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Salient features of the orb-web of the garden spider, *Argiope luzona* (Walckenaer, 1841) (Araneae: Araneidae)

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ABSTRACT

Many orb-web building spiders such as the garden spider *Argiope luzona* (Walckenaer, 1841) add conspicuous, white zigzag silk decorations termed stabilimenta onto the central portion of the webs. We studied the features of the web of this species by examining the stabilimenta, variations in form and quantity, presence and absence of stabilimentum and structure to be able to understand the nature of web building especially the factors that affect the nature of the built web. Field observations reveal that the stabilimenta of *A. luzona* are mainly discoid or cruciate which significantly depended on body size. Smaller individuals (body size < 0.6 cm) produced mainly discoid stabilimenta and larger individuals (body size > 0.6 cm) produced strictly cruciate stabilimenta that are 1-armed, 2-armed, 3-armed, 4-armed, or 5-armed. Results also showed that the spiders' body size was positively correlated to the number of stabilimentum arms, length of upper arms and to the length difference between upper and lower arms. Smaller individuals (body size :≤ 0.8 cm) built 2-armed and 4-armed only while larger individuals (body size :≥ 0.8 cm) built 1-armed, 2-armed, 3-armed, 4-armed and 5-armed stabilimenta.

Keywords: stabilimentum, descriptive statistics, *Argiope luzona*, UTHSCSA Image Tool, arm asymmetry.

INTRODUCTION

All orb-weaving spiders use webs as an excellent device for catching prey that includes intersection (intercepting the prey), stopping (absorbing the momentum without breaking), and retention (trapping the prey by entangling it or sticking to it). Several economic importances of webs had been reported. Many of these spiders also spin highly visible decorations at the center of their webs (Scharff and Coddington, 1997; Herberstein *et al*., 2000a) especially in spiders that forage diurnally. The decorations can be made entirely of silk, a combination of silk and other items such as egg sacks, vegetation and detritus, decaying prey items and the exoskeletons of arthropod prey. These structures have been variously termed decorations by McCook (1889), stabilimenta by Comstock (1912), or devices by Hingston (1927) and Ewer (1972). Stabilimenta are often variable within webs of a species at any given locality, both in frequency of occurrence and in form or pattern (Robinson and Robinson, 1970; Ewer, 1972). Among these types, silk stabilimenta have many forms and have been of interest to researchers for over 100 years which remains an exciting area of research today.

Stabilimenta are best known and have been most intensively studied from spiders of the genus *Argiope* Audouin 1826 (Araneidae) which consists of moderately large orb-weaver spiders (Barrion and Litsinger, 1995). Its occurrence among *Argiope* spiders have attracted most attention to people since these are obvious unusual white zigzag structures at the center of the orb-web even clearly visible to naked eyes, either one below and one above the hub (linear decoration), disc-shape (discoid) or four bands forming a St, Andrew's cross typically with a gap at the hub (cruciate).

Stabilimentum is produced by aciniform and piriform glands (Peters 1993; Foelix 1996) and is the same that used to wrap prey. When you look at the structure of the stabilimenta, there are differences in form and in the frequency of spiders that spun decorations in their webs, both within and between species. This suggests that their functions can be species-specific and vary even within a single species (Uhl, 2008; Lubin, 1980) probably to suit multiple functions throughout their life history. In *Argiope*, even within the same species, the shape of a stabilimentum differs at different developmental stages. Moreover, some juvenile spiders spin disk-like stabilimenta surrounding web hubs, but adults spin cross or linear forms (Nentwig and Rogg, 1988). Thus, this study was conducted to characterize the stabilimentum structure and to be able to understand the nature of web building in a species of *Argiope luzona* (Walckenaer, 1841), especially the factors that affect the nature of the built web. Specifically, this study aimed to answer the following questions: (1) is the occurrence of stabilimenta an obligatory component of orb web? (2) is the any correlation between the spider size and the occurrence and type or form of stabilimenta? and (3) does intraspecific differences in stabilimentum structure among *Argiope luzona* individuals exist? This study also aimed to describe some distinguishing external topology of female *A. luzona*.

