

Orb-web Design of Garden Spider, *Argiope Appensa* (Walckenaer, 1841) (Araneae:araneidae)

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Abstract: This study was conducted to describe the stabilimentum structure in the garden spider, *Argiope appensa* both in field conditions and in the laboratory. The presence or absence of stabilimenta was examined in the field and in the laboratory; the influence of foraging success in stabilimentum building behavior was also investigated. Results from field survey and laboratory experiments show that stabilimenta is not an obligatory component in web building of *A. appensa* since some spiders did not add web decoration on their webs. The form and occurrence of stabilimenta varied with spider size. Smaller individuals (body size :< 0.6 cm) commonly built discoid (disc-shaped) stabilimenta while larger individuals (body size: >0.6cm) spun strictly cruciate (cruciform) or part of cruciate stabilimenta. Among the juveniles, the stabilimentum size is positively correlated with the spider's body size; hence, larger individuals tend to spun larger discoid stabilimenta than the smaller ones. In the laboratory, well-fed *A. appensa* built more stabilimenta and more often than starved spiders. These results argue against the prey attraction hypothesis, but not the predator defense hypothesis, since well-fed spiders invested more in stabilimenta than those starved spiders. Also, *A. appensa* may adjust the structure and frequency of their stabilimenta probably to suit multiple functions throughout their life history. *A. appensa* are able to increase or decrease their web sizes, capture area (portion of the web with sticky or capture spirals), and mesh height (distance between sticky spirals) in response to changing prey size and density. Starved spiders spun significantly larger webs and capture area than well-fed spiders. In the absence of potential prey, spiders significantly constructed very narrow- meshed webs or tightly spaced capture spirals than in the presence of potential prey. The present study may demonstrate that spiders can manipulate their web architecture in response to different prey availability.

Key words: stabilimentum, *Argiope appensa*, orb-web, prey size and density.

INTRODUCTION

Orb-web spiders spin circular or ellipsoid web as an excellent tool for prey-capture. Although the orb web is made up primarily of radial and frame threads, and catching spiral, some diurnal species (Family: Araneidae, Uloboridae and Tetragnathidae) spin highly visible white zigzag silk decorations to the center of their orb webs (Scharff and Coddington 1997; Herberstein *et al.*, 2000a) after a typical orb-web construction. These structures have been termed silk decorations by McCook (1889), stabilimenta by Comstock (1912) and Simon (1895), or devices or adornment by Nentwig and Heimer (1987), Hingston, (1927) and Ewer (1972). Silk decoration is built either one below and one above the hub (linear decoration), discoid (disc-shape) or four bands forming a St. Andrew's cross typically with a gap at the hub (cruciate). Individuals within species display different decorating behaviors (Adamat *et al.*, 2009) that may be influenced by changes in local factors and food availability (Pasquet and Lebogne, 1994). Obviously, there is considerable within-species ontogenetic variation in decorating behavior among *Argiope* spiders (Herberstein, *et al.*, 2000a; Uhl, 2008; Bruce *et al* 2005; Adamat *et al.*, 2009). In this study, the term stabilimenta is used to denote silk decorations. Over the years, several functions of stabilimenta have been proposed (e.g thermoregulation, stabilizing the web,

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act as camouflage, prevent web damage by birds, helps guide males to females for mating (Crome and Crome, 1961), and increase foraging success or silk regulation (Stark, 2000), but these functions have been the subject of continued debate (Bruce 2006). It is often assumed that web decorations serve different roles in different species, and even multiple functions for a single species. The functions best studied are prey attraction (hunger-related), predator avoidance and web advertisement to prevent accidental damage by other flying animals (Herberstein *et al.*, 2000a; Bruce *et al.*, 2005). Based on prey-attraction hypothesis, spiders may improve their foraging success by improving their web attractiveness, thus starved spiders should invest more in silk decoration despite a probable increased risk of predations (Blackledge, 1998). Alternatively, the predator-avoidance hypothesis argues that satiated spiders are expected to invest more in them, despite a probable decreased in prey capture (Blackledge, 1998).

