

Describing frequency of occurrence, size and stabilimentum-building behavior of four species of orb-web building *Argiope* spiders

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Abstract. This study was conducted to describe the frequency of occurrence, variations in size and shapes of stabilimenta of four species of *Argiope* - *A. luzona*, *A. catenulata*, *A. appensa* and *A. aemula* found in their natural habitat. The description was based on size, shape and frequency of occurrence. Out of 1,094 orb-webs observed, the spinning of stabilimenta is an optional component of web-building since 8%-29% were undecorated. The frequency of occurrence of stabilimentum-building and the cruciate type vary among the four species which may indicate an interspecific variation in stabilimentum structure. Cruciate and discoid types were observed to be dependent of spider size. Larger individuals were observed to be spinning cruciate stabilimenta while the smaller ones spinning the discoid form. This result demonstrates an ontogenetic shift from discoid to cruciate form. Though linear stabilimentum was not observed in the present study, the within-species variation in cruciate stabilimentum (e.g 1-5 arms, continuous or discontinuous) suggests variation in stabilimentum-building behavior among the four species. Spider size was moderately positively correlated with the number of stabilimentum arms or bands in *A. luzona*, moderately negatively correlated in *A. aemula*, but no relationship in *A. catenulata* and *A. appensa*. The spider size is not correlated with the presence of decoration. The size of discoid stabilimentum as well as the length of cruciate type are both positively correlated with the web size in the four species observed. The spider size is significantly positively correlated with web size in *A. aemula* but not in the other 3 species. It was also observed that the length of cruciate stabilimentum was significantly negatively correlated with the web size, spinning wider webs with shorter stabilimenta or smaller webs with longer stabilimenta. Spinning wider undecorated or smaller decorated webs was only observed in *A. appensa*. The results in this study may suggest evidence for a trade-off between the two alternative prey-capture strategies of orb spiders, that is, stabilimentum-building activity and building a web with a large capture area.

Key Words: *Argiope luzona*, *Argiope catenulata*, *A. appensa*, *A. aemula*, descriptive statistics, UTHSCSA Image Tool, stabilimentum, web size.

Introduction. Just like the typical orb-webs, many diurnal spiders like *Argiope* spp. also spin highly visible decorations called stabilimenta at the center of their webs (Abrenica-Adamat et al 2009; 2011; Scharff & Coddington 1997; Herberstein et al 2000a). These structures vary in forms and composition (Herberstein et al 2000a). While some are made up of silk, others are made of combination of silk and other items such as egg sacks, vegetation and detritus, decaying prey items and exoskeletons of arthropod prey. Among these types, the silk stabilimenta have many forms and have been the center of debate in spider literature for over a century. The functions of stabilimenta can be thought as species-specific and vary even within a single species (Uhl 2008; Lubin 1980) probably to suit multiple functions throughout their life history (Li et al 2003). For example, within a single population of *Argiope*, the type of stabilimenta varies at different developmental stages. Some juveniles spin disk-like stabilimenta surrounding web hub while the adults spin cruciate or linear forms (Abrenica-Adamat 2009; Nentwig & Rogg 1988). This field study was therefore conducted to describe and compare the

stabilimentum structure in orb-webs within and between four *Argiope* species and to be able to understand their stabilimentum-building behaviors and be able to understand the factors that affect the nature of the built web-decoration.

Materials and Methods

Study Species and Study site. Observation on occurrence and structure of stabilimentum of the four *Argiope* spiders conducted in selected areas of Region X and Region XII, Mindanao, Philippines (Figure 1). The sampling areas include Iligan City (8°13'N 124°14'E), along the Coastal Areas of Lugait, Misamis Oriental (8°20'0"N,124°16'0 E), Mantigue Island, Camiguin (9 °10 '35 "N, 124 ° 49 '32 "E), Gingoog City (8° 50 "N, 125° 06 "E), Ozamis City (8°9'N 123°51'E), Kirondong, Magpet, North Cotabato (7°03'11.3"N, 125°14'47.5"E), Kidapawan City (7°00'40"N 125°05'28"E) and Tangub, Misamis occidental (8°04'N 123°45'E).

