**, 215-225.
- Enquist, M. and Johnstone, R. A. (1997). Generalization and the evolution of symmetry preferences. *Proc. R. Soc. Lond. B* **264**, 1345-1348.
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783-791.
- Fleishman, L. J. (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.* **139**, 36-61.
- Foelix, R. F. (1996). *Biology of Spiders*, 2nd edition. Oxford: Oxford University Press.
- Forrest, T. G. (1994). From sender to receiver: propagation and environmental effects of acoustic signals. *Am. Zool.* **34**, 644-654.
- Giurfa, M., Dafni, A. and Neal, P. (1999). Floral symmetry and its role in plant-pollinator systems. *Int. J. Plant. Sci.* **160** (6 Suppl.), S41-S50.
- Grether, G. F. (2000). Carotenoid limitation and mate preference evolution: A test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution* **54**, 1712-1714.
- Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Series* **41**, 95-98.
- Hauber, M. E. (2002). Conspicuous colouration attracts prey to stationary predator. *Ecol. Entomol.* **27**, 686-691.
- Haynes, K. F., Gemenio, C., Yeagan, K. V., Millar, J. G. and Johnson, K. M. (2002). Aggressive chemical mimicry of moth pheromones by bolas spider: how does this specialist predator attack more than one species of prey? *Chemoecology* **12**, 99-105.
- Herberstein, M. E. (2000). Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* (Karsch 1878)? *Aust. J. Zool.* **48**, 217-223.
- Herberstein, M. E., Craig, C. L., Coddington, J. A. and Elgar, M. A. (2000). The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biol. Rev.* **75**, 649-669.
- Horridge, G. A. (2006). Visual processing of pattern. In *Invertebrate Vision* (eds E. Warrant and D.-E. Nilsson), pp. 494-524. Cambridge: Cambridge University Press.
- Huelsenbeck, J. P. and Ronquist, F. R. (2001). MrBayes: Bayesian inference of phylogeny. *Biometrics* **17**, 754-755.
- Humphreys, W. F. (1992). Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behaviour. *Bull. Br. Arachnol. Soc.* **9**, 47-52.
- Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L. and Bussière, L. F. (2004). High-quality male field crickets invest heavily in sexual display but die young. *Nature* **432**, 1024-1027.
- Johnstone, R. A. (1997). The evolution of animal signals. In *Behavioural Ecology: An Evolutionary Approach*, 4th edition (ed. J. R. Krebs and N. B. Davies). Oxford: Blackwell Scientific Publications.
- Kilner, R. M., Noble, D. G. and Davies, N. B. (1999). Signal of need in parent-offspring communication and their exploitation in the common cuckoo. *Nature* **397**, 667-672.

- Lehrer, M. (1999). Shape recognition in the honeybee: symmetry as a global framework. *Int. J. Plant. Sci.* **160** (6 Suppl.), S51-S65.
- Lehrer, M., Horridge, G. A., Zhang, S. W. and Gadagkar, R. (1995). Shape vision in bees: innate preference for flower-like patterns. *Philos. Trans. R. Soc. Lond. B* **347**, 123-137.
- Li, D. (2005). Spiders that decorate their webs at higher frequency intercept more prey and grow faster. *Proc. R. Soc. Lond. B* **272**, 1753-1757.
- Li, D., Lim, M. L. M., Seah, W. K. and Tay, S. L. (2004). Prey attraction as a possible function of discoid stabilimenta of juvenile orb-spinning spiders. *Anim. Behav.* **68**, 629-635.
- Lloyd, J. E. (1975). Aggressive mimicry in *Photuris* fireflies: signal repertoires by *femmes fatales*. *Science* **197**, 452-453.
- Lunau, K. (2004). Adaptive radiation and evolution - pollinator biology case studies. *Org. Divers. Evol.* **4**, 207-224.
- Maddison, D. R. and Maddison, W. P. (2003). *MacClade, Release Version 4. 06*. Sunderland, Massachusetts: Sinauer Associates.
- Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* **362**, 149-152.
- Neal, P. R., Dafni, A. and Giurfa, M. (1998). Floral symmetry and its role in plant-pollinator systems: terminology, distribution and hypotheses. *Annu. Rev. Ecol. Syst.* **29**, 345-373.
- Nentwig, W. and Rogg, H. (1988). The cross stabilimentum of *Argiope argentata* - non-functional or a non-specific stress reaction? *Zool. Anz.* **221**, 246-266.
- Okamura, J. Y. and Strausfeld, N. J. (2007). Visual system of Calliphoridae flies: motion- and orientation-sensitive visual interneurons supplying dorsal optic glomeruli. *J. Comp. Neurol.* **500**, 189-208.
- Pagel, M. and Meade, A. (2006). Bayesian analysis of correlated evolution of discrete characters by Reversible-Jump Markov Chain Monte Carlo. *Am. Nat.* **167**, 808-825.
- Panhuis, T. M. and Wilkinson, G. S. (1999). Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). *Behav. Ecol. Sociobiol.* **46**, 221-227.
- Platnick, N. I. (2009). *The World Spider Catalog, Version 9. 5* (online catalog). Available on <http://research.amnh.org/entomology/>.
- Posada, D. and Crandall, K. A. (1998). MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14**, 817-818.
- Proctor, H. C. (1992). Sensory exploitation and the evolution of male mating behavior: a cladistic test. *Anim. Behav.* **44**, 745-752.
