ISOLATED SPIDER WEB STABILIMENTUM ATTRACTS INSECTS

by

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Summary

The insect-attraction function of silk stabilimenta spun by *Argiope* spiders was directly tested by examining if isolated stabilimenta will increase insect interception in artificial webs. Artificial webs were made from basswood frames and fine monofilaments coated with a sticky substance and were divided into two groups, experimental and control. In the experimental group, silk stabilimenta isolated from stabilimentum-decorated webs spun by *Argiope aurantia* were introduced. In the control group, corresponding areas collected from the undecorated webs of *A. trifasciata* were introduced. A general linear model was used to examine the effect of stabilimenta, web location, and date of data collection on insect interception in artificial webs. When the effects of location and date were simultaneously considered, artificial webs containing isolated stabilimenta intercepted significantly more flying insects (41.6% more) than those in the control group. However, there was no difference in orthopteran interception rates between experimental and control groups. These results indicate that silk stabilimenta of *Argiope* spiders do attract insects, although not all insects exhibit a strong orientation response to them.

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Introduction

Stabilimenta are distinctive structures on the webs of at least 17 genera (estimated from Levi, 1968, 1983; Eberhard, 1990; Tso, pers. obs.) of orb-weaving spiders (Araneae, Araneidae and Uloboridae). Stabilimenta can be composed entirely of silk bands in a circular, linear or cross form; or can be composed of both silk and objects such as detritus, prey remains, or egg sacs (Levi, 1968, 1977; Eberhard, 1973, 1990; Nentwig & Heimer, 1987). Among them, the zig-zag silk bands spun by garden spiders (genus *Argiope*) have received the most attention. Arachnologists have proposed many functional hypotheses for silk stabilimenta spun by *Argiope* spiders, such as stabilizing the web, regulating body temperature of spiders, camouflaging the spider, advertising the presence of the web, deterring predators by making the spider look larger, and attracting potential prey (see discussions in Edmunds, 1986; Nentwig & Heimer, 1987; Nentwig & Rogg, 1988; Eberhard, 1990; Craig & Bernard, 1990; Humpreys, 1992; Schoener & Spiller, 1992).

Although these functional hypotheses are not mutually exclusive, the empirical support each hypothesis has received varies. Among all hypotheses, the insect-attraction hypothesis has accumulated a great amount of support from both field manipulative studies and natural experiments. Craig & Bernard (1990) and Craig (1991) argued for the insect-attraction hypothesis by demonstrating that stabilimenta of the garden spider *Argiope argentata* reflected ultra-violet (UV) light, and webs decorated with stabilimenta intercepted more insects than undecorated webs. Tso (1996a) also found that decorated webs of *Argiope trifasciata* intercepted more flying insects, but not more orthopteran insects. The silk stabilimenta spun by *Cyclosa conica* were also found to greatly increase insect interception of decorated webs (Tso, in press).

From this short review, it appears that most previous studies on the insect-attraction hypothesis examined if stabilimenta increase insect interception in webs containing them. However, in addition to stabilimenta, insect interception is also affected by web characteristics such as silk diameter, mesh size, and orb size, as well as spatial and temporal variations in insect abundance. Silk diameter and mesh size determine both prey retention and the visibility of the orb web (Rypstra, 1981; Craig, 1986; Craig & Freeman, 1991). Orb size has been demonstrated to correlate positively

with number of prey trapped (Brown, 1981; Higgins & Buskirk, 1992; but see Tso, in press). Because the distribution of insects is heterogeneous in space and time (on a seasonal, daily, and hourly basis), the estimated interception rate of an orb will be affected by the orb's location and the time of data collection. Although these factors have been controlled with various experimental designs and statistical methods in previous studies, a test using isolated stabilimenta and artificial webs with identical web parameters is still lacking. Therefore, I conducted a field manipulative study using isolated stabilimenta and artificial webs to provide a straightforward test of the insect-attraction hypothesis.

