

Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant

I-MIN TSO

Museum of Zoology and Department of Biology, University of Michigan

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Abstract. Stabilimenta are silky structures on the webs of some orb-weaving spiders, whose function is still not well understood. This study tested the prey-attraction hypothesis as a possible function of stabilimenta with the banded garden spiders *Argiope trifasciata* in southeastern Michigan. Spider webs' stabilimentum length, prey interception rates and web characteristics were recorded daily. The daily insect interception rates and web characteristics were compared between stabilimentum-decorated and undecorated webs. An intra-web comparison was performed between decorated and undecorated halves of webs on the daily insect interception rates and web characteristics. The effects of location and characteristic of webs on insect interception rates were further examined at decorated and undecorated webs. A higher interception rate for flying insects was found in webs decorated with stabilimenta, but orthopteran interception rate was the same when compared with undecorated webs. The decorated web's higher interception rate for flying insects did not seem to result from locations or characteristics of webs. The length of a stabilimentum had little effect on increasing its attractiveness to flying insects. There was no difference in flying insect interception rates between decorated and undecorated halves of webs, but orthopteran interception rates were always higher in lower halves of webs. The results from intra-web comparison indicated that a stabilimentum did not increase insect interception rate of the adjacent area but did increase that of the whole web. © 1996 The Association for the Study of Animal Behaviour

Stabilimenta are the ribbon-like silky structures on the webs of some orb-weaving spiders (Araneidae and Uloboridae) which have attracted the attention of arachnologists for a century. Investigators have described various types of stabilimenta (silk, egg and detritus stabilimenta) from at least 12 genera of orb-weaving spiders (Eberhard 1973, 1990; Levi 1983; Nentwig & Heimer 1987). Among these types, silk stabilimenta have many forms and have been the subject of most studies. For example, in the garden spider (genus *Argiope*) the shape of a stabilimentum can be a linear zig-zag (e.g. *A. trifasciata*) or a diagonal cross (e.g. *A. argentata*) (Levi 1968). In *Argiope*, even within the same species, the shape of a stabilimentum differs at different developmental stages. Some juvenile spiders spin disk-like stabilimenta surrounding web hubs, but adults spin cross or linear forms (Nentwig & Rogg 1988).

Ever since Simon introduced the term stabilimentum in 1895 and asserted a web-stabilizing function for it (Robinson & Robinson 1970a), workers have proposed many functional hypotheses including helping to adjust web tension, serving as moulting platforms, advertising presence of the web, protecting spiders from predators and aiding in thermoregulation (Eberhard 1990).

Recently, Craig & Bernard (1990) provided evidence that the stabilimenta of *Argiope* might attract ultraviolet light (UV)-oriented insects and thereby increase the foraging efficiency of spiders. They measured the reflectivity of silks from different spider taxa and found that the stabilimenta of *A. argentata* and *Uloborus glomosus* reflect UV. Then they tested the prey-attraction hypothesis in two ways. First, in a choice experiment, more fruit flies (*Drosophila* spp.) were attracted to UV-reflecting webs. Second, in a field experiment, stabilimentum-decorated webs spun by *A. argentata* intercepted more insects than undecorated webs. Despite these provocative data, the prey-attraction hypothesis has received

Correspondence: I. M. Tso, Museum of Zoology, University of Michigan, Ann Arbor, MI, 48109-1079, U.S.A. (email: SPIDER@UMICH.EDU).

no further examination compared to other functional hypotheses (thermoregulation: Humphreys 1992; predator defence: Schoener & Spiller 1992; web advertisement: Kerr 1993). Nevertheless, some workers have provided negative evidence for or argued against the prey-attraction hypothesis. Nentwig & Heimer (1987) introduced artificial stabilimenta (of unknown reflectance properties) to sticky traps but found no increase in insect trapping ability. Ewer (1972) argued that stabilimenta can not be a lure device for insects because the area on the web around a stabilimentum lacks sticky spirals, and the prey caught by spiders did not concentrate around a stabilimentum. Therefore, the prey-attraction hypothesis needs further testing.

