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Molting interferes with web decorating behavior in *Argiope keyserlingi* (Araneae, Araneidae)

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Abstract. Various orb weaving spiders decorate their webs with extra silk structures. In the araneid genus *Argiope*, these web decorations consist of flimsy aciniform silk threads arranged in zig zag shaped bands. The adaptive value of these structures is still unclear and controversy over a suite of possible functional explanations persists: the high variation of web decoration adds further uncertainty. Web decorations can differ in shape, size, and frequency across species and even within species. Physiological processes may influence individual variation in web decorating behavior. Molting events are major physiological transitions combined with fundamental alterations of the metabolic state of the spiders. For gaining new insights into possible proximate mechanisms driving web decorating behavior, we observed subadult *Argiope keyserlingi* Karsch 1878 females in the laboratory and registered the individual variation of web decorations associated with the maturity molt under laboratory conditions.

We found substantial individual variation of web decorations of *A. keyserlingi*. The most striking result was that subadult spiders built dramatically oversized decorations prior to the last molt. Since aciniform silk is used for both constructing web decorations and immobilizing prey we suggest that these extensive decorations might provide a store for the swift replenishment of aciniform silk after the molt. High silk recycling rates make temporary outsourcing less costly and facilitate a rapid resumption of prey capture following lost foraging opportunities during the molting phase. Thus, we argue that the solution of the riddle of web decorations might reside in the physiology of molting spiders.

Keywords: Orb-web spiders, web decorations, maturity molt, gland regulation

Web decorating is a characteristic behavior of various orb weaving spiders (Robinson & Robinson 1973; Edmunds 1986; Bruce 2006), yet the possible functional explanations remain controversial despite extensive investigations (Herberstein et al. 2000; Eberhard 2003; Bruce 2006). "Web decorations" (first mentioned as such by McCook 1889, but also called "stabilimenta" by Simon 1895 and many modern authors) in the araneid genus *Argiope* consist of numerous flimsy aciniform silk threads (Peters 1993), mostly arranged in zig zag shaped bands (Bruce 2006). Although web decorations of *Argiope* are considered as prey attractants by some (Craig & Bernard 1990; Tso 1996; Bruce et al. 2001; Li 2005; Cheng & Tso 2007), this view is not unanimous and alternative functional explanations include anti-predator devices (Ewer 1972; Schoener & Spiller 1992; Blackledge & Wenzel 2001); advertisement for web protection (Eisner & Nowicki 1983; Kerr 1993; Blackledge & Wenzel 1999); thermoregulation (Humphreys 1992); mechanical support [Robinson & Robinson 1970; see also Watanabe 2000 for *Octonoba sybotides* (Bösenberg & Strand, 1906), Uloboridae]; and acting as a molting platform (Robinson & Robinson 1973, 1978). In the rapidly growing literature on this topic, tests for non-visual functions are clearly underrepresented (Bruce 2006). In particular the potential relationship between physiological processes and web decorating behavior has been addressed in only a very few studies (e.g., Peters 1993; Tso 2004; Walter et al. 2008a).

Typically, decorating behavior in species of *Argiope* is highly variable (Bruce & Herberstein 2005) and web decorations can differ in shape (number and arrangement of zig zag bands), size and frequency (Lubin 1975; Edmunds 1986; Nentwig & Heimer 1987; Schoener & Spiller 1992). One problem for determining the adaptive value of web decorations stems from this high variation (Robinson & Robinson 1974), which occurs across species and within species at both the population and individual level (Herberstein et al. 2000; Starks 2002; Bruce & Herberstein 2005; Rao et al. 2007). Most studies explore the adaptive significance of these structures (e.g., Blackledge 1998; Craig et al. 2001), although phylogenetic analyses of web decoration patterns suggests that interspecific variance shows weak homologies at best and yields phylogenetically feeble signals (Herberstein et al. 2000; see also Scharff & Coddington 1997). We agree with Eberhard (2003) that an accumulation of single "experiments *per se* … are no guarantee of reliable conclusions." Thus, understanding the intra-individual variance of web decorations in detail is necessary before embarking on the interpretation of web decorating behavior in general.

The production of web decoration is governed by an enhanced activity of the silk glands and hence physiological processes are expected to impact web decorating behavior (Tso 2004; Walter et al. 2008a). The major physiological transitions in the life history of spiders are the repeated molting events. Molting requires a drastic change of anabolic and metabolic biochemical pathways requiring fundamental alterations of the physiological state of the animal. Apart from hormonal changes (Bonaric 1987; Foelix 1996; Craig 2003), molts are particularly vulnerable events in the life of spiders, in terms of both increased physiological stress (Pulz 1987; Vollrath 1987a) and increased risk of predation (Tolbert 1975; Tanaka 1984; Vollrath 1987b; Baba & Miyashita 2006). It would, therefore, be surprising if web decoration behavior was not affected by molting. Indeed several studies suggest that molting might have profound effects on the web decorating activity of *Argiope* (Robinson & Robinson 1970, 1973; Edmunds 1986; Nentwig & Heimer 1987). Yet if we observe consistent changes in the patterns of decoration behavior associated with the molting process, this might provide insights into the proximate mechanisms driving web decoration and their potential adaptive value.

