

# Wrap attack activates web-decorating behavior in *Argiope* spiders

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Various orb-weaving spiders add extra silk structures—“web decorations”—to their webs. The adaptive value of these web decorations is still unclear, and the suite of functional hypotheses remains controversial. Spiders in the genus *Argiope* decorate their webs with densely woven zigzag ribbons made of fibrous aciniform silk. This type of silk is also used by the spiders for “wrap attacks” to immobilize the prey by wrapping it with a dense silk cover. Previous studies suggested that the spiders use accumulated excess silk for building web decorations due to a constant secretion in the aciniform glands. We test if this hypothesis holds for 3 species, which construct different types of web decorations: linear in *Argiope bruennichi*, irregular in *Argiope sector*, and cruciate in *Argiope keyserlingi*. We show that depletion of aciniform silk has a stimulating effect on web-decorating behavior in 3 species of *Argiope*. The aciniform glands apparently readily overcompensated experimentally induced silk losses, and so silk depletion may result in the activation of the according glands. We suggest that the aciniform gland activation might be an important mechanism for *Argiope*'s wrap attack to ensure sufficient wrapping of silk under high prey density and repeated wrapping events. The web decorations might function as a mechanism to maintain high gland activity, thereby maximizing the efficiency of the wrap attack strategy of *Argiope*. **Key words:** aciniform silk, *Argiope*, capture strategy, gland activation, web decorations. [*Behav Ecol* 19:799–804 (2008)]

Predators either actively search and hunt for prey or inconspicuously wait for potential prey. If combined with high-speed locomotion, active hunting is often highly energy consuming. Sit and wait predators save this energy but have to rely on sufficiently high prey densities and effective foraging mechanisms. Both strategies exist in spiders, and evolutionary processes have led to several specializations. The orb-weaving spiders are typical sit and wait predators, and the web structure provides an excellent study system to investigate the evolutionary significance of behavioral traits. Orb webs are evolutionarily highly developed devices for prey-capture (Nentwig and Heimer 1987), and they are typical for several spider families including the Araneidae, Tetragnathidae, Nephilidae, and Uloboridae. The principle of catching prey with a web seems simple: construct an almost invisible silken web and optimize shape and size to maximize the trapping of airborne insects. From this perspective, it seems to be an evolutionary paradox that many araneid, uloborid, and nephilid spiders incorporate highly conspicuous web decorations into their orb webs (Hingston 1927; Robinson MH and Robinson B 1973; Scharff and Coddington 1997; Herberstein et al. 2000). Structures, such as silk bands, silk tufts, egg sacs, or detritus (Eberhard 2003) clearly enhance the visibility of the webs (Bruce et al. 2005) and hence should reduce the trap efficiency. Even worse, several studies showed that these web decorations can attract predators and reduce spider survival (Bruce et al. 2001; Craig et al. 2001; Seah and Li 2001; Li and Lee 2004; Cheng and Tso 2007).

Numerous proximate and ultimate explanations that account for web decorations have been proposed (review in Herberstein et al. 2000; Bruce 2006; see also Robinson MH and Robinson B 1970). Web decorations are thought to act

as camouflage devices that hide the exposed spider and its outline from visually hunting predators (Hingston 1927; Ewer 1972; Eberhard 1973; Lubin 1975; Tolbert 1975; but see also Robinson MH and Robinson B 1970), to enhance the visibility of the web to nonprey species that might inadvertently damage the web (Horton 1980; Eisner and Nowicki 1983; Kerr 1993) or to provide a molting platform (Robinson MH and Robinson B 1973; Nentwig and Heimer 1987). The web decorations of spiders belonging to the genus *Argiope* are generally thought to increase the foraging success of the spider by attracting prey insects (Craig and Bernard 1990; Tso 1996, 1998; Hauber 1998; Bruce et al. 2001; Li 2005), an explanation that may also apply to detritus bands (Bjorkman-Chiswell et al. 2004).

Alternatively, web decorations may have no adaptive function at all and merely reflect a nonspecific stress response (Nentwig and Rogg 1988) or simply a sign of a nonfunctional evolutionary relic behavior (Nentwig 1986). Because web decorations differ considerably in shape, size, and the frequency of occurrence among various species of *Argiope* (Wiehle 1927; Nentwig and Heimer 1987; Herberstein et al. 2000; Bruce and Herberstein 2005; Bruce 2006), they may well serve different (Herberstein et al. 2000) or multiple functions (Starks 2002).