The principle of catching prey with a web seems simple: construct an almost inconspicuous silk web and optimize shape and size to efficiently trap airborne insects (Walter *et al.*, 2008). Since orb-web represents a behavioral and material investment in foraging by the orb-web spider (Eberhard, 1986), web design is an essential part of their foraging strategy. Spiders' foraging success depends largely on the prey-capture efficiency of the web, which is tightly related to its design such as web size, web capture area (portion of the web covered with sticky or capture spirals), web mesh size (width between spiral threads; Watanabe, 1999) and probably presence of stabilimenta (Herberstein *et al.*, 2000b). According to Herberstein *et al.* (2000b), the orb-web spiders (Araneae, Araneidae) employ flexibility in their foraging behavior. Hence, in response to periods of starvation, orb-web spiders increase the web size and attack prey unselectively, while satiated spiders decrease the web size and reject less profitable prey. The web variations can directly influence the number and types of prey entangled. For example, a larger web will increase the rate of prey interception but more expensive to construct than smaller ones (Chacon and Eberhard, 1980; Higgins and Buskirk, 1992; Herberstein and Elgar, 1994). As suggested by Craig (1986), web mesh height may affect the visibility of the web and the size of prey entangled (Uetz *et al.*, 1978; Murakami, 1983; Miyashita and Shinkai, 1995; Herberstein and Heiling, 1998). The web with a large mesh may be less efficient in keeping insects entangled than the web with smaller mesh. It is therefore likely that spiders possess a behavioral repertoire to adjust the design of webs to varying requirements for successful prey capture (Prokop, 2006). But several field studies failed to find a consistent correlation between the average distance between sticky spirals and prey size (Herberstein and Heiling, 1998; McReynolds & Polis, 1987, Herberstein & Elgar 1994).

In the present study, we conducted a field survey to describe the web decorating behavior of garden spider, *Argiope appensa* Walckenaer, 1841 (Araneae, Araneidae, Argiopinae), locally called "Spider X" or "Mr. X". In the laboratory, feeding experiments were conducted to investigate the effect of foraging success on the frequency of web decoration, and length of stabilimenta spun by *A. appensa* and the effect of the different prey sizes and density on their web building behavior.

Specifically, this study aims to answer the following questions: (1) Does prey body length variation result in the differences in web mesh height?; (2) Does the variation in foraging success influence the architecture of the web (hence, well-fed or satiated spiders build smaller web size, web capture area and mesh height than starved spiders)?; (3) Does the presence or absence (prey density) decrease the web size and capture area?; and (4) Does foraging success influence the web decorating behavior?. To eliminate the prediction that the mesh height is a result of the length of the leg used to fix the spider thread onto the radials; the same spiders were utilized in the three prey treatments.

MATERIALS AND METHODS

Field Observation:

Field survey on *A. appensa* spiders (Figure 1; $N=141$) was conducted along the coastline of Lugait ($8^{\circ} 20' 0'' \text{N}$, $124^{\circ} 16' 0'' \text{E}$), Misamis Oriental, Philippines and Mantigue Island ($9^{\circ} 10' 35'' \text{N}$, $124^{\circ} 49' 32'' \text{E}$), Camiguin Province, Philippines. Presence and absence of web decoration were recorded. There are only two basic forms of stabilimenta in *A. appensa*: "disc" stabilimentum or discoid (tightly woven disc of white silk covering the hub) and "cross" stabilimentum" or cruciate. If web decorations were present, it was classified either discoid or cruciate (Figure 2). For cruciate web decoration, the number of bands (arms) was noted. Juvenile spiders were collected and reared in the laboratory for identification.

Feeding Treatment:

After field survey, thirty (30) spiders were collected and each spider was housed in a wooden cage 60 x 60 x 60 cm, covered with clean plastic sheeting on the top, front, and back. Screen sides provided ventilation.