METHODS

Study species and experimental design.—We chose the St. Andrew's cross spider, *Argiope keyserlingi* Karsch 1878, to study the variation in web decoration under highly controlled laboratory conditions. This orb web spider is distributed along the east coast of Australia (northern Queensland to Victoria in the south), building their webs between branches and leaves of bushes, e.g., in parks and gardens. *Argiope keyserlingi* is a well studied species in terms of its natural history (Rao et al. 2007), its sexual cannibalism (Elgar et al. 2000; Herberstein et al. 2005) and its web decorating behavior (Herberstein 2000; Bruce et al. 2001, 2005; Herberstein & Fleisch 2003). St. Andrew's cross spiders typically build cruciate web decorations consisting of up to four zig zag bands forming a large "X" in the orb web (Rao et al. 2007). This allows an unambiguous interpretation of deviations from the "complete cross."

We collected 55 subadult female spiders in Ku-ring-gai Bicentennial Park (West Pymble/Sydney, Australia) and transferred them individually to Perspex frames (58 cm × 58 cm × 15 cm) in the laboratory, where they were kept under natural light conditions. Every other day, each spider was fed with one blowfly (*Lucilia* spp.). At this life stage the spiders are still of a similar size as the blowflies; thus, it has turned out in preliminary observations that this feeding regime is sufficient to keep spiders "well-fed." At this same time, each web was moistened with five shots from a water spray. Given that spiders typically build a new web each day, we recorded daily the number of decoration bands (shape) and decoration size to assess the variation of web decorating behavior within a total observation period of 30 days. We estimated the size of the web decoration by computing a trapezium area similar to Tso (1999): $(a+c)/2 \times h$ (a and c = upper and lower width of zig zag bands, h = height of zig zag bands, see Fig. 1). Additionally, we quantified the size of all newly built webs following Herberstein & Tso (2000): $(d_v/2) \times (d_h/2) \times \pi$ (d_v = vertical and d_h = horizontal diameter of the capture area, see Fig. 1) and measured the spider body size (length from clypeus to the end of the opisthosoma). Voucher specimens were deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg (Zoological Institute), Germany (identification number 2569).

Statistical analyses.—We used STATISTICA® (version 6.0) for all statistical analyses including the paired *t*-test to evaluate differences in the sizes of decorated and undecorated webs. Chi square-tests and *t*-tests were used to detect differences in the proportion of decorated web parts and constructed decoration patterns. Web and web decoration sizes prior, during, and after molting events were analyzed with an ANOVA. Pearson-correlations were computed between web size and decoration size.

RESULTS

Web decorating frequency.—All females could be observed over the whole 30 day period. Forty-six of the 55 subadult *A. keyserlingi* molted to maturity within this time. The spiders constructed new webs every second day (mean 2.29 ± 0.07 SE day). Typically, the new web decorations were built together with new webs, and therefore the decorating activity mostly followed an equal rhythm (a mean value of every 2.37 ± 0.37 SE day). The few exceptions were all in the context of molting events (see below). However, 233 (37.5%) of all newly built webs (n = 622) did not contain a web decoration. Many spiders occasionally failed to decorate their webs, but only five animals (9.1%) never built a web decoration at all during the observation period.

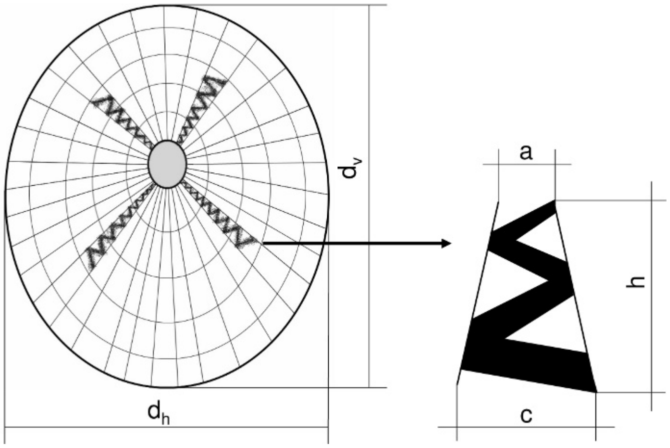

Figure 1.—Web and decoration measurements from the webs of *A. keyserlingi*: Left: determination of the size of capture areas (including hub region), d_h = horizontal diameter, d_v = vertical diameter; Right: determination of decoration band sizes, a = upper width of the band, c = lower width of the band, h = length of the band (lettering after trapezium formula).