The variability of web decorations among the genus *Argiope* makes it a model taxon for investigating the various explanations for decorating behavior (Edmunds 1986; Craig 1991; Kerr 1993; Tso 1996, 1998, 1999, 2004; Blackledge 1998a, 1998b; Blackledge and Wenzel 1999, 2001; Herberstein 2000; Bruce et al. 2001, 2005; Craig et al. 2001; Seah and Li 2001; Li and Lee 2004; Bruce and Herberstein 2005). The web decorations in this genus are constructed from fibrous silk produced by the aciniform glands (glandulae aciniformes) that are used both for the wrap attack and for constructing the typical zigzag-shaped decoration bands (Peters 1993; Foelix 1996; Griswold et al. 1998). Thus, the cue to solve the riddle about the function of these curious structures might reside in this coherency.

We here test the possibility that web-decorating behavior of *Argiope* is directly linked to its prey-capture strategy through

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Received 26 September 2007; revised 7 February 2008; accepted 7 February 2008.

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**Figure 1**

Adult females of the 3 *Argiope* species and their web decorations in the laboratory. left: *Argiope bruennichi* with linear-shaped decoration; middle: *Argiope sector* with cruciate-like (irregular) decoration; and right: *Argiope keyserlingi* with cruciate decoration pattern.

the activity of the aciniform glands. Several araneid spiders have a very distinct prey-catching behavior that differs from other orb-weaving spiders (Olive 1980; Foelix 1996). *Argiope* spiders do not immediately kill their prey by biting but rather throw a dense mesh of silk bands around the prey to immobilize it. This technique has been described as the “wrap attack” strategy (Olive 1980). After the prey is immobilized, the spiders will bite and kill it. This wrap attack strategy relies on a ready availability of aciniform silk in the highly active glandulae aciniformes (Olive 1980; Peters 1993; Foelix 1996). Peters (1993) suggested that the constant secretion in the aciniform glands may result in the accumulation of silk, and individuals may be forced to build decorations in order to utilize this excess material. When prey-capture rates are low, only small amounts of silk will be used resulting in much excess silk. Consequently, web-decorating behavior should be increased the following day (Peters 1993). Indeed, Eberhard (1988) showed that a manipulation of the fill level of silk glands affected several design features of orb webs, and experimental data obtained by Tso (2004) are consistent with Peters’ (1993) explanation. After the experimental removal of aciniform silk, *Argiope aetheroides* spiders built less web decorations in subsequent webs after the treatment. Tso (2004) proposed a threshold fill level in the aciniform glands. Hence, spiders ought to cease decorating their webs at a certain threshold point, and the size of the web decoration should be determined by the excess silk above this threshold. Peters’ proximate hypothesis predicts a high variance in decorating behavior, which nicely matches the huge variance observed in both the quantity and the quality of web decorations (Herberstein et al. 2000; Bruce 2006). Moreover, it is an appealing hypothesis because it can be experimentally tested (see Tso 2004) by manipulatively removing silk. However, in Tso’s experiments, both silk removal and observation periods were only brief (4–5 days). It is unclear whether the aciniform silk was really removed below the proposed threshold. Moreover, the absence of a control group means that it remains unclear whether the effects on web-decorating behavior were truly significant.

An experiment with more intensive silk removal over a longer period of time may demonstrate a clearer effect on decoration behavior. We investigate the influence of a depletion of the aciniform glands on the decorating behavior of *Argiope* over a period exceeding 2 weeks. We also use a comparative approach with 3 species that express very different web-decorating behavior to obtain greater taxonomic generality: 1) *Argiope bruennichi* with linear web decorations consisting of 2 zigzag bands, 2) *Argiope sector* with irregularly arranged zigzag bands,

and 3) *Argiope keyserlingi* as a representative species with cruciate web decorations (similar to *A. aetheroides* used by Tso).