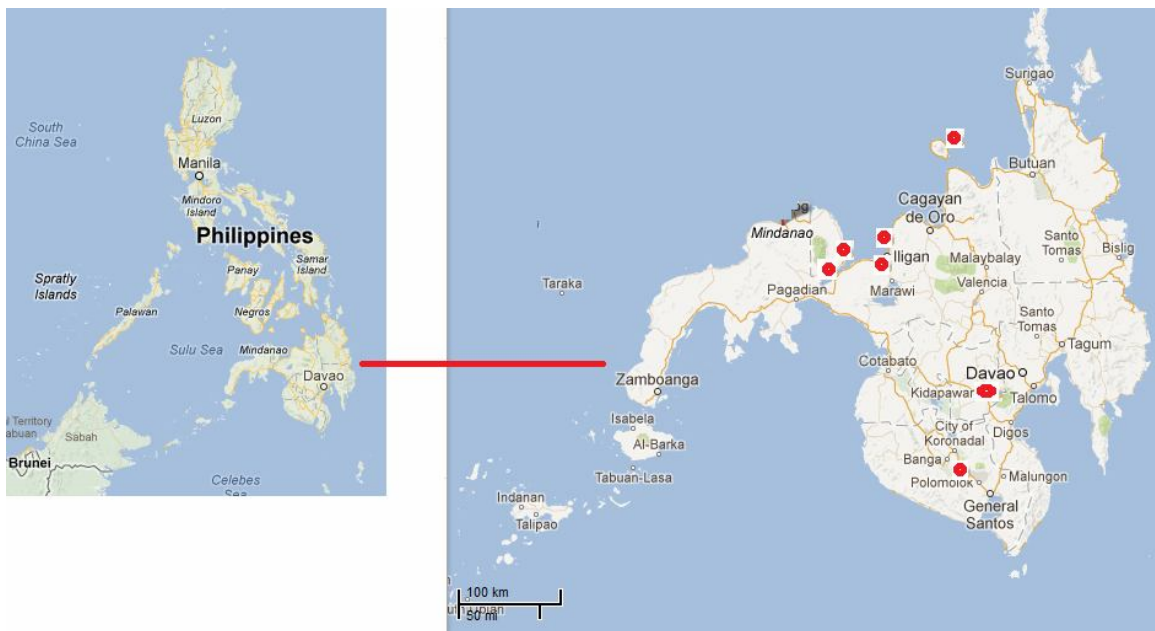


Figure 1. Sampling areas in Mindanao, Philippines.

Web parameters. Field observations were made on four species of orb spiders for the presence of stabilimenta (Figure 2). A total of 1074 webs were described - *A. luzona* (N=302, 28.2%), *A. appensa* (N=346, 32.2%), *A. catenulata* 273 (25.4%) and to *A. aemula* (153 (14.2%).



Figure 2. The four *Argiope* species: *A. appensa* (A), *A. catenulata* (B), *A. aemula* (C) and *A. luzona* (D).

The stabilimentum was categorized as either discoid (disc-shaped) or cruciate (cross-shaped, Figure 3). For cruciate stabilimenta, the number of bands or arms was recorded. For comparison purposes, arms that crossed each other at the hub are continuous arms while those that leave a gap are called discontinuous arms.

The spiders in their webs were photographed with a ruler on the side (for calibration). The images were then imported to UTHSCSA *Image Tool* software (compdent.uthscsa.edu/dig/download.html) where necessary measurements were done. The spider size was measured based on the total body length (Barrion & Litsinger 1995). Small juvenile spiders observed, these were collected and reared in the laboratory for taxonomic identification.

Spiders were classified according to size classes or categories: <4.0 cm (A); 0.4-0.59 cm (B); 0.6-0.79 cm (C); 0.8-0.99 cm (D); and >1.0 cm (E).

