

Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae)

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Abstract

Many spiders include conspicuous designs of white silk called stabilimenta in the centre of their orb webs. Stabilimenta are highly variable in their form and frequency and are hypothesized to function in either defence against predators or attraction of prey. These hypotheses generate different predictions about the effect of foraging success on variation in the form and frequency of stabilimenta. If stabilimenta serve as prey attractants, then starved spiders should invest more in them than well-fed spiders, while the opposite pattern is expected if stabilimenta function as a predator defence mechanism. This study examines the effect of variation in foraging success of the yellow garden argiope *Argiope aurantia* and the banded argiope *Argiope trifasciata* on variation of their stabilimenta and orb webs. Both species built smaller stabilimenta when fed less, even though a stabilimentum accounts for only 10% of the dry weight of an orb web. Poorly fed *A. trifasciata* also included stabilimenta in their webs less often than did well-fed *A. trifasciata*. Differences in stabilimenta were independent of differences between treatments in the orb webs themselves. These results argue against the prey attraction hypothesis, but not the predator defence hypothesis, since well-fed spiders invested more in stabilimenta.

Key words: stabilimenta, *Argiope*, spider webs, predator, prey

INTRODUCTION

Stabilimenta are conspicuous designs of white silk included in the otherwise cryptic orb webs of several genera of orb-weaving spiders. They are highly variable in shape, including spiral disks, crosses or vertical lines, and are often incomplete (Hingston, 1927; Eberhard, 1973). Detritus or egg sacs included in orb webs are also sometimes termed stabilimenta (Eberhard, 1990), but these structures are not discussed here.

Many functions have been proposed for stabilimenta, though evidence is lacking for most. They were initially thought to mechanically stabilize orb webs (McCook, 1889; Simon, 1895; Robinson & Robinson, 1970a). Yet the silk that stabilimenta are built from is too loosely attached to the web to affect it mechanically (Eberhard, 1973; Foelix in Edmunds, 1986). Other early hypotheses suggested that stabilimenta functioned as 'love paths' to guide male spiders to the female (Wolfram in Eberhard, 1973) or deposits of excess or reserve prey swathing silk (Vinson in Eberhard, 1973). Yet, stabilimenta are common in webs of juvenile spiders, built long before sexual maturity (Eberhard, 1973; Edmunds, 1986). It is unlikely that stabilimenta are reserve swathing silk since the silks are structurally different (Eberhard, 1973) and

stabilimenta are often included in moulting webs, which do not contain the sticky silk necessary for prey capture (Robinson & Robinson, 1973). A thermoregulatory, sun shading, function has been suggested for disk-shaped stabilimenta in *Neogea* sp. (Humphreys, 1992) but is unlikely for linear designs which often do not occlude the bodies of spiders (Nentwig & Heimer, 1987).

Stabilimentum production has evolved many times in the Araneidae but is found only among spiders that rest at the hub of their webs in daylight (Eberhard, 1973; Scharff & Coddington, 1997). Stabilimenta are therefore thought to function as visual signals used in either predator defence or attraction of prey. The designs may camouflage spiders (Eberhard, 1973; Edmunds, 1986), startle predators (Tolbert, 1975; Schoener & Spiller, 1992), or even serve as an aposematic warning to flying birds or large insects (Ewer, 1972; Eisner & Nowicki, 1983; Kerr, 1993). Prey may be attracted to the webs of spiders by ultraviolet (UV) light reflected off the stabilimenta (Craig & Bernard, 1990; Tso, 1996).

Both classes of functional hypotheses have had difficulty accounting for the great amount of variation in shape and frequency of stabilimenta (Eberhard, 1990). Within a species, individual spiders vary in how often

they build these designs (Eberhard 1973; Edmunds, 1986). Spiders may also produce several different types of designs over their lifetime and often include incomplete designs in their webs (Ewer, 1972; Edmunds, 1986; Nentwig & Rogg, 1988). Some of this variability has been correlated with the maturation of spiders (Ewer, 1972; Robinson & Robinson, 1973; Edmunds, 1986; Nentwig & Rogg, 1988). Yet few correlations between stabilimentum construction and environmental parameters have been demonstrated (Edmunds, 1986; Nentwig & Rogg, 1988).