## MATERIALS AND METHODS

### Study species and experimental design

Experiments were conducted on the Panpaleartic *A. bruennichi* (Scopoli, 1772), the North African *A. sector* (Forskål, 1775), and the Eastern Australian *A. keyserlingi* Karsch, 1878. All 3 species exhibit different basic web decoration types, constructing linear, irregular, and cruciate forms, respectively (Figure 1). Egg sacs (*A. bruennichi* and *A. sector*) and adult female spiders (*A. keyserlingi*) were sampled in the field (*A. bruennichi*: meadows north of Halle, Germany; *A. sector*: dry scrublands near Tripoli, Libya; *A. keyserlingi*: Pymble Park, Sydney, Australia) and brought to the laboratory (*A. bruennichi* and *A. sector*: Halle; *A. keyserlingi*: Melbourne). *Argiope bruennichi* and *A. sector* females were reared from the emergence from the egg sacs in environmentally controlled terraria (80 × 40 × 50 cm) with long day conditions (16:8 light:dark, at 26 ± 1.5 °C, RH: 56 ± 11.4%; for details, see Walter et al. 2005). One week prior to the tests, the experimental spiders were set on web frames (wooden frames for *A. bruennichi* and *A. sector*: 35 × 35 × 7 cm; perspex frames for *A. keyserlingi*: 58 × 58 × 15 cm) and kept under natural light conditions. Each spider was fed with a single prey item (1 honeybee for *A. bruennichi*, 1 house cricket for *A. sector*, and 1 blowfly for *A. keyserlingi*) and sprayed with water every other day, which ensured a normal development and is close to food intake under natural conditions.

Following Tso (2004), we experimentally removed aciniform silk from the spiders’ gland repository to deplete the reservoir of excess silk. We removed the silk by offering additional prey items to the spiders, which were readily wrapped, but then removed the prey from the web before the spiders could consume it.

Spiders of each species were randomly assigned to an experimental or a control group. Individuals in the experimental treatment received, every other day, additional prey items that were removed after wrapping. We used 3 honeybees (*Apis mellifera*) for *A. bruennichi* ( $n = 11$  spiders), 3 house crickets (*Acheta domesticus*) for *A. sector* ( $n = 11$  spiders), and 4 blowflies (*Lucilia spec.*) for *A. keyserlingi* ( $n = 22$  spiders). The prey items were pressed with tweezers to immobilize them and keep web damage low (following Tso 2004). The spiders had to wrap each prey item in succession. Prey items were removed, by

careful excision from the sticky spiral, immediately after the spider had completed wrapping. This procedure ensured that spiders in both the experimental and the control groups had the same feeding regime with 1 prey item every second day. Because *Argiope* spiders typically construct a new capture web every day, we observed the decorating behavior on the day after the experimental treatment. We observed the spiders of all species for 17 days.

For each web, we measured: 1) the web-decorating frequency, 2) the size of web decorations, and 3) the spider size. All observed web decorations were integrated in the decorating frequency of each group each day. The decoration size was calculated by using the formula of Tso (1999) for determining a trapezium area:  $(a + c)/2 \times h$  ( $a$  and  $c$  = upper and lower width of zigzag bands,  $h$  = height of zigzag bands). For calculating the web area, we determined the web capture area (including hub area) of all webs following Herberstein and Tso (2000):  $(d_v/2) \times (d_h/2) \times \pi$  ( $d_v$  = vertical and  $d_h$  = horizontal diameter of the orb web). We measured total body length from the clypeus to the end of the opisthosoma.

### Statistical analyses

For general statistical analyses, we used STATISTICA® (version 6.0). Differences in decorating frequencies over the observation period were examined using chi-square tests for independence. Paired  $t$ -tests were used to examine body size comparisons and to test for differences in web decoration size.

## RESULTS

Spiders increased in body size over the time period consistent with a regular growth rate. In this context, treatment groups and control groups did not differ significantly in any species (paired  $t$ -tests:  $t = -1.52$ ,  $P = 0.15$  for *A. bruennichi*;  $t = 0.04$ ,  $P = 0.97$  for *A. sector*; and  $t = 1.32$ ,  $P = 0.21$  for *A. keyserlingi*). On average, *A. bruennichi* spiders ( $n = 22$ ) grew up from  $8.5 \pm 0.16$  mm standard error (SE) to  $11.36 \pm 0.12$  mm SE, *A. sector* ( $n = 22$ ) from  $6.86 \pm 0.14$  mm SE to  $9.4 \pm 0.28$  mm SE, and *A. keyserlingi* ( $n = 4$ ) from  $10.48 \pm 0.28$  mm SE to  $11.61 \pm 0.21$  mm SE within the 17-day observation period. This indicates that the silk depletion treatment did not generally interfere with spider constitution.