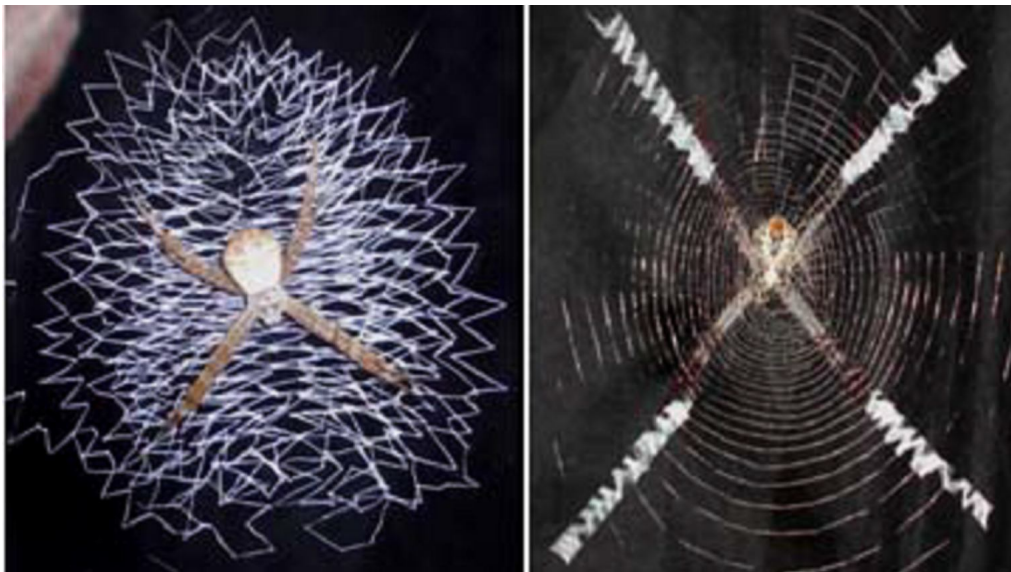


Figure 3. Types of stabilimentum of the garden spider, *Argiope* spp: discoid (magnification 3x) (A), and cruciate (magnification 1x) (B).

Statistical Analysis. Linear Regression Correlation analysis was used to determine relationship between spider size and stabilimentum structure based on type, size and number of arms. In terms of stabilimentum type, ranking was employed: discoid=1 and cruciate=2. For the presence and absence of decoration: non-decorated=1, and decorated=2. Descriptive analysis was also used to describe the stabilimentum structure of *Argiope* spp.

Results and Discussion. Results from field observations of 1074 webs revealed 72%-92% had stabilimenta (Table 1). The spiders spin only discoid or cruciate types. Few of the juveniles were observed to have a discoid with incomplete cruciate stabilimentum, a transition between a discoid to a cruciate design.

Table 1
Summary on the occurrence of Stabilimentum. Percent Frequencies are given in parenthesis (N= 1074)

	<i>A. luzona</i> No. of Webs	<i>A. catenulata</i> No. of Webs	<i>A. appensa</i> No. of Webs	<i>A. aemula</i> No. of Webs
Decorated	272 (90%)	246 (71%)	196(72%)	140 (92%)
Non-decorated	30 (10%)	100 (29%)	77 (28%)	13 (8%)
<i>N</i>	302	346	273	153

It was observed that for all the four species the occurrence of either discoid or cruciate stabilimenta is significantly dependent on spider's size (Figures 4 and Figure 5). Very small spiders (Spider Size: < 0.4cm) spin only the discoid type while the larger spiders (Spider Size: > 6.0 cm) spin only the cruciate type. The results of Mann-Whitney pairwise comparison suggest that the type of stabilimentum significantly varies within species of different ontogenetic stages: *A. luzona* (discoid vs cruciate: $p < 0.0001$); *A. catenulata* (discoid vs. cruciate: $p < 0.0001$); *A. appensa* (discoid vs. cruciate: $p < 0.0001$), and *A. aemula* (discoid vs. cruciate: $p < 0.0001$). Undecorated webs were also observed for all size categories.