Hypotheses for a prey attraction or predator defence function for *Argiope* stabilimenta generate mutually exclusive predictions about the effect of foraging success on stabilimentum variation, based upon the trade-offs that spiders must make between foraging and defence. Many species of orb-weaving spiders increase their foraging effort, when starved, through an increase in the capture area of their webs (Higgins & Buskirk, 1992; Pasquet, Ridwan & Leborgne, 1994; Sherman, 1994). It has been argued that webs with more stabilimentum silk should catch more prey (Craig & Bernard, 1990) and that *Argiope aetherea* adjusts the amount of silk in stabilimenta to increase insect attraction in dimly lit habitats (Elgar, Allen & Evans, 1996). Therefore, an increase in stabilimentum size and frequency in the webs of starved spiders seems likely if these designs are prey attractants, particularly if they are cheap to build. At the same time, these highly visible structures could also attract predators to webs. Pompilid and sphecid wasps as well as salticid spiders are important predators of orb-weaving spiders (Tolbert, 1975; Hoffmaster, 1982; Coville, 1987) and are likely to have visual pigments similar to the arthropod prey of *Argiope* (Chittka, 1996). Furthermore, vertebrate predators such as birds can perceive and use the UV light (Bleiweiss, 1994; Derim-Oglu & Maximov, 1994) thought to be so crucial to prey attraction. Birds can also associate artificial stabilimenta with potential prey (Robinson & Robinson, 1970a). Thus, if stabilimenta are prey attractants, satiated spiders are likely to decrease investment in them to avoid increased predation risk. Alternatively, if stabilimenta function as a predator defence mechanism, then starved spiders would be expected to build them less often, particularly if stabilimenta are energetically costly. The silk in stabilimenta could be calorically expensive. More likely, a highly visible stabilimentum designed to advertise webs to predators may also help prey avoid webs. Web visibility has been demonstrated to be a very important factor in prey capture success (Olive, 1980; Craig & Freeman, 1991) and there is evidence that araneid orb webs have evolved to be visually cryptic (Craig, 1986, 1988; Craig, Bernard & Coddington, 1994). Craig (1994) has argued that variation in stabilimenta in *A. argentata* functions to prevent some prey from learning to avoid webs. Thus, satiated spiders would be more likely to include conspicuous defensive structures in their webs.

If stabilimenta are prey attractants, spiders experiencing poor foraging success should invest more in them

despite a probable increased risk of predation. Alternatively, if stabilimenta are defensive structures, then spiders experiencing good foraging success should invest more in them despite a probable decrease in prey capture. Such trade-offs between foraging success and predation risk may be already made by juvenile *Argiope* when they include a non-sticky silk barrier around their web. While the barrier may physically deter predators, it may also inhibit prey from reaching the webs (Tolbert, 1975). Foraging-defence trade-offs are also well documented in colonial orb-weaving spiders (Rayor & Uetz, 1990; Uetz & Hieber, 1997).

Although these predictions have not been explicitly tested, Eberhard (1973) and Nentwig & Rogg (1988) found no influence of short-term fluctuations in the foraging success of *Uloborus diversus* or *Argiope argentata* on stabilimentum frequency. But, neither study examined the effect on stabilimenta of differences in the foraging success between spiders, which could easily result from variation in prey abundance between web sites (Craig 1989).

I examined the effect of longer term differences between groups of spiders in the amount of prey captured and of variance in capture rate on the frequency of inclusion and size of stabilimenta in the webs of the yellow garden argiope *Argiope aurantia* Lucas and the banded argiope *Argiope trifasciata* (Forsk.)

MATERIALS AND METHODS

All of the spiders used in this experiment were collected on 30 August 1996 from a prairie reserve at the Marion campus of The Ohio State University (latitude 40°34', longitude 83°05'). *Argiope aurantia* and *Argiope trifasciata* are common as adults in old fields of Ohio in late summer and early autumn. Both species build disc stabilimenta when juveniles and vertical line stabilimenta as mature adults. After collection, all spiders were starved for 5 days to allow them to evacuate their guts (Nakamura, 1987). Spiders were weighed to the nearest mg on a Mettler PM400 balance before and after the experiment.

