A study on web asymmetry and prey capture in Argiope pulchella Thorell, 1881 (Araneae: Araneidae)

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A study on web asymmetry and prey capture in *Argiope pulchella* Thorell, 1881 (Araneae: Araneidae)

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ABSTRACT

For a sit and wait forager like *Argiope* spiders, the web is their ultimate foraging strategy, therefore investment in web building is crucial for their survival. For understanding this foraging strategy, studying of web architecture and web symmetry become essential as any change in web can severely affect the prey capture success. The present study focused on studying the web asymmetry in *Argiope pulchella* Thorell, 1881, from juvenile to the adult stage. We observed a deviation from the original circular orb web as the spider grows. Adult webs had higher vertical asymmetry in comparison to the juvenile webs. The reason for such asymmetry was tested by correlating it with the number of prey captured in the upper and lower halves of the webs. The study showed significant relationship between the lower web area and the number of prey captured in the webs. This study concludes that web transition takes place from symmetrical to asymmetrical as the spider matures and larger lower web parts in adult spiders aids in higher prey capture success.

Key words: *Web asymmetry, Orb-web spiders, Prey capture, Argiope pulchella, Web area, Capture area.*

Introduction

Argiope pulchella Thorell, 1881 of family Araneidae is a downward facing spider known to build the classical vertical orb webs. Araneids are known as 'sit and wait' foragers owing to its specialized foraging strategy in which it resides at the central portion of the web, known as hub from where it usually attacks its prey (Zschokke, 1999). Several proximate factors are reported to affect the architecture of vertical orb webs such as nutritional and reproductive status, prey and predator species present in the surrounding environment (Eberhard, 1975; Herberstein, 2011; Robinson and Robinson, 1972), space available for web construction (Adams, 2000; Harmer and Herberstein, 2009) and, gravity (Herberstein and Heiling, 1999; Nakata and Zschokke, 2010; Zschokke and Nakata, 2010). Various investigators have tried to explain the web variation and web asymmetry occurring across the developmental stages of orb web spiders (Eberhard *et al.,* 2008). The best theory explained so far is the biogenetic law that states- the ontogenetic changes that occur during an individual's development occur in similar order that take place in lineages (Hesselberg, 2010). In other words, the web characteristics of juveniles would resemble the phylogenetic ancestral taxa but as the juveniles grow to more mature stages, more derived features are accumulated to the basic developmental plan (Eberhard *et al.,* 2008; Hesselberg, 2010). Since the ultimate foraging strategy of orb web spiders is to build a web as a trap for its prey, therefore the success of prey capture should be directly dependent on captive ability of the orb webs (Herberstein and Heiling, 1999). Web asymmetry is simply the deviation of the

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web from circularity and may result from behavioral adaptation to prey capture. Asymmetrical nature of orb webs has been reported in many species but was never studied for *A. pulchella* which is a common synanthropic species of India (ap Rhisiart and Vollrath, 1994; Das *et al.,* 2018; Masters and Moffat, 1983; Zschokke and Nakata, 2015). The present study attempts to analyze the web variation across the developmental stages of *A.pulchella* and to verify the relationship between web asymmetry and amount of prey captured by the web.

Materials and Methods

The study was conducted in Kamrup metropolitan district, Assam, India from November 2014 to June 2018. This area extends from 25° 59' 52.45" N to 26° 15' 31.54" N latitude and from 91° 33' 08.04" E to 92° 10' 49.8" E longitude occupying an area of 1527.84 km^2. It is a mosaic of hills, semi-urban, urban areas, forests and wetlands.Field surveys were conducted twice a week at 8:00-12:00 and 13:00-16:00 hours along 15 fixed trails of one kilometer length and five meters width on both the sides. To equalize the effort size, the survey duration was kept constant (Coddington *et al.*, 1996). When a web was encountered, 20-30 mins of field observations per web was performed in order to record the number of prey items captured at different sectors of the webs. Indirect evidence of prey capture such as counting damaged sectors of the web and prey already present in the hub were not considered in order to avoid faulty results. Three developmental stages based on size and morphology, viz. juvenile, sub-adult and adult were selected for the study. At the end of the observation period,individuals were photographed and webs were measured (Figure 1a, 1b and 1c). Analyzing Digital Images Suite software was used for analyzing the stage classes of *A. pulchella* and prey size. Since female webs were larger, occurred in higher numbers and could be easily found both in breeding and non- breeding season; for adult and sub adult stages, only female webs studied. Each web was divided into two halves – upper and lower and two sides- left and right with reference to the observer. Each half had two quadrants, i.e. upper half with quadrant 1 on the left, quadrant 2 on the right and lower half with quadrant 3 on left whereas quadrant 4 on the right side (Figure 2). Prey items intercepted on the web were classified into 3 categories based of their size– 1) small sized prey: 0 to 5 mm, 2) medium sized prey:>5 mm but<15 mm and, 3) large sized prey: >15 mm.Prey captured in each of these quadrants was counted to quantify which quadrant of the web has higher prey capture rates.