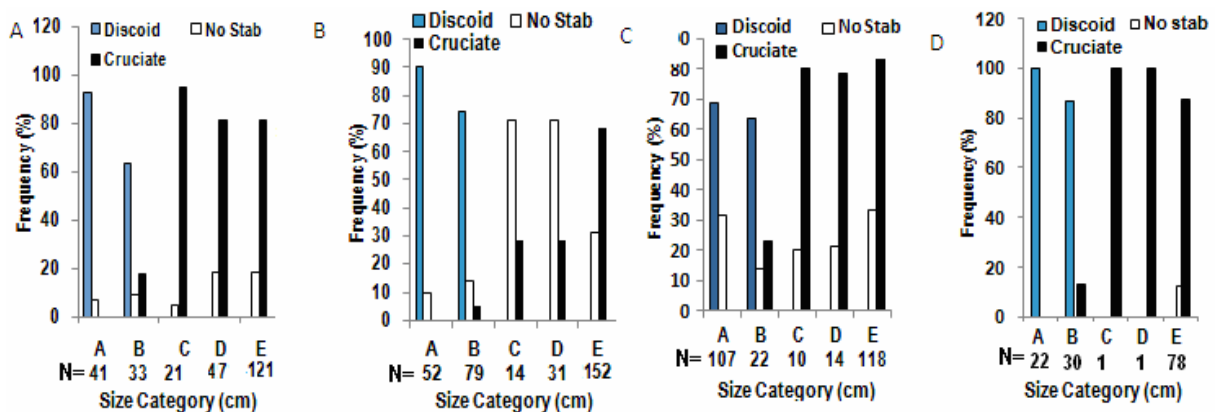


Figure 4. Presence, absence and stabilimentum form in orb-webs in different size categories: A: < 4.0 cm; B: 0.4-0.59 cm; C: 0.6-0.79 cm; D: 0.8-0.99 cm; and E: >1.0 cm among the three *Argiope* spiders: *A. luzona* (A), *A. appensa* (B), *A. catenulata* (C) and *A. aemula* (D).

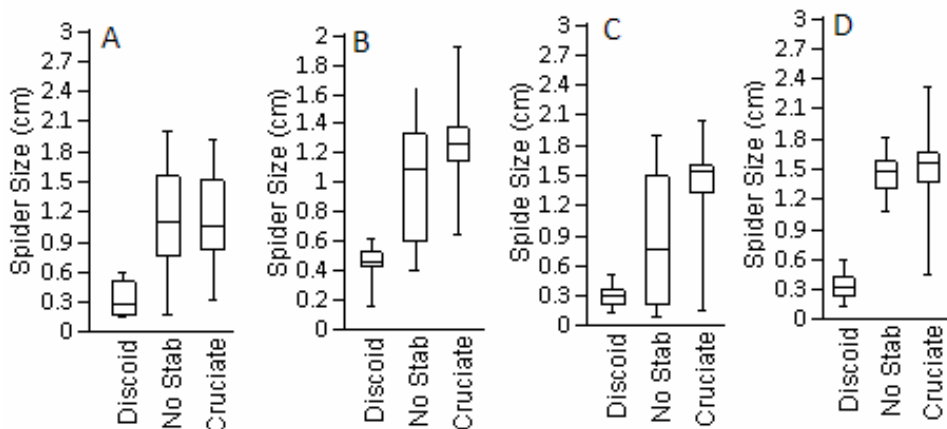


Figure 5. Relationship between Spider Size (cm) and occurrence of stabilimentum: *A. luzona* (A), *A. catenulata* (B), *A. appensa* (C), and *A. aemula* (D).

In addition to the size-dependent occurrence of the different stabilimentum types, there were at least five different forms of cruciate stabilimenta in *Argiope* (Table 2). These were observed to be having 1 arm, 2 arms, 3 arms, 4 arms or 5 arms. Some of these arms crossed each other at the hub (continuous arms) while others leave a gap at hub (discontinuous arms). Differences in frequency of stabilimentum-building as well as stabilimentum structure within and between species were also observed. *A. catenulata* will spin only 1-armed (37%) or discontinuous 2-armed (63%) stabilimenta while *A. luzona* spin all possible combinations of continuous and discontinuous arms in its stabilimentum. A high proportion of the web with a complete cross (4-armed) stabilimenta was displayed among *A. luzona*. We rarely observed a complete cross stabilimenta among *A. appensa* and none among *A. catenulata* (Table 1). Results have

also shown that though *A. aemula* spin 1-armed to 5-armed decorations, none of these arms have crossed the hub. Likewise, *A. appensa* spin all possible combinations except 3-armed and 5-armed stabilimenta. These results suggest that the type or form of stabilimenta can vary within and between species of *Argiope*.

