Size dependent occurrence of different types of web decorations and a barrier web in the tropical spider *Argiope argentata* (Fabricius 1775) (Araneae Araneidae)

GABRIELE UHL

*Universität Bonn Institut für Zoologie, Abteilung Neuroethologie, Endenicher Allee 11-13, D-53115 Bonn, Germany*

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Web decorations occur in a wide range of spiders and are constructed using various materials such as leaves, carcasses or silk. Silk decorations, so called stabilimenta, have attracted most attention since they are an obvious feature of the webs of several orb web species and are highly visible to the human eye. Silk decorations are mainly disc-shaped, linear or cruciate. The functions of silk decorations remain a controversial issue. More comparative and experimental work is needed, apart from the assessment of environmental prerequisites for the construction of web decorations. I collected data on the occurrence and type of silk decorations, along with a measure of body size, for a population of the tropical spider *Argiope argentata* (Fabricius 1775) in the Bijagual biological reserve in Costa Rica. In addition, I recorded whether a barrier web was present or not. I found that whether a discoid or cruciate decoration was produced significantly depended on body size: smaller spiders constructed mainly discoid decorations whereas larger spiders constructed at least part of a cruciate decoration or none at all. Barrier webs predominantly occurred in smaller spiders and were rarely present in larger spiders. The data contradict those of an earlier census performed on the Galapagos Islands, which suggested that the difference in biotic and abiotic environmental parameters not only causes differences in variability of web building behaviour but near complete reversal.

KEY WORDS: St Andrews cross spider, stabilimentum, web decoration, barrier web, ontogenetic changes, plasticity, predator-prey relationship.
INTRODUCTION

So called web decorations or stabilimenta are interesting features of webs of a wide range of orb web spiders. Spiders can “decorate” their web by including leaves, pieces of plant material, leftovers from previous meals, egg sacs or only silk material, which in one or the other combination was suggested to camouflage the spider (Herberstein et al. 2000a, Eberhard 2003). However, decorations that consist only of silk have attracted most attention. Silk decorations occur in at least 22 genera (Scharff & Coddington 1997) and are arranged in various patterns on the web, mostly occurring as cruciate, linear, discoid, spiral, or irregular silk material. The function of these structures has remained the subject of considerable controversy with little consensus. The functions best studied are prey attraction, protection against predators and web advertisement to prevent accidental damage by non-prey animals (see Herberstein et al. 2000a, Bruce et al. 2004, Bruce 2006 for review). A stabilizing function, as suggested by the term “stabili-mentum”, seems very unlikely (but see Neet 1990). However, web tuning by means of different web decorations was suggested for an uloborid spider that produces different decorations when food-deprived resulting in higher response speed to small prey (Wantanabe 2000).

Silk decorations have been most intensively studied in the genus Argiope Audouin 1826 in which they occur as zigzag bands of wrapping silk, either one below and one above the hub (linear decoration: e.g. A. aurantia Lucas 1833) or four bands forming a St Andrew’s cross typically with a gap at the hub (cruciate decoration: e.g., A. argentata (Fabricius 1775), A. florida Chamberlin & Ivie 1944, A. bruenichitii (Scopoli 1772) (from Levi 1968)). The spider sits at the hub of the web with legs extended two by two in a similar cruciate manner. Obviously, in the genus Argiope the expression of silk decorations is characterized by high interspecific variability, suggesting that their function or combination of functions can be species-specific. Even 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 (Levi 1968, Lubin 1975). Moreover, there are reports of ontogenetic variability, suggesting or demonstrating that juveniles produce different decorations compared to adult spiders (Robinson & Robinson 1978, Herberstein et al. 2000a, Li et al. 2003, Nentwig & Heimer 1987).

In the present study, a field survey was performed on a population of A. argentata in the Sarapiquí region of Costa Rica in order to quantify variation in decorating behaviour within and between ontogenetic stages. The presence or absence of a barrier web was also registered. A barrier web is an irregular tangle of non-sticky threads on one or both sides of the orb web that occurs for example in species of Argiope, Nephila Leach 1815 and Metepeira F.O.P.-Cambridge 1903. Its function is debated: it may act as a mechanical barrier protecting the spider from predators (= stopping maze) (Higgins 1992) or may support the orb web, as proposed by Lubin (1975). The data of the present study are compared to existing data on the same species collected on two Galapagos Islands (Lubin 1975) and under laboratory conditions (Robinson & Robinson 1978).
**MATERIALS AND METHODS**

*Argiope argentata* (Fabricius 1775) is found in grassy areas in tropical and subtropical regions of America. It is a large silver species with a predominantly silver and yellow or orange pattern on the dorsal side of the opisthosoma. The opisthosoma is equipped with 6 protuberances of different sizes that extend sideways (Fig. 1). In contrast to the similar looking sympatric *A. blanda* O.P.-Cambridge 1898, the colouration of the protuberances is distinctly different from the rest of the body, especially when viewed ventrally, whereas in *A. blanda* the brownish colouration of the venter extends into the whitish protuberances, which are also more pointed than those of *A. argentata*. Furthermore, the species can easily be distinguished from the sympatric but much rarer *A. savignyi* Levi 1968 (legs dark brown, almost black, and thornlike protrusions extending backwards) and the pantropical *A. trifasciata* (Forskål 1775) that has no protrusions.