In this study, I tested the prey-attraction hypothesis as a function of stabilimenta by comparing the insect interception rates between stabilimentum-decorated and undecorated webs. I also tested whether stabilimenta could increase insect interception rate of those web areas immediately adjacent by comparing the interception rates between decorated and undecorated halves of webs. I examined factors other than stabilimenta that could potentially affect insect interception abilities of webs, such as web locations, catching areas and mesh sizes, to determine the effect of stabilimenta unambiguously. In addition, because herbivore and pollinator insects respond differently to UV cues (Silberglied 1979; Propok 1983), I examined whether the effectiveness of stabilimenta varied in increasing the interception rates of orthopterans and other flying insects.

MATERIALS AND METHODS

Study Site and Spiders

This study was conducted between 15 August and 25 September 1993 in the University of Michigan Matthaei Botanical Gardens in Ann Arbor, Michigan, U.S.A. Banded garden spiders, *A. trifasciata* (Forsk.), were abundant in the prairie of the Gardens. Adult female spiders frequently built a linear stabilimentum on either lower halves or both lower and upper halves of their webs. During the study, none of the decorated webs was found to contain a stabilimentum on only the upper half of web. Only adult female spiders were included in this study, because mature male spiders do not build large webs

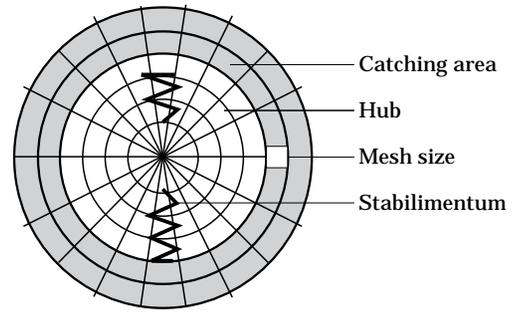


Figure 1. A schematic web of *Argiope trifasciata* demonstrating the web parameters measured. Hub is the area in the center of a web covered by non-sticky spirals and is present in both decorated and undecorated webs. Catching area is the rest of web area covered by sticky spirals. Mesh size is the distance between two consecutive sticky spirals. Stabilimentum, if present, may consist of one arm in the lower half or two arms in both lower and upper halves of a web. Sometimes stabilimenta may extend into the area covered by sticky spirals.

(Emerton 1961; Tso, personal observation). The major vegetation in the study site was spotted knapweed, *Entaurea maculosa*.

Web Characteristics

I marked web sites of 53 spiders by fastening green tapes on bamboo sticks placed beside the webs. Webs from all sites were monitored twice each day, between 0800 and 1100 hours and between 1600 and 1800 hours. In the morning I recorded the following web characteristics for webs from each site: length and location of stabilimenta (in lower web half only or in upper and lower web halves), hub diameter, number of sticky spirals and length of radius of the upper and lower halves of webs. I used these data to calculate mesh size and catching area of lower and upper web halves. I defined mesh size as the average distance between two consecutive sticky spirals, and I defined the catching area as the area on the web covered by sticky spirals (Fig. 1). Mean mesh size and overall catching area were calculated as follows:

Mean mesh size = $\frac{1}{2}$ (upper web half mesh size + lower web half mesh size)

$$= \frac{1}{2} \left[\frac{\left(r_u - \frac{H}{2} \right)}{S_u} + \frac{\left(r_l - \frac{H}{2} \right)}{S_l} \right]$$

Overall catching area=(catching area of upper web half)+(catching area of lower web half)

$$= \left[\frac{1}{2} \pi r_u^2 - \frac{1}{2} \pi \left(\frac{H}{2} \right)^2 \right] + \left[\frac{1}{2} \pi r_l^2 - \frac{1}{2} \pi \left(\frac{H}{2} \right)^2 \right]$$

where H equals hub diameter, r_u and r_l equal the length of radius of upper and lower halves of webs, and S_u and S_l equal the number of sticky spirals of upper and lower web halves.