MATERIAL AND METHODS

Field Observations. This study was conducted in 2008 in a three-hectare banana plantation at Sitio Paitan, Dalipuga, Iligan City, Philippines. A total of 128 female and juvenile *A. luzona* were observed with body sizes ranging from 0.14 to 2 cm (mean=0.89$\pm$0.54; N=124). Identification and descriptions of female *A. luzona* were based on the descriptions of Barrion and Litsinger (1995). The presence and absence of web decoration or stabilimentum, classification as either discoid (disk-shaped) or cruciate (cross-shaped) shapes were determined (Fig. 1). For cruciate web decoration, the number and pattern of stabilimentum arms were noted. Spider size was measured as total body length and stabilimentum arm length and their asymmetries were determined with the aid of UTHSCA Image Tool software, Version 3.00 (available on the internet at http://ddsdx.uthscsa.edu/dig/itdesc.html). This was done by measuring the images of spiders and stabilimentum scaled with rulers. For comparison purposes, spiders were assigned 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 $\leq$1.0 cm (E). Juvenile spiders without visible alternating bands on the dorsal side of abdomen were excluded. The spiders in the A category were observed in enclosure reared from egg sacs of *A. luzona* collected from the field. Sample sizes varied because some measures were added after some data collection had taken place, and not all measures could be taken successfully on all webs.

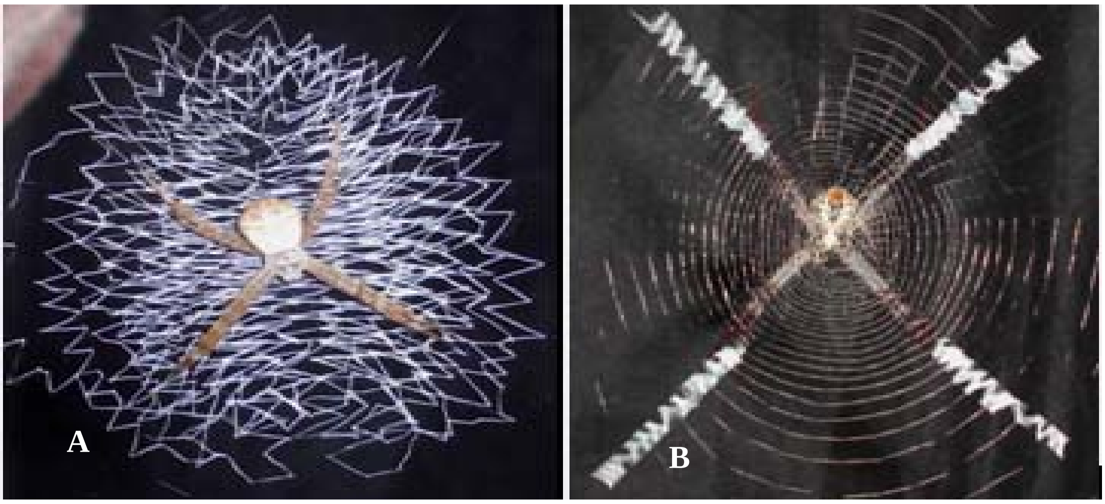

Fig.1. Types of stabilimentum of the garden spider, *Argiope luzona* (Walckenaer, 1841). Discoid (magnification, 3x) (A), Cruciate (magnification 1x) (B).

Statistical Analysis. Pearson Regression Correlation analysis was used to determine relationship between spider size and stabilimentum structure. Descriptive statistics (Univariate Analysis) were also used. All tests were performed two tailed and alpha set to 0.05 in all cases. Statistical analysis was performed using the software SPSS ver. 13 (Statistical package for the Social sciences).

