

Intraspecific and Interspecific Variation of Stabilimenta in Orb Webs of *Argiope* Spiders (Araneae: Araneidae)

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Received: August 06, 2015; Accepted: October 26, 2015; Published: October 29, 2015

Research Article

Abstract

Argiope spiders decorate their orb-webs with very conspicuous white zigzag silk construct called stabilimenta. This study was conducted to describe and compare the stabilimentum structure within and among the four *Argiope* species - *Argiope luzona*, *A. catenulata*, *A. Appensa* and *A. Aemula*. Results showed that stabilimenta is an optional component of the orb-web across the four *Argiope* species. The frequency, type (cruciate or discoid) form (thickness, extend: continuous or discontinuous, number of bands or arms) vary from web to web of a single individual (intra-individual variation), same species (intraspecific variation), or webs of different species (interspecific variation) which might be correlated with variety of environmental factors such as presence of prey, predators, conspecifics and other abiotic factors. The stabilimentum types of *Argiope* spp. were either discoid or cruciate which vary with spider size or ontogenetic stage. Small juveniles (body length < 0.4 cm) decorate their webs with discoid type while large adult/sub adult ones (body length: >0.6 cm) spun strictly cruciate form which vary in the number of arms (1-arm to 5-arm).

Keywords: *Argiope luzona*; *A. Appensa*; *A. Catenulata*; *A. aemula*; Stabilimentum structure.

1. Introduction

Some diurnal orb-web spiders (Araneae: Araneidae, Tetragnathidae, Uloboridae) also spin highly visible decorations called stabilimenta at the hub of their webs. These structures vary in form and composition [1]. 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 [2]. Among these types, the silk stabilimenta have many forms and have been the centre of debate in spider literature for over a century [3]. In general, silk stabilimenta are characterized by their shape (discoid, spiral, cruciate, linear), location with the web (center or in

the periphery of the web), and number of arms.

Argiope spiders (Araneae: Araneidae) are diurnal stationary species that decorate their webs with very conspicuous white zigzag silk stabilimenta. In the Philippines, *Argiope* spiders are locally known as "Mr. X" or "Spider X" since these spiders rest at their webs with legs extending in "X" position. When you look at the structure of stabilimenta, its occurrence and specific form (type and number of arms) a spider may construct were likely to vary with spider size, across the spider's life history, spider species, and response to abiotic and biotic factors of its immediate surroundings [1]. Several hypotheses were proposed to describe the function of stabilimenta. Some researchers thought that these constructs may serve as warning design against birds that might fly through the web [4,5], may be used to startle predators by changing its size and body shape/outline [6], and may be used for hiding their body [1,3,7]. However, some of these functions were not explicitly tested. To date, two of the most accepted theories of the adaptive function of these constructs are predator avoidance and prey attraction. Both hypotheses rely on the fact that silk stabilimenta reflect ultraviolet (UV) light, and insects are attracted to UV range since it mimics an open sky/open vegetation serving as escape route or food source [8-10]. This field study aims primarily to describe and compare the stabilimentum structure in orb-webs within and among the four *Argiope* species -*Argiope luzona*, *A. catenulata*, and *A. Aemula*, and investigate some of the proposed functions of stabilimenta.

2. Methods

2.1 Study species and study sites

Field survey on the occurrence and form of stabilimentum in orb-webs of the four *Argiope* spiders-*Argiope luzona*, *A. catenulata*, and *A. aemula* (Figure 1) was conducted from October 28, 2008 to June 20, 2015 in selected areas of Mindanao, Philippines.

The spider size was measured based on the total body length [11]. Unidentified small juvenile spiders collected in the field were reared in the laboratory for taxonomic identification. For comparison purposes, spiders with body in size <0.60 cm were considered juveniles while spiders in size of ≥ 0.60 cm were considered adults.

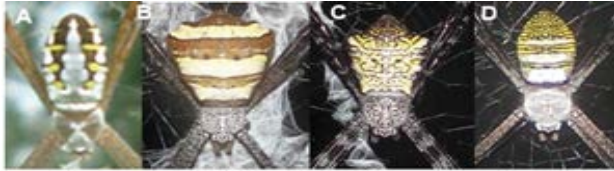


Figure 1. The four Argiope species: *A. catenulata* (A), *A. luzona* (B), *A. appensa* (C) and *A. aemula* (D).

