The adaptive value of web decorations for *Argiope* spiders (Araneae, Araneidae)

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Chapter 1

General introduction

Spiders are a large invertebrate predator-guild (approx. 40.000 species) that has not substantially changed its fundamental lifestyle over millions of years. Unlike insects spiders show much fewer diversifications in terms of morphology and foraging strategies. Species of different families possess a very similar body plan and all feed almost exclusively on insects (Foelix 1996). Nevertheless, spiders conquered a broad spectrum of habitats. From the evolutionary point of view these order-specific features demonstrate that "They are obviously doing something right" (Craig 2003). One reason for the success of spiders resides in the ability to produce silk. Silk is used by spiders in diverse ways and allows them to remain morphologically unmodified. For example, they build silken retreats or tubes to protect themselves and egg sacs covered by silk to protect offspring. They spin silken webs for trapping prey and use silk threads for immobilising prey. Overall, most interactions between spiders and environment are silk-mediated (Nentwig & Heimer 1987) and responsible also for the striking behavioural plasticity of these evolutionary relatively unchanged animals.

Many spider families use silken webs as prey capture devices. As a result of the adaptation on different ecological niches, the evolution of web weavers has been generating also a high diversity of web shapes and sizes, with the orb web as an evolutionary highly developed structure (Nentwig & Heimer 1987). Orb webs are used for prey capture by several families, such as Araneidae, Nephiliidae, Tetragnathidae and Uloboridae. The construction plan of these webs combines a minimum usage of silk with a maximum area for catching prey. To be effective, spider webs should be as invisible as possible. But then, why do certain orb weaving species add conspicuous attachments to their webs?

Web attachments

It seems to be a paradox that several orb weaving spiders ‘decorate’ their inconspicuous webs with highly visible attachments. The terminology of such additional constructions is inconsistent. They are called “web decorations”, “devices”, “adornments” or “filaments” (Herberstein et al. 2000a). Very different types of web attachments are known, e.g. silk bands and silk tufts, but also attachments consisting of egg sacs or detritus (Eberhard 2003). Moreover, some species combine silk attachments with non-silk materials (Hingston 1927; Eberhard 2003). However, enhancing the visibility of a trap by including attachments should reduce the trapping efficiency, and a couple of studies already show that this behaviour can reduce spider survival (Bruce et al. 2001; Craig et al. 2001; Seah & Li 2001). The fact that a number of species do perform web decorating indicates that there has to be an adaptive value of additional web structures.

Since web attachments occur only in species that do not build retreats (Eberhard 2003) the functional significance of these structures has been discussed in the context of protective devices (Comstock 1967; Schoener & Spiller 1992; Blackledge & Wenzel 2001; Gonzaga & Vasconcellos-Neto 2005). This hypothesis is applicable for various detritus, egg sac and silk band decorations (see reviews in Herberstein et al. 2000a and Eberhard 2003). However, in general, silken decorations are the best studied web attachments (Bruce 2006). These structures occur in different spider genera such as *Uloborus* (Uloboridae), *Nephila* (Nephilidae), *Cyclosa*, *Gea* and *Argiope* (Araneidae).

Silken web decorations

Silk band attachments constructed by several orb weavers are often called “web decorations” (McCook 1889; Marples 1969). Simon (1895) described the zigzag-shaped silk bands built by *Argiope* spiders alternatively as “stabilimentum”, based on a supposed stabilising function of these structures. Web decorations or stabilimenta have evolved independently several times in the different groups of orb weaving spiders (Scharff & Coddington 1997; Levi 2001), indicating a potential adaptive significance. Despite of the wide range of web decorating species, recent decoration-research is mainly concentrated on a few species of the genus *Argiope* (e.g. Chmiel et al. 2000; Herberstein et al. 2000a; Seah & Li 2001, 2002; Herberstein & Fleisch 2003; Li & Lee 2004; Li et al. 2003, 2004; Tso 2004; Li 2005; Bruce & Herberstein 2006).

The basic construction plan of silken web decorations is very similar within the genus *Argiope*. The silken bands consist of densely woven flimsy silk threads which are spanned in a zigzag-pattern between two adjacent radii of the orb web (Fig. 1). Due to different opportunities how to arrange these bands in the web, a lot of partly species-specific decoration shapes are described. In a more or less rough classification arachnologists distinguish between linear (two silk bands vertically arranged, one above and one beneath the web hub), cruciate (four silk bands aligned to a large 'X' in the web) and circular (zigzag-bands forming a circle around the hub region of the web) shapes (Bruce 2006). Most of the species can be assigned to one of these decorating types, but curiously, there are also *Argiope*-species that exhibit indistinct decoration patterns, e.g. *A. lobata*, *A. sector*, *A. ocyaloides*.