The study was conducted at the Reserva Ecológica Bijagual de Sarapiquí (REBS) in northern Costa Rica, about 10 km south-east of La Virgen de Sarapiquí and 4 km west of Braulio Carrillo National Park. All developmental stages of *A. argentata* were found in a grass strip along the side of the gravel road that leads along the rim of the reserve over 2 km between the administration building and the researcher’s refugio. The data were collected in the course of 3 consecutive days and the investigated webs in the vicinity were marked with a small pole made from a twig. It is unlikely that the spiders changed website within these three days since five animals that could be individually recognized due to one or more mutilated legs were found at the same spot on 5 consecutive days.

I recorded the presence or absence of web decorations. If web decorations were present, I classified them as either discoid or cruciate (Fig. 2) and noted whether a cruciate decoration was complete (four bands) or incomplete (one to three bands). The presence or absence of a barrier web was also recorded.

Spider body size was measured as total body length to the nearest 0.5 mm. Web area was calculated from the horizontal and vertical diameter of the sticky spiral using the following calculation: web area = \( \pi \times ((0.5 \times \text{horizontal diameter}) \times (0.5 \times \text{vertical diameter})) \). Developmental stage was recorded as juvenile, subadult or adult.

![Fig. 1. — *Argiope argentata* from Costa Rica. A, dorsal view; B, ventral view.](image-url)
Subadult females can be distinguished by a protrusion covering the genital opening in adult females (scape), which is already visible through the cuticle. Subadult males are easily distinguished by their already enlarged pedipalps. Sex was categorised as male, female or unknown (in cases of very small spiderlings). Since male body size ranges between 3-4 mm and subadult males can be easily recognized by their already inflated palps, individuals larger than 4 mm and lacking inflated palps could safely be assumed to be female.

To allow comparison between this study on *A. argentata* and a similar study on three *Argiope* species from Australia (Bruce & Herberstein 2005), I also assigned spiders to size classes depending on their body size but added a further size class due to the overall larger size of *A. argentata* (A: < 4.0 mm; B: 4.0-5.9 mm; C: 6.0-7.9 mm; D: 8.0-9.9 mm and E: > 10.0 mm).

Statistical analyses were performed using the programme SPSS 13.0. Data were checked for normality, and parametric or non-parametric tests were applied when appropriate. All tests were performed two tailed and alpha was set to 0.05 in all cases.

One adult female voucher specimen was deposited at the Zoological Museum of the University of Costa Rica, San Pedro (MZ-UCR 1129).

**RESULTS**

In total, 132 webs were examined of which 79 originated from juvenile, 22 from subadult and 31 from adult spiders. Among these, 6 subadult males were found in their own webs and 4 adult males in the periphery of webs of females (2 with subadult females, 2 with adult females). Male size was 0.31 ± 0.049 mm on average and did not significantly differ between subadult and adult males (subadult males: 0.32 ± 0.05 mm, adult males: 0.29 ± 0.02; U-
test: $U = 6.0, P = 0.257$). Of the six subadult males, one had no web decoration and five had a discoid web decoration. For the following analyses, subadult and adult males are excluded from the dataset.

Of the 122 remaining individuals, 31 had no web decoration, 45 had a discoid decoration, and 46 had a complete or part of a cruciate decoration. Body size measured as body length was found to be a strong predictor of web decoration (Multinomial logistic regression, with body size and web area as covariates: $\chi^2 = 56.81, \text{df} = 4, P < 0.001$): discoid web decorations occurred predominantly in smaller individuals, whereas larger individuals either showed no web decoration or at least part of a cruciate decoration (body size: $\chi^2 = 22.09, P < 0.001$. Pairwise comparison: discoid versus none: $P < 0.001$; discoid versus cruciate: $P < 0.001$; none versus cruciate: $P = 0.682$; Fig. 3). The area of the sticky spiral did not predict the occurrence and type of web decoration (web area: $\chi^2 = 2.77, P = 0.251$). Fig. 4 depicts the distribution of web decorations over five size classes similar to the graphical presentation by Bruce & Herberstein (2005) for three Australian Argiope species.