Web size.—The spiders more than doubled the catching area of their webs within the 30 day observation period. The mean size of the first web we measured was 635.30 ± 44.46 SE cm^2 (n = 55) and the mean size of the last measured web was 1630.61 ± 21.99 SE cm^2 (n = 55). Over the whole observation period, undecorated webs were significantly larger than decorated webs, ranging from 625.21 ± 56.88 SE cm^2 to 646.54 ± 70.57 SE cm^2 at the beginning of to the experiment to between 1563.21 ± 42.56 SE cm^2 and 1700.50 ± 37.42 SE cm^2 at the end of the period (paired t-test: t = 2.11, $P < 0.05$). However, the mean decoration size did not significantly change over time, and ranged from 55.17 ± 72.72 SE mm^2 (n = 55) at the beginning to 46.25 ± 54.06 SE mm^2 (n = 55) at the end of the observation period (Pearson, r^2 = 0.04, P = 0.29). We found a significant positive correlation between spider size and web area (Pearson, r^2 = 0.31, $P < 0.01$; n = 621). In contrast, we found no significant correlation between spider size and web decoration size. Consequently, the size of the decorated web area in relation to the total web decreased over time.

Variation of web decorating behavior.—The variation in web decoration shapes was very high and the "typical" cruciate type was rarely constructed (Fig. 2); females of *A. keyserlingi* most often constructed single arm decorations (n = 47 spiders in 65.13%, n = 282 observations), and decorations with two (n = 31 spiders in 24.48%, n = 106 observations), three (n = 10 spiders in 5.54%, n = 24 observations), or four (n = 15 spiders in 4.85%, n = 21 observations) zig zag bands were less frequent. In all partial cross shapes (one to three arms), the bands were added to the lower web half significantly more often (85.2% vs. 14.8%, n = 50; X^2 = 9.12, $P < 0.01$). There

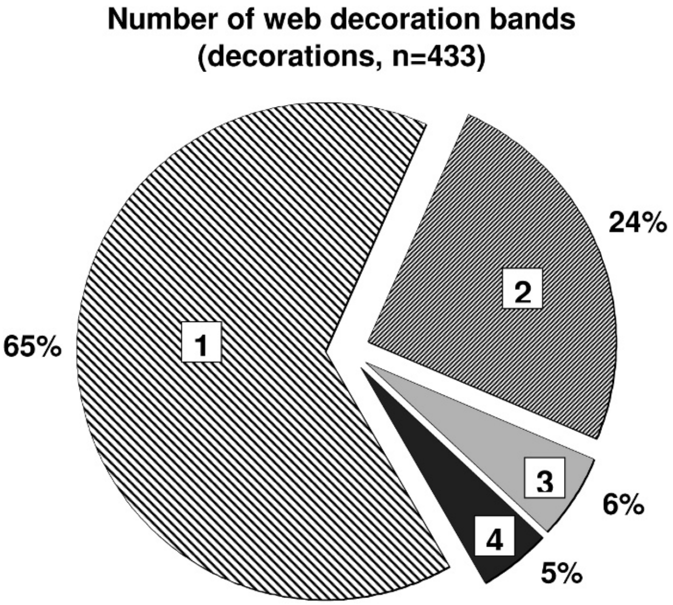

Figure 2.—The variation in web decoration patterns of *A. keyserlingi* females under laboratory conditions. Partial cross shapes (one to three decoration bands = number 1–3 in the diagram) are more frequent than the typical cruciate shape (number 4).

was also strong intra-individual variance; most spiders (65.45%, $n = 36$) altered the web decoration pattern up to four times over the observation period: Thirteen spiders (23.64%) altered their web decoration pattern once; nine (16.36%) altered the pattern twice; six individuals (10.51%) altered it three times; and three spiders (5.46%) altered the decoration four times. Only 19 spiders (with 34.55% significantly less, $X^2 = 9.55$, $P < 0.01$) constructed the same number of arms within the observation period and five individuals (9.09%) built no web decoration at all. These latter spiders also had a significantly lower web decorating frequency (new decoration every 3.7 ± 4 SE days) than individuals that constructed more variable shapes over time (new decoration every 1.5 ± 0.9 SE days, $n = 31$; t-test: $t = 2.91$, $P < 0.01$).

Web decorating behavior in the context of molting events.—Within the 30 day observation period 46 of 55 subadult spiders molted to maturity. Spiders suspended the two-day web building rhythm a few days before molting, and on average 3.3 ± 1.6 SE days elapsed between the "last" web building and the start of the molt. The mean interval between constructing the "last" web decoration prior to the final molt into sexual maturity (2.8 ± 1.5 SE days) was also longer than the mean decorating interval at other times (every 2.37 ± 0.37 SE day, see above). The molting events coincided with an increase in overall web size: the web size had increased by 19% (mean +260 cm^2) in the ten day period after the molt (from 1080.37 ± 42.9 SE cm^2, $n = 101$ prior to the molt to 1340.36 ± 25.56 SE cm^2, $n = 205$; paired t-test: $t = -4.88$, $P < 0.01$). Ten spiders (22%) added a new web decoration to an old web prior to the molt. The change in web decorating and web building frequency was exclusively observed in combination with molting events, and the most conspicuous change was the dramatic increase in the web decoration size (Fig. 3) during the pre-molting phase (last subadult webs). The size of the "regular" web decorations, both in penultimate webs before and in the first webs after the molt, were significantly smaller (68.78 ± 10.45 SE mm^2, $n = 43$ vs. 58.39 ± 9.24 SE mm^2, $n = 45$) than those constructed directly in the last web before molting (211.74 ± 35.94 SE mm^2, $n = 46$; ANOVA: $F = 14.36$, $P < 0.01$).