The size of the capture area of orb webs showed no significant differences between treatment and control group in *A. bruennichi* (paired  $t$ -test:  $t = -0.89$ ,  $P = 0.39$ ) and *A. keyserlingi* (paired  $t$ -test:  $t = -1.67$ ,  $P = 0.11$ ) within the observation period. Web size remained unchanged in *A. bruennichi* (treatment: from  $336.52 \pm 57.62$  cm<sup>2</sup> SE to  $332.06 \pm 46.72$  cm<sup>2</sup> SE,  $n = 11$ , and control:  $280.18 \pm 38.66$  cm<sup>2</sup> SE to  $299.92 \pm 52.53$  cm<sup>2</sup> SE,  $n = 11$ ), and in *A. keyserlingi*, web size increased over time, but similarly among the groups (treatment: from  $657.66 \pm 68.69$  cm<sup>2</sup> SE to  $1479.57 \pm 61.38$  cm<sup>2</sup> SE,  $n = 22$ , and control:  $731.32 \pm 102.27$  cm<sup>2</sup> SE to  $1586.85 \pm 59.27$  cm<sup>2</sup> SE,  $n = 22$ ). Interestingly, individuals of *A. sector* decreased the size of the capture area in both the treatment and the control group (treatment: from  $746.08 \pm 93.22$  cm<sup>2</sup> SE to  $323.08 \pm 47.71$  cm<sup>2</sup> SE,  $n = 11$ , and control:  $783.14 \pm 107.55$  cm<sup>2</sup> SE to  $599.36 \pm 66.92$  cm<sup>2</sup> SE,  $n = 11$ ). Treated spiders decreased their web size significantly more strongly than spiders of the control group (paired  $t$ -test:  $t = 6.69$ ,  $P < 0.01$ ).

The silk depletion treatment did not result in a reduction but rather in a significant increase in web-decorating behavior for all 3 species. The proportion of decorating spiders was higher in the experimental than in the control groups in all 3 species shortly after commencing the treatment and remained that way for the duration of the trial (Figure 2). On average, the decorating frequency of treated *A. bruennichi*

individuals was  $66.33 \pm 5.93\%$  SE ( $n = 11$ ) compared with  $46.22 \pm 7.05\%$  SE ( $n = 11$ ) in the control group, and similar differences were recorded in *A. sector* (treatment:  $81.4 \pm 3.04\%$  SE,  $n = 11$ , vs. control:  $62.71 \pm 3.82\%$  SE,  $n = 11$ ) and *A. keyserlingi* (treatment:  $78.37 \pm 2.78\%$  SE,  $n = 22$ , vs. control:  $62.14 \pm 1.82\%$  SE,  $n = 22$ ). The frequency of web decorating was significantly higher in silk removal than in control groups in all 3 species (chi square; *A. bruennichi*:  $\chi^2 = 214.4$ ,  $P < 0.01$ , degrees of freedom [df] = 16; *A. sector*:  $\chi^2 = 120.67$ ,  $P < 0.01$ , df = 16; and *A. keyserlingi*:  $\chi^2 = 48.91$ ,  $P < 0.01$ , df = 16).