- Quillfeldt, P. (2002). Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. *Anim. Behav.* **64**, 579-587.
- Rodd, F. H., Hughes, K. A., Grether, G. F. and Baril, C. V. (2002). A possible non-sexual origin of male preference: are male guppies mimicking fruit? *Proc. R. Soc. Lond. B* **269**, 475-481.
- Rodríguez, I., Gumbert, A., Ibarra, N. H., Kunze, J. and Giurfa, M. (2004). Symmetry is in the eye of the 'beeholder': innate preference for bilateral symmetry in flower-naïve bumblebees. *Naturwissenschaften* **91**, 374-377.
- Ruxton, G. D., Sherratt, T. N. and Speed, M. P. (2004). *Avoiding Attack: the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: Oxford University Press.
- Schaefer, H. M., Schaefer, V. and Levey, D. J. (2004). How plant-animal interactions signal new insights in communication. *Trends Ecol. Evol.* **19**, 57-584.
- Scharff, N. (1997). A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zool. J. Linn. Soc. Lond.* **120**, 355-434.
- Seah, W. K. and Li, D. (2001). Stabilimenta attract unwelcome predators to orb webs. *Proc. R. Soc. Lond. B* **268**, 1553-1558.
- Srinivasan, M. V., Zhang, S. W. and Witney, K. (1994). Visual discrimination of pattern orientation by honeybees: performance and implications for 'cortical' processing. *Philos. Trans. R. Soc. Lond. B* **343**, 199-210.
- Su, Y. C., Chang, Y. H., Lee, S. C. and Tso, I. M. (2007). Phylogeography of the giant wood spider (*Nephila pilipes*, Araneae) from Asian-Australian regions. *J. Biogeogr.* **34**, 177-191.
- Swofford, D. L. (2001). PAUP*. *Phylogenetic Analysis Using Parsimony (*And Other Methods)*. Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Théry, M. and Casas, J. (2002). Predator and prey views of spider camouflage. *Nature* **415**, 133.
- Théry, M. and Casas, J. (2009). The multiple disguises of spiders: web colour and decorations, body colour and movement. *Philos. Trans. R. Soc. Lond. B* **364**, 471-480.
- Thomas, J. A., Knapp, J. J., Akino, T., Gerty, S., Wakamura, S., Simcox, D. J., Wardlaw, J. C. and Elmes, G. W. (2002). Parasitoid secretions provoke ant warfare. *Nature* **417**, 505-506.
- Tso, I. M. (1996). Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Anim. Behav.* **52**, 183-191.
- Tso, I. M. (1998a). Stabilimentum-decorated webs spun by *Cyclosa conica* (Araneae, Araneidae) trapped more insects than undecorated webs. *J. Arachnol.* **26**, 101-105.
- Tso, I. M. (1998b). Isolated spider web stabilimentum attracts insect. *Behaviour* **135**, 311-319.
- Tso, I. M. (2004). The effect of food and silk reserve manipulation on decoration-building of *Argiope aetheroides*. *Behaviour* **141**, 603-616.
- Tso, I. M., Tai, P. L., Ku, T. H., Kuo, C. H. and Yang, E. C. (2002). Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Anim. Behav.* **63**, 175-182.
- Tso, I. M., Lin, C. W. and Yang, E. C. (2004). Colourful orb-weaving spiders through a bee's eyes. *J. Exp. Biol.* **207**, 2631-2637.
- Tso, I. M., Liao, C. P., Huang, R. P. and Yang, E. C. (2006). Function of being colorful in web spiders: attracting prey or camouflaging oneself? *Behav. Ecol.* **17**, 606-613.
- Van Hateren, J. H., Srinivasan, M. V. and Wait, P. B. (1990). Pattern recognition in bees: orientation discrimination. *J. Comp. Physiol. A* **167**, 649-654.
- Walter, A., Elgar, M. A., Bliss, P. and Moritz, R. F. A. (2008a). Wrap attack activates web-decorating behavior in *Argiope* spiders. *Behav. Ecol.* **19**, 799-804.
- Walter, A., Elgar, M. A., Bliss, P. and Moritz, R. F. A. (2008b). Molting interferes with web decorating behavior in *Argiope keyserlingi* (Araneae, Araneidae). *J. Arachnol.* **36**, 538-544.
- Watanabe, T. (1999). Prey attraction as a possible function of the silk decoration of the uloborid spider *Octonoba sybotides*. *Behav. Ecol.* **10**, 607-611.
- Wehner, R. (1971). The generalization of directional visual stimuli in the honey bee *Apis mellifera*. *J. Insect Physiol.* **17**, 1579-1591.
- Wignall, A. E., Heiling, A. M., Cheng, K. and Herberstein, M. E. (2006). Flower symmetry in honeybees and their crab spider predators. *Ethology* **112**, 510-518.
- Witte, K. and Sawka, N. (2003). Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ. *Anim. Behav.* **65**, 195-203.
- Yang, E. C. and Maddess, T. (1997). Orientation-sensitive neurons in the brain of the honey bee (*Apis mellifera*). *J. Insect Physiol.* **43**, 329-336.
- Yin, C. G., Wang, J. F., Zhu, M. S., Xie, L. P., Peng, X. J. and Bao, Y. H. (1997). *Fauna Sinica (Arachnida, Araneae: Araneidae)*. Beijing: Science Press (in Chinese).