Spiders were subjected to three sequential feeding regimes. These were: (A) small-size prey no prey; (B) large-size prey; (C) no-prey. Spiders in small-size prey regime were given fruit flies (*Drosophila sp.*: body size: 0.25-0.30cm; weight: 0.0011-0.0018g) *ad libitum* and one grasshopper (Body size: 1.2-1.6 cm; weight: 0.1309±0.071g) was given to spiders in large-size prey regime. For the first three (3) consecutive days, spiders were given fruit flies *ad libitum*. For the next 3 days (day 4-6), spiders were given one medium size grasshopper (g; length:) every day. For five (5) days (day 7-11) the spiders were fasted. The presence and absence and the length of stabilimenta, web size, web capture area and mesh height were recorded every day in small prey and large prey regime, while in no prey regime, only webs spun in the final 3 days (day 9-11) were recorded to ensure that the spiders are already starving. Observation on the occurrence and length of stabilimentum was done for five days.

For the purpose of comparison, spiders in no prey feeding regime are categorized as starved or fasted while in small-size prey and large prey regime are considered poorly-fed and well-fed respectively. Water was provided to spiders *ad libitum* through wet sponge.

Measurements:

The spider and web with ruler (for calibration) were photographed and imported to UTHSCSA *Image Tool* software, UTHSCSA *Image Tool* Version 3.00 where necessary measurements were done. For the purpose of comparison, the field-observed spiders were grouped into three based on its body size: below 0.21 cm, 0.21-0.60 cm, and above 0.60 cm. Sub adult and adult male spiders were not included in the observation. The web with ruler (for calibration) were photographed and imported to UTHSCSA *Image Tool* software, UTHSCSA *Image Tool* Version 3.00 where necessary measurements were done.

Statistical Analyses:

Statistical Analysis was performed using the PAST (Paleontological Statistics) Software. Linear Regression Correlation analysis was used to determine relationship between spider size and stabilimentum structure. Linear Regression, Kruskal Wallis and One-way ANOVA were used to compare between feeding treatments in terms of stabilimentum length, web size, capture area, and mesh height.

Results

Field Observation:

A total of 141 webs were observed, of which 40(28%) had no stabilimentum, 32 (22%) discoid decoration, and 69 (50%) had cruciate or part of the cruciate decoration. This result suggests that the presence of stabilimentum is not an obligatory component of web construction. The relationship between body size and occurrence and type of web decoration is shown in Figure 3. Discoid stabilimentum occurred predominantly in smaller spiders (body size: <0.60cm) while larger spiders (body size: >0.60 cm) showed complete or partial type of cruciate decoration. Results of Mann-Whitney pairwise comparison: discoid versus none: $p=0.0809$; discoid versus cruciate: $p<0.0001$; none versus cruciate: $p<0.001$ reveal that the type of stabilimenta significantly varies among the spiders of different ontogenetic stages. Webs with no decoration were also observed in all size groups. Though few smaller spiders (body size: 0.21-0.60 cm) add cruciate decoration, larger spiders add strictly cruciate decoration. The frequency of occurrence of stabilimenta increased with size (age) of the spider.

There is a positive correlation between spider's size and discoid stabilimentum size. Larger juveniles tend to construct larger stabilimentum size (Linear Regression: $r = 0.6915$; $p<0.0001$; $N = 31$). Cruciate stabilimenta (Figure 1B and Figure 5) were rarely complete (4-arms). The continuous 2-arms were the most frequently observed (80%) while complete cross (4-arms) was rarely observed (10%). Stabilimenta with 1-arm were the least frequently observed (10%). Stabilimenta with 2-arms either in both upper or lower portion of the hub (V-form) were not observed. This result is also true under laboratory condition.

Feeding Treatment:

The frequency of occurrence of stabilimenta varies with prey treatment (Figure 6a). The spiders in small-size prey treatment constructed web decoration less frequently (19%, $N=167$) than in no prey (30%, $N=91$) and large-size prey treatments (58%; $N=107$), which suggests that starved (no prey group) and poorly-fed

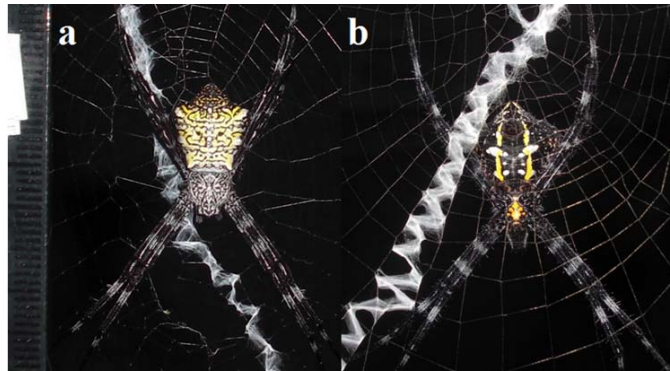


Fig. 1: Female *Argiope appensa* (Walckenaer 1841): dorsal view (A), ventral view (B).