2.2 Web parameters

A total of 3,087 webs were observed- *A. luzona* (N=824, 26.7%), *A. catenulata* (N=949, 30.7%), *A. appensa* (N=753, 24.4%), *A. aemula* (N=547, 17.7%). 2,234 (72.4%) webs were occupied with adults and 853 (27.6%) were occupied with juveniles. The stabilimentum was described based on type (Figure 2), number of arms and extend of arms (continuous, discontinuous). For comparison purposes, arms that crossed each other at the hub (without a gap at hub) are called continuous arms while those that leave a gap are called discontinuous arms (Figure 2).

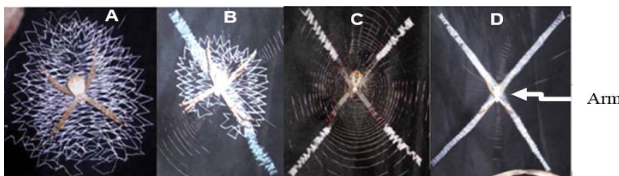


Figure 2. Types of stabilimentum of Argiope spp: discoid (A), discoid with part of cruciate (B), discontinuous cruciate (C) and continuous cruciate (D). A cruciate type can be incomplete/partial cruciate where one or more arms are missing (not shown here).

2.3 Statistical analyses

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

3. Results and Discussion

The results showed that not all webs were decorated suggesting that stabilimenta are optional component of the web (Figure 3). The web decorating frequency

range from 46.6% to 93.5% among adults and 62.2% to 90.1% among juveniles. The stabilimentum

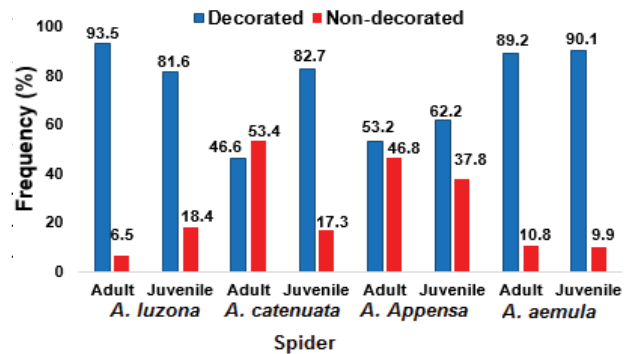


Figure 3. Summary on the occurrence of Stabilimentum in *A. luzona* (adult: N=626; juvenile: N=212), *A. catenulata* (adult: N=770; juvenile: N=179), *A. appensa* (adults: N=412; juvenile: N=341), and *A. aemula* (adult: N=426; juvenile: N=121),

Figure 4 shows the relationship between spider size and occurrence of stabilimentum among the four Argiope spiders. Argiope spp. spun only two types of stabilimentum: cruciate and discoid type which varied with spider size (developmental stage), suggesting an ontogenetic polymorphism on stabilimentum structure. Very small spiders (spider size: < 0.4 cm) spun the discoid type while the larger spiders (spider size: > 6.0 cm) spun only the cruciate type which differs in patterns (1-arm to 5-arm). Few of the juveniles were observed to have a discoid with incomplete cruciate stabilimentum- 3 webs, 5 webs, 4 webs, and 4 webs for *A. luzona*, *A. catenulata*, *A. appensa* and *A. aemula* respectively, a transition between a discoid to a cruciate design (Figure 2B).

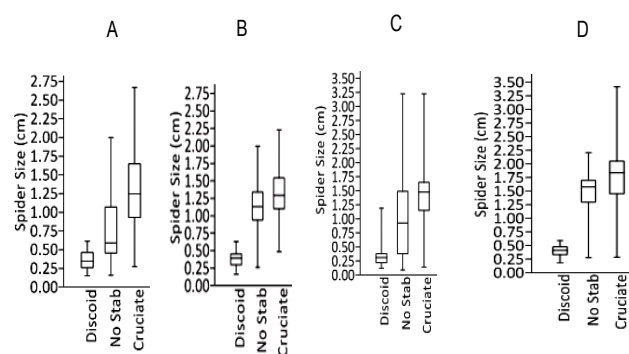


Figure 4. Relationship between Spider Size (cm) and occurrence of stabilimentum among the four Argiope spiders: *A. luzona* (A), *A. catenulata* (B), *A. appensa* (C) and *A. aemula* (D).