Table 2

Summary on the frequency of stabilimentum arms of orb-webs

Spider	Stabilimentum Arm					Discoid with cruciate
	1-arm	2-arm	3-arm	4-arm	5-arm	
<i>A. luzona</i> ; N=194	6 (3.1%)	52 (26.8%)	10 (5.2%)	121 (62.4%)	1 (0.52%)	4 (2.1%)
<i>A. catenulata</i> ; N=124	45 (36.3%)*	76 (61.3%)*	-	-	-	3 (2.4%)
<i>A. appensa</i> ; N=115	26 (22.6%)	85 (73.0%)	-	4 (4.4%)	-	-
<i>A. aemula</i> ; N=117	14 (12.0%)	33 (28.0%)*	7 (6.0%)*	56 (48%)*	7 (6.0%)*	-

Legend: *- discontinuous stabilimentum only.

Linear regression show spider's size is positively correlated with the discoid stabilimentum size among juveniles. Larger juveniles tend to spin larger disc stabilimenta in all four species [*A. luzona* ($r = 0.87738$; $p < 0.0001$; $N = 59$), in *A. catenulata* ($r = 0.79465$; $p < 0.0001$; $N = 107$), in *A. appensa* ($r = 0.86543$; $p < 0.0001$; $N = 72$), and in *A. aemula* ($r = 0.92272$; $p < 0.0001$; $N = 48$). It is not however correlated with the presence of stabilimenta. While the number of stabilimentum arms is positively correlated with the spiders' size in *A. luzona* ($r = 0.3341$; $p < 0.0001$; $N = 227$), it is negatively correlated in *A. aemula* ($r = -0.38357$; $p = 0.01$; $N = 44$). We found no correlation in *A. catenulata* ($r = 0.087918$; $p = 0.4462$; $N = 78$) and *A. appensa* ($r = 0.1098$; $p = 0.06721$; $N = 80$).

The relationship between spider size and the cruciate stabilimentum length show positive correlation in all four species [*A. luzona* ($r = 0.6847$; $p < 0.001$; $N = 205$), *A. catenulata* ($r = 0.3413$; $p = 0.0026$; $N = 78$); *A. aemula* ($r = 0.8769$; $p = 0.0424$; $N = 41$) and *A. appensa* ($r = 0.54076$; $p = 0.007$; $N = 76$)].

No correlation between the spider size and web size was observed in *A. luzona* ($r = -0.15585$; $p = 0.113$; $N = 137$), *A. catenulata* ($r = 0.16226$; $p = 0.0701$; $N = 124$), and in *A. appensa* ($r = 0.2103$; $p = 0.3502$; $N = 76$). A positive correlation was observed among *A. aemula* ($r = 0.30622$; $p = 0.0416$; $n = 45$).

The cruciate stabilimentum length is moderately negatively correlated with the web size in *A. luzona* ($r = -0.33308$; $p = 0.001$; $N = 92/127$) and *A. aemula* ($r = -0.3236$; $p = 0.0338$; $N = 43$). However, we found no correlation in *A. appensa* ($r = -0.18367$; $p = 0.1135$) and *A. catenulata* ($r = 0.13353$; $p = 0.2405$; $N = 77$). However, in *A. appensa*, the web area is significantly larger ($Q = 3.289$; $p = 0.0205$) in non-decorated webs than decorated webs (Non-decorated: Mean = $1721.61 + 564.01 \text{ cm}^2$; Min = 1021.18 ; Max = 3423.15 cm^2 vs. Decorated: Mean = $1527.24 + 506.19 \text{ cm}^2$, Min = 225.47 cm^2 ; Max = 2457.56 cm^2). We found no significant difference in web size between decorated and undecorated webs in *A. catenulata*.

The present study shows that spinning of stabilimenta can be argued to be an optional component of web-building behaviours among the four species of *Argiope* since a number of the observed webs were underdecorated (7-28%). The options not to decorate their webs can be due to their foraging needs or moulting (Shermann 1994), quantity of available silk (Pasquet & Leborgne 1997; Walter et al 2008), specific abiotic factors (Ap Rhihiart & Vollrath 1994; Pasquet & Leborgne 1997), physiological state (Humpreys 1992) and conspecifics (Lubin 1980; Buskirk 1986; Leborgne & Pasquet 1987; Pasquet & Leborgne 1997). Our results on the occurrence of stabilimenta failed to support the web stabilization function since not all webs were decorated. Likewise, the male guidance function cannot be argued since not only sexually matured individuals do decorate their webs but also the juveniles. Also, observations under laboratory conditions showed that high proportion of sexually matured *A. appensa* (Abrenica-

Adamat et al 2011) and *A. catenulata* (actual field observations) did not spin stabilimenta.