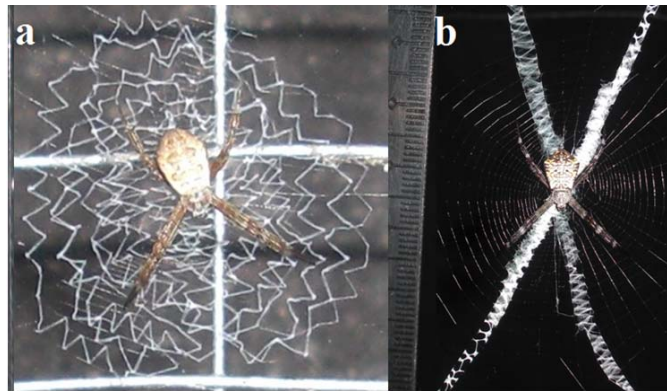


Fig. 2: Type of Stabilimenta: discoid (A) and cruciate (B). The spider is located upside down in the hub (center portion) of the web.

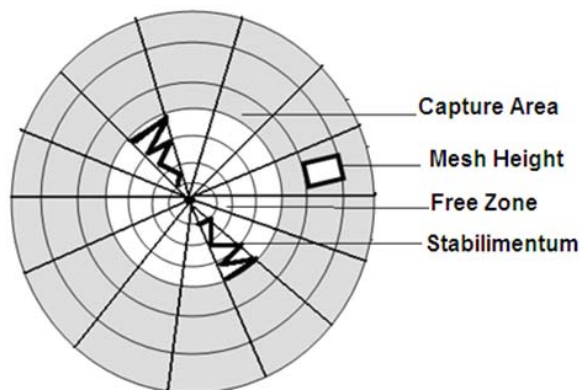


Fig. 3: A schematic web of *Argiope appensa* demonstrating the web parameters measured. Free zone (white-color) is the area in the center of a web covered by non-sticky spirals and is present in both decorated and undecorated webs. Capture area (gray-color) is the rest of web area covered by sticky spirals. Mesh height/size/width is the distance between two consecutive sticky spirals.

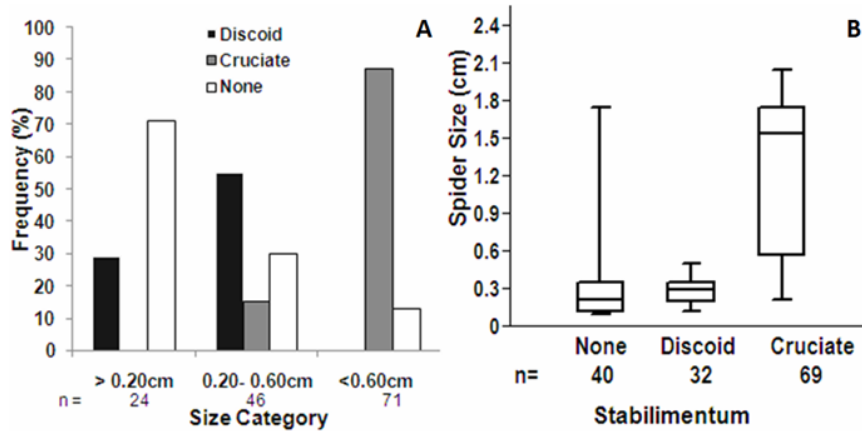


Fig. 4: Frequency of webs with discoid (black bars), at least part of cruciate (gray with black bars) or no decoration (open bars) for the three size groups (A). Relationship between spider size and the occurrence and shape of stabilimenta in *Argiope appensa* (B). N=141. Subadult and adult males excluded.