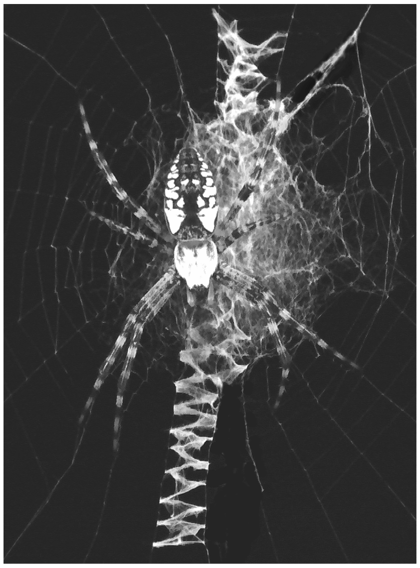

Figure 1. Linear web decoration pattern: Typical zigzag-shaped silk band in the web of a female *Argiope aurantia*.

Adaptive significance of web decorations in Argiope

The question remains: Why do *Argiope* spiders decorate their inconspicuous webs with highly visible silk bands? Although a couple of researchers have been studying the web decorating behaviour of *Argiope*-species, the adaptive value of these web attachments is beyond a conclusive evaluation (Bruce 2006). Over the last decades, a suit of partly contradictory proximate and ultimate functional hypotheses has been claimed. So web decorations are supposed to represent, for example:

1. an enhancement of the stability of the orb web – Simon (1895),
2. auxiliary silk for wrapping of larger prey items – Vinson 1863 (cit. in Wiehle 1928),
3. a deposit of excess silk – Wiehle (1928) and Peters (1993),
4. an abutment for grasping larger prey items – Voigt (1929),
5. a "pathway" for males to find females at the web hub – Crome & Crome (1961),
6. a moulting platform – Robinson & Robinson (1973) and Nentwig & Heimer (1987),
7. a sun shield to avoid overheating and excessive water losses – Robinson & Robinson (1978),
8. an unspecific stress reaction – Nentwig & Rogg (1988),
9. a camouflage/anti-predator device – Schoener & Spiller (1992); Blackledge & Wenzel (2001) and Eberhard (2003),
10. a web advertisement to avoid inadvertent web damaging by non-prey animals – Horton (1980); Eisner & Nowicki (1983) and Blackledge & Wenzel (1999),
11. a prey attractant – Craig & Bernard (1990); Elgar et al. (1996); Tso (1996, 1998); Blackledge (1998b); Herberstein (2000) and Bruce et al. (2001).

Recently, the last hypothesis (11) is the most frequently addressed functional explanation for the occurrence of web decorations - in the controversial debate only the 'predator defense' hypothesis (9) is considered in a similar extent.

Above all, the high variability in decorating behaviours among *Argiope*-species appears to complicate any comprehensive adaptive explanation. Often silk band arrangements (linear, cruciate or circular shapes) are not only species-specific but also underlie substantial intraspecific variation affecting both a varying number of decoration bands and the overall web architecture. The decorating behaviour can differ at both the population and the individual level but also vary over time within an individual (Lubin 1975; Craig et al. 2001; Starks 2002). Moreover, spiders may temporarily decide to cease web decorations altogether. It is certainly possible that the web decorating behaviour in *Argiope* spiders serves multiple functions. In that case, the aim to identify a single adaptive function to the highly variable decoration patterns may be inappropriate. If a suite of different factors affects web decoration behaviour this would explain the variety of competing hypotheses in the debate about their adaptive significance (see Herberstein et al. 2000a; Starks 2002).

Study structure and aims

Despite of the large amount of functional hypotheses only a few authors have considered the proximate mechanisms behind the web decorating behaviour. Nentwig & Rogg (1988) suggested that web decorations might be functionless in the orb web representing simply the product of an unspecific stress reaction. Peters (1993) argued that the silk compiling the web decorations originates from an accrued excess of silk not used for wrapping prey items, since both decorating and wrapping silk are mainly built by the Glandulae aciniformes (see also Vollrath & Knight 2001). Given that the aciniform glands are continuously secreting, an excess of silk should arise if it is not used for wrapping prey. Peters (1993) argued that spiders use this excess for constructing web decorations when rebuilding the orb web. Hence, web decorations are considered to regulate the aciniform silk glands. Alas, an experimental proof of this hypothesis was missing (Herberstein et al. 2000a; Starks 2002), and the main focus of this study was to test this regulatory hypothesis in *Argiope* spiders.