The "supersized" decorations of the molting webs were characterized by a partial loss of the typical zig zag look (Fig. 3, right). Moreover, these peculiar decoration bands overlapped in the hub region of the web, which was never observed in intermolt webs. Finally, only one individual molted in a web without a web decoration.

All in all, individuals of *A. keyserlingi* reduced their web building frequency (Fig. 4A) and increased the size of their web decorations prior to their final molt to sexual maturity (Fig. 4B).

DISCUSSION

Although individuals of *A. keyserlingi* usually build cruciate web decorations (Rao et al. 2007) consisting of up to four zig zag-shaped silk bands (Bruce 2006), we observed substantial individual variation in web construction and decorating behavior in *A. keyserlingi* in our study. Web size strongly correlated with the spider's size and larger females built larger webs. Moreover, we could confirm previous reports by Hauber (1998) and Craig et al. (2001) on a negative correlation between web size and decoration size. Undecorated *Argiope* webs were larger than decorated ones. Since we kept the feeding regime constant, this might indicate a tradeoff between web size and decoration as suggested by Craig et al. (2001).

Although web size was positively correlated with spider size, larger spiders did not build larger web decorations. Consequently, the relative decoration area of the web decreased over time, which may reflect previous reports of reduced web decorating behavior in later adult stages of *Argiope* spiders (Peters 1953; Edmunds 1986; Nentwig & Heimer 1987). The intra-individual variation in the shape of the decoration was remarkably high. Very few spiders consistently built only one particular pattern. An explanation for this may be given by the results of Craig et al. (2001) on *Argiope argentata* (Fabricius 1775). They argue that individual decoration patterns have a genetic component and any variation represents the influence of ecological conditions. Most spiders in our study alternated the web decoration type, some individuals up to four times. Although this high variation may have been affected by the laboratory conditions it has also been observed in many other *Argiope* species (e.g., Blackledge 1998 in *A. aurantia* Lucas 1833 and *A. trifasciata* (Forskål 1775); Hauber 1998 in *A. appensa* (Walckenaer 1842); Seah & Li 2002 in *A. versicolor* (Doleschall 1859); Bruce & Herberstein 2005 in *A. picta* L. Koch 1871 and *A. aetherea* (Walckenaer 1842)).

Argiope keyserlingi females in our study regularly rebuilt their orb webs every second day, and the web decorating frequency followed this rhythm. The only exceptions occurred on those days leading up to the commencement of the final molt to sexual maturity. During this time, some spiders added web decorations to their old webs. Typically, *Argiope* spiders do not rebuild orb webs several days before they molt to maturity (Robinson & Robinson 1978; Nentwig & Heimer