Estimating Daily Insect Interception Rate

I recorded the number and position of both damaged areas and wrapped prey on webs in the afternoon to estimate webs' daily insect interception rate (IIR). For each wrapped prey observed I also noted whether it was flying insect or orthopteran. Usually no insects were trapped on webs at the time of morning monitoring. I excluded those damaged areas and wrapped prey already present at the time of morning monitoring from the estimation of daily IIR. Thus, I only considered the insects intercepted between morning and afternoon in this study. The positions of damage on webs were used to compare IIRs between decorated and undecorated halves of webs. I excluded data collected on rainy and extremely windy days from the analysis.

I used the number of damage areas on webs, instead of number of wrapped prey, to estimate the daily IIR for the following reasons. First, even when insects hit *Argiope* spiders' webs, spiders frequently failed to subdue them (Olive 1980; Pasquet & Leborgne 1990). The catching success of *A. trifasciata* ranged from 17% (Lepidoptera) to 53% (Orthoptera) (Olive 1980). Second, *A. trifasciata* frequently remove consumed prey from the webs and dropped them to the ground. Both events resulted in damage but no wrapped prey on webs, and *A. trifasciata* did not seem to repair those areas during the rest of the day. Thus, number of areas of web damage was a more valid estimate of IIR than number of wrapped prey.

I also examined the response of different categories of insects to the stabilimenta. Because counting the number of damaged areas was used to estimate the insect interception rate, a comparison of the IIRs of different taxa of insects was not possible. I could reliably use the size of the damage area on webs, however, to distinguish between small flying insects and large orthopterans. When a small flying insect hit the web, the

spider moved towards it and tried to subdue it, resulting in a small hole around where the insect was intercepted and wrapped. When a large orthopteran was caught, the activities of both the attacking spider and the struggling prey resulted in the loss of a whole sector of the web ($\frac{1}{4}$ to $\frac{1}{3}$ the area of the web). Thus, the distinct difference in the size of damage (small holes versus loss of whole sector) enabled the identification of prey type. To test the reliability of IIR estimation using web damages, I performed a Spearman correlation between number of damaged areas and number of wrapped prey, which was significant for both categories of insects (Spearman $r=0.536$ for flying insects and $=0.914$ for orthopterans, $P_S=0.000$). Thus, I could reliably use the number and size of damaged area on webs to estimate IIRs of small flying insects and large orthopterans.

Data Analysis

In addition to stabilimenta, web locations and web characteristics such as catching area and mesh size could potentially affect the IIR of a web. To determine whether differences existed between the IIRs of webs recorded from different locations, I used a Kruskal-Wallis one-way ANOVA. To perform this test appropriately, each web site used in analysis must contain both decorated and undecorated webs. For 20 of the 53 web sites marked, the sites remained occupied for more than 6 consecutive days. Four of the 20 web sites had no undecorated webs during the study. Thus, I only used the IIRs of 184 webs measured from the remaining 16 web sites. To prevent an interaction between stabilimentum and web location effects, the data collected from decorated webs ($N=104$) and undecorated webs ($N=80$) were examined separately. Because I was testing whether web location affects a web's IIR, whether the same spider built the webs recorded from a certain web site would not affect the result. Then, I used a Mann-Whitney U -test to compare the IIRs, catching area and mesh size between decorated and undecorated webs. The effect of stabilimenta could be unambiguously determined if there was (1) a significant difference in IIR between decorated and undecorated webs, (2) no significant difference in catching area and mesh size between decorated and undecorated webs and (3) no significant difference in IIR between web sites.

Table I. Results of Kruskal–Wallis one-way ANOVA testing the effect of web site location, catching area, mesh size and stabilimentum length on daily flying insect and orthopteran interception rates of decorated ($N=104$) and undecorated ($N=80$) webs spun by *Argiope trifasciata* in the field

	Web site	Catching area (cm ²)	Mesh size (mm)	Stabilimentum length (mm)
Flying insect interception rate				
Decorated webs				
<i>H</i>	18.068	0.306	3.901	3.114
<i>P</i>	0.259	0.858	0.272	0.211
Undecorated webs				
<i>H</i>	20.301	1.007	1.614	
<i>P</i>	0.161	0.604	0.656	
Orthopteran interception rate				
Decorated webs				
<i>H</i>	17.870	3.538	4.143	0.728
<i>P</i>	0.270	0.170	0.246	0.695
Undecorated webs				
<i>H</i>	9.539	2.408	3.016	
<i>P</i>	0.848	0.300	0.389	