RESULTS AND DISCUSSION

Both sexes of *A. luzona* observed and collected from a three-hectare banana plantation in Paitan, Dalipuga, Iligan City are locally named “Spider X” since they sit and wait at the hub of the orb-web with legs extended two by two in a similar cruciate manner, forming an “X”. Penultimate and adult females are characterized by a flat yellow brown cephalothorax, covered with a thick layer of short white hairs. Their chelicerae are brown, with yellowish tinge, a promargin with four teeth and a retromargin with three teeth. The eyes are recurved in two rows and the lateral eyes are likely continuous. A six alternating yellow and brown transverse bands that form a pattern can be seen on the dorsal side of the abdomen starting from the anterior to the posterior positions. Patches of irregularly scattered obovate to globular yellow spots are found in brown patches. A pair of sublateral chalk-white longitudinal bands, subapical and submedian parts bulging, enclosed black area between epigynum and spinnerets, with eight pairs of yellow spots are evident in venter of abdomen (Figure 2A & B). The epigynum (female genital structure) is characterized by a prominent anterior bulge, a narrow septum deeply notched anteriorly but well rounded in lateral view, a posterior plate which is a little wider than septum, and a depression moderately narrow. The epigynum bears spermathecae (receptacles that receive sperm) with a pair of parallel oblong structures with a slight constriction in the middle. The legs are long and slender with thin short spines with a leg formula of 2143. Adult males are smaller than females (body size: 0.41 ± 0.05cm. Fig. 2C) with a light reddish brown cephalothorax and abdomen. Unlike female, male’s cephalothorax is bigger than its abdomen with the six alternating yellow and brown transverse bands completely absent. Male’s web were not included in the study.

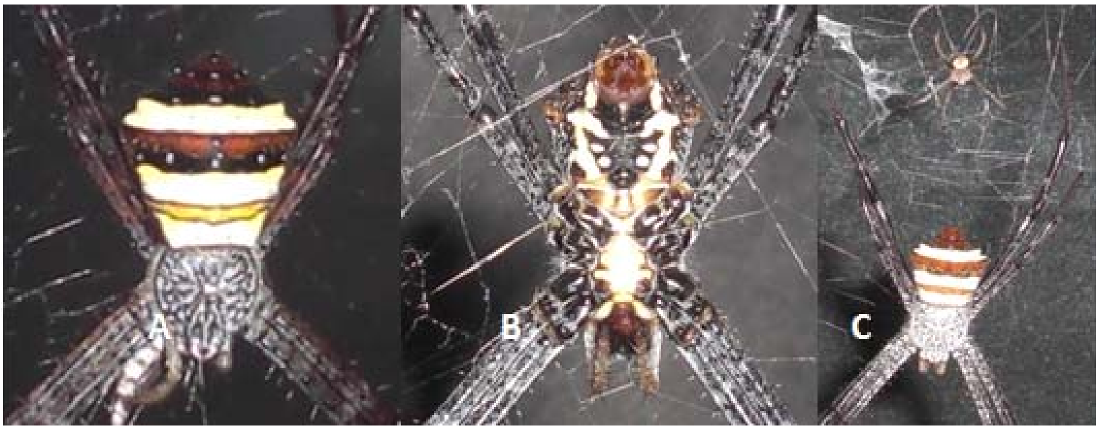

Fig. 2. Garden spider, *Argiope luzona* (Walckenaer, 1841) sampled from Sitio Paitan, Dalipuga, Iligan City. A, female dorsal view; B, ventral view; and C, female (lower) and male (upper). Magnifications: ca. 2.5x (A), 2.8x (B) and 0.91x (C) respectively.

Stabilimentum Structure.

Based on field observations, there are only two basic forms of stabilimenta in *A. luzona* (Fig.1): "disc" stabilimentum or discoid (tightly woven disc of white silk covering the hub) and "cross" stabilimentum" or cruciate. Cruciate can be four ribbons of zigzag silk forming the arms of a diagonal cross, with or without crossing each other at the hub. Incomplete cross stabilimenta may be found, with one to three arms of the cross in several possible combinations.

As observed, the presence of web decoration was not an obligatory part of web construction. Of the 128 orb-webs observed, 23 (18%) had no stabilimenta, 27(21%) had discoid stabilimenta, one (0.78%) had discoid and cruciate stabilimenta, and 77 (60%) had cruciate stabilimenta (Fig. 2). The occurrence of different types of stabilimentum was observed to be dependent on spider size (Pearson Correlation: *$r=0.597$; $P<0.05$; $n=124$)*). Discoid stabilimentum predominantly occurred in smaller spiders (category A and B; while larger spiders (category C, D and E) showed complete or partial type of cruciate decoration. It is interesting to note here that one individual in category B was observed to add cruciate decoration in its discoid web stabilimenta (Table 1 and Fig.3).