The high frequency of occurrence of stabilimentum in the webs (72%-93%) indirectly supports the high aciniform gland activity hypothesis. Since stabilimenta is made of aciniform silk which is used by spiders in wrap attack, spiders may have used accumulated excess silk for building web decoration due to constant secretion in the aciniform gland. Constant secretion of silk and the web decoration might function as mechanism to maintain high gland activity, thereby maximizing the efficiency of the wrap attack strategy of *Argiope* (Walter et al 2008). Active silk glands are not only crucial to prey-capture success such as pursuing larger prey (actual field observations) or when multiple prey must be caught in short succession but are also essential for defense (e.g. attacking opponent spiders in gaming spiders).

Findings regarding ontogenetic variation in stabilimentum-building behavior and stabilimentum type in *A. savigny* (Nentwig & Heimer 1987), *A. flavipalis* (Ewer 1972; Edmunds 1986), *A. aetherea* (Clyne 1969), *A. keyserlingi* (Herberstein et al 2000b) were also observed in *A. luzona*, *A. catenulata*, *A. appensa* and *A. aemula*. Juveniles usually spin discoid stabilimenta and sexually mature individuals spin cruciate stabilimenta. Li et al (2003) suggest that the ontogenetic shift from discoid to cruciate may indicate that stabilimentum function varies throughout the spider's life history, hence, might serve different functions in juveniles and adults.

In addition to ontogenetic variation in decoration type, there is interspecific variation in both the form (e.g. number of bands or arms) and frequency of web decoration. Though none of the four species of *Argiope* under study displayed a linear type decoration, the number (1-arm to 5-arm) and extent of bands or arms (continuous or discontinuous) of cruciate stabilimenta vary between species. *A. luzona* displayed a highly variable stabilimentum form ranging from 1-5 arms with or without a gap at hub, *A. catenulata* displayed only 1 or 2 discontinuous arms, *A. appensa* displayed only 1, 2, and 4 continuous or discontinuous arms, and *A. aemula* displayed only 1, 2, 3, and 4 discontinuous arms. Herberstein (2000) observed a tri-radiate form of stabilimentum in *A. catenulata*. Chen et al (2009) constructed a molecular phylogeny of Asian members of genus *Argiope* using mitochondrial markers to infer the evolutionary relationship of linear and cruciate stabilimenta. Results of ancestral character state reconstruction showed that the linear form was ancestral and the cruciate form derived, and the cruciate form has reversals back to the linear form. By manipulating the number and orientation of stabilimentum arms or bands in the field, they found out that bands arranged in a cruciate form were significantly more attracted to insects than those arranged in linear form. Such results suggest that pollinator insects' innate preference for a particular stabilimentum pattern might be one of the driving forces shaping the arrangement pattern of spider stabilimentum.

The idea that discoid stabilimenta might provide an amount of visual occlusions from potential predators, particularly for juvenile spiders (Eberhard 1973) is partly supported in this study. The size of disc-shaped stabilimentum is significantly correlated with the spider's size where larger spiders tended to spin larger disc-stabilimenta. Basically, the presence of disc-shaped stabilimenta changes the basic outline of the spider, and hiding behind it conceals its entire body. During our observations, a slight disturbance of the web causes them to shuttle behind the disc which distorts the image of the juveniles. The cruciate stabilimentum not only changes the outline of the spider but also augments the original spider's size, particularly, as spiders vibrate the web, a common predatory response among *Argiope* spp. Building a cruciate stabilimenta probably a simple response to gape-size limited predators such as lizards and other potential predators. The presence of stabilimenta make the web more visible to flying animals, hence, may serve as warning signals for web protection (Eisner and Nowicki 1983). Most of the undecorated webs were located in shaded areas (per. obs.). This is in congruent with the notion that discoid stabilimentum is used for thermoregulation by smaller spiders since smaller spiders are more prone to temperature fluctuation than those larger ones (Humphreys 1992).