I also examined the effects of stabilimentum length and web characteristics on IIRs. I examined data from decorated webs separately from those of undecorated webs to reduce the interaction between stabilimenta and web parameters. I divided those web characteristics (catching area, mesh size and stabilimentum length) into groups of approximately equal sample size then compared the insect interception rates among those groups. For both decorated and undecorated webs, I divided catching area into three groups (<400, 400–800, >800 cm²), mesh size into four groups (<3, 3–4, 4–5, >5 mm) and stabilimentum length into three groups (<23, 23–30, >30 mm). A Kruskal–Wallis one-way ANOVA was used to compare the IIRs between the groups of each web characteristic examined.

To determine whether a stabilimentum increased the IIR of an adjacent area, I used the Wilcoxon signed-rank test to compare IIRs between decorated and undecorated halves of webs. I performed this intra-web comparison by comparing the IIRs between upper and lower web halves and also between left and right web halves. I also compared catching area, mesh size and stabilimentum length between upper and lower web halves to see whether they contributed to any difference in IIR. Because I compared IIRs between different halves of each individual web and did not need to consider the location of a web, I used data from all 53 web sites. I performed the

test separately on webs without stabilimenta ($N=88$), webs with one arm of stabilimentum on the lower web halves ($N=118$) and webs with stabilimenta on both halves of webs ($N=46$).

RESULTS

Effects on Insect Interception Rates

For both decorated and undecorated webs, there were no differences in either flying insects or orthopteran interception rates between those 16 web sites (Table I). Decorated webs intercepted more flying insects but not more orthopterans than undecorated webs (Table II). Catching area of decorated webs did not differ from that of undecorated webs, but mesh size differed significantly between two kinds of webs. The average mesh size of undecorated webs was only 0.5 mm larger than that of decorated webs, however.

When the IIRs were assorted into groups according to their size of catching area, mesh size and stabilimentum length and the comparisons made between the groups, no web characteristic significantly affected webs' insect interception rate (Table I). Among decorated and undecorated webs, webs with different size categories of catching area or mesh size did not differ in IIRs of either type of insects. Among decorated webs, webs with different size categories of stabilimentum length again did not differ in IIR (Table I).

Table II. Means, standard deviations, and Mann-Whitney *U* statistics of daily flying insect and orthopteran interception rates (number insects intercepted per web per day), catching area, mesh sizes and stabilimentum length of decorated and undecorated webs spun by *Argiope trifasciata* in the field

	<i>N</i>	Flying insects	Orthopterans	Catching area (cm ²)	Mesh size (mm)	Stabilimentum length (mm)
Decorated webs	104	2.21 ± 2.1	0.17 ± 0.4	687 ± 355	3.87 ± 1.4	26.09 ± 10.1
Undecorated webs	80	1.28 ± 1.3	0.18 ± 0.4	606 ± 300	4.38 ± 1.6	0.00 ± 0.0
<i>U</i>		3040.000	4295.000	3664.500	5010.500	
<i>P</i>		0.001	0.551	0.167	0.018	

Table III. Means, standard deviations and Wilcoxon signed rank test statistics (*T*) of daily flying insect and orthopteran interception rate (number insects intercepted per web per day), catching area, mesh sizes and stabilimentum length of upper and lower halves of webs spun by *Argiope trifasciata* in the field