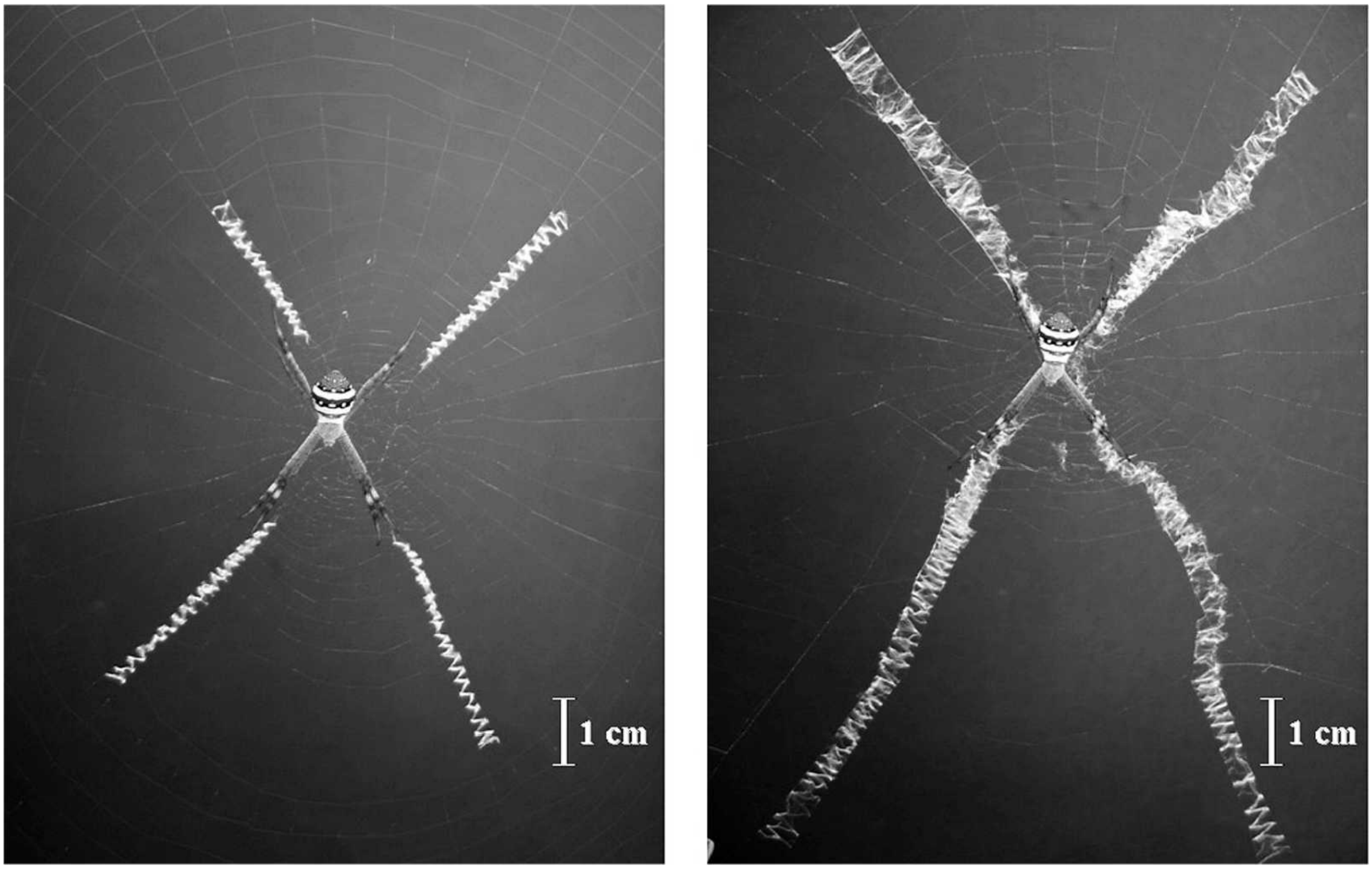

Figure 3.—The "regular" web decoration (left) and the "supersized" web decoration (right) of *A. keyserlingi*.

1987; Eberhard 1990). Robinson & Robinson (1973) suggest that a tradeoff between silk production and the biosynthetic efforts in preparation of the molt provides an adaptive explanation for this phenomenon. However, the frequency of web decorating prior to molting did not decline, despite the reduction in web building, because some spiders added new decorations to already existing, old, and dilapidated webs.

Indeed, the dramatically oversized decorations that spiders built prior to the molt (Fig. 4) were the most conspicuous difference to the intermolt webs of subadult and the webs of adult individuals. The phenomenon that spiders build more frequent and/or more perfect web decorations prior to the molt was already observed in *A. argentata* and *A. savignyi* Levi 1968 in the laboratory (Nentwig & Heimer 1987). Moreover, Edmunds (1986) noticed larger and denser decorations prior to moltings in a wild population of *A. flavipalpis* (Lucas 1858). These anecdotal reports, however, have never been empirically quantified. In our study we could show that web decorations in *A. keyserlingi* were three times larger shortly before the maturation molt and did not correspond with the individual variation in decoration shape. Decoration size decreased to the intermolt level immediately after the molt. Consequently, very large decorations were thus directly linked to the molting procedure.

Do our findings contribute to resolving the controversy over the adaptive significance of web decorations (see Bruce 2006)? Web decorations have been discussed in a variety of contexts, including in the context of prey attraction (Herberstein 2000; Herberstein & Fleisch 2003; Li 2005). Although we cannot exclude this explanation for decorations in regular webs, the observed increase in web decorating activity in *A. keyserlingi* prior to the molt is not predicted by this hypothesis. Spiders decrease their foraging efforts during the pre-molt phases (Higgins 1990), presumably because there is little opportunity to consume food during molting. Nevertheless, web decorations may provide particular mechanical support for orb webs (Simon 1895) during the molting phase (Robinson & Robinson 1970, 1973, 1978; Nentwig & Heimer 1987). Higgins (1990) argued that the web decorations of *Nephila clavipes* (Linnaeus 1767) (Nephilidae) help prevent the spiders contacting the sticky spiral, which could interrupt the molting procedure by hindering individuals from freeing themselves from the old exoskeleton. Since molting events are generally vulnerable phases in the life of a spider (Robinson & Robinson 1973; Baba & Miyashita 2006) the potentially protective properties of web decorations may be relevant in preserving the integrity of the web during the molt (Horton 1980; Eisner & Nowicki 1983; Kerr 1993). Additionally, the potential protection against predators (Eberhard 1990; Schoener & Spiller 1992; Blackledge & Wenzel 2001) would also predict an increase in decorating investment because spiders are especially vulnerable to predators during the molt or shortly afterwards (Tanaka 1984; Baba & Miyashita 2006).