Materials and methods

The study site and the spiders

This study was conducted between mid-August and early September 1995 in the University of Michigan Matthaei Botanical Gardens in Ann Arbor, Michigan, USA. Two species of garden spiders, *Argiope trifasciata* (Forskal 1775) and *A. aurantia* Lucas 1833, occur in the prairie of the Gardens. Adult *A. aurantia* females usually build a linear stabilimentum on both lower and upper halves of their webs. During the study only adult *A. aurantia* could be found, and all the webs spun were decorated. Adult *A. aurantia* males were not included in this study because they do not build foraging webs (Levi, 1983; Tso, pers. obs.).

Constructing artificial webs

Artificial webs were made from basswood frames (30×30 cm) and monofilament (Stren 2 lb. test fishing line, Remington Arms Co.) following the design of Eberhard (1977) (Fig. 1). The monofilaments were woven onto the frames at intervals of 5 mm and then a clear and odorless sticky substance (Bird Repellent, Tanglefoot Co.) was applied to the monofilaments following the method of Uetz & Biere (1980). A total of 32 artificial webs were constructed, and during the experiment each web was used for four sunny days. After four days of use, the monofilaments were removed from the frames and new monofilaments were re-woven and the sticky substance re-applied. Sixteen web sites of *Argiope trifasciata* were randomly located in the field and 16 artificial webs were installed immediately adjacent to those webs at the same orientation and height and with minimum change to the surrounding vegetation. The webs were secured by hooking them to two bamboo sticks inserted deeply into the soil. After web installation, the neighboring spider and web were removed.

Collecting stabilimenta from webs

Twenty-four frames (9 × 2.5 × 0.5 cm) were made from transparency films (Labelon XTR650S) (Fig. 1) to collect stabilimenta from the webs. To collect a stabilimentum, I applied clear glue (Ross School Glue, Conros Co.) to one side of the transparency frame, pressed the sticky side of the frame on the web, then burned the silk around the frame

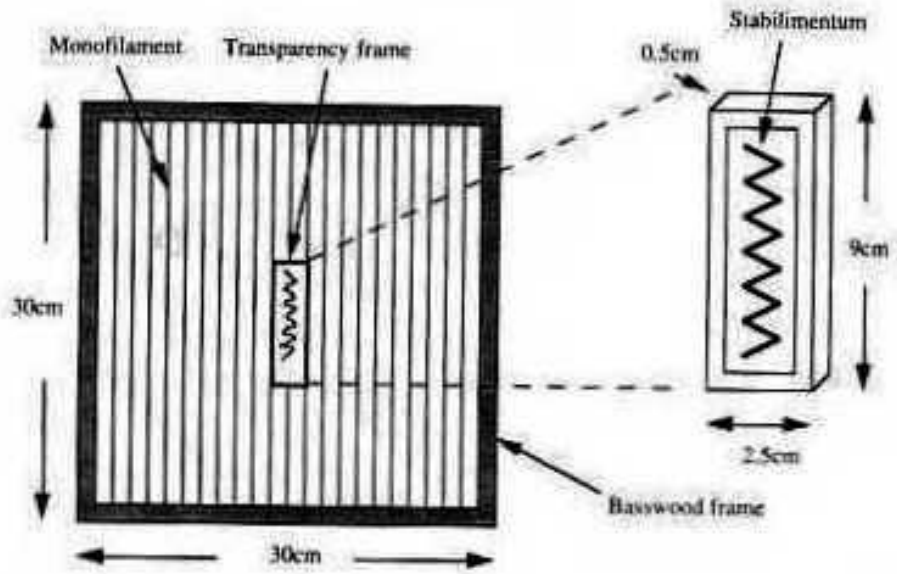

Fig. 1. Schematic drawing showing the design and dimensions of the artificial webs and transparency frame.

to free it. With this method, the stabilimentum could be collected intact and the tension of the supporting silk could be maintained. Twelve stabilimenta (including upper arms, hubs and lower arms) were collected from decorated webs of *A. aurantia* to be used in the experimental group. I used another 12 frames to collect the corresponding area of the undecorated webs spun by *A. trifasciata*, because I could not find and use undecorated webs spun by *A. aurantia* as control.