	<i>N</i>	Flying insects	Orthopterans	Catching area (cm ²)	Mesh size (mm)	Stabilimentum length (mm)
Undecorated						
Upper half	88	0.835 ± 1.103	0.034 ± 0.166	230 ± 156	4.445 ± 1.989	
Lower half	88	0.733 ± 0.997	0.148 ± 0.365	417 ± 212	4.375 ± 1.984	
<i>T</i>		-0.873	2.887	6.357	-1.014	
<i>P</i>		0.383	0.004	0.000	0.310	
Lower half decorated						
Upper half	118	1.017 ± 1.138	0.025 ± 0.205	230 ± 150	3.998 ± 1.568	
Lower half	118	1.072 ± 1.190	0.178 ± 0.465	415 ± 235	3.744 ± 1.427	22.180 ± 7.490
<i>T</i>		0.468	3.227	7.101	-2.843	
<i>P</i>		0.640	0.001	0.000	0.004	
Both halves decorated						
Upper half	46	1.250 ± 1.246	0.022 ± 0.103	259 ± 217	3.901 ± 1.645	16.570 ± 5.699
Lower half	46	1.163 ± 1.216	0.239 ± 0.418	435 ± 217	3.595 ± 1.724	24.977 ± 5.939
<i>T</i>		-0.480	3.162	4.226	-1.440	5.736
<i>P</i>		0.631	0.002	0.000	0.150	0.000

This result suggested that stabilimentum length does not significantly affect the IIR of decorated webs.

The low daily IIR of *A. trifasciata* may have affected the reliability of IIR estimation. Some workers using tropical *Argiope* species in their studies suggested that the mapping of damage areas on webs must be practised within four to five hours after completion of webs and must be done hourly because as damage to a web accumulated, the web sometimes went beyond identification (C. L. Craig, personal communication). Although this might be the case for those tropical *Argiope* spiders that can intercept as many as two insects per hour (Craig & Bernard 1990), the temperate *A. trifasciata*, on average, intercept only one to two insects per day (Table II). This low daily IIR left the webs fairly intact at the end of day, which

enabled precise recording and identification of web damage. None the less, I also excluded insect interception data collected from rainy and extremely windy days to avoid incorporating damages caused by rain and wind. Thus, a single daily census of damage pattern should be appropriate for this temperate *A. trifasciata*.

Results From Intra-web Comparison

Presence of a stabilimentum did not increase IIR of decorated web half compared to the other half (Table III). Flying insect interception rate of upper web halves of undecorated webs did not differ from that of lower web halves. Those webs decorated in lower halves did not intercept more flying insects in their decorated halves. No significant difference was found in flying insect

Table IV. Means, standard deviations and the Wilcoxon signed rank test statistics (T) of daily flying insect and orthopteran interception rates (number insects intercepted per web per day) of left and right halves of webs spun by *Argiope trifasciata* in the field

	N	Flying insects	Orthopterans
Undecorated			
Left half	88	0.761 ± 1.069	0.102 ± 0.314
Right half	88	0.835 ± 0.964	0.102 ± 0.285
T		0.740	0.190
P		0.459	0.850
Lower half decorated			
Left half	118	1.055 ± 1.141	0.127 ± 0.371
Right half	118	1.081 ± 1.288	0.085 ± 0.295
T		0.009	- 1.107
P		0.993	0.268
Both halves decorated			
Left half	46	1.141 ± 1.134	0.098 ± 0.271
Right half	46	1.293 ± 1.397	0.163 ± 0.350
T		0.768	1.000
P		0.442	0.317

interception rates between lower and upper halves of webs decorated in both web halves, although lower halves tended to have a longer stabilimentum. In contrast, orthopteran IIRs were higher in lower web halves in all three types of webs. For all three types of webs, both categories of insects were equally intercepted between right and left web halves (Table IV), and the mean catching area was larger in lower web halves. Except in those webs decorated in lower web halves, mesh size did not differ significantly between web halves. The mesh size difference between web halves of those webs decorated in lower half was only 0.254 mm, however.

DISCUSSION

The prey-attraction hypothesis as one of the functions of stabilimenta is supported by the daily IIRs of flying insects but not by those of orthopterans. The average IIR of flying insects was 2.212 (± 2.112) insects per web per day for the stabilimentum-decorated webs and 1.288 (± 1.333) for the undecorated webs, a 72% difference. This value is greater than that estimated by Craig & Bernard (1990; 31.3%, inferred value). The average orthopteran IIR of decorated webs did not differ from that of undecorated webs. These results suggest that stabilimenta on webs of *A. trifasciata* attract flying insects, but not orthopterans.