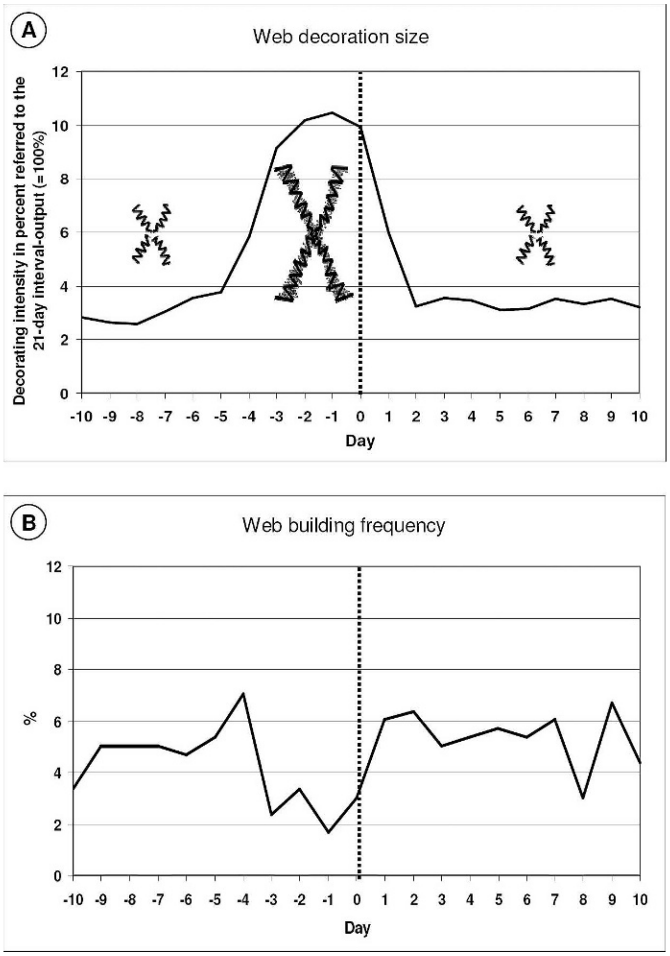

Figure 4.—A. The size of the web decoration of *A. keyserlingi* dramatically increases prior to the maturation molt and then returns to the level prior to the molting event; B. Web building frequency decreases prior to the last molt; *dotted line*: day of molting (= day 0).

Shortly after a molt spiders are vulnerable to desiccation due to the slowly sclerotizing exoskeleton. In this phase it must be particularly important to balance the hygric status through water ingestions. In this context (large) web decorations might be practical tools: some *Argiope* spiders directly ingest water from parts of their web decorations (Olive 1980; Walter et al. 2008a).

Since *Argiope* spiders can also successfully molt on webs without a web decoration (Nentwig 1986; own observations) the adaptive effects of the decorations may play a subsidiary role. Instead, the increase in web decoration investment may proximately derive from direct physiological processes, particularly since resource allocations directly influence interactions between molting, silk composition and web building behavior (Townley et al. 2006). Thus, it might be necessary to "outsource" a certain amount of nutrients for optimizing the molting procedure. Higgins & Rankin (2001) showed that "well-fed" individuals of the orb weaving spider *N. clavipes* more often suffer from molting failures when exceeding a critical pre-molt mass. They concluded that this might be the cost for the ability of rapid growth based on an almost non-limited food intake in this species. This may also be relevant for the rapid growth of *Argiope* spiders. Outsourcing body mass in the form of silk proteins may ensure an "optimal" molt-weight. In this context it is possible that *N. clavipes* builds web decorations only shortly before a molt (Higgins 1990). Conversely, a molt is always combined with a loss of body mass (through the failure to consume exuvia) (Hutchinson et al. 1997), and outsourcing silk proteins may allow spiders to minimize nutrient waste.

The link between the increase of web decorating behavior and moltings might also be explained by a requirement to outsource specific, physiologically important compounds that would be otherwise metabolized during the molting procedure or the non-foraging days shortly before and after the molt. Such allocation occurs for different compounds in several spider species [e.g., choline, Higgins & Rankin 1999 for *N. clavipes* and Townley et al. 2006 for *Argiope trifasciata* and *A. aurantia*; GABamide, Townley & Tillinghast 1988 for *Araneus cavaticus* (Keyserling 1881)]. Perhaps the enlarged decoration simply provides a storage area for the silk proteins themselves. The aciniform decoration silk is also used for immobilizing prey (Peters 1993; Tso 2004). Thus, web decorating might be crucial for maintaining a certain level of activity in the aciniform glands for an optimal performance of *Argiope*'s typical "wrap attack" strategy of prey capture (Olive 1980; Tso 2004; Walter et al. 2008b). After molting, spiders must swiftly resume capturing prey to compensate for lost foraging opportunities of the previous days. For subsequent capture events, *Argiope* requires large amounts of wrapping silk that has to be newly synthesized after the molt. Since several types of silk glands are remodeled during a molt, they may not be fully operative in the days immediately after the molt (Townley et al. 2006). If this is also true for the *glandulae aciniformes*, the extensive web decorations may provide an ideal store of the crucial silk components, allowing the swift replenishment of the aciniform silk following molting. The highly efficient recycling of web parts (Peakall 1971) thereby clearly reduces the costs of silk production (Janetos 1982; Opell 1998) by reusing the relevant amino acids.