I based my studies on laboratory experiments to single out potential factors affecting web decorations between groups of spiders by keeping all other conditions equal. However, before evaluating the ecological relevance of treatmentrelated effects on web decorating behaviour under laboratory conditions, I first determined the basic variation of web decorating in the field (chapter 2) of the main study animal of this thesis, the Palearctic wasp spider *Argiope bruennichi*. In a second step I developed a suitable laboratory rearing method to ensure a sufficiently high number of individuals available for the experiments. Follner & Klarenberg (1995) found that *A. bruennichi* spiderlings do not build webs under laboratory conditions without a ballooning-phase prior to the caging. Because this prerequisite would clearly aggravate the rearing, I studied the obligation of the ballooning behaviour in this species (chapter 3).

After these two initial steps, I started the actual experimental part of the study examining the adaptive significance of *Argiope*'s web decorating behaviour primarily testing the possible gland-regulation mechanism. Consequently, the amount of silk used for decorating rather then the decoration pattern was in the centre of my research. This allowed for straight forward interspecific comparisons (Herberstein et al. 2000a; Eberhard 2003) among three different *Argiope*-species (chapter 4). This comparative approach also allowed for generalisations within the genus *Argiope*. The experiments were based on manipulatively removed silk from the aciniform glands in *A. bruennichi*, *A. sector* and *A. keyserlingi*. All three species build different basic decoration patterns and are endemic to different continents (*A. bruennichi* – Eurasia, *A. sector* – Northern Africa and *A. keyserlingi* – Eastern Australia).

If web decorating behaviour in *Argiope* is proximately influenced by the spider's physiology, life history phases with most dramatic changes may be most suitable for studying any relationship between physiology and web decoration behaviour. Clearly, the moult represents one of the most drastic physiological changes in the spider's life. Hence, I studied the web decorating behaviour specifically in the context of moulting events (chapter 5) in *A. keyserlingi*. This species builds large cruciate decorations consisting of up to four silk bands, ensuring a maximum resolution of differences in the size of the web decorations.

Most studies on the web decorating behaviour in *Argiope* spiders address ultimate adaptive functions of web decorations, mostly based on effects created by visual characteristics of the decoration silk. Even given the proximate physiological mechanisms for building the web decorations in *Argiope* were understood, than this does not explain why different decoration shapes are added to the web. So after having addressed how web decorations are constructed, I deal with testing two deliberately chosen adaptive hypotheses in chapters 6 and 7.

Several authors stated that web decorations might be maladaptive because they attract predators. To clarify this question I examined whether web decorations of *A. bruennichi* are attractive to a potential predator, *Mantis religiosa*. Bruce et al. (2001) had tested this using a Y-maze experimental setup with a similar species-pair and found that the mantids were attracted by web decorations. However, it is not clear if this was a result primarily driven by the experiment and does not reflect natural behaviour. So testing the attractiveness of the decorations seems to make only sense, if this testing system is useful for investigating the predator attraction hypotheses at all, a topic dealt with in chapter 6.

Among orb weavers *Argiope* spiders are especially vulnerable to biotic and abiotic environmental changes since they do not build protecting retreats. Such influences also include the water metabolism; permanently exposed to the sun, sitting on the web hub aggravates dry stress situations. During the rearing of *A. bruennichi* spiders I recognized a potential link between the water metabolism and the web decorating behaviour. Spiders that were sprayed with water, following the rearing protocol, repeatedly ingested droplets from web hub decorations. A similar behaviour was yet reported only anecdotally and I therefore tested individuals of *A. bruennichi* for the regularity of this behaviour to close this research gap.

Chapter 2

Web decorating behaviour in *Argiope bruennichi* (Araneae, Araneidae): Is short-term variation an indication of a conditional strategy?

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Abstract. Web decorating is a conspicuous feature of the web building behaviour of several orb weaving spiders. In the genus *Argiope* these decorations are represented by zigzag shaped silk bands in the orb web. Over the last decades, a large suite of sometimes contradictory hypotheses have been proposed to explain the adaptive value of web decorations. Inter- and intraspecific variation of different shapes of *Argiope*'s web decorations is the prime problem for assigning a single adaptive function. We here study the individual variation of web decorations of *A. bruennichi* in the field. We found a high variation of web decorating behaviour. In particular, spiders showed a significant decrease of the web decorating behaviour but more often altered the decoration pattern after web relocation. This result may represent the response to the specific local micro habitat conditions and therefore supports the hypothesis that variable web decorations are tactically used as multifunctional tools.