Data analysis

Total web area was calculated as per Koh and Li, 2002 - $\pi \times a \times b$ where, *a* is calculated as-[(upper radius + lower radius)/2] and *b* as - (left radius + right radius)/2 (Figure 2). Asymmetrical Index (A.I.) was

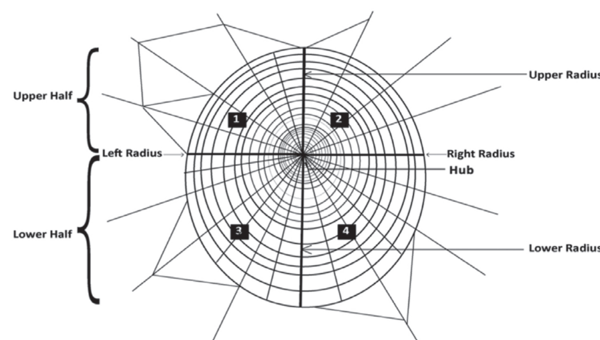

Fig. 2. Segments of a typical orb web. 1, 2, 3 and 4 represent four quadrants of an orb web. Area covered by quadrant 1 and 2 forms the upper web area and by 3 and 4 forms the lower web area; vertical diameter = upper radius+lower radius; horizontal diameter = left radius+right radius.

Fig. 1a. Juvenile *Argiope pulchella*

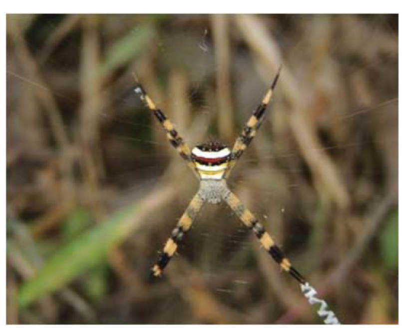

Fig. 1b. Sub adult *Argiope pulchella*

Fig. 1c. Adult female *Argiope pulchella*

calculated for each web using web area (Nakata and Zschokke, 2010; Zschokke and Nakata, 2015). We calculated the upper and lower web area using the formula–[(π x upper radius x b)/2] and [(π x lower radius x b)/2], respectively. The left and right web area was calculated as-[(π x left radius x a)/2] and [(π x right radius x a)/2], respectively. For vertical web symmetry, asymmetrical index (A.I.) is calculated as-(U-L)/(U+L), where, U = upper web area and L = lower web area; for horizontal web symmetry, A.I. is calculated as- (Lft-R)/(Lft+R), where, Lft = left web area, R= right web area. Positive A.I. value indicates asymmetrical web with larger upper web half, negative A.I. value indicates asymmetrical web with larger lower web half and zero A.I. value indicates perfect symmetrical web with both upper and lower equal halves. Prey densities were calculated by counting the number of prey captured by the web per cm^2 for each web half and size based prey composition was tabulated to check which prey size category contributed more towards the total prey captured by the webs. Linear regression analysis was performed in SPSS ver. 16.0 to study the relation between the size of web and number of prey captured by it. Since, *A. pulchella* is an upside-down oriented spider, therefore, upper and lower area of the web were only considered for the analysis to predict which half of the web had higher prey capture rates owing to vertical symmetry.

Results

Web variation

A total 111 webs of *A. pulchella*, 38 juveniles, 23 sub-adults and 50 adults, were studied and was found that from the juvenile to sub-adult and adult stages, *A. pulchella* webs showed a large variation in symmetry at different life history stages. The study revealed both the symmetrical and asymmetrical nature of webs in *A. pulchella* from juvenile to adult stage with higher proportion of negative A.I. (webs with larger lower parts) than positive A.I. (webs with larger upper parts) in vertical asymmetrical webs (Figure 3). In case of horizontal asymmetry, the three stages showed more or less similar proportions of positive and negative A.I. (Figure 4). In all three developmental stages, majority of webs were asymmetrical but juvenile spiders were recorded to construct more symmetrical webs in comparison to adults and sub adults. Adults had the least symmetrical webs (Table 1).