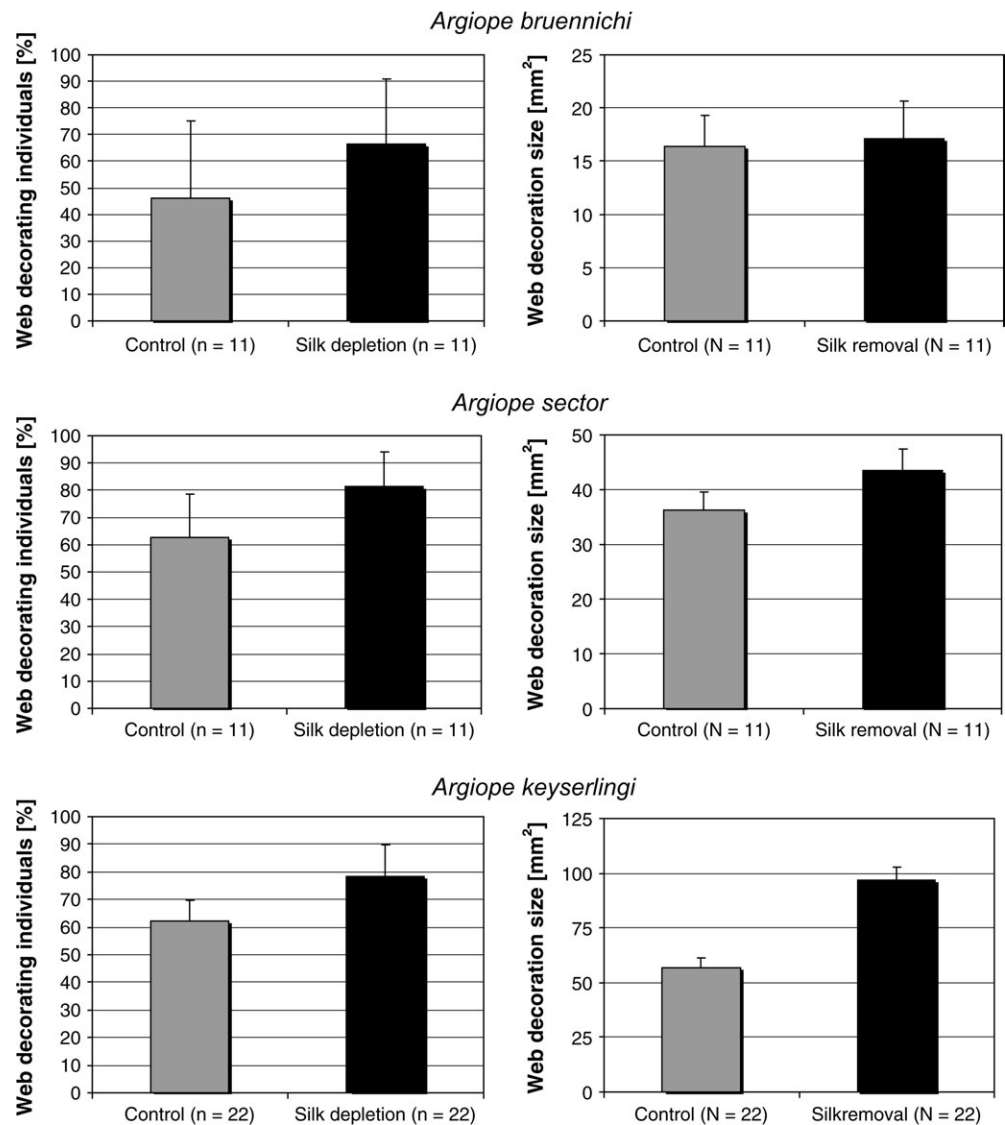
The size of decorations was not consistently lower in the depletion than in the control treatment in any of the tested species (Figure 2). There was no significant difference in the size of decorations between the 2 treatments in either *A. bruennichi* ( $17.14 \pm 3.52$  mm<sup>2</sup> SE for the treatment group vs.  $16.38 \pm 2.95$  mm<sup>2</sup> SE for the control group; paired  $t$ -test:  $t = -0.26$ ,  $P = 0.8$ ) or *A. sector* ( $43.6 \pm 3.84$  mm<sup>2</sup> SE for the treatment group vs.  $36.22 \pm 3.37$  mm<sup>2</sup> SE for the control group; paired  $t$ -test:  $t = -1.83$ ,  $P = 0.09$ ). The size of decorations was significantly higher in the silk removal treatment compared with the control treatment in *A. keyserlingi* ( $96.61 \pm 6.11$  mm<sup>2</sup> SE for the treatment group vs.  $56.97 \pm 4.38$  mm<sup>2</sup> SE for the control group; paired  $t$ -test:  $t = -5.09$ ,  $P < 0.01$ ).