Measuring insect-interception of artificial webs

The experiment was conducted on 12 non-consecutive sunny days between August 14 and September 1 (rainy and windy days were skipped). At initiation of the experiment (day 1), the web sites were randomly assigned to experimental or control groups. For each succeeding day, the treatment at each site was alternated such that all sites had six days of each treatment and on each day there were eight replicates of each treatment. Because there were no spiders on the artificial webs, some of the insects intercepted might have escaped the trap. To reduce the potential data loss due to escapes, insects trapped on the artificial webs were collected hourly. Those insects intercepted by the artificial webs were categorized as either flying insects or orthopterans because they are known to respond differently to stabilimenta (Tso, 1996a). Insects smaller than 2 mm were excluded from the analysis, because *Argiope* spiders in the study site normally do not consume prey of this size (Tso, unpubl. data). The webs and frames were removed from the sites each day at 6:00 PM and were re-installed the next experimental day.

Data analysis

Daily interception rates (DIRs, number of insects per artificial web per day) of flying insects and orthopterans were analyzed separately. I used a general linear model to simultaneously

examine the effect of stabilimenta, location, and date on DIRs (C.L. Craig, pers. comm.). The model was expressed as:

$$\text{DIRs} = \text{Constant} + b_1 \times \text{stabilimentum} + b_2 \times \text{location} + b_3 \times \text{date}$$

Since the DIRs of both flying insects and orthopterans were not normally distributed, I estimated the parameters of the model by maximum likelihood approximation as described by Craig (1994a) and Craig *et al.* (1996). In this approach, the relative effects of stabilimentum, location, and date can be evaluated by examining if the corresponding parameters b_1, b_2 and b_3 are statistically different from 0 by a Student t-test (Snedecor & Cochran, 1980). After estimating the parameters by SYSTAT 5.2.1, I divided the parameters by their standard errors to generate Student t-values, then acquired a level of significance by comparing them to critical t-values with $N - k - 1$ degrees of freedom (N = sample size = 192, k = number of parameters = 3).

Results

The parameters and their standard errors generated by maximum likelihood approximation are given in Table 1. Also given in Table 1 is the result of Student t-tests examining if those parameters were statistically different from 0. The DIR of flying insects was significantly increased by the presence of the stabilimentum (b_1, $p < 0.01$), but not web location, or date of data collection. The DIR of orthopterans was significantly altered by location (b_2, $p < 0.01$). This result suggests that the distribution of orthopterans in the study site was patchy, and presence of stabilimenta did not significantly increase orthopteran interception rates on artificial webs. The

TABLE 1. *Results of maximum likelihood approximation estimating the parameters of the model DIRs = constant + b_1 × stabilimentum + b_2 × location + b_3 × date*

Effect	Parameter	Estimate	SE	t-value	p
(a) Flying insects					
Stabilimentum	b_1	−1.021	0.336	3.039	<0.01
Location	b_2	−0.552	0.036	1.444	>0.05
Date	b_3	−0.015	0.049	0.306	>0.05
(b) Orthopterans					
Stabilimentum	b_1	−0.052	0.121	0.430	>0.05
Location	b_2	−0.039	0.013	3.000	<0.01
Date	b_3	0.026	0.018	1.444	>0.05

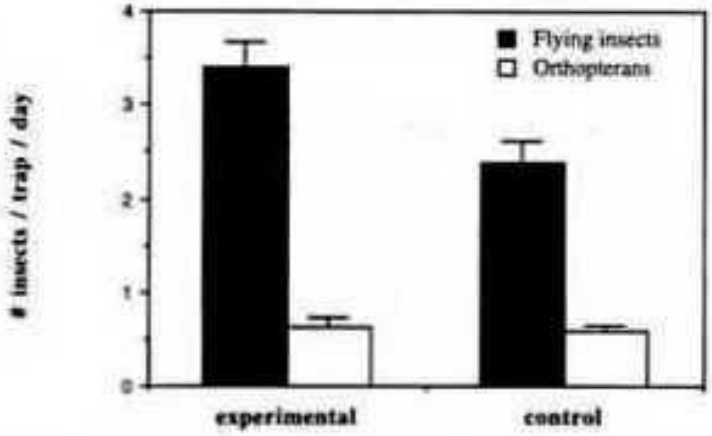

Fig. 2. Mean (± SE) daily flying insect and orthopteran interception rates of artificial webs containing an experimental frame and webs containing a control frame.

average DIRs of both types of insects trapped by artificial webs containing experimental frames and control frames are given in Fig. 2.