A comparison between 16 subadult (body size: $1.32 \pm 0.05 \text{ cm}$) and 27 adult females ($1.52 \pm 0.03 \text{ cm}$) showed that discoid decorations only occurred in two cases of subadult females (4.65%), whereas the majority of

![Fig. 3. — Relationship between body length and the occurrence and shape of a silk decoration in 122 A. argentata individuals (subadult and adult males excluded).]
spiders produced either no decoration ($n = 17, 39.53\%$) or a cruciate decoration ($n = 24, 55.81\%$). The frequency of occurrence of none versus at least part of a cruciate decoration was 8:6 for subadult and 9:18 for adult females, which was not significantly different ($\chi^2$ test: $\chi^2 = 2.15, P = 0.142$). Furthermore, a logistic regression including developmental stage of the female as a categorical variable (subadult or adult) as well as their body size as a covariate did not explain whether a female produced no decoration or a cruciate decoration (developmental stage: Wald = 1.32, $P = 0.251$; body size: Wald = 0.13, $P = 0.717$; df = 1, $n = 41$).

Cruciate decorations were rarely complete: of 46 webs of individuals of all sizes, 17 showed a single band, 24 two bands, a single web was found with three bands and four webs with a complete cruciate decoration. Considering only subadult versus adult females, the probability of a cruciate silk decoration being complete or not was not significantly different between the two developmental stages (complete versus incomplete: 0 versus 6 in sub-
Web decorations in *Argiope argentata* adult and 1 versus 17 in adult females (Fischer's exact test, $P = 1.00$). One to four bands occurred in subadult females in 3:3:0:0 cases and in adult females in 11:5:1:1 cases. These distributions were not significantly different ($\chi^2 = 1.43$, df = 3, $P = 0.699$).

Barrier webs occurred on one side of the web, facing the spider's dorsal side. The presence of a barrier web was not an obligatory part of web construction. Of the six subadult males in their webs, five had a barrier web and one had none. Of the 122 individuals that remained after the exclusion of males, 82 had a barrier web and 40 did not. The presence of a barrier web was significantly predicted by the spider's size: large individuals tended to have no barrier web, whereas in the webs of smaller individuals a barrier web was mostly present (Fig. 5; Logistic regression: body size: Wald = 7.68, $P = 0.006$). Web area as a covariate did not significantly predict the presence of a barrier web (Wald = 2.53, $P = 0.111$). Webs with a barrier web were more likely to have a stabilimentum (Wald = 6.41, $P = 0.011$, df = 1, n = 122).

Fig. 5. — Absence or presence of a barrier web in relation to the spider's size. Data are based on the examination of 122 webs of female *A. argentata*.
DISCUSSION

The results clearly demonstrate that silk decorations in *Argiope argentata* are not an obligatory component of the spider's web, since 25% of webs did not contain a decoration. This finding argues against a stabilizing function. It also excludes a male guidance function meaning that the decoration helps to guide the males to the females for mating, as suggested by Crome & Crome (1961), especially since there is a high proportion of subadult and adult females that did not add a decoration to their webs (65.5%).

Comparing these data to those available in the literature reveals a high variability between populations of *A. argentata* in the probability of producing a decoration: three populations investigated on two Galapagos Islands showed that only 22, 27 and 42% of 78, 63 and 134 individuals of different size classes produced a decoration (Lubin 1975). This is in contrast to the 75% found in the present study. Moreover, the probability of a web being decorated increased with increasing body size in the Galapagos populations but decreased with increasing body size in the Bijagual population. Under laboratory conditions, the production of silk decorations was found to be related to abiotic factors (Herberstein & Fleisch 2003) and to the amount of food available: satiated spiders are more likely to include decorations than hungry spiders (Herberstein et al. 2000b on *A. keyserlingi* Karsch 1878; Blackledge 1998 on *A. aurantia* and *A. trifasciata*; Tso 1996 on *A. trifasciata*; Seah & Li 2002 on *A. versicolor* (Doleschall 1859)). Tso (2004) found, in fact, that food-deprived *A. aetheroides* Yin et al. 1989 reduced the size of their web decorations but did not economize on wrapping silk. Tso argued that spiders may have a threshold in silk reserves, below which silk decorations are less likely to be produced. If this trade-off equally applies to natural conditions, larger spiders in the Bijagual population are less satiated than smaller spiders, whereas on the Galapagos Islands the reverse should be the case. It would be interesting to test size-related satiation in the field using latency and degree of aggressive responses towards potential prey or at least body mass indices as indirect indicators of satiation.