## DISCUSSION

We show that an experimentally induced increase in prey interception and wrapping behavior resulted in a consistent increase in the frequency of web-decorating behavior in 3 species of *Argiope* and increased the size of web decorations in *A. keyserlingi*. Although these data do not provide a definitive adaptive explanation for web-decorating behavior, they reveal that this behavior is not independent from gland physiology. It is possible that the individual's prey-capture experience also contributed to the observed increase in web-decorating behavior. However, food ingestion rate was not a mechanism informing individuals of their prey-capture history because the spiders from the control and experimental treatments received the same quantity of prey.

Prey-capture experience may influence the web-building behavior in orb weavers in several ways. Although the actual prey type seems not to affect web design in *A. bruennichi* (Prokop 2006), some orb web spiders assess past foraging success to relocate their webs more often when prey abundance is low (Nakata and Ushimaru 2004). Also, *Argiope* spiders can readjust web characteristics or change the web-building frequency as a consequence of past capture experience (Heiling and Herberstein 1999; Herberstein et al. 2000). Although wrapping many prey items is a good indicator of high prey abundance and high web efficiency, Tso (1999) showed that recent capture success alone does not affect web-decorating behavior in *Argiope trifasciata*. Nevertheless, our results with *A. bruennichi*, *A. sector*, and *A. keyserlingi* are consistent with the prey-attracting function of web decorations (Craig and Bernard 1990; Herberstein 2000; Bruce et al. 2001; Li 2005). Spiders experiencing a higher capture rate (but not higher ingestion rate) may compensate for the loss of prey by increasing the prey encounter rate through constructing more web decorations. This explanation may not be widespread because an increase in web-decorating activity does not necessarily translate into higher prey-capture rate (see Blackledge and Wenzel 1999; Prokop and Grygláková 2005).

Blackledge (1998b) suggests that, given a metabolic cost for silk production, decorating behavior might reflect a balance between foraging effort and energy intake. Indeed, in many *Argiope* species, well-fed spiders are more likely to produce decorations than poorly fed individuals (Herberstein 2000;



**Figure 2**

Average web-decorating frequency (left chart) and web decoration size (right chart) over the observation period in all 3 tested *Argiophe* species. The frequency of web-decorating behavior was significantly increased in the treatment group (chi square; *Argiophe bruennichi*:  $\chi^2 = 214.4$ ,  $P < 0.01$ ,  $df = 16$ ; *Argiophe sector*:  $\chi^2 = 120.67$ ,  $P < 0.01$ ,  $df = 16$ ; *Argiophe keyserlingi*:  $\chi^2 = 48.91$ ,  $P < 0.01$ ,  $df = 16$ ). The increase of decoration size in the silk depletion group was only significant for *A. keyserlingi* (paired *t*-test:  $t = -5.09$ ,  $P < 0.01$ ) but not for *A. bruennichi* (paired *t*-test:  $t = -0.26$ ,  $P = 0.8$ ) and *A. sector* (paired *t*-test:  $t = -1.83$ ,  $P = 0.09$ ).

Craig et al. 2001; Seah and Li 2002). Thus, sated spiders are better placed to take advantage of other benefits of web decorations, including camouflaging the spider (Schoener and Spiller 1992; Blackledge and Wenzel 2001; Eberhard 2003; Li et al. 2003) or protecting the web (Eisner and Nowicki 1983; Kerr 1993). Our experiments provide little support for this idea. Spiders that wrapped additional prey items were not rewarded with a greater food intake. Hence, there was no increased energy uptake in our study that might have translated to an increase in web-decorating behavior. However, aciniform silk removal in *A. sector* caused an increase in web-decorating activity combined with a significant decrease in web size, suggesting a trade-off between both parameters. Hauber (1998) described a similar phenomenon in *Argiophe appensa* and argued that this might reflect different foraging strategies. Thus, large webs without decorations may yield a similar capture success as small webs with “prey-attracting” decorations. This ultimate function of web decorations would not be effective in *A. bruennichi* and *A. sector*, in which web-decorating behavior was independent of web size. Although we cannot explain why *Argiophe* builds such conspicuous decorations into a web, when inconspicuous webs might be more effective traps, the high visibility of web decorations indicates that there must be benefits to web-decorating behavior.