The correlation between higher IIR of flying insects and presence of a stabilimentum on a web may not necessarily result from insects being attracted to decorated webs. Alternatively, flying insects may be more capable of avoiding undecorated webs, thus leading to higher IIRs for decorated webs. The web-avoiding ability of flying insects is greatly determined by webs' visibility, however. Web visibility in turn is determined by mesh size and light intensity (Rypstra 1982; Craig 1986, 1988; Craig & Freeman 1991). When light intensity is the same, webs with more spirals per unit area (smaller mesh size) are more visible to flying insects and thus are easier to avoid. In this study, the average mesh size of decorated webs was significantly smaller (3.87 ± 1.4 mm) than that of undecorated webs (4.38 ± 1.6 mm). This result indicates that when the presence of stabilimenta is not considered, decorated webs are more visible and easier to avoid than undecorated webs. Thus, the higher IIR of flying insects in decorated webs is unlikely to result from insects being less able to avoid them.

The difference in flying insect interception rates between decorated and undecorated webs did not result from locations of web sites or characteristics of webs. The foraging success of orb-weaving spiders can be greatly affected by the location of web sites, because the distribution of insects is sometimes patchy (Craig 1989). The characteristics of a web can also affect its insect interception ability. Larger webs tend to trap more prey

(Brown 1981; Craig 1989; Higgins & Buskirk 1992). Mesh size, as previously discussed, determines a web's visibility to approaching insects and thus can potentially affect the web's insect interception ability. Different web sites in this study did not significantly differ in insect interception rates, however, nor did catching area and mesh size significantly differ between decorated and undecorated webs (the 0.5 mm mesh size difference could be ignored because the size of prey greatly exceeded that). None of the Kruskal-Wallis one-way ANOVAs performed to examine the effects of catching area and mesh size on interception rates of undecorated webs showed significance. These results suggest that the difference in flying insect interception rates between decorated and undecorated webs arise from presence or absence of stabilimenta. One cannot conclude, however, that location of web sites, catching area and mesh size are unimportant for determining foraging success of orb weaving spiders. The non-significance of those characteristics in this study only suggests that they did not contribute to differential interception success between different types of webs when data were collected.

The difference in responses to UV light between herbivore and pollinator insects seems responsible for the differential attractiveness of stabilimenta to those insects. Insects tend to match the visual cues they receive with some pre-formed template of stimulus perception (Craig 1994). A UV-reflecting stabilimentum may be perceived as an escape route or potential foraging site by flying pollinators (Goldsmith 1962; Craig & Bernard 1990). Although UV light is an attractant for pollinator insects, however, yellow tends to be a strong foraging stimulus to most herbivorous insects (Prokopy 1983). Because most orthopterans are herbivores, they may not associate UV cues with the foraging stimulus, which may explain why stabilimenta cannot increase the interception rate of orthopterans.

The effectiveness of stabilimenta in attracting flying insects can be important for the following reasons. First, large orthopterans are not always available to *Argiope* spiders, but flying insects are the major type of prey available to some *Argiope* species. For instance, Murakami (1983) collected 387 trapped insects from the webs of *A. amoena* and found only one orthopteran. Nentwig (1985) analysed prey composition of two tropical

Argiope (*A. argentata* and *A. savignyi*) in Panama and found that only 1.7–1.9% of the prey trapped were orthopterans. Second, even though orthopterans are available in the habitats of *Argiope* spiders, their abundance may fluctuate with season or with spiders' microhabitats. Robinson & Robinson (1970b) examined the prey composition of *A. argentata* in Panama for a year and found orthopterans to be extremely scarce in March and April. Olive (1980) surveyed prey availability in different habitats of *A. trifasciata* in Michigan and found orthopterans to be more abundant in grassy than in herbaceous habitats. Thus, under situations when *Argiope* spiders must rely on capturing flying insects, stabilimenta can greatly increase the webs' interception rate.