Twenty-eight female *A. aurantia* and 10 female *A. trifasciata* were used in the experiment. All were mature except for one of the High Prey *A. trifasciata* which moulted to maturity on the fourth day of the experiment. *A. aurantia* were housed in wooden cages (35 × 35 × 10 cm) covered with clear plastic sheeting on the top, front, and back. Screen sides provided ventilation. Wooden rods, 35 cm high, at either end of each cage were connected at the top by a thread to provide web attachment sites. *A. trifasciata* were housed in metal cages (45 × 45 × 8 cm) with a Plexiglas front and back. Here, the screen top and sides provided a continuous web building substrate. The experiment was conducted in a south-east room of the OSU insectary greenhouse where vents maintained temperature near outdoor levels. Light intensity was not homogeneous throughout the room. Therefore, *A. aurantia* cages for

each of the 2 feeding treatments were placed alternately on shelves around the room, with *A. trifasciata* cages mixed among them, so that both species and all treatments were subjected to similar variation in light. All spiders were sprayed with a fine mist of water every day.

Feeding treatments

Individuals of both species were randomly assigned to either a High Prey or a Low Prey treatment (15 *A. aurantia* and 4 *A. trifasciata* were in the High Prey treatments, and 13 *A. aurantia* and 6 *A. trifasciata* were in the Low Prey treatments). Prey were placed directly in the capture area of webs. If a spider had not built a web, prey was instead offered to it by gently rubbing the larva against the chelicerae of the spider until accepted or until 90 s elapsed. High Prey spiders were offered one large *Tenebrio molitor* larva (13.3 ± 1.0 mg) daily for the entire 27 days of the experiment. Low Prey spiders were offered approximately one-third this amount, in 2 sequential feeding regimes.

All Low Prey spiders were included first in a high variance regime and then in a low variance regime. During the high variance regime, frequency of prey capture was altered. Low Prey spiders were offered the same size of larvae as High Prey spiders, but one-third as often. They received one large *T. molitor* larva (13.3 ± 1.0 mg) every 3 days for the 13 days of the high variance regime. Then size of prey was manipulated in the low variance regime. Low Prey spiders were now offered smaller prey than the High Prey spiders, but at the same rate, for the final 14 days of the experiment. In the low variance regime 1 small *T. molitor* larva (3.6 ± 0.8 mg) was offered to Low Prey spiders daily. This change in feeding regime allowed me to determine if prey size or variance of capture rate had a confounding influence.

Data collection

I used callipers to measure, to the nearest mm, the maximum height and width of each web, from outermost sticky spirals, and the maximum height and width of the free zone, from innermost sticky spirals (Fig. 1). Overall web area and free zone area were estimated using the formula: $\text{area} = \pi * 0.5 (\text{height}) * 0.5 (\text{width})$. Capture area of the web was then computed as: $\text{capture area} = \text{web area} - \text{free zone area}$.

Stabilimenta consisted of either a single lower vertical arm or both a lower and an upper vertical arm. I measured the length of each arm to the nearest mm with callipers. Stabilimenta were generally contained within 2 adjacent radii which diverged from the centre of the web (Fig. 1). Therefore, stabilimentum width was highly dependent upon stabilimentum length and I did not include it in the analysis.

Often spiders did not build new webs every day, but data were only collected from new webs. If a spider remained in an old web for 2 days, I broke several radii