Introduction

Wasp spiders attach conspicuous silk structures to their orb-webs which enhance the visibility of the web (Herberstein et al. 2000a). These additional web elements, termed stabilimenta (Simon 1895) or decorations (McCook 1889), are constructed with aciniform silk fibres similar to those used in the 'wrap attack' behavioural sequence of *Argiope* spiders (Robinson 1975; Peters 1993). A high variability of these curious silk attachments is typical for a number of spider species of the genus *Argiope* (Nentwig & Heimer 1987; Bruce & Herberstein 2006).

A large suite of proximate and ultimate hypotheses has been proposed to explain the adaptive value of the web decorating behaviour in *Argiope* spiders (e.g., Crome & Crome 1961; Craig & Bernard 1990; Blackledge & Wenzel 1999; Chmiel et al. 2000; Herberstein et al. 2000b, Bruce et al. 2001; Seah & Li 2001, 2002; Li 2005). Unfortunately, many of these hypotheses are contradictory and do not unambiguously resolve the issue (reviews and discussions in Robinson & Robinson 1970; Nentwig & Heimer 1987; Herberstein et al. 2000a; Starks 2002; Eberhard 2003; Bruce 2006). In particular, the high intra- and interspecific variability in web-decorating behaviour (see also Lubin 1986; Blackledge 1998b; Craig et al. 2001; Seah & Li 2002) does not support the idea of a single, universal function of decorations and it renders an adaptive explanation difficult (Nentwig 1986; Nentwig & Heimer 1987; Nentwig & Rogg 1988; Peters 1993; Starks 2002). Nevertheless, the contradictions of adaptive versus non-adaptive explanations in the long-standing controversy about web decorations may not be mutually exclusive (Herberstein et al. 2000a). A phylogenetic analysis of decoration patterns suggests that the different types are little homologous and do not form a phylogenetic signal (Scharff & Coddington 1997; Herberstein et al. 2000a). Numerous convergences and independent evolutionary gains support the notion that different types of web decorations serve different functions, both at the inter- and intraindividual level, and web decorations may act as a multifunctional tool (Herberstein et al. 2000a). Starks (2002) argued that web decorations might result from a conditional strategy and multiple possible selective benefits are the reason for contradictory results in the literature. On the one hand, this model includes the possibility that a particular decoration type may fulfil a species-specific function. On the other hand, web decorating behaviour might be a mechanism for tactical decisions in a rapidly changing environment. These changes include abiotic and biotic influences as well as the physiological status of the spider itself (Starks 2002).

Starks' (2002) approach allows for a large variation in decoration types and overcomes the problem of those hypotheses which are focusing on a single adaptive function for web decorations. The first step in examining the function of web decorations should be to record the intra- and interspecific variation of decoration shapes rather than immediately starting with experiments to test selected potential web functions (Eberhard 2003).

A. bruennichi seems to be an excellent study species because it shows a fundamental ontogenetic shift in the form of web decorations between juveniles and adults (Crome & Crome 1961). Spiderlings often adorn their webs with a circular zigzag structure (Sacher 1991), whilst adult females mostly spin two linear zigzag bands, one above and one below the web hub (Wiehle 1927; Sacher 1991). A considerable intraindividual variation in both the form and frequency in *A. bruennichi* females' web decorations has been reported (Gerhardt 1924; Wiehle 1927, 1928; Malt 1996; Diener 2000), as well as the lack of decorating in the 'rudimentary webs' of adult males (Wiehle 1928; Sacher 1991). We here study the individual short-term variation of web decorating behaviour in *A. bruennichi* in the field to screen if changes in frequency, shape and size of the web decorations support the notion of a multifunctional tool.

Methods

Study site and study species

We examined the inter- and intraindividual web decorating behaviour in an *A. bruennichi* population from 15 Aug. to 18 Aug. 2003 near the village Brachwitz

(011°52'24"E, 51°33'05"N Saxony-Anhalt, Germany). No rain fall occurred during the 4 day-observation period with average midday air temperatures of 35.9±2.5 °C.

We individually marked 34 adult female spiders (mean body length: 13.39±1.02 mm) at the opisthosoma with long-lasting acrylic paint Edding Lackmarkers 751 (colours: signal red, red-violet, blue, white). All webs were marked with a flag to ensure the recovery of spiders on the next day and to test whether web locations were changed by the spiders on subsequent days. We controlled the flagged orb-webs daily between 10:30 and 11:00 and estimated the capture area of each web by the maximum horizontal and vertical diameters of the viscid spiral using the equation of Blackledge (1998b): capture area = π x ½ vertical spiral diameter x ½ horizontal spiral diameter. Finally, we recorded the shape of the web decoration, if present, of all webs.