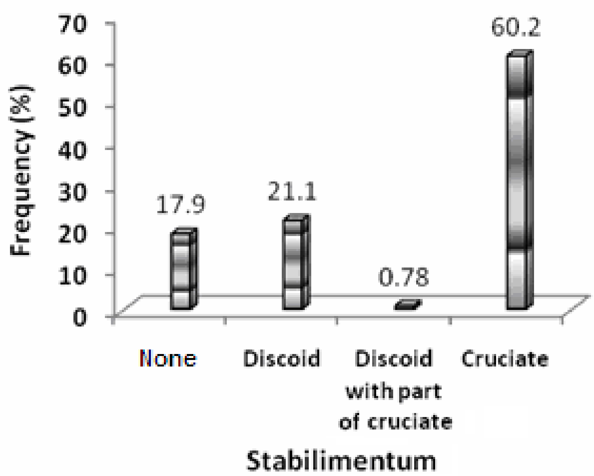

Fig. 3. Presence and absence of stabilimentum and frequency of occurrence of different kinds of stabilimenta in *A. luzona* (n=128*)*.

Table 1: Distribution of the type of stabilimentum among five size categories of *Argiope luzona (Walckenaer, 1841)* sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008. Frequencies are given in parenthesis. Subadult and adult males excluded.

Types of Stabilimenta	A <0.4 cm	B 0.4-0.59 cm	C 0.6-0.79 cm	D 0.8-0.99 cm	D >1.0 cm	Total
Discoid	17(73.9%)	10(52.6%)	0	0	0	27(21.1%)
Discoid with part of cruciate	0	1(5.3%)	0	0	0	1
Cruciate	2(8.7%)	5(26.3%)	15(88.3%)	17(77.3%)	38(80.9%)	77 (60.2%)
N	23	19	17	22	47	128

Fig. 4 shows the discoid type of stabilimentum was observed to have two size categories (<0.4 and 0.4-0.59 cm) and the cruciate type in three size categories (0.6-0.9 cm, 0.8-0.99 and >1.0 cm). Webs with no silk decoration were also observed in all size classes. The ratios of occurrences of decorations between and among stabilimentum types are presented in Table (2). It can be observed from the results that the occurrences of stabilimentum types vary with increasing sizes among *A. luzona* individuals.

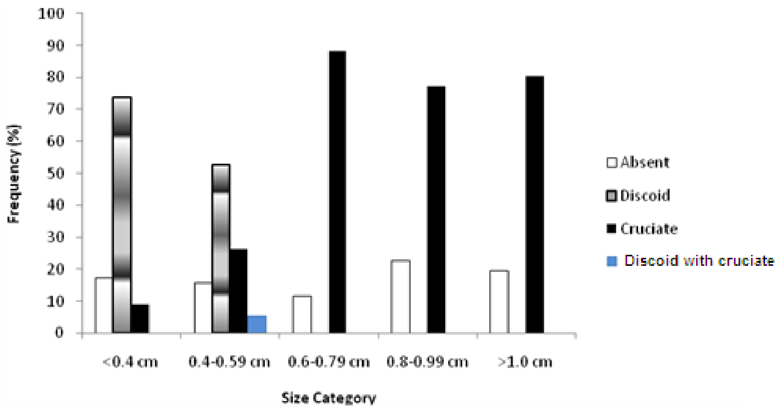

Fig. 4: Frequency of webs with discoid (broken bars) or cruciate stabilimenta (black bars) or no decoration (white bars) or discoid with cruciate decoration (blue bar) among the size categories of 128 *Argiope luzona* (Walckenaer, 1841) females sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008 (Subadult and adult males excluded).

Table 2: Frequency (ratio) occurrences between and among stabilimentum types of *Argiope luzona* (Walckenaer, 1841*)* sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008 (*n=124*) (Subadult and adult males excluded).