To confirm the physiological background of our observations, further studies should concentrate on the impact of different metabolic processes on the web decorating behavior prior to moltings, with a focus on those spiders that nonetheless molt without decorations. However, irrespective of the actual ultimate adaptive mechanisms of web decorations, it seems that these structures may play a more specific role in the molting web than in the regular capture web in *Argiope*. Given the large size of the molting decorations in contrast to relatively small and highly variable decorations in regular webs, it may well be that the clue to solving the riddle of these structures lies in the physiology of the molting spider.

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LITERATURE CITED

Baba, Y. & T. Miyashita. 2006. Does individual internal state affect the presence of a barrier web in *Argiope bruennichi* (Araneae: Araneidae)? Journal of Ethology 24:75–78.

Blackledge, T.A. 1998. Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). Journal of Zoology 246:21–27.

Blackledge, T.A. & J.W. Wenzel. 1999. Do stabilimenta in orb webs attract prey or defend spiders? Behavioral Ecology 10:372–376.

Blackledge, T.A. & J.W. Wenzel. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. Behaviour 138:155–171.

Bonaric, J.-C. 1987. Moulting hormones. Pp. 111–118. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer, Berlin.

Bruce, M.J. 2006. Silk decorations: controversy and consensus. Journal of Zoology 269:89–97.

Bruce, M.J., A.M. Heiling & M.E. Herberstein. 2005. Spider signals: are web decorations visible to birds and bees? Biology Letters 1:299–302.

Bruce, M.J. & M.E. Herberstein. 2005. Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. Journal of Natural History 39:3833–3845.

Bruce, M.J., M.E. Herberstein & M.A. Elgar. 2001. Signaling conflict between prey and predator attraction. Journal of Evolutionary Biology 14:786–794.

Cheng, R.-C. & I-M. Tso. 2007. Signaling by decorating webs: luring prey or deterring predators. Behavioral Ecology 18:1085–1091.

Craig, C.L. 2003. Spiderwebs and Silk. Tracing Evolution from Molecules to Genes to Phenotypes. Oxford University Press, New York. 230 pp.

Craig, C.L. & G.D. Bernard. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. Ecology 71:616–623.

Craig, C.L., S.G. Wolf, L.D. Davis, M.E. Hauber & J.L. Maas. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. Evolution 55:986–993.

Eberhard, W.G. 1990. Function and phylogeny of spider webs. Annual Review of Ecology and Systematics 21:341–372.

Eberhard, W.G. 2003. Substitution of silk stabilimenta for egg sacs by *Allocyclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. Behaviour 140:847–868.

Edmunds, J. 1986. The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. Pp. 61–72. *In* Proceedings of the Ninth International Congress of Arachnology, Panama. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington, D.C.

Eisner, T. & S. Nowicki. 1983. Spider web protection through visual advertisement: role of the stabilimentum. Science 219:185–187.

Elgar, M.A., J.M. Schneider & M.E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. Proceedings of the Royal Society of London B 267:2439–2443.

Ewer, R. 1972. The devices in the web of the West African spider *Argiope flavipalpis*. Journal of Natural History 6:159–167.

Foelix, R.F. 1996. Biology of Spiders. Second edition. Oxford University Press, New York. 330 pp.

Hauber, M.E. 1998. Web decorations and alternative foraging tactics of the spider *Argiope appensa*. Ethology, Ecology & Evolution 10:47–54.

Herberstein, M.E. 2000. Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? Australian Journal of Zoology 48:217–223.

Herberstein, M.E., C.L. Craig, J.A. Coddington & M.A. Elgar. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. Biological Reviews 75:649–669.

Herberstein, M.E. & A.F. Fleisch. 2003. Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). Animal Ecology 28:622–628.

Herberstein, M.E., A.C. Gaskett, J.M. Schneider, N.G.F. Vella & M.A. Elgar. 2005. Limits to male copulation frequency: sexual cannibalism and sterility in St Andrew's Cross spiders (Araneae, Araneidae). Ethology 111:1050–1061.

Herberstein, M.E. & I-M. Tso. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). Journal of Arachnology 28:180–184.

Higgins, L.E. 1990. Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae: Araneidae). Journal of Insect Behavior 3:77–783.

Higgins, L.E. & M.A. Rankin. 1999. Nutritional requirements for web synthesis in the tetragnathid spider *Nephila clavipes*. Physiological Entomology 24:263–270.

Higgins, L.E. & M.A. Rankin. 2001. Mortality risk of high rate of weight gain in the spider *Nephila clavipes*. Functional Ecology 15:24–28.

Horton, C.C. 1980. A defense function for the stabilimenta of two orb weaving spiders (Araneae, Araneidae). Psyche 87:13–20.

Humphreys, W.F. 1992. Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae: Argiopinae) and its thermal behaviour. Bulletin of the British Arachnological Society 9:47–52.

Hutchinson, J.M.C., J.M. McNamara, A.I. Houston & F. Vollrath. 1997. Dyar's rule and the investment principle: optimal moulting strategies if feeding rate is size-dependent and growth is discontinuous. Philosophical Transactions of the Royal Society B 352:113–138.