Prey density and size composition

We studied the prey density and prey size composition in *A. pulchella* webs in order to find which area of web has higher capture success. Out of 111

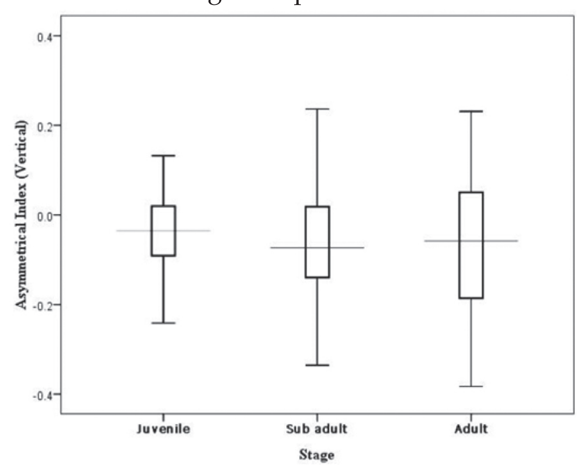

Fig. 3. Box plot showing variation in vertical Asymmetrical Index of webs of three different stages of *A. pulchella.* Negative A.I. indicates that web has larger lower part, positive A.I. indicates web has larger upper part.

Table 1. Relative proportion of webs showing positive, negative and zero A.I.

Direction of Asymmetry	Stage	Percentage of webs with larger upper area ('+'ve A.I.)	Percentage of webs with larger lower area ('-'ve A.I.)	Percentage of webs with equal upper and lower area ('0' A.I.) i.e. perfectly symmetrical
Vertical	Juvenile	26.31%	63.15 %	10.53%
	Sub adult	26.08%	65.21%	8.69%
	Adult	32.00%	64.00%	4.00%
Horizontal	Juvenile	44.73%	39.47%	15.80%
	Sub adult	56.52%	34.78%	8.70%
	Adult	50.00%	40.00%	10.00%

webs under study, we found prey items only in 66 webs (12 juveniles, 16 sub-adults and 38 adults) in which the prey density was higher at the upper web half than the lower half for the three developmental stages. To understand why the upper web half had more prey capture than the lower web half, we checked the size- based prey composition captured by the webs. In all three developmental stages, webs captured considerably higher proportions of small sized prey in comparison to medium or large sized prey items. The higher prey density observed at the upper web half was primarily due to large number of small sized prey captured at the upper half in comparison to the lower half (Table 2). In case of sub adult and adult spiders, medium to large sized preys were caught in lower web half at higher proportion than the upper web half (Table 3).

Relationship between web area and prey captured

To check whether web area influenced the number of prey captured, we performed linear regression analysis for the number of prey captured by –i. the whole web area, ii. upper area of the web and, iii. lower area of the web. For the total web area versus the number of prey captured, our model ($F_{1,64}$ = 3.648, p= 0.061) was found to be insignificant (Figure 5). Further, analysis was done to check whether owing to the web asymmetry, the upper web half and the lower web half independently showed any relation with the number of prey captured for small (juvenile) and large spiders (sub adult and adult). The models forlarge spiders, upper area versus number of prey captured ($F_{1,52}$ = 0.108, p= 0.744), lower area versus number of prey captured ($F_{1,52}$ = 1.452, p= 0.234) and small spiders, upper area versus number of prey captured ($F_{1,10}$ = .096, p= 0.763),

Table 3. Proportion of middle-large sized prey captured at upper and lower halves of the *A. pulchella* webs

Stage	Prey captured at upper half (%)	Prey captured at lower half (%)
Juvenile	11.11	15.38
Sub adult	0	7.14
Adult	8.64	13.54

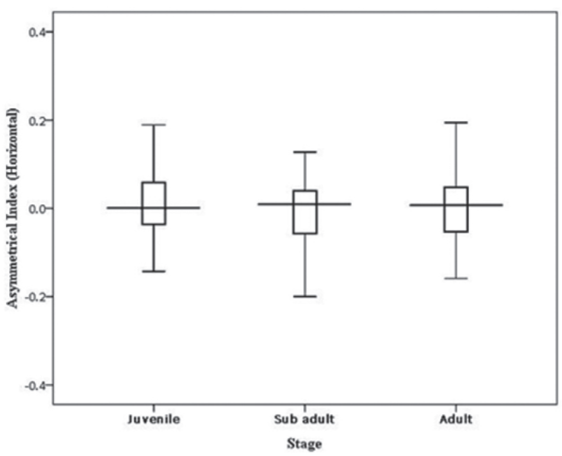

Fig. 4. Box plot showing variation in horizontal Asymmetrical Index of webs of three different stages of *A. pulchella*. Negative A.I. indicates that web has larger right part, positive A.I. indicates web has larger left part.