	A <0.4 cm	B 0.4-0.59 cm	C 0.6-0.79 cm	D 0.8-0.99 cm	E >1.0 cm
None versus discoid	4:17	3:10	2:0	5:0	9:0
None versus cruciate	4:2	3:5	2:15	5:17	9:38
Discoid versus cruciate	17:2	10:5	0:15	0:17	0:38
None:discoid:cruciate	2:8:2	1:3:2	1:0:7	1:0:3	1:0:4
N	23	19	17	22	47

Variable stabilimentum arm pattern were also observed (1-arm to 5-arms, or none at all; Fig. 5). This result suggests that within a single species, different types of silk decorations can be found or one type can be extremely variable with webs lacking one or several silk bands or being completely without decoration. Stabilimentum may have one lower arm, 2 arms where it may have two lower arms or 1 upper and 1 lower arm or a continuous upper to lower arm. Four-arm stabilimentum may consist of either two continuous upper to lower arms or four discontinuous arms. Stabilimentum with 1 arm, 3 arms or 5 arms were the least frequently observed while 4 arms and 2 arms stabilimenta were the most frequently observed (Fig. 6).

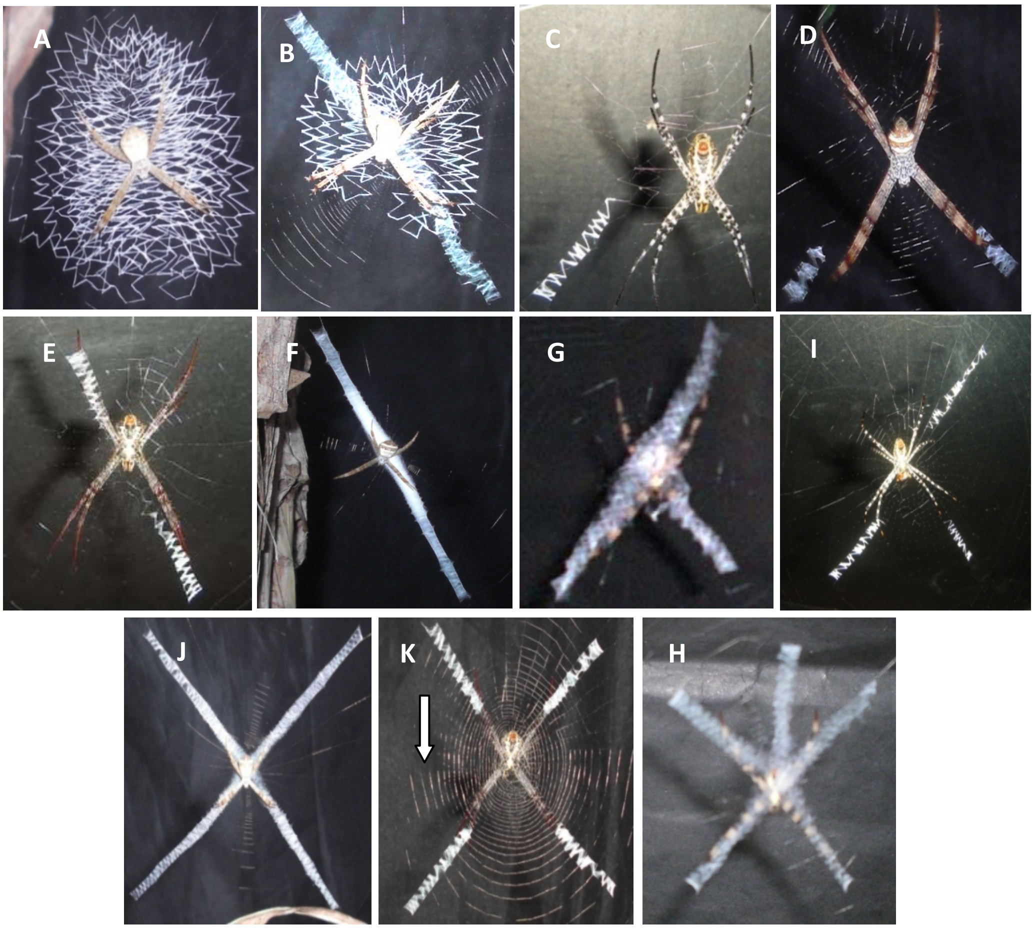

Fig.5. Decoration (stabilimentum) types: discoid (*A*), discoid with cruciate (*B*), and cruciate (*C-K*). Cruciate web decoration includes 1-arm (***C***), 2-arm either with 2 lower arms (*D*), a discontinuous upper arm and lower arm (*E*), or a continuous upper arm to lower arm (*F*). Three-arm may have 2 continuous arms and a discontinuous arm (*G*), or a discontinuous (*H)* 3- arm. Four-arm is either continuous (*J*), or discontinuous (*J*) or 5-arm continuous (*K*). The spider is located up side down in the hub (white arrow) of the web. Stabilimentum can be continuous (crosses the hub) or discontinuous (do not cross the hub). Magnifications are ca. 3x (*A*)*;* 1.5x (*B*) 0.90x (*C*) 1.6x (*D*); 0.7x (*E*); 0.48x (*F*); 0.5x (*G*); 4.7x (*H*); 0.7x (*I*); 0.5x (*J*); and 0.4x (*K*) respectively (Subadult and adult males excluded).

The descriptive statistics on the measurements of stabilimentum and Pearson Correlation results are given in Tables 3 and 4. Spiders' body sizes were not significantly related to the length of lower right arm (Pearson Correlation*:* r =00.496; P>0.05; $n=29$), and the lower left arm (Pearson correlation: r=0.455; P>0.05; $n=28$), but it is related to the length of both the upper left arm (Pearson Correlation*:* r= 0.*624*; $P<0.05$; $n= 27$) and upper right arm (Pearson Correlation: r= 0.*587*; $P<0.05$; $n=33$).