(small-size prey group) *A. appensa* also spin stabilimenta in their webs but less often than well-fed (grasshopper group). This result did not support the prey attraction hypothesis, that is, stabilimentum is used to attract prey since starved and poorly-fed spiders were unlikely to add decoration on their webs. The length of stabilimenta was significantly different between the three treatments (One-way ANOVA: $F=14.75$; $df=2$; $p<0.001$; Figure 2B). A significant difference between starved and well-fed spiders (Tukey's pairwise comparison: $Q=4.793$; $p=0.003$), and between poorly-fed and well-fed ($Q=4.793$; $p=0.0001$). However, there is no significant difference between poorly-fed and starve spiders ($Q=2.534$; $p=0.177$).

Prey treatment had a confound effect on the web size (ANOVA: $F=43.86$; $df=2$; $p<0.001$), web capture area ($F= 32.12$; $df=2$; $p<0.001$) and web mesh height ($F=34.25$; $df=2$; $p <0.001$) (See Figure 6). The web size was significantly different between the three treatments. The no-prey spiders spun significantly larger webs than large-prey spiders (NP=2079.74+461.06 cm² vs. LP=1249.75+468.04 cm²; Tukey's Pairwise Test: $Q=13.57$, $p<0.001$). Similarly, spiders in small-prey regimes spun larger webs than spiders in large prey (SP=1600.40+487.17 cm² vs. LP=1249.75+468.04 cm² $Q=5.89$, $p<0.001$).

In the absence of potential prey, spiders not only increased the web size but also the capture area. A significant difference in web capture area was observed among spiders in different feeding treatments ($p<0.001$). The no prey spiders constructed significantly larger capture area than in the presence of small prey (NP=2017.16+405.43cm² vs. SP=1600.40+487.17cm²; $Q=5.805$, $p<0.001$) and large prey (NP=2017.16+405.43cm² vs. LP=1168.41 ± 494.12 cm²; $Q=11.82$, $p<0.001$). This result further shows that fasted or starved spiders constructed the largest web capture area than those poorly-fed and well-fed spiders.

In the presence of small prey, spiders significantly constructed very narrow- meshed webs or tightly spaced capture spirals than the presence of larger prey (SP=0.3537 ± 0.0824 cm vs. LP=0.4837±0.0896cm; $Q=11.32$, $p<0.001$). Moreover, in the absence of prey, spiders constructed significantly narrower- meshed compared to spiders in the presence of large prey (NP=0.4293±0.0642 vs. LP= 0.4837±0.0896; $Q=4.737$, $p<0.001$) and in the presence of small prey (NP=0.4293±0.0642 vs. SP=0.3537 ± 0.0824 cm; $Q=6.585$, $p<0.001$). Our results demonstrate that spiders able to manipulate web mesh height response to different prey sizes. Spiders in small-size prey decrease the mesh height but increase the capture area to improve retention of smaller prey because more silk can adhere to the prey.

Discussion and Conclusion:

Field and laboratory observation results clearly demonstrate that stabilimenta in *A. appensa* are not an obligatory component of the web of *A. appensa* since some of them did not add stabilimenta on their webs. If stabilimenta are present, they can be discoid or cruciate only. This observation argues against a stabilizing function as suggested by Comstock (1912) and Simon (1895). It also do not support a male guidance function (helps guide males to females for mating) as suggested by Crome and Crome (1961) since there is high