Statistical analyses

We used STATISTICA® (version 6.0) for statistical analyses. Differences in web size were calculated with t-tests. Chi-square tests were performed, to compare sequences of web decoration patterns and to test for differences between spiders with and without web relocations.

Results

Web decoration shapes

In the observed population of *A. bruennichi,* 73% of all webs had a web decoration. We found three basic decoration patterns (Fig 1). Type A, with two arms, one above and one below the web hub, was found in 39.15% (*n*=53) of all cases. Type B, with only a single arm below the hub, was found in 32.47% (*n*=44) of all webs. Type C, with only a single arm above the hub, was only built twice (=1.48%). Approximately a quarter of all webs (26.91%, *n*=37) had no web decoration at all (type '0').

We found no significant correlation between the presence of web decorations and the mean web size. Although undecorated webs tended to be larger (480.54±27.2 SE cm^2, n=37) than decorated webs (402.21±20.98 SE cm^2, n=99) this difference was statistically not significant (t-test, t=-1.79, p=0.08).

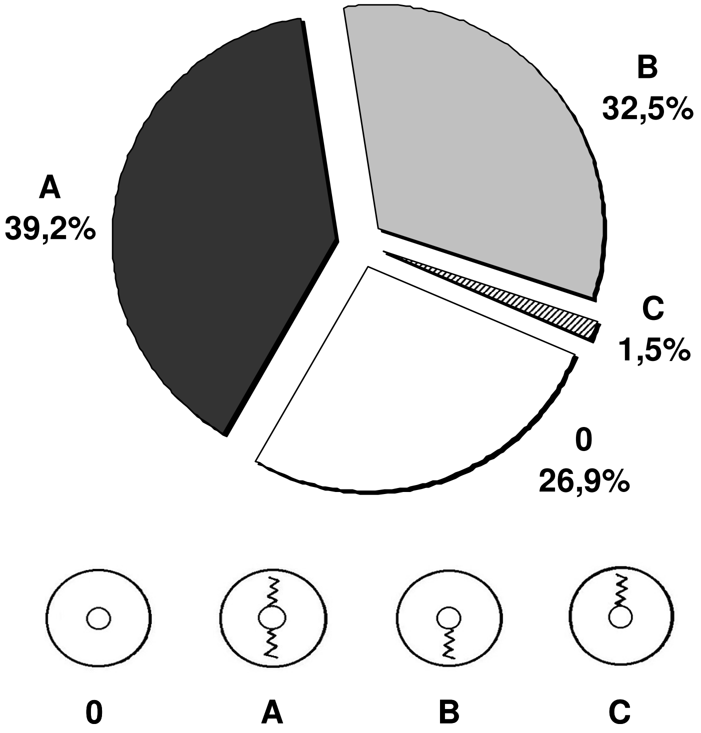

Figure 1. Midday web decoration shapes in webs of *A. bruennichi* over a four-day-interval (legend with schematic representation of the basic forms).

Variation of web decorating behaviour

The web decoration shapes of most individuals changed considerably from day to day. Almost half of all spiders (48.04%, n=49 observations) changed the decoration type in newly built webs the next day. By recording the individual temporal dynamics of the day-to-day changes in web decoration pattern, we identified 19 different pattern sequences for the 34 spiders (Table 1). The pattern sequences were evenly distributed among the spiders and only up to four individuals showed the same sequence (Chi²-test, χ^2=12.94, p=0.8).

Table 1. Recorded sequences of web decoration shapes of 34 females of *A. bruennichi* in the four-day-interval.

Sequence No.	**Sequence**				**Individuals**
1	*A*	*A*	*A*	*A*	2
2	*A*	*A*	*B*	*A*	1
3	*A*	*A*	*B*	*B*	4
4	*A*	*A*	*B*	*0*	4
5	*A*	*A*	*0*	*0*	2
6	*A*	*B*	*A*	*A*	1
7	*A*	*B*	*A*	*C*	1
8	*A*	*B*	*B*	*B*	1
9	*A*	*C*	*0*	*B*	1
10	*B*	*A*	*A*	*A*	3
11	*B*	*A*	*A*	*B*	2
12	*B*	*B*	*B*	*B*	1
13	*B*	*0*	*B*	*0*	1
14	*B*	*0*	*0*	*B*	1
15	*B*	*0*	*0*	*0*	4
16	*0*	*A*	*B*	*B*	2
17	*0*	*B*	*0*	*0*	1
18	*0*	*0*	*B*	*0*	1
19	*0*	*0*	*0*	*0*	1

Although we classified the various decoration shapes into four types only, the individual pattern of decoration construction was highly variable. Only four spiders (11.76%) did not vary their web decoration type within the four-day observation period. All other spiders altered web decoration shapes up to three times in this narrow time window (one change: 41.18%, *n*=14; two changes: 38.24%, *n*=13; three changes: 8.82%, *n*=3; Fig. 2).