If decorations are present in *A.argentata* of the Bijagual population, they can be discoid or cruciate and the probability of producing one or the other kind depends on the spider's body size. Smaller individuals produce mainly discoid decorations and larger individuals produce mainly cruciate decorations. On the Galapagos Islands, the census by Lubin (1975) provided contrasting results: both populations on Daphne Island lacked discoid decorations and the population on Bahia Island showed discoid decorations in only 3% of the webs (n = 78). Size variability, however, was comparable between the Galapagos and Bijagual populations. All males of the Bijagual population that produced a decoration had a discoid one. Since males are much smaller and mature at the sixth or seventh instar whereas females are larger and mature at the 13, 14 or 15 instar (Robinson & Robinson 1978), males behave according to their body size in the production of a decoration. The present field data correspond with data from the laboratory: a rearing study by Robinson & Robinson (1978) on *A. argentata* from Panama demonstrated that discoid decorations were mainly constructed from the third to the eighth instar and were gradually superseded by the linear decoration.
After the eighth moult, individuals only produced linear decorations or none at all. The percentage of individuals producing no decoration increased from 78 to 98% until the final moult in their study (see also comparable results by Nentwig & Heimer 1987). However, in the Bijagual population, webs of subadult and adult females were found without decoration with lower probability (65%), suggesting that web decoration may be more common under natural conditions and that spiders economize on the production of material under laboratory conditions. Preliminary data show that individuals of the congeneric A. bruennichi that constructed decorations in the field stopped doing so under laboratory conditions even under a high feeding regime (G. Uhl unpublished). This suggests not only that data derived from laboratory settings have to be treated with care but more importantly it shows that an external stimulus — be it biotic or abiotic — is required to trigger the construction of a web decoration (but see Bruce & Herberstein 2005 for A. aetherea and A. picta).

An ontogenetic shift in decoration type and frequency was also demonstrated for a population of A. argentata on Bahama Islands (Schoener & Spiller 1992). Here, the distribution of decoration types also differed from that of the Bijagual population. The fact that discoid decorations occurred mostly among intermediate size classes led the authors to conclude that they make the spiders appear larger — a possible adaptation to gape-size limited predators such as lizards. In other Argiope species, A. keyserlingi, A. aetherea (Walckenaer 1842) and A. picta L. Koch 1871, discoid decorations only occur during the smaller stages, albeit to a variable degree (Bruce & Herberstein 2005). In A. keyserlingi and A. aetherea webs without decorations were more common (50 to 85%) than in A. argentata. Further research should focus not only on the function of the decoration but also on why it is omitted so frequently in the field and in the lab.

Studies that explore the function of web decorations in Argiope have focussed on adult female individuals. However, the ontogenetic differences in decoration types may indicate different functions at different life-history stages, especially since Li et al. (2003) demonstrated that individuals of A. versicolor show different predator avoidance behaviours depending on the developmental stage. They suggested that behaviour and the type of web decorations are causally related. The experimental studies that have been performed to date were designed to test one specific hypothesis each (see review in Bruce et al. 2004) but since the hypotheses are not mutually exclusive, data supporting one hypothesis do not necessarily refute the other hypotheses. The example of A. aurantia demonstrates that several functions may indeed interact. The presence of silk decorations contemporaneously reduces web damage by birds and predatory attacks by wasps (Blackledge & Wenzel 1999). Prey attraction also seems to play a role since isolated silk decorations of this species attracted prey to the web (Tso 1998). However, another study found that the presence of a decoration led to avoidance of the web (Blackledge and Wenzel 1999). Avoidance and attraction are only possible if web decorations are visible to prey or predator. In fact, web decorations were shown to be visible to honey bees and birds over long and short distances, at least under laboratory conditions (Bruce et al. 2005).
In the Bijagual population, barrier webs were predominantly present in webs of smaller spiders and only on one side of the web. Again, this finding differs from that of Lubin (1975) for Galapagos populations of A. argentata, where the probability of barrier web construction increased significantly with increasing size for all three populations and two-sided barrier webs occurred with a probability of 1.6 to 8.2%. Lubin suggested that strong winds make it necessary to anchor the web securely, or the barrier webs are built when web supports are scarce. Alternatively, a barrier web may have a protective function, as suggested by Comstock (1912) and supported in a study on Nephila clavipes (Higgins 1992). Furthermore, if an Argiope web is equipped with a barrier web, the spider is always found on the side of the barrier web, suggesting that it may act as an early warning system against predators approaching from behind or the side.

Smaller spiders produced both barrier webs and web decorations with higher probability than larger spiders. Possibly both phenomena are related in that they have evolved in the context of predation avoidance: the barrier web as an early warning system and the web decorations for concealment against predators approaching from the front. The contrasting occurrence of barrier webs in webs of smaller or larger individuals in different populations, as found by Lubin (1975), would then suggest that size-dependent predation depends on the habitat, which certainly requires further investigation.

These findings demonstrate the need to investigate ecological parameters that may shape population-specific adaptations in the construction and type of web decoration, such as size-dependent predation risk, site-specific prey type availability, differential habitat use and differential exposure or crypsis of different developmental stages in different populations.

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REFERENCES