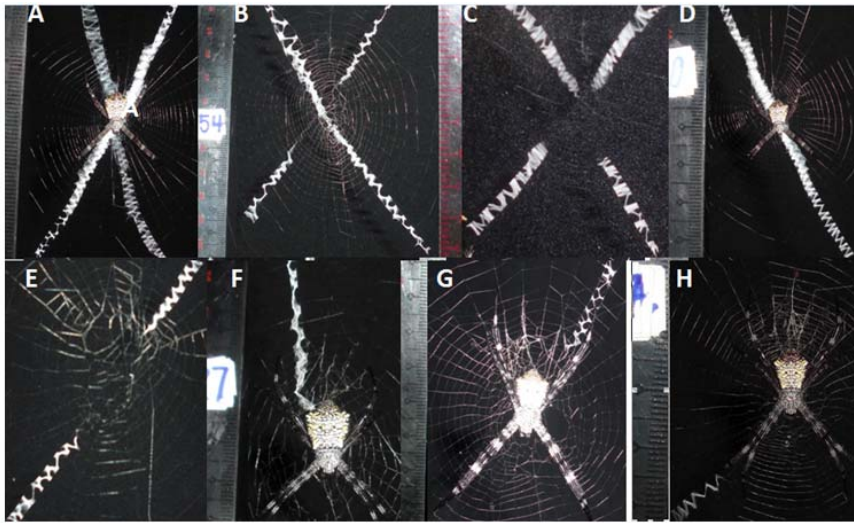


Fig. 5: Cruciate Stabilimenta. (A,B,C) 4-arms (2-4 diagonal arms, forming an X). (D,E) 2-arms (1 diagonal arm). (F,G,H) 1-arm (upper or lower). Cruciate stabilimentum can be continuous (without gap at hub) or discontinuous (leaving a gap at hub).

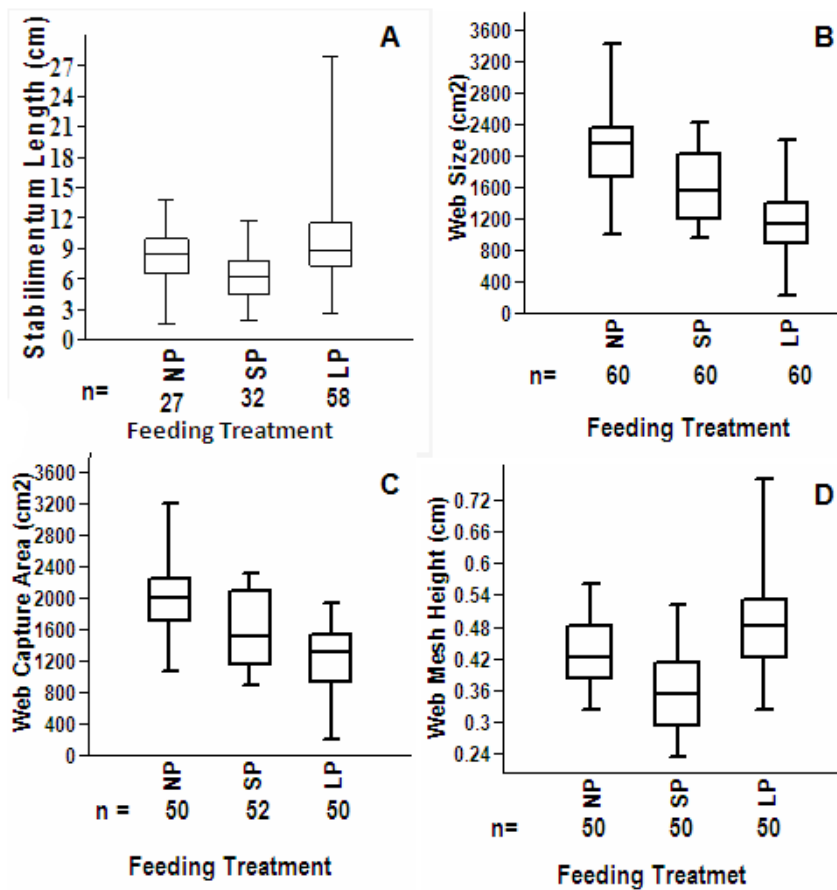


Fig. 6: Stabilimentum Length of *A. appensa* (A), Web Size (B), Web Capture Area (C) and Web Mesh Height (D). NP (No Prey), SP (Small-size prey), LP (Large-size prey).

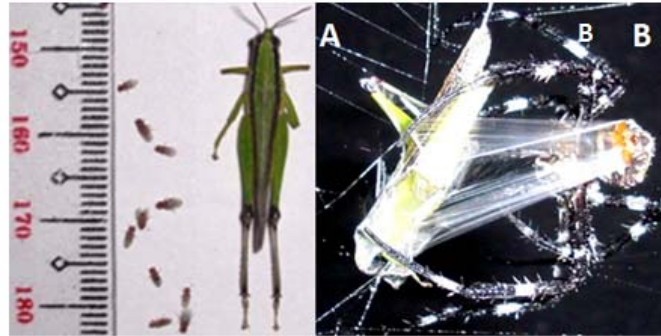


Fig. 7: (A) Prey used in the study: *Drosophila* sp. (body size: 0.25-0.30cm; weight 0.0011-0.0018g) and Grasshopper (body size: 1.0-1.4 cm; body weight: 0.1309±0.071g). (B). Wrapping attack prior to consumption of prey.

proportion of subadult and adult females observed in the laboratory that did not spin stabilimenta to their webs (68%; $N=365$ webs).