Longer stabilimenta do not seem to attract significantly more insects than shorter ones. There was no significant difference in interception rates of either type of insect between the three groups of decorated webs sorted according to their stabilimentum length. Moreover, those webs decorated in both halves (mean stabilimentum length = 41.54 ± 9.4 mm) did not intercept more insects than those decorated in the lower halves (mean stabilimentum length = 22.18 ± 7.5 mm).

The intra-web comparison indicated that a stabilimentum will not increase the flying insect interception rate of the adjacent area. Lower halves of undecorated webs did not intercept more flying insects than upper halves, despite the larger catching area in the lower web halves. For those webs in which both web halves are decorated, IIR of flying insects again did not vary between web halves, although the mean stabilimentum length and catching area of lower halves are greater than the upper halves. These results do not contradict the prediction that a stabilimentum increases the insect interception rate of adjacent areas, because the upper web did not differ from lower web halves in stabilimentum pattern. For those webs in which only lower halves were decorated, however, no difference in flying insect interception rates was found between decorated and undecorated halves despite the larger catching area in decorated halves. Therefore, although the presence of a stabilimentum will attract more flying insects to a web, those areas on a web with a stabilimentum did not intercept more prey than those areas without it.

The result that stabilimenta do not increase the IIR of adjacent areas offers an answer to the

argument made by Ewer (1972) on the validity of stabilimenta as insect attractants. Damage patterns of all the webs mapped in this study indicate an even distribution of prey intercepted on most webs (except orthopterans) instead of a concentration around a stabilimentum. Moreover, for all the decorated webs examined, no difference in flying insect IIR was found between upper and lower or between left and right web halves. This even distribution suggests that stabilimenta might increase IIR by attracting insects to fly towards the web, instead of flying directly for a stabilimentum. When insects approach a stabilimentum and perceive the presence of a spider and a web, they may try to orientate away from the web (Craig 1986, 1988; Craig & Freeman 1991). Unless insects do not avoid the web and try to land on a stabilimentum, the insects intercepted and the damage caused will be away from a stabilimentum and will distribute randomly on webs. Therefore, the lack of sticky spirals around a stabilimentum should not affect its effectiveness in increasing spiders' foraging efficiency. Thus the avoiding behaviours of flying insects might explain why decorated and undecorated halves of a web intercept the same amount of flying insects.

Although flying insects were evenly intercepted across both halves of webs, more orthopterans were intercepted in the lower web halves of all three types of webs. If a stabilimentum increases the rate of orthopteran interceptions in proximity, the interception rate should not be higher in lower halves of undecorated webs and lower halves of webs decorated in both halves. This result again suggests that a stabilimentum does not increase the insect interception rate of the area immediately adjacent to it. Two explanations are possible for the higher orthopteran interception rate in lower web halves. First, orthopterans might be intercepted by the webs of *A. trifasciata* purely by chance, because they do not seem to be attracted by stabilimenta. Thus, lower web halves might intercept more orthopterans simply by having larger catching areas. Second, because of some orthopterans' large size, once they are intercepted they may slide down the webs while struggling to get free.

The results of this study provide an insight regarding the foraging ecology of stabilimentum-building spiders. Studies of the foraging behaviour of other orb-weaving spiders have shown a correlation between web size and foraging gain (Brown 1981; Higgins & Buskirk 1992) or an increase in

web diameter when spiders experience low foraging success (Sherman 1994). In this study, the flying insect interception rate of *A. trifasciata* was increased up to 72% by the presence of stabilimenta. To achieve the same magnitude of foraging gain, those non-stabilimentum-builders must considerably increase their web size. Although an orb web takes a spider 30–60 minutes and about 20 meters of silk (Foelix 1982), stabilimentum construction only takes less than 5 minutes and relatively little silk (Tso, personal observation). Considering both the foraging gain and building cost, building a stabilimentum, rather than building a larger web, is probably more effective to increasing foraging success of *A. trifasciata*. Although some orb-weaving spiders respond to low foraging success by building larger webs, perhaps *Argiope* spiders respond by building stabilimenta on their webs, or both. How *Argiope* spiders adjust stabilimentum building and web size to respond to different prey availability needs further study.

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