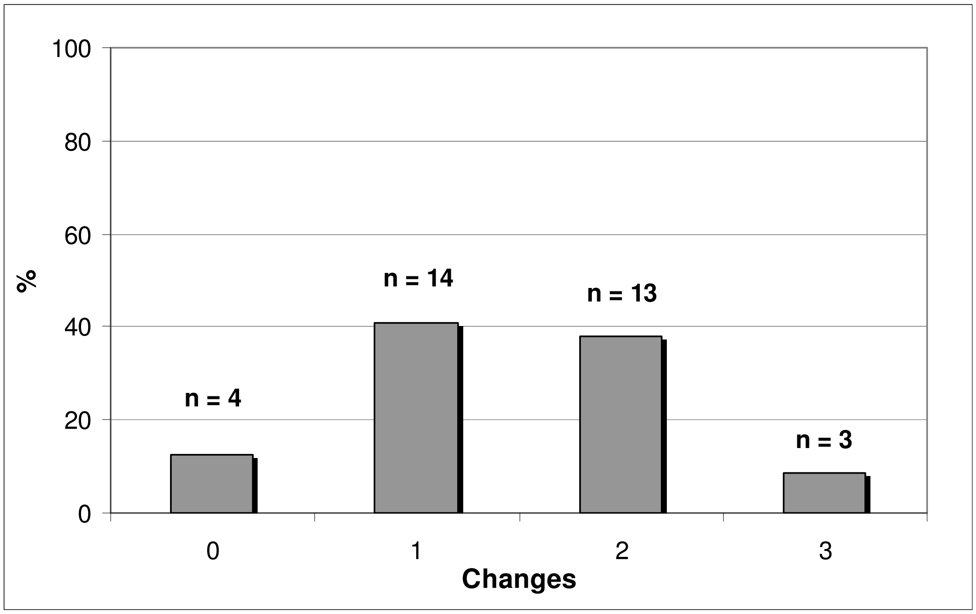

Figure 2. Frequency of alternation of web decoration shapes of *A. bruennichi* in a four-day-interval.

Web-site relocation and web design

Most spiders showed a web-site tenacity and 78.43% (*n*=80) of the new webs were constructed at the same location of the previous day. We recorded 15 individuals (44.12%, *n*=34) relocating their web from one day to the next, which were at the average slightly less than one meter apart from the old site (94.55±14.56 cm). Seven spiders changed the web-site even twice within the observation period.

The web decorating behaviour was clearly affected by web-site relocation. Spiders less frequently added a decoration to their new webs after moving to a new site (after relocation: 59.09% decorated webs, *n*=22; without relocation: 70% decorated webs, *n*=80; Chi^2-test, χ^2=5.67, p<0.05). Additionally, moving spiders significantly more often changed the decorating pattern compared to the stationary spiders. Only 43.75% of the stationary spiders altered the decoration type, whereas

63.63% of the relocated webs had a change in decoration type (Fig. 3, Chi²-test, $\chi^2=16.1$, $p<0.01$).