A remarkable ontogenetic difference in web decoration types was observed among *A. appensa* in which the occurrence of different types of stabilimentum (discoïd and cruciate decoration) was observed to be dependent on spider size (Linear Regression: $r=0.7614$; $p<0.0001$; $N=101$). Smaller individuals (body size: <0.6 cm) produced mainly discoïd stabilimenta while larger individuals (body size: >0.6 cm) produced strictly cruciate stabilimenta. Few of the juveniles (15%; $n=7$; $N=46$) add cruciate stabilimentum, however, none of the sub-adult and adult females spun discoïd stabilimentum. This observation is also true to other species of *Argiope* - *A. argentata* (Uhl, 2008), *A. versicolor* (Li *et al.*, 2003), *A. keyserlingi*, and *A. trifasciata* (Herberstein *et al.*, 2000a), *A. luzona* (Adamat *et al.*, 2009).

Within- ontogenetic stage variation was also evident, in which stabilimentum can be one-arm, two-arm or four-arm, with or without crossing the hub which varies on daily basis (personal observation). The diagonal band (2-arms) were the most frequently observed (80%) while complete cross (4-arms) and other forms were rarely observed (10%). This result is also true under laboratory condition. Moreover, the frequency of occurrence of stabilimenta increased with increase spiders' size (96% occurrence; spider size: >0.6 cm. These results may reflect different functions of stabilimenta across different history stages (Herberstein *et al.* 2000a; Bruce *et al.* 2005; Uhl, 2008).

There is a positive correlation between spider's size and discoïd stabilimentum size. The discoïd stabilimentum, a typical of immature individuals, is generally considered a concealing device (McCook, 1889). It also functions in thermoregulation (Starks 2002) and as defense against wasps (Blackledge and Wenzel, 2001), enhancing defensive dropping behaviors (frequently observed when spiders are disturbed during the study). Based on personal observation, when the spider is disturbed, it shuttles through the web and hides behind the disc. In this type of stabilimenta, the decoration overlaps the entire spider (Figure 2a), thus may provide camouflaging against predators or even protect the spider from direct heat from sunlight. A low proportion of juvenile spiders (body size: >2.0 cm) spun disc stabilimenta on their webs probably because these spiders are found in shaded areas (e.g. window screens), hence, they are sun-protected and protected from non-prey species that might accidentally damage their web.

Feeding treatments were chosen to approximate moderate variation in foraging success of common garden spider *A. appensa*. Our study reveals that foraging success of *Argiope appensa* has a significant effect on stabilimentum building. Well-fed spiders spun stabilimenta on their webs more often than hungrier spiders. Also, well-fed spiders built longer stabilimenta than starved and poorly-fed spiders. These results somehow agree with predator- avoidance (predator defense) hypothesis but argue against prey attraction hypothesis since well-fed spiders invested more in stabilimenta. Furthermore, starved and poorly-fed spiders invest less into the production of stabilimenta than do well-fed spiders. *A. appensa* reduces stabilimentum frequency by 40-50% when offered less or no prey and build stabilimentum arm that are 20-40% shorter when starved or fed less. Similarly, this result partly agree the excess silk regulation function as suggested by Walter *et al.*, (2008), thus spiders use accumulated excess silk for building stabilimenta due to constant secretion in the aciniform gland, given that the same silk is used in wrap-attack of large-size prey. As observed spiders in large prey treatment

used more silk to attack and wrap the prey (wrapping precede consumption) (Figure 7B). In contrast, during encounters of *Drosophila* (small-prey), spiders bite and consume the prey directly without wrapping (personal observation). This could probably explain the low occurrence and shorter stabilimenta in spiders fed with small-size prey.