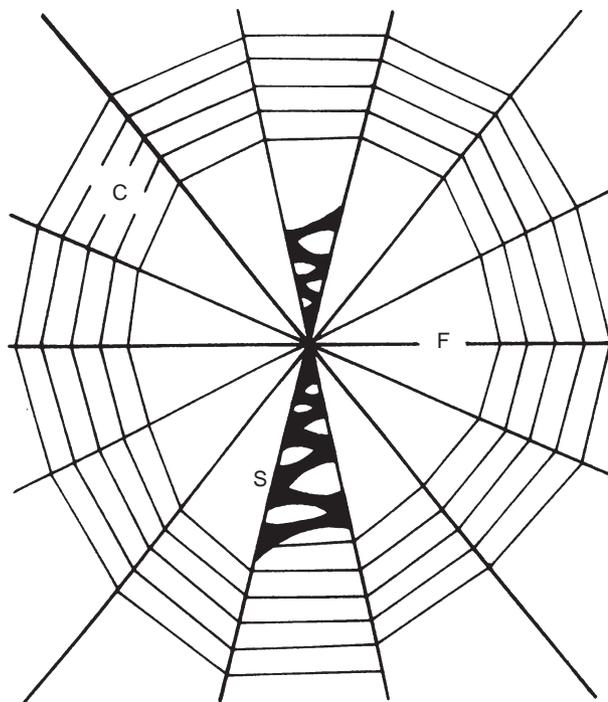


Fig. 1. A stylized orb-web containing a stabilimentum (S) consisting of both a lower and an upper arm. The capture area (C) is that portion of the orb-web covered by sticky spirals. The free zone (F) is the inner portion of the orb web and contains no sticky spirals. *Argiope aurantia* and *Argiope trifasciata* both rest at the centre of the free zone of their webs during daylight.

to collapse the web and encourage rebuilding. I occasionally damaged webs during data collection. This prevented complete data collection for 5 *A. trifasciata* orb webs.

Web collection

I collected 19 *A. aurantia* laboratory webs on the final 4 days of the experiment and weighed them to compare how much silk was invested in stabilimenta and webs. *Argiope aurantia* characteristically filled in the hub of their orb webs with an amorphous shield of white silk that was laid down just before the stabilimentum, with similar movements of the abdomen. I assumed that the hub silk was homologous to that in the stabilimentum itself. I cut out the hub and stabilimentum using forceps heated in a clean blue flame and wrapped it around a small, pre-weighed piece of nylon fishing line. Finally, I cut the orb web from the frame and wrapped it around a second piece of pre-weighed fishing line. Because the sticky silk of the web absorbed water, all samples were dried at 50°C for at least 48 h before I weighed them, to the nearest μg , on a Mettler UMT2 balance. Although dehydration of the nylon line was minuscule, I dried and weighed 12 additional pieces of fishing line to obtain a correction factor for dehydration of the nylon itself.

Table 1. Mean (\pm SE) stabilimentum parameters for High Prey (HP) and Low Prey (LP) *Argiope aurantia*

Parameter	HP ($N = 15$)	LP ($N = 13$)	P
Upper arm			
Frequency	0.59 ± 0.05 , $N_w = 111$	0.56 ± 0.04 , $N_w = 132$	< 0.100
Length (mm)	23.8 ± 1.1 , $n = 65$	20.1 ± 1.0 , $n = 74$	< 0.010
Lower arm			
Frequency	0.87 ± 0.03 , $N_w = 111$	0.88 ± 0.03 , $N_w = 132$	< 0.100
Length (mm)	38.0 ± 1.2 , $n = 97$	30.5 ± 0.8 , $n = 116$	< 0.001

P values are from nested ANOVAs comparing the treatments, except for stabilimentum arm frequencies where P values are from χ^2 tests comparing the number of spiders which built a stabilimentum arm more or less often than the average of the treatments combined (a null hypothesis of no difference). N , number of spiders in a treatment; N_w , total number of webs built in a treatment; n , number of webs containing the appropriate stabilimentum arm.

Table 2. Mean (\pm SE) stabilimentum parameters for High Prey (HP) and Low Prey (LP) *Argiope trifasciata*

Parameter	HP ($N = 4$)	LP ($N = 6$)	P
Upper arm			
Frequency	0.75 ± 0.05 , $N_w = 65$	0.16 ± 0.04 , $N_w = 88$	< 0.001
Length (mm)	17.8 ± 1.5 , $n = 49$	10.8 ± 1.7 , $n = 14$	< 0.050
Lower arm			
Frequency	0.88 ± 0.04 , $N_w = 65$	0.63 ± 0.05 , $N_w = 88$	< 0.001
Length (mm)	32.4 ± 1.7 , $n = 57$	24.0 ± 1.4 , $n = 55$	< 0.025

P values are from nested ANOVAs comparing the treatments, except for stabilimentum arm frequencies where P values are the probability that the observed distribution of spiders building stabilimenta arms more or less frequently than the average of both treatments combined could occur by chance (i.e. that this distribution could occur if every spider had a 50% chance of building a stabilimentum arm more often than expected). N , the number of spiders in a treatment; N_w , total number of webs built in a treatment; n , number of webs containing the appropriate stabilimentum arm.

Data analysis

All comparisons of web and stabilimentum measurements between treatments were made separately for the 2 species.