The apparent dependence of the occurrence of either discoid or cruciate stabilimenta with spider's size (Figure 4) was confirmed with Linear Correlation Analysis (Linear Correlation between spider's size and stabilimentum type [*A. luzona* (r=0.62; p<0.0001), *A. catenulata* (r=0.82; p<0.0001), *A. appensa* (r=0.72;

$p < 0.0001$) and *A. aemula* ($r = 0.86$; $p < 0.0001$]. Results of Mann-Whitney pairwise comparison further confirmed that the type of stabilimenta significantly varies within species of different ontogenetic stage: *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 (webs without stabilimenta) were also observed from small to large spider. The findings regarding ontogenetic variation in stabilimentum-building behaviour are also true to *Argiope savigny* [12], *A. flavipalis* ([13,14], *A. aetherea* [15], *A. keyserlingi* and *A. trifasciata* [4], *A. argentata* [16,17], and *A. versicolor* [18].

There were at least five different forms of cruciate stabilimenta (1-arm, 2-arm, 3-arm, 4-arm or 5-arm) among *Argiope* spiders (Table 1), which is not predicted with spider's size [Linear Correlation Analysis: *A. catenulata* ($r = 0.012$; $p = 0.83$), *A. appensa* ($r = 0.05$; $p = 0.32$), in *A. luzona* ($r = 0.142$; $p = 0.61$) and *A. aemula* ($r = 0.06$; $p = 0.42$)]. Some of these arms crossed each other at the hub (continuous arms) while others left a gap at hub (discontinuous arms). The proportions of specific stabilimentum pattern (number of stabilimentum arms) varied among the four *Argiope* species.

In particular, *A. catenulata* spun only 1-armed (75.5%), discontinuous 2-armed (23.1%) and 3-armed (1.4%) stabilimenta (Table 1, Figure 5) while *A. luzona* spun all possible combinations (Table 1, Figure 6). Webs with a complete cross (4-armed) stabilimenta were displayed more often among *A. luzona* (56.9%), least often among *A. appensa* (only 2.2 %), and none among adult *A. catenulata* (Table 1). A discontinuous 4-armed stabilimenta were only observed among juvenile *A. catenulata* (body size = 0.4-0.6 cm). *A. appensa* spun all possible combinations except 5-armed stabilimenta (Table 1, Figure 7). Likewise, *A. aemula* spun 1-armed to 5-armed decorations; however, none of these arms have crossed the hub (Table 1, Figure 8). Thickest stabilimentum was observed in webs of *A. luzona*, followed by *A. aemula*, *A. appensa* and *A. catenulata* has the least conspicuous silk stabilimenta.

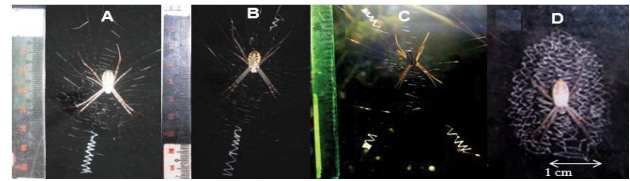


Figure 5. Cruciate stabilimenta in orb-webs of *A. catenulata*: 1-arm (A), 2-arms (B), and Discoid (C). *A. catenulata* also spun 3-armed, 4-armed, and continuous 2-armed in a discoid stabilimenta (not shown here).

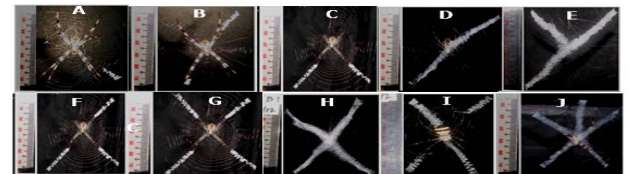


Figure 6. Cruciate stabilimenta in orb-web of *A. luzona*: 1-arm (A), 2-arms (B-C), 3-arms (D) and 4-arms (E-G) and 5-arms (H).