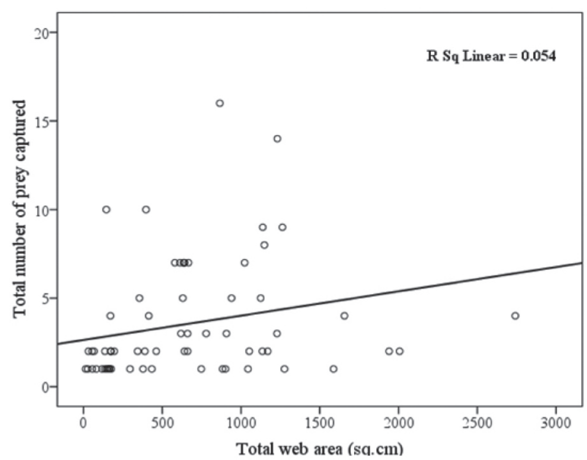

Fig. 5. Scatter plot showing the regression analysis between web area and number of prey captured

Table 2. Prey density and per cent composition of prey captured by *A. pulchella* webs

Stage	Prey density (Individuals/cm²)		Prey composition at upper half (%)			Prey composition at lower half (%)		
	Upper web half	Lower web half	Small sized prey	Medium sized prey	Large sized prey	Small sized prey	Medium sized prey	Large sized prey
Juvenile	0.19	0.15	88.89	11.11	0	84.62	0	15.38
Sub adult	0.37	0.19	100	0	0	92.86	3.57	3.57
Adult	0.34	0.25	91.36	8.64	0	86.46	8.33	5.21

lower area versus number of prey captured ($F_{1,10}$ = 3.180, p= 0.105) were found to be insignificant. One probable reason might be the sample sizes for individual stages were less as webs with prey enmeshed in it were less frequently encountered. To check whether the results were affected by small sample size, we analyzed all the webs together and checked the cumulative effect of prey captured at upper and lower halves of the web. The model for upper web area versus number of prey captured in it was found to be insignificant ($F_{1,64}$ = 1.473, p= .229) (Figure 6) whereas the model for the lower web area versus number of prey captured in it was found to significant at 0.05 level ($F_{1,64}$ = 4.730, p= 0.033; $y = .002x + 1.305$, R sq. = .069) (Figure 7). Approximately 6.9% of the variance in the prey caught was accounted by the web size of the lower half.

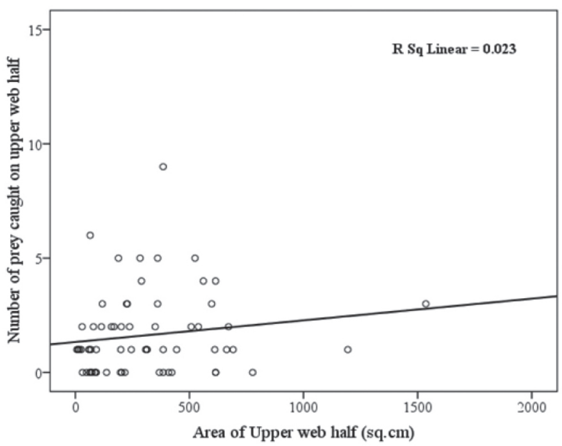

Fig. 6. Scatter plot showing the regression analysis between area of upper web half and number of prey caught on upper half

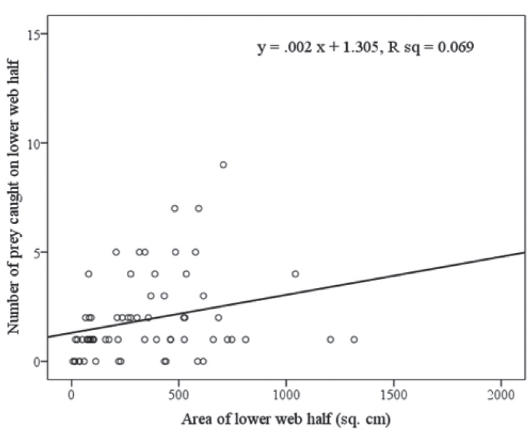

Fig. 7. Scatter plot showing the regression analysis between area of lower web half and number of prey caught on lower half