I compared the frequency with which spiders built stabilimenta between treatments using contingency tests. Each spider was classified according to whether it built stabilimenta more or less often than the mean frequency of all the spiders. I then used a chi-square goodness of fit test to compare the distribution of spiders above and below that overall mean.

Stabilimentum length was normally distributed and I compared it between treatments using nested ANOVAs (Sokal & Rohlf, 1981). The multiple stabilimenta built by individual spiders were nested within each treatment to avoid pseudo-replication. Many web parameters were not normally distributed so nested ANOVAs could not be performed. Instead, I examined all web parameters using t -tests to compare the means of each spider, thereby preventing pseudo-replication.

I examined the effect of prey variance regime within the Low Prey treatment by using Wilcoxon signed rank tests to compare the means for each spider between the high variance and low variance regimes.

RESULTS

Initial spider mass was similar between treatments for *A. aurantia* (High Prey = 542.4 ± 62.7 mg, Low

Prey = 440.7 ± 66.0 mg; $t = 1.11$, $P > 0.25$) and mass did not change significantly over the experiment for either High Prey treatment ($t = 0.771$, $P > 0.45$) or Low Prey treatment ($t = 1.471$, $P > 0.16$). *Argiope aurantia* produced egg sacs throughout the experiment (High Prey $n = 8$, Low Prey $n = 7$). *Argiope trifasciata* initial mass was similar between treatments ($t = 0.28$, $P > 0.75$) but mass increased significantly in both the High Prey treatment (initial = 181.7 ± 30.6 mg, final = 420.3 ± 66.4 mg; $t = 3.67$, $P < 0.05$) and Low Prey treatment (initial = 192.3 ± 22.7 mg, final = 400.3 ± 54.3 mg; $t = 4.86$, $P < 0.005$). However, there was no significant difference between treatments in the increase ($t = 0.412$, $P > 0.65$). Egg sacs were produced by *A. trifasciata* only on the last 8 days of the experiment (High Prey $n = 4$, Low Prey $n = 1$).

Effect of variance regime

Low Prey treatment webs and stabilimenta were relatively similar between prey variance regimes, for both species. Wilcoxon signed rank tests revealed that *A. aurantia* built significantly longer free zones during the low variance regime ($P < 0.05$; 105.8 ± 2.3 mm vs 98.3 ± 2.5 mm). They also built longer lower stabilimentum arms during the low variance regime ($P < 0.05$; 31.8 ± 1.0 mm vs 28.6 ± 1.5 mm). *Argiope trifasciata* orb webs were significantly wider in the low variance regime ($P < 0.05$; 296.1 ± 8.3 mm vs 268.9 ± 10.8 mm). For each of these three parameters, the mean of both regimes and

Table 3. Mean (\pm SE) web parameters for High Prey (HP) and Low Prey (LP) *A. aurantia*

Parameter	HP ($N = 15$)	LP ($N = 13$)	P
Web			
Area (mm^2)	40 165 \pm 1206, $n = 111$	39 719 \pm 1164, $n = 132$	<0.37
Height (mm)	243.6 \pm 3.9, $n = 111$	238.5 \pm 4.2, $n = 132$	<0.32
Width (mm)	206.7 \pm 3.6, $n = 111$	205.4 \pm 3.6, $n = 132$	<0.32
Free zone			
Area (mm^2)	8635 \pm 381, $n = 111$	7362 \pm 259, $n = 132$	<0.04
Height (mm)	112.6 \pm 2.7, $n = 111$	102.7 \pm 1.7, $n = 132$	<0.02
Width (mm)	92.8 \pm 2.3, $n = 111$	88.3 \pm 1.6, $n = 132$	<0.11
Capture area (mm^2)	31 816 \pm 1159, $n = 111$	32 357 \pm 1108, $n = 132$	<0.45

P values are from t -tests comparing the means of each spider. N , number of spiders in a treatment; n , number of webs measured for a parameter.