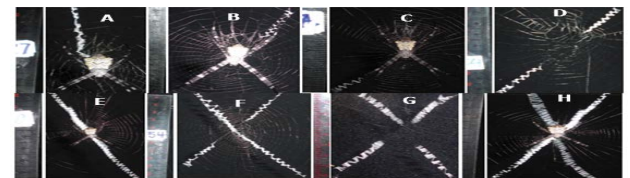


Figure 7. Cruciate stabilimenta in orb-webs of *A. appensa*: 1-arm (A-C), 2-arms (D-E), and 4-arms (F-H). Cruciate stabilimentum can be continuous (without gap at hub), discontinuous (leaving a gap at hub) or a combination of continuous and discontinuous arms.

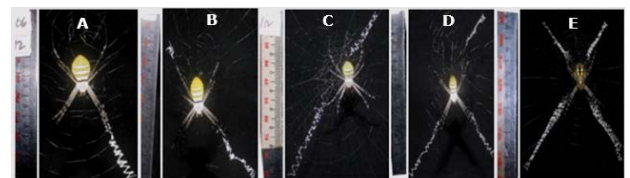


Figure 8. Cruciate stabilimenta in orb-webs of *A. aemula*: 1-arm (A), 2-arms (B-C), 3-arms (D) and 4-arms (E).

The above results showed that the presence of stabilimenta is optional component of the web. The stabilimentum structure varies within (intraspecific) and between (interspecific) species of *Argiope*. These observations suggest that the function of stabilimenta can be species-specific and vary within species to suit multiple functions throughout the spider's life history [16,18,19].

Table 1. Summary on the frequency of the different cruciate stabilimentum patterns (arms) in orb-webs of adult spp. Percent frequencies are within parenthesis.

Species	Stabilimentum form								
	1	2C	2D	3C	3D	4C	4D	2C;2D	5C;5D*
<i>A. luzona</i> (N=585)	31 (5.3)	20 (3.4)	152 (26)	4 (0.7)	16 (2.7)	196 (33.5)	146 (25)	16 (2.7)	4 (0.7)
<i>A. catenulata</i> (N=359)	271 (75.5)	-	83 (23.1)	-	5 (1.4)	-	-	-	-
<i>A. appensa</i> (N= 219)	13 (5.9)	102 (46.6)	80 (36.5)	3 (1.4)	-	10 (4.6)	10 (4.6)	1 (0.5)	-
<i>A. aemula</i> (N=380)	20 (5.3)	-	136 (35.8)	-	27 (7.1)	-	187 (49.2)	-	10* (2.6)

It is noteworthy that spider size is not correlated with the presence of discoid stabilimenta [Linear Regression Analysis: *A. luzona* ($r=0.05$; $p=0.43$), *A. catenulata* ($r=0.03$; $p=0.37$), *A. appensa* ($r=0.05$; $p=0.43$), and *A. aemula* ($r=0.08$; $p=0.54$)] and cruciate stabilimenta [Linear Regression Analysis: *A. luzona* ($r=0.12$; $p=0.067$), *A. catenulata* ($r=0.33$; $p=0.50$), *A. appensa* ($r=0.12$; $p=0.064$), and *A. aemula* ($r=0.24$; $p=0.10$)]. Hence, web decorating behaviour among these spiders was not influenced by ontogenetic stage. Several studies have shown that the spider's options to spin stabilimenta in their webs can be due to foraging needs/hunger-related [20] or moulting [21], quantity of available aciniform silk use in prey-wrapping and stabilimentum-building [22,23], specific abiotic and biotic factors (i.e. prey, predator) in their habitat [22,24,25], physiological state [26] and conspecifics or resource competition [17,19,22,27,28].