Because *Argiophe* uses aciniform silk for both prey wrapping and web decoration (Peters 1993), spiders in our study apparently overcompensated aciniform silk removal by increasing the secretion to construct more and/or larger decorations. The rapid silk resynthesis is thought to be a general mechanism that allows spiders to respond instantly to the immediate needs of efficient prey capture (Craig 2003). Silk gland secretion is stimulated by silk removal in the nondecorating spider *Araneus cavaticus* (Tillinghast and Townley 1986), and the efficiency of silk glands can be stimulated by manipulative silk depletion in *Araneus diadematus* (Peakall 1966). Therefore, aciniform silk removal may also stimulate gland activation in *Argiophe*, resulting in the observed overcompensation of the depleted silk reserves in the repository. All species showed a significant increase in web-decorating frequency after aciniform gland depletion. Moreover, *A. keyserlingi* also enhanced the size of the decorations.

Our data contradict Tso (2004), which may reflect a true biological difference among the tested species because web-decorating behavior varies profoundly within the genus *Argiophe* (Bruce 2006). Several factors may affect web-decorating activity, including the genotype (Edmunds 1986; Craig et al. 2001) and the environment (e.g., an enhanced risk of predation: Bruce et al. 2001; Craig et al. 2001; Seah and Li 2001), and

they may have contributed to the comparatively inconsistent results. Alternatively, this inconsistency with Tso (2004) may derive from differences in experimental procedures. The duration of Tso's (2004) experiment may not have been sufficiently long to completely empty the aciniform glands and thus stimulate the same behavioral change we report.

An increase of aciniform gland activity in response to the depletion treatment may be highly adaptive for *Argiope* because the aciniform silk is used to immobilize prey insects in the wrap attack (Olive 1980). Sufficiently large silk stores are essential to ensure prey capture at any time. Therefore, spiders must rely on highly active glands to ensure sufficient wrapping material for serial capture events, even under high prey densities. In times of low prey density (e.g., during the night), the nonusage of wrapping silk combined with ongoing secretion in the aciniform glands may lead to an accumulation of aciniform silk (Peters 1993). Decorating the web may be an effective mechanism to ensure an appropriate gland activity: greater gland activity may lead to more and larger decorations and vice versa. Decorating the web more extensively enhances the aciniform silk usage and therefore the gland activity. The high efficiency of 95% of web recycling (Peakall 1971) ensures that this temporary outsourcing of rather precious silk is less costly. Accordingly, spiders that show an increased decorating behavior should be better at catching abundant prey with wrap attacks by having a higher amount of wrapping silk available. This positive feedback loop should enhance the efficiency of an already established capture strategy to respond to higher prey abundances. This model predicts that the number of sequential wrap attacks might be reduced if the spider is experimentally prevented from constructing web decorations, simply because it has less activated aciniform glands. Further studies might focus on the intensity of the capture behavior of *Argiope*, depending on the presence or size of web decorations at that time. Because some *Argiope* species specifically decorate their webs more often than others (Starks 2002; Bruce and Herberstein 2005; Bruce 2006), it would be particularly interesting to compare the capture behavior of *Argiope* species that have different decorating frequencies.

Perhaps the decorating silk was initially a by-product of regulating the aciniform glands and was placed haphazardly on the web in order to ensure that it will be recycled (Janetos 1982). Due to their signalling effect, the species-specific decoration patterns (cf., Figure 1) may then have subsequently fulfilled an important, perhaps species specific, function. In this way, the described mechanisms nicely reveal the results of an extended phenotype. Based on the initial physiological adaptation on a specialized capture strategy, the consequences of this coherency became selected secondarily. Irrespective of the adaptive mechanisms behind the decoration construction, we show that it is possible that the wrap attack strategy of *Argiope* further activates the glandulae aciniformes, and web decorations represent the visible result.

## FUNDING

Deutsche Forschungsgemeinschaft (P.B.); the Deutscher Akademischer Austauschdienst (A.W.); the Federal State of Saxony-Anhalt, Ministry for Science and Culture (A.W.).

We thank Taher Shaibi for providing *Argiope sector* from Libya. The experiments carried out in this study comply with the current laws of Germany and Australia.

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