Discussion and Conclusion

In the present study, we found that *A. pulchella* showed a large variation in web symmetry at different life history stages. Displacement of hub in the web largely contributed to the web's asymmetrical nature and the web symmetry decreased from the juvenile stage to the adult stage (Zschokke and Nakata, 2010). Similar observations were reported in *Nephilengys cruentata* (Japyassú and Ades, 1998), *Larinoides sclopetraius* (Heiling and Herberstein, 1998) and in *Neoscona oaxacensis* and *Araneus diadematus* (Witt and Baum, 1960) where juveniles were seen to construct semi-orb or more circular webs than adults. Though the present study revealed that juveniles do not have perfectly circular webs in *A. pulchella*, but it does assume that as the juvenile spider grows to adult stage, there is an increase in web asymmetry owing to the increase in the lower web half. Several workers have reported the variation in orb webs between and within species due to biotic factors such as the state of satiation and prey capture rates and across different developmental stages (Sandoval, 1994; Witt and Baum, 1960). Adams in 2000 reported that large-sized spiders preferred larger sized prey but caught large range of prey items in their web whereas small sized spiders captured a narrow range of small sized prey items. In this study, small sized preys though were caught effectively by the webs of all three stages, but may only be of importance as food for juvenile *A. pulchella*. One reason explained for large capture of small sized prey is that- being light weighted, is easily drifted by wind and is vulnerable to be trapped by orb webs (Gillespie and Caraco, 1987; Nentwig, W. 1980; Venner and Casas, 2005). Due to light weight, they may even fail to confer significant vibration and load on the web, and are subjected to non-consumptive mortality (Nentwig, 1982; Sunderland, 1999). Such prey items though may not be valuable in terms of energetic gain, but may play a complementary role to keep the spider alive until it catches rare but larger preys (Venner and Casas, 2005). Being an upside-down spider, we assume that there is quick attack and removal of the prey from the lower half as *A. pulchella* may locate prey stuck in front more precisely and faster than the ones which are behind (Klärner and Barth, 1982). Thus, we assume that in need of large but valuable prey item, downward facing spider may adjust their web size by increasing the lower half of the web. Our regression models for prey captured at upper and lower half of the web for large and small spiders were found to be insignificant. One probable reason might be the sample sizes for individual stages were less as webs with prey enmeshed in it were less frequently encountered during the field study. On analyzing the web area with number of prey captured for all webs that had captured preys, our models suggest - i. Increase in the total web area do not reflect higher prey capture, ii. Increase in the upper area do not show any significant relationship number of prey captured at the upper half, and iii. Increase in the lower web area however showed significant relationship number of prey captured at the lower web half. We assume that number of prey capture increases with the increase in lower half of the web and larger lower parts of the web increases the capture area along with the probability of prey interception. As *A.pulchella* is downward facing spider, prey captured at lower area decreases the time required for locating and capturing thereby conserving both time and energy (apRhisiart and Vollrath, 1994; Masters and Moffat, 1983). Due to gravity, travelling downwards becomes easier than locating and capturing a prey at the upper web half (Herberstein and Heiling, 1999). Body weight also plays a pivotal role as, heavier the spider, more time would be spent to orient itself to the direction of the prey and finally run to capture the prey intercepted on the web. This leads us to an assumption that as an orb web spider grows from juvenile to adult stage, increase in body size which also results in increase in body weight, may contribute towards the web asymmetry. This may result in construction of webs with larger lower area in order to compensate the time required to process the prey intercepted at the upper web half. An additional advantage of constructing vertical webs and building larger lower part is to capture insects which struggle to get away from the web, thus having larger lower capture area would favour holding back those insects which drops down from the upper web area while escaping (Eberhard, 1990). Owing to the benefits of higher foraging success with increased web lower half, it can be concluded that asymmetrical web of a downward facing spider with larger lower parts at the adult stage is very advantageous at least in terms of capturing large sized prey. Along with preserving the upper reduced web half which is also necessary in order to conserve the overall web stability (Herberstein and Heiling, 1999). Thus, changes in web structure in terms of symmetry can be considered as an adaptation to the food requirement by the spider and is reflected in its ontogeny.

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