Table 3: Frequency distribution of stabilimentum arm among the five size categories of *Argiope luzona* (Walckenaer, 1841) sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008. (*N=77*) (Subadult and adult males excluded).

Stabilimentum Arm	Size Category (N=77)				
	A <0.4 cm	B 0.4-0.59 cm	C 0.6-0.79 cm	D 0.8-0.99 cm	E >1.0 cm
1-arm	0	0	0	0	1(2.6%)
2-arm	1(50%)	3(60%)	7(46.7%)	6 (35.3%)	3(7.9%)
3-arm	0			2(11.8%)	4(10.5%)
4-arm	1(50%)	2(40%)	8(53.3%)	9(52.9%)	29(76.3%)
5-arm	0	0	0	0	1(2.6%)
n	*2*	*5*	*15*	*17*	*38*

Spider size was also observed to be significantly correlated with the number of stabilimentum arms (Pearson Correlation: $r= 0.334$; $P<0.05$; $n=79$). Smaller spiders showed less variable arm (2-arm or 4-arm) while larger individuals showed more variable arm patterns (1-arm, 2-arm, 3-arm, 4-arm or 5-arm; Figure 6, Table 4).

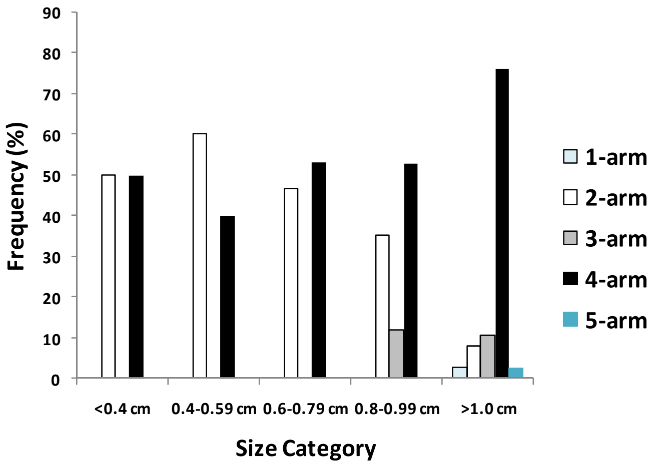

Fig.6: Frequency of stabilimentum arms (field-observation) of *Argiope luzona* (Walckenaer, 1841) sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008 ($N=77$) (Subadult and adult males excluded).

In terms of stabilimentum arms length, there were substantial differences between upper arms, between lower arms, between upper and lower arms, and between upper and lower arms in the same side of the web. The length of upper arms and lower arms can also be symmetrical (one web only; length difference= 0.0). Spider's size was not significantly related to the difference between upper arms (Pearson Correlation: $r=0.166$; $P>0.05$; $n= 24$) and between lower arms (Pearson Correlation: $r=-0.043$; $P>0.05$; $n= 23$). In contrast, spider size was significantly related to the difference between upper and lower arms of the left side (Pearson Correlation: $r=0.408$; $P<0.05$; $n=24$), the difference between upper and lower arms of the right side (Pearson Correlation: $r=0.376$; $P=0.05$; $n=27$), and the difference between upper and lower arms (Pearson Correlation: $r= 0.383$; $P<0.05$; $n=32$) (Table 4).