Although, the predictions of prey attraction and predator avoidance were not directly tested in the present study, however, it has been argued that if stabilimenta function as a predator defense mechanism, then starved spiders would be expected to build less often, if stabilimenta are energetically costly. Similarly, if stabilimenta are prey attractants, then spiders experiencing poor foraging success should invest more in them despite a probable increase in 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 (Craig and Bernard, 1990). According to Sandoval (1994), a potential for undertaking prey-specific web adjustments requires that the spider can classify prey types and respond to a change in prey types by altering features of the web in an adaptive way.

The results of the present study show that in addition to facultative decorating their webs (personal observation), *A. appensa* adjust their web size and design based upon previous foraging history and success. *A. appensa* significantly increase or decrease their web size, web capture area and mesh height in response to changing prey size and density. It has been suggested that the ability of web-building spiders to function as predators is intimately linked to the construction of webs, such that, they manipulate the sizes (Sherman, 1994) and design (Craig, 1987) of webs as either evolutionary or behavioral responses to changes in prey density or type.

The starved spiders were able to manipulate their web size and capture area probably to increase the prey interception rates. The spiders were fed first with large-size and then allowed to starve, where the former built smaller webs and capture area than the latter. The increase in the web size and capture area could have been due to foraging success but not due to prey size since spider in no prey treatment built the largest web and capture area than those in small-prey and large-prey treatment. The prey (Figure 7A) used in the experiment strongly differ in weight and body size: (SP: 0.25cm; 0.0011-0.0018g) vs. (LP: 1.2-1.6 cm; 0.1309±0.071g). These differences in prey size and weight might have affected the web size and web capture area obtained after prey digestion due to the differences in satiation between treatments rather than the effect of experience with different types of prey.

Although, the effect of web design on prey capture rates was not directly tested in the present study, however, based on several studies (e.g. Miyashita & Shinkai, 1995; Craig, 1987), these web variations can directly influence the length, number and types of prey entangled. Manipulation of investment in webs as means to alter foraging effort requires that web architecture affects prey capture. For example, increasing the web area will reflect in a higher prey interception, hence, higher prey capture rate (Herberstein & Elgar 1994); a greater number of radii enable the web to absorb more kinetic energy and thus retain heavier and faster flying prey (Craig, 1987).

Our present study indicates a short-term response of mesh height to size of prey. There is remarkable increase in the distance between spirals as prey shifted from *Drosophila* to grasshopper. The observed difference in web mesh height can be due to the differences in prey body length and prey kinetic energy (Prokop, 2006). In the presence of small prey, spiders significantly spun closely spaced capture spirals compared to the presence of larger prey probably to efficiently intercept and capture detected small-sized prey. This suggest that spiders in different feeding groups adopted different foraging strategies (e.g. narrow-spaced or larger-spaced mesh height) based upon an assessment of their previous foraging success (presence of small-prey or large-prey or interception and consumption of small-prey and large prey) to maximize prey capture. This further suggest that starved or food-deprived spiders increased their foraging effort in terms of silk investment by spinning more tightly spaced sticky spirals compared to satiated or well-fed spiders. Furthermore, in the absence of prey, spiders constructed narrower-meshed compared to spiders in the presence of large prey but larger than in the presence of small-size prey. This is probably because spiders were unable to detect presence of any potential prey, so spider in no prey treatment, made a compromise strategy between increasing and decreasing the mesh height to unselectively capture potential prey.

Finally, this study suggest that some of the variations in size and frequency of stabilimentum among *A. appensa* can be caused by the variation in the foraging success of the spiders, which has important implications for the study of stabilimentum structure. The food-deprived spiders did not only increase the web size and capture area but also increased the number of spiral turns while decreasing the distances between spiral turns to maximize the trapping of airborne insects. It further suggest that starved spiders should increase their web construction effort (increased investment on web spirals) to efficiently increase their foraging effort. In addition,

the increasing web construction effort could be ultimately directed to increasing prey capture rates thus increase foraging success which has a significant implication to spiders' survival. The direct correlation between the effect of mesh height and prey capture rates of different prey types as well as the effect of body condition on web design in *Argiope appensa* will be considered in the future study.

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