The spider size is not a predictor of the occurrence of stabilimenta across all *Argiope* species under study. However, in congruence with aciniform gland activity hypothesis (Walter et al 2008), larger juvenile *Argiope* spp. tend to spin larger disc-shape stabilimentum. In spiders with cruciate stabilimentum, the body size is significantly correlated with the stabilimentum length among the four species observed (*A. luzona*, *A. catenulata*, *A. appensa*, and *A. aemula*), where larger individuals tend to spin longer stabilimenta. This is probably because the nutritional requirements tend to increase with increasing body size (Sensenig et al 2011). The sizes of prey targeted by spiders are also likely to increase as spiders grow. Since larger preys such as grasshoppers, dragonflies and some coleopterans the most commonly observed prey caught by larger spiders, an increase aciniform activity is required to completely immobilized these larger prey or to wrap and store more smaller prey.

In the present study, the length of cruciate stabilimentum was significantly negatively correlated with the web size in *A. luzona*, and *A. aemula*, spinning wider webs with shorter stabilimenta or smaller webs with longer stabilimenta. Alternatively, spinning wider undecorated or smaller decorated webs as observed in *A. appensa*. These results may suggest a trade-off between decorated small webs and undecorated large webs, hence, might be alternative foraging strategies among these spiders. This idea that large, undecorated web and small, decorated webs are alternative strategies is consistent with those findings from other studies testing the relationship between occurrence or stabilimentum length and web size (e.g. *Araneus eburnus*: Bruce et al 2004; *Argiope appensa*: Hauber 1998 and Abrenica-Adamant et al 2011; *A. keyserlingi*: Walter et al 2008; Herberstein et al 2000b; *A. trifasciata*: Tso 1999; *A. aurantia* and *A. trifasciata*: Blackledge 1998 and Crowe 2005). Herberstein et al (2000b) found that less satiated spiders tend to spin larger webs, but were less likely to spin stabilimenta than those more satiated. This finding supports the idea that stabilimentum-building is a different foraging strategy compared to building webs with a large capture area. The stabilimentum - building strategy is conceivably more easily adopted by well-fed or well-satiated spiders as these individuals have the option to invest more heavily in directed efforts toward particular prey types (Crowe 2005). The no correlation result between web size and stabilimentum length among *A. catenulata* can be thought as trade-off in energy investment between web construction and egg sac construction, thereby maximizing energy for egg sac construction. As observed, most of *A. catenulata* individuals were sexually matured or gravid (as indicated by presence of some egg sacs in the periphery of the webs). Other local ecological factors might also have contributed to this result.

In addition, within-species variation in stabilimentum-building behavior can be due to conflicts in investment between foraging enhancements and defense, considering that the silk stabilimenta attract both prey (Craig et al 1994; Elgar et al 1996) and predators (Eberhard 1973; Scharff and Coddington 1997; Blackledge and Wenzel 2001) to the web. Individual spiders respond to this conflict by varying their stabilimentum-building behavior relative to proportions of prey or predator types (Blackledge 1998; Blackledge & Wenzel 1999; Starks 2002). Tolbert (1975) has suggested that ontogenetic shifts in stabilimentum shape as spiders mature are responses to changes in predation risk as spider increase in size. Since spiders do not hunt continuously and spider predators were presumed to use stabilimenta in their search image (Blackledge & Wenzel 2001). There seems to be a cost to predictable stabilimentum production (Herberstein et al 2000b). Some prey learns to avoid stabilimenta (Craig et al 1991), thus forcing spiders to vary the pattern stabilimentum (Starks 2002). Craig et al (2001) suggest that the stabilimentum-building behavior of spiders has a genetic component and that expression of stabilimentum-building behavior is subject to local ecological conditions, specifically the presence of prey or predator. Foraging success favors the retention of stabilimentum-building polymorphism within population, as well as variability in individual stabilimentum-building response. Accordingly, the stabilimentum structure also reflects physiological states. As such, it is predicted that spiders with high-decorating phenotype and forage in favorable environment will grow faster and reach maturity earlier than those that do not.

An enclosure study is recommended to address the issue whether stabilimenta attracts prey or predators or both and that web size and stabilimentum-building are alternative foraging strategies which are dependent on local environmental conditions. Subjecting spiders of different species to different densities of only prey, only predators or both would address the question of when it is profitable to add stabilimentum, and what aspects might it be too risky. Examining the intra-individual variation in stabilimentum-building behavior over time (e.g. frequency of decoration, ontogenetic variation, response to perceivable environmental factors) would also help us understand the plasticity of stabilimentum-building as a behavioral response to variation in environmental conditions.

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