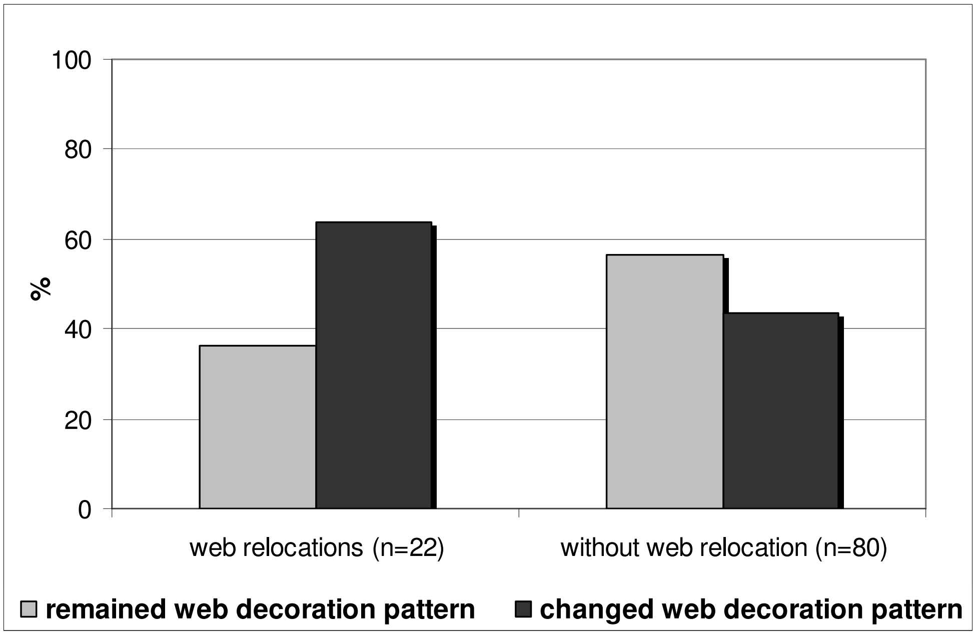

Figure 3. Influence of web-relocations on web decoration alternation in *A. bruennichi* in a field population.

Discussion

Our study reveals that *A. bruennichi* shows a high inter- and intra-individual variation of web decorating behaviour. Individual spiders varied the decoration pattern often on a day-to-day basis, even within the short observation period of four days. The decoration types did not depend on web size, but whenever a spider changed the web-site, the decorating frequency was decreased in the rebuilt webs on the subsequent day. Moreover, relocating spiders altered the decoration type more often than individuals that remained stationary on an established site.

Intraspecific variation in web decorating behaviour is already known for a broad range of *Argiope*-species (Herberstein et al. 2000a; Bruce 2006), including the temporary lack of decorations (Hauber 1998). However, most of the studies describe the differences in decorating frequencies at the population rather then the individual level (Edmunds 1986; Schoener & Spiller 1992; Craig et al. 2001). Indeed, the large individual variation and day to day changes in decoration patterns in this study (see also Edmunds 1986; Nentwig & Heimer 1987) seem to contradict many adaptive explanations of web decoration construction resulting in an obvious problem: How can completely different decoration types function in the same adaptive way on different days?

Tactical adaptations to local and rapidly changing conditions have been invoked to explain high pattern diversity. Craig et al. (2001) found that *A. argentata* builds more web decorations when prey abundance is high and conclude that the variance in decoration pattern might preventing prey insects to associate decorations with the risk of being caught, so that they do not learn to avoid the webs (Craig 1994). Alas, this does not seem to hold for our study species because Prokop & Grygláková (2005) found that the web decorating behaviour of *A. bruennichi* does not increase its prey capture success.

Ewer (1972) and Eberhard (1973) argue along a similar route, but focus on the potential attraction of predators by the web decoration (Bruce et al. 2001; Seah & Li 2001). They state that varying decoration patterns might prevent araneophagic predators to associate a particular decoration shape with a food source. However, this hypothesis cannot explain why particularly web relocating spiders build less web decorations and more often change the decoration pattern than stationary ones.

Argiope spiders typically show a high degree of web site tenacity. Enders (1975) found 80% of *A. trifasciata* and *A. aurantia* do not change the web site which corresponds well with our results for *A. bruennichi* (78%). The search for more profitable foraging sites has been claimed to be a main reason for web relocation. *Argiope*-spiders more often relocate their webs if the capture success is low until they find trap sites with higher prey abundances (McNett & Rypstra 1997; Tso 1998; Chmiel et al. 2000). Since in our study spiders often changed both web site and web decoration pattern, this may reflect local adaptations to the microhabitat.

Our data do not support hypotheses that claim unique single adaptive functions of web decorations; otherwise we would have seen a much higher consistency of decoration patterns in *A. bruennichi*. The hierarchical approach of the conditional strategy described by Starks (2002) might resolve the dilemma. If web decorations are multifunctional tools, different shapes may fulfil different functions. Hence, spiders might use a specific pattern depending on their own physiological and local environmental conditions. In the case that spiders evaluate which web decoration type might be most advantageous in any given set of internal and external conditions they could respond in a tactical way. If, for example, a spider were sated than it might cease web decorating behaviour because there is no need to attract further prey (prey attraction hypothesis) and avoid predator attraction (predator attraction hypothesis). Since Starks' approach allows including a large suite of highly variable abiotic and biotic factors, and the resulting individual variation of web decorations is expected to be high as well. Although our field observations of a high short-term variation of web decorations in *A. bruennichi* are most compatible with Starks' (2002) model, it remains to be experimentally tested whether *Argiope* spiders are actually intentionally varying the decoration shape in response to environment or whether stochastic processes are the main driver of the variance in decoration pattern.