Table 4: Descriptive statistics and correlation analysis (*Pearson Correlation*) of stabilimentum measures on stabilimentum structure of *Argiope luzona* (Walckenaer, 1841) sampled from Sitio Paitan, Dalipuga, Iligan City on December 28, 2008 ($n=77$). Sample sizes (n) refer to the number of webs. If a web has two upper arms and two upper arms, their measures were averaged and the averages were used in the analysis between upper and lower arms. Measurements are in centimeter (cm) (Subadult and adult males excluded).

VARIABLE	*n*	*Mean*	*S.D.*	*Min*	*Max*	Pearson Correlation	
						R	*P*
Arm Length							
Upper left arm	27	1.95	0.99	0.31	4.71	0.064*	<0.05
Upper right arm	33	1.92	0.91	0.56	3.58	0.587*	<0.05
Lower left arm	28	1.84	0.62	0.66	3.23	0.96	>0.05
Lower right arm	29	1.78	0.72	0.64	3.25	0.55	>0.05
Length Asymmetry							
Difference between upper arms (left & right arms)	24	0.41	0.52	0.20	2.56	0.166	>0.05
Difference between lower arms (left &right arms)	23	0.33	0.30	0.01	1.09	-0.043	>0.05
Difference between upper and lower arms of the left side	24	0.51	0.39	0.07	1.48	0.408*	<0.05
Difference between upper and lower arms of the right side	27	0.50	0.42	0.02	1.72	0.376*	=0.05
Difference between upper arm and lower arm	32	0.40	0.35	0.0	1.51	0.382*	<0.05
Stabilimentum Area (cm^2)	26	1.75	0.75	0.08	5.75		

*- Correlation is significant at the 0.05 level (2-tailed).

Results of this study showed remarkable variations in stabilimentum structure of *A. luzona*. First, as also observed in other species of *Argiope*, it is not always true that orb web structurally determines, *a priori*, stabilimentum length in *A. luzona*. The stabilimentum arms were observed to extend beyond the free zone (inner portion of the web that contains non-sticky spiral), where it often stopped for short of the first sticky spiral into the capture area (sticky spirals). This can be attributed to the fact that stabilimentum silk are produced by aciniform glands while web silk are produced by aggregate, ampullate, and flagelliform glands (Foelix, 1996).

Second, changes in form from disc shaped (discoid) to cruciform (cruciate) designs were observed to be significantly correlated with body size. Discoid web predominates in smaller animals while cruciate web decoration predominates in larger spiders. This observation is also true to other species of *Argiope*, i.e., *A. argentata* (Uhl, 2008), *A. versicolor* (Li *et al*., 2003), *A. keyserlingi*, and *A. trifasciata* (Herberstein *et al*., 2000a). This current study showed one spider displayed a discoid web with a part of cruciate decoration, probably a transition between discoid to cruciate design. Studies on other species of the genus *Argiope* add linear web decorations (Bruce *et al*., 2005).

Third, spider size was observed to be related to the number of arms. If present, larger spiders add extremely variable stabilimentum pattern (1 to 5 arms). Cruciate decoration is extremely variable in the number of arms and size. A high proportion of webs with a complete cross (64%; *n=128*) was observed. The result of the study is similar to those observed in *A. florida* (Uhl, 2008). In contrast however, 13 other species of *Argiope* are known to add stabilimenta but webs with full crosses were relatively rare (Herberstein *et al.,*2000b, Justice *et al.,* 2005). Our study shows that the 2-arm and 4-arm stabilimenta which vary in thickness (visible zigzag or very thick zigzag in band) may cross or may not cross the hub. The length of upper arms and lower arms were predominantly asymmetrical although we have observed one web to have a symmetrical arm length.