Janetos, A.C. 1982. Foraging tactics of two guilds of web-spinning spiders. Behavioral Ecology and Sociobiology 10:19–27.

Kerr, A.M. 1993. Low frequency of stabilimenta in orb webs of *Argiope appensa* (Araneae: Araneidae) from Guam: an indirect effect of an introduced avian predator? Pacific Science 47:328–337.

Li, D. 2005. Spiders that decorate their webs at higher frequency intercept more prey and grow faster. Proceedings of the Royal Society of London B 272:1753–1757.

Lubin, Y.D. 1975. Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galapagos. Journal of Arachnology 2:119–126.

McCook, H.C. 1889. American Spiders and Their Spinning Work. Academy of Natural Sciences, Philadelphia. 373 pp.

Nentwig, W. 1986. Stabilimente in Radnetzen von *Argiope*-Arten (Araneae: Araneidae): ein funktionsloses Relikt? Verhandlungen der Deutschen Zoologischen Gesellschaft 79:182.

Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 211–225. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer, Berlin.

Olive, C.W. 1980. Foraging specializations in orb-weaving spiders. Ecology 61:1133–1144.

Opell, B.D. 1998. Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. Functional Ecology 12:613–624.

Peakall, D.B. 1971. Conservation of web proteins in the spider, *Araneus diadematus*. Journal of Experimental Zoology 176:257–264.

Peters, H.M. 1953. Beiträge zur vergleichenden Ethologie und Ökologie tropischer Webespinnen. Zeitschrift für Morphologie und Ökologie der Tiere 42:278–306.

Peters, H.M. 1993. Über das Problem der Stabilimente in Spinnennetzen. Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere 97:245–264.

Pulz, R. 1987. Thermal and water relations. Pp. 26–55. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer, Berlin.

Rao, D., K. Cheng & M.E. Herberstein. 2007. A natural history of web decorations in the St Andrew's Cross spider (*Argiope keyserlingi*). Australian Journal of Zoology 55:9–14.

Robinson, B.C. & M.H. Robinson. 1974. The biology of some *Argiope* species from New Guinea: predatory behaviour and stabilimentum construction (Araneae: Araneidae). Zoological Journal of the Linnean Society 54:145–159.

Robinson, B. & M.H. Robinson. 1978. Developmental studies of *Argiope argentata* (Fabricius) and *Argiope aemula* (Walckenaer). Symposia of the Zoological Society of London 42:31–40.

Robinson, M.H. & B. Robinson. 1970. The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. Canadian Entomologist 102:641–655.

Robinson, M.H. & B. Robinson. 1973. The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. Psyche 80:277–288.

Scharff, N. & J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120:355–434.

Schoener, T.W. & D.A. Spiller. 1992. Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support of the predator-defense hypothesis. Behavioral Ecology and Sociobiology 31:309–318.

Seah, W.K. & D. Li. 2002. Stabilimentum variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. Journal of Zoology 258:531–540.

Simon, E. 1895. Histoire Naturelle des Araignées, Volume 1, fascicle 4. Libraire Encyclopédique de Roret, Paris. Pp. 761–1084.

Starks, P.T. 2002. The adaptive significance of stabilimenta in orb-webs: a hierarchical approach. Annales Zoologici Fennici 39:307–315.

Tanaka, K. 1984. Rate of predation by a kleptoparasitic spider, *Agyrodes fissifrons*, upon a large host spider, *Agelena limbata*. Journal of Arachnology 12:363–367.

Tolbert, W.W. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). Psyche 82:29–52.

Townley, M.A. & E.K. Tillinghast. 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, GABamide. Journal of Arachnology 12:303–319.

Townley, M.A., E.K. Tillinghast & C.D. Neefus. 2006. Changes in composition of spider orb web sticky droplets with starvation and web removal, and synthesis of sticky droplet compounds. Journal of Experimental Biology 209:1463–1486.

Tso, I-M. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. Animal Behaviour 52:183–191.

Tso, I-M. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. American Midland Naturalist 141:238–246.

Tso, I-M. 2004. The effect of food and silk reserve manipulation on decoration-building of *Argiope aetheroides*. Behaviour 141:603–616.

Vollrath, F. 1987a. Growth, foraging and reproductive success. Pp. 274–286. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer, Berlin.

Vollrath, F. 1987b. Kleptobiosis in spiders. Pp. 357–370. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer, Berlin.

Walter, A., P. Bliss, M.A. Elgar & R.F.A. Moritz. 2008a. *Argiope bruennichi* shows a drinking-like behaviour in web hub decorations (Araneae, Araneidae). Journal of Ethology. Doi 10.1007/s10164-007-0077-5.

Walter, A., M.A. Elgar, P. Bliss & R.F.A. Moritz. 2008b. Wrap attack activates web-decorating behavior in *Argiope* spiders. Behavioral Ecology. doi: 10.1093/beheco/arn030.

Watanabe, T. 2000. Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. Proceedings of the Royal Society of London B 267:565–569.

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