Table 4. Mean (\pm SE) web parameters for High Prey (HP) and Low Prey (LP) *A. trifasciata*

Parameter	HP ($N = 4$)	LP ($N = 6$)	P
Web			
Area (mm^2)	62 649 \pm 3563, $n = 63$	70 877 \pm 3000, $n = 88$	<0.63
Height (mm)	288.8 \pm 9.9, $n = 65$	304.9 \pm 8.3, $n = 88$	<0.45
Width (mm)	257.8 \pm 71.3, $n = 63$	285.11 \pm 6.3, $n = 88$	<0.45
Free zone			
Area (mm^2)	6811 \pm 283, $n = 62$	7495 \pm 248, $n = 86$	<0.25
Height (mm)	98.9 \pm 2.9, $n = 63$	100.7 \pm 2.1, $n = 87$	<0.84
Width (mm)	84.9 \pm 2.2, $n = 62$	90.8 \pm 2.0, $n = 86$	<0.11
Capture area (mm^2)	55 564 \pm 3599, $n = 62$	62 507 \pm 3054, $n = 86$	<0.50

P values are from t -tests comparing the means of each spider. N , number of spiders in a treatment; n , number of webs measured for a parameter.

the Low Prey treatment mean itself were consistently all higher or all lower than the mean of the High Prey treatment.

Effect of prey treatment

Lower and upper stabilimentum arms were significantly shorter in Low Prey treatment orb webs for both *A. aurantia* (Table 1) and *A. trifasciata* (Table 2). *Argiope trifasciata* webs included both stabilimentum arms significantly less often in the Low Prey treatment than in the High Prey treatment (Table 2). All of the High Prey *A. trifasciata* built both stabilimentum arms more often than average. While all Low Prey treatment *A. trifasciata* built the upper stabilimentum arm less often than average, and all but one built the lower arm less often than average. Chi-square tests could not be conducted because of the empty cells and P -values were instead calculated as the probability of these skewed distributions occurring by chance (i.e. that these distributions would occur if every spider had a 50% chance of building stabilimenta more often than average).

Prey treatment had little effect on the webs of either *A. aurantia* (Table 3) or *A. trifasciata* (Table 4), except that Low Prey *A. aurantia* built significantly shorter free zones ($P < 0.02$) and consequently had significantly smaller free zone areas ($P < 0.04$).

Stabilimentum and web mass

Web mass was $1404 \pm 632 \mu\text{g}$ while the mass of the stabilimentum and hub together was $304 \pm 210 \mu\text{g}$. The hub and stabilimentum of an additional three webs were collected and were of equal mass ($111 \pm 23 \mu\text{g}$ and $111 \pm 30 \mu\text{g}$, respectively). Thus, stabilimenta alone accounted for approximately 10% of the dry mass of silk in webs that included them.

DISCUSSION

My study demonstrates that the foraging success of *Argiope* has a significant effect on stabilimentum building. Well-fed *A. trifasciata* included stabilimenta in their webs more often than hungrier spiders. Both *A. aurantia* and *A. trifasciata* built larger stabilimenta when well fed. These results agree with the predictions of the predator defence hypothesis but do not support those of the prey attraction hypothesis.

Feeding treatments were chosen to approximate moderate variation in foraging success of temperate *Argiope* spp. Change in spider mass did not differ between feeding treatments for either species and both *A. aurantia* treatments produced similar numbers of egg sacs. (*Argiope trifasciata* produced egg sacs too late in the experiment for real comparison.) Therefore, web and stabilimentum differences were likely the result of relatively minor variation in foraging success rather

than traumatic starvation of Low Prey spiders. While several studies have catalogued the prey caught by *Argiope*, few have examined the average daily consumption rate of *Argiope* in the field. Olive (1980) estimated the dry weight of prey captured by *A. trifasciata* to be 0.73 mg/h (this extrapolates to 10.2 mg/day, assuming a 14 h day) with a capture rate of 0.65 prey/h (9.1 prey/day, assuming a 14 h day). Tso (1996) estimated a capture rate of 1–2 prey/day for *A. trifasciata*. Horton & Wise (1983) found 21–23% of *A. aurantia* webs and 13–19% of *A. trifasciata* webs contained prey when surveyed. Brown (1981) found that *A. aurantia* webs contained an average of 0.6–1.3 prey/web and *A. trifasciata* webs contained 0.5–1.1 prey/web. Prey capture rates tend to be higher in tropical species of *Argiope* (Robinson & Robinson, 1970b; Craig & Bernard, 1990).