The continued debate on the ecological function of stabilimenta decelerates the understanding of the exact function of these constructs. The male guidance/love path function [29], thermoregulation/shield the sun preventing overheating of spiders [13,12,15,26], warning signal/predator avoidance [7,25], and prey attraction [1,8,10,18,30-33] are few of the proposed functions of silk decoration or stabilimenta. Several authors have suggested that stabilimenta may serve more than one function, either simultaneously or at different stages in a spider's development [12,34,35]. To date, several researchers presumed that the ontogenetic shift from discoid to cruciate form and variations in cruciate stabilimentum reflect different selection pressures across spider's life history [18,35,36].

The stabilimentum may have anti-predatory function. As depicted in Figure 4, the presence of stabilimenta might serve as visual occlusion against visual predators. *Argiope* spp. often shuttled through and hides at the back of their discoid or cruciate stabilimenta. Hiding behind the disc-shape or thick cruciate stabilimentum reduces the visibility the spiders' body (Figure 8A-8C). Most of the juveniles, build their webs behind trunks, behind big leaves (i.e. banana leaves) or in window screens of abandoned human habitations, hence, shuttling and hiding behind the disc-stabilimentum hides them from visual predators. Moreover, the presence of stabilimenta displayed in "X" manner camouflaged the spider and increased the actual size of the spider making it less spider-like which was presumed to be defence tactics against gape-sized limited predators such as lizards [16], and attacking wasps [37]. In webs with stabilimenta, body angling accompanied with web shaking for 30 sec. or more (common response to slight web disturbance) changed the spider's

actual image which could startle visual predators. Stabilimenta may have thermoregulatory function. *Argiope* spiders (95%, $N=50$) found in open field or in less dense vegetation tend to hide behind their cruciate stabilimenta against direct sun light/rays (observed between 9:00am to 10:00 am.). Discoid stabilimenta may also have thermoregulatory effects [12]. Since smaller spiders are more susceptible to fluctuating temperature, spinning of discoid stabilimenta may be more beneficial to smaller individuals than the larger ones [36]. The love path function [29] is not supported since both juveniles, sub adult and adult spiders decorate their webs, and male courting female in non-decorated webs (5 out of 11 webs) were also observed (Figure 9).

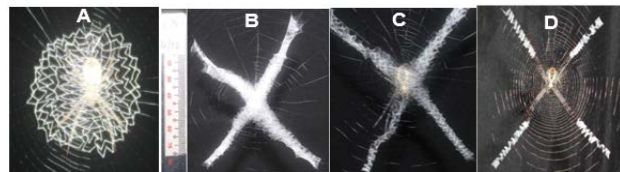


Figure 9. Juvenile spider hiding at the back of the disc-shaped stabilimentum (A), adult spider at the back of cruciate stabilimentum (B&C), spider resting at hub with discontinuous 4-armed stabilimentum (D).

Among *Argiope* spiders, the stabilimentum spun by a single individual often varies in daily basis. In particular, when observed daily for five days in the field, *A. luzona* spun 3-armed stabilimenta at Day1, 1-armed stabilimenta at Day2, 2-armed stabilimenta at Day3, and no stabilimenta at Day 5. This intra-individual variation in stabilimentum structure was also true in webs of *A. aemula*, *A. appensa*, and *A. catenulata* observed in field and in enclosures (actual observation). The intra-individual variation in stabilimentum-building behaviour can also be a response to conflict between prey attraction (increasing foraging success) and predator avoidance or defence [20,34-39]. Individual spiders might have responded to this conflict by varying their building of stabilimenta relative to proportions of predators or prey [20,36,38].

4. Conclusions

The presence of stabilimenta is an optional component of the web across the four *Argiope* species. The frequency, type (cruciate or discoid) form (thickness, extend: continuous or discontinuous, number of bands or arms) vary from web to web of a single individual (intra-individual variation), same species (intraspecific variation), or webs of different species (interspecific variation) which were reported by several researchers to be correlated with variety of environmental factors such as presence of prey, predators, conspecifics and other abiotic factors.

The male-guidance function is not supported. The predator avoidance and thermoregulation function of stabilimenta were indirectly supported in the present study.

Acknowledgements

The author would like to acknowledge the Department of Biological Sciences for the partial support through the Faculty Development Program (FDP) of the Office of the Vice Chancellor for Academic Affairs and to those whose names are too numerous to mention for the extended support in the conduct of this study.

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