Discussion

This study provides strong support that stabilimenta of *Argiope* spiders attract flying insects, even when they are isolated from the webs. Compared to artificial webs containing a control frame, the presence of stabilimenta significantly increased DIRs of flying insects by 41.6%. The use of artificial webs to determine the insect-attraction function of stabilimenta was previously attempted (see Nentwig & Heimer, 1987) but no significant effect was found. In that attempt, artificial stabilimenta of unknown reflectance property were used. Because reflectance property of the silk has been shown to be important in the visual interactions between araneoid spiders and prey (see review in Craig *et al.*, 1994), artificial stabilimentum's lack of effect in that attempt may due to the material's inappropriate reflectance. In this study, although artificial webs were also employed, real stabilimenta from webs spun by *Argiope aurentia* were used. Compared to a natural experiment conducted by Tso (1996a) on *A. trifasciata* at the same site, this study provides a better control on variables affecting DIRs. By using artificial webs with the same parameters, the effects of web-related variables such as orb size, mesh size, and silk diameter were effectively controlled. By placing artificial webs in 16 sites for 12 days, and by the use of a general linear model, the long term effect of spatial or temporal variation in insect

gain of *Argiope* spiders, and seem to be one form of foraging effort, their synthesis is not influenced by manipulating food intake (Nentwig & Rogg, 1988; Tso, 1996b). An attempt to compare the building patterns between adults and offspring of *A. trifasciata* revealed a higher similarity between related individuals than between unrelated ones, suggesting some degree of genetic linkage (Edmunds, 1986). But the data are insufficient to establish whether genetic programming plays a role in controlling stabilimentum-building. To understand how stabilimentum-building behavior is involved in the ecology of *Argiope* spiders, an investigation on how the temporally inconsistent pattern of stabilimentum-building is proximately generated is needed.

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distribution is incorporated in the analysis while testing for the effect of stabilimenta.

Stabilimentum's lack of attractiveness to orthopterans further supports the hypothesis proposed by Craig regarding which prey *Argiope* spiders specialize in catching. Craig suggested that *Argiope* spiders may specialize in catching insect pollinators, because, a UV-reflecting stabilimentum provides a supernormal stimulus to those insects seeking UV-reflecting nectar guides (Craig & Bernard, 1990; Craig & Ebert, 1994; Craig, 1994b). This hypothesis was supported by the evidence that insect pollinators (such as hymenopterans) constituted more than 70% in the diet of *A. argentata* (Robinson & Robinson, 1970; Nentwig, 1985), and non-orthopteran insects represented more than 95% in the diet of *A. amoena* (Murakami, 1983). In this study, no difference in orthopteran interception rates was found between artificial webs with or without stabilimenta. Tso (1996a) also found that decorated webs of *A. trifasciata* did not intercept greater numbers of orthopterans. These findings provide further support to Craig's hypothesis by demonstrating that a UV-reflecting stabilimentum is ineffective in attracting non-pollinating insects such as orthopterans.

Although this field manipulative experiment provides strong evidence that isolated stabilimenta spun by *Argiope* spiders attract insects, how stabilimentum-building behavior is regulated still remains unknown. Individual *Argiope* spiders do not always decorate their webs. Craig (1994b) manipulated position and number of stabilimentum arms in an attempt to understand how inconsistent building of stabilimenta affects interaction between stingless bees and *Argiope argentata*. She concluded that an unpredictable pattern prevented those bees from learning to associate stabilimenta with danger. Craig (1994b) then suggested an inconsistent building of stabilimenta (in both shape and frequency) to be beneficial to *Argiope* spiders. However, although stabilimenta's UV-reflecting properties and the unpredictable way spiders build them greatly benefit *Argiope* spiders, we still do not understand how their construction is proximately controlled. Edmunds (1986) and Nentwig & Rogg (1988) examined the effects of microclimatic conditions, habitat type, web characteristics, presence of males, illumination, and even hormones (ecdysone) on stabilimentum-building of various *Argiope* spiders. However, no satisfactory conclusion can be drawn from these factors. Although stabilimenta can potentially increase foraging

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