Two previous studies had found no immediate effect of feeding on stabilimentum frequency in the orb webs of *U. diversus* (Eberhard, 1973) and *A. argentata* (Nentwig & Rogg, 1988) over 3–5 days of starvation. But *Argiope* are sit-and-wait predators and may not alter stabilimenta based on foraging success over such a short time. In this study, the short-term foraging success of Low Prey treatment spiders changed between prey variance regimes but this did not result in large changes in web or stabilimentum parameters. Along with Eberhard (1973) and Nentwig & Rogg (1988), this suggests that stabilimentum building by spiders is not strongly affected by daily fluctuations in prey capture.

Many araneoid spiders will construct larger webs or increase the capture area of their webs during times of low prey capture success (Higgins & Buskirk, 1992; Pasquet *et al.*, 1994; Sherman, 1994). Neither *A. aurantia* nor *A. trifasciata* had significantly larger overall web areas or capture areas in the Low Prey treatments (Tables 3 and 4). This may have been because spiders were confined in cages smaller than their maximum possible web size. However, the decrease in free zone area by Low Prey *A. aurantia* is consistent with a pattern of increased foraging effort by spiders with reduced prey capture (Higgins & Buskirk, 1992; Sherman, 1994; but see Witt 1963).

There is little reason to believe that an orb web structurally determines, *a priori*, stabilimentum length. Stabilimentum arms could extend beyond the free zone into the capture area of webs, but often stopped far short of the first sticky spiral. Also, stabilimentum silk is produced by the aciniform glands while web silks are produced by the aggregate, ampullate, and flagelliform glands (Foelix, 1996). Finally, the frequency and overall size of stabilimenta were strongly affected by biomass of prey captured (Tables 1 and 2) while webs were relatively homogeneous (Tables 3 and 4).

There are many other potential influences on stabilimentum variation. Changes in form, particularly from disc shapes to linear designs, are well correlated with maturation in many species of spiders (Eberhard, 1973; Edmunds, 1986). Moulting and sexual receptivity can be correlated with an increased frequency of stabilimenta (Robinson & Robinson, 1973; Nentwig & Heimer,

1987). But this study suggests that some of the variation in size and frequency of stabilimenta within populations of orb-weaving spiders is caused by variation in the foraging success of the spiders. This has important implications for the study of stabilimentum function.

The prey attraction hypothesis has been supported by field studies that have demonstrated correlations between prey capture success and the presence of stabilimenta (Craig & Bernard, 1990; Tso, 1996). However, this study indicates that foraging success influences stabilimentum form and frequency. Those correlations may have been caused by an increase in stabilimentum building due to successful foraging rather than an increase in prey capture due to attractiveness of stabilimenta. Craig & Bernard (1990) and Tso (1996) used natural variation in stabilimenta in their comparisons of decorated and undecorated webs. Thus, both studies contained an *a priori* bias toward demonstrating correlations between foraging success and stabilimentum presence. Even the restriction of comparisons to capture rate differences between webs at the same site (Tso, 1996) may not adequately control for this effect if prey abundance varies temporally or if different spiders with different foraging histories sequentially build webs at the same site. Comparison of insect interception rates between stabilimentum-containing webs and webs where the stabilimenta have been artificially removed would eliminate this influence of past foraging success and provide a clearer test of the prey attraction hypothesis. While Craig & Bernard (1990) did remove existing stabilimenta from some webs, their analysis combined them with an unspecified number of webs which did not naturally include stabilimenta, making it difficult to interpret their results.

More importantly my study directly tests the mutually exclusive predictions generated by the predator defence and prey attraction hypotheses. It demonstrates that starved *Argiope* put less effort into the production of stabilimenta than do well-fed spiders. Both *A. aurantia* and *A. trifasciata* build stabilimentum arms that are 10–40% shorter when fed less. *Argiope trifasciata* reduces stabilimentum frequency by as much as 60% when offered less prey. These reductions occur even though stabilimenta appear to be relatively inexpensive to build, accounting for only 10% of the silk in a web. It is difficult to believe that a structure which attracts prey and is energetically inexpensive would be less common and smaller in the webs of starved spiders. Conversely, the pattern reported here is expected if linear stabilimenta serve as a predator defence mechanism, particularly if prey are able to use stabilimenta to avoid webs. This possibility must be more closely examined.

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