There are several published studies that explain potential influences on stabilimentum variation. Edmunds (1986) recorded changes in form from discoid to cruciate design. Moulting and sexual receptivity can be correlated with an increased frequency of stabilimenta (Nentwig & Heimer, 1987). Some of the variations in size and frequency of stabilimenta within population may have been caused also by variation in the foraging success of the spider (Blackledge, 1998). Since the stabilimenta is also made of aciniform silk which is used by the spiders for "wrap attacks", spiders may have used accumulated excess web for building web decoration. Constant secretion in the aciniform gland 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*).

The size and structure differences of webs (i.e. presence of stabilimenta and barrier webs) may have also varied due to differences in the needs of the spider (egg maturation, moult: Shermann, 1994) or with the quantity of available silk (Pasquet and Leborgne, 1997). Variations may also be due to environmental factors: abiotic (Ap Rhisiart and Vollrath, 1994; Pasquet and Leborgne, 1997) or biotic: i.e. prey (Pasquet *et al*., 1994; Pasquet and Leborgne, 1997) and conspecifics (Lubin, 1980; Buskirk, 1986; Leborgne and Pasquet, 1987; Pasquet and Leborgne, 1997).

Variation in stabilimentum-building behaviors may also be due to conflicts from selective pressures from investment in foraging and defense at many different levels. While most of the orb-weaving spiders are nocturnal or stay at retreats during the day, thus are protected from predators, spiders in the genus *Argiope, Cyclosa,* *Micrathena*, and some *Uloborids,* however, sit-and-wait at the centers of the webs during the day. The presence of web decoration could probably allow these spiders to respond more quickly to any environmental stimulus but also exposes them to predators (Eberhard, 1973; Schcarff and Coddington, 1997; Blackledge and Wenzel, 2001). Individual spiders respond to this conflict by varying their building of stabilimenta relative to proportions of predator types (Blackledge, 1998; Blackledge and Wenzel, 1999; Starks, 2002). Tolbert (1975) has suggested that changes in stabilimentum shape as spiders mature are responses to changes in predation risk as spider increase in size. Other studies show varied predator avoidance behaviors on different developmental stage suggesting that ontogenetic differences in stabilimentum types may reflect different function at different history stages (Li *et al.*, 2003). Discoid stabilimentum of juvenile spiders and cruciform stabilimentum may be used for deception by shielding a spider from a predator's view (Eberhard, 1973), or act as a visual signal that attracts insects (Tso, 1998), supporting prey attraction hypothesis or make the spiders appear larger which is a possible adaptation to gape size limited predators such as lizards (Uhl, 2008). Presence of stabilimenta functions as defenses against wasps. It can enhance defensive dropping behaviors, perhaps by distracting (or startle) attacking wasps or by camouflaging spiders (Blackledge and Wenzel, 2001). In this type of decoration, the entire or almost the entire spider overlaps with the decoration (Figure 1A), thus may provide camouflaging against arthropod predators. However, a study conducted by Bruce *et al.* (2005) stated that these decorations are inefficient at camouflaging against birds, despite the fact that the entire or almost the entire spider overlap with the stabilimentum. If discoid decoration is still inefficient at camouflaging against birds, then, it is definitely unclear how cruciate decorations could function to obscure the spider, since, there is minimal overlap between stabilimentum and spider's body (Figure 2B). Spiders also vary the stabilimentum building behavior for foraging enhancement (Starks, 2002). Spiders do not hunt continuously and spider predators were presumed to use stabilimenta in their search image (Blackledge and Wenzel, 2001). There seems to be a cost to predictable stabilimentum production (Herberstein *et al.*, 2000b). Some prey learns to avoid stabilimenta (Craig, 2004), thus forcing spiders change to the pattern of stabilimenta (Starks, 2002).

Variation in stabilimentum structures may also reflect different selection pressures across a spider's life history (Starks, 2002). Stabilimenta are likely to have any thermoregulatory effects especially in juvenile spiders which display discoid decoration (Nentwig & Heimer, 1987). Given that smaller spiders are more susceptible to fluctuating temperature, the use of stabilimenta for thermoregulation may more beneficial to smaller individuals of a given developmental stage but not to large ones (Starks, 2002). Finally, variation in the number of arms, length of each arm in the stabilimentum, design (arm arrangement, thickness) and extent (cross the hub or leave a gap between arms), could all related to several proposed ecological functions of the stabilimentum and should be considered in the future studies of stabilimentum structure and function.

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