Chapter 3

The wasp spider *Argiope bruennichi* (Arachnida, Araneidae): Ballooning is not an obligate life history phase.

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Abstract. Aerial dispersal ("ballooning") of *Argiope bruennichi* spiderlings has been claimed to be an obligate life history trait and a prerequisite for spinning prey-capture webs. If this were true, a ballooning phase would be essential for any laboratory rearing of *A. bruennichi* making rearing protocols particularly elaborate. We tested the significance of ballooning for second-instar spiderlings in the laboratory and showed that the ballooning behavior is not essential for building prey-capture orb webs. Our results also give no evidence for the hypothesis that recent natural selection has changed ballooning behavior in newly founded field populations.

Introduction

Ballooning is a common dispersal mechanism for many modern spiders (Coyle 1983; Dean & Sterling 1985; Weyman 1993), and this behavior is particularly important for maintaining genetic cohesion among *Argiope* populations (Ramirez & Haakonsen 1999). The life history in *Argiope* is characterized by ballooning, the aerial transport on wind-blown silk threads. A good example for the importance of ballooning for range expansion is the Palearctic wasp spider *Argiope bruennichi* (Scopoli, 1772). The spider is an r-strategist (Guttmann 1979), characterized by high aerial dispersal capability and an on-going post-glacial expansion of its geographical range in Europe (van Helsdingen 1982). Females of *A. bruennichi* produce up to five cocoons in the field, often containing several hundred eggs (Crome & Crome 1961; Köhler & Schäller 1987). The expansion of the species has accelerated in the second half of the last century probably due to factors favoring dispersal by ballooning (Guttmann 1979; Levi 1983; Sacher & Bliss 1990; Scharff & Langemark 1997; Jonsson & Wilander 1999; Smithers 2000). The wasp-spider prefers grassy or herbaceous vegetation in open, ephemeral or shrubby sites (Wiehle 1931; Pasquet 1984; Malt 1996) in coarse-grained (patchy) landscapes (Gillandt & Martens 1980; Sacher & Bliss 1989) and has regionally benefited from an extension of farming production and urbanization (Lohmeyer & Pretscher 1979; Arnold 1986; Nyffeler & Benz 1987). River valleys have been identified as favored dispersal corridors further supporting the importance of ballooning for dispersion (Gauckler 1967; Puts 1988).

Follner & Klarenberg (1995) claimed ballooning to be an obligate phase in the development of *A. bruennichi*. These authors monitored the pre-ballooning and ballooning behavior of spiderlings in a grassland study site near Munich (Germany). Since they never found aggregations of orb webs in the neighborhood of the cocoons from which the overwintering second-instar spiderlings eclosed and they only observed the construction of first prey-capture orb webs after a ballooning trip, they concluded "that aeronautic behaviour in Bavarian populations of

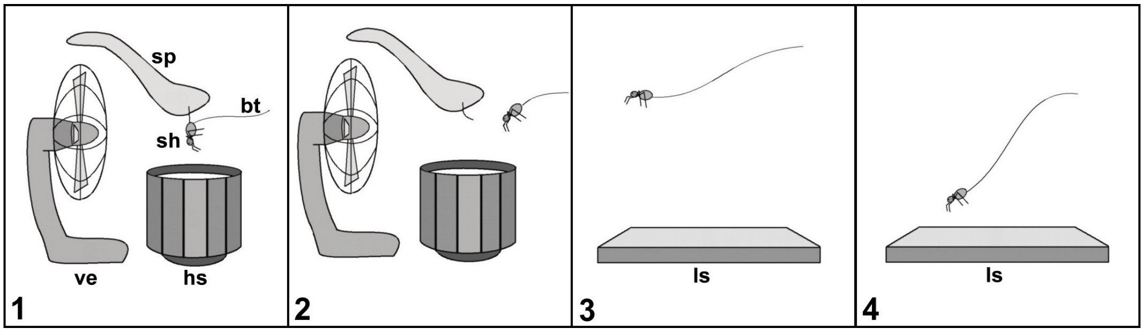
A. bruennichi is obligatory". Moreover, these authors suggested that spiderlings, which have hatched from the cocoon, will starve to death, unless they perform a ballooning trip. Ballooning should thus be an obligate phase to switch from a non-predatory, passive phase to one of active predation by spinning prey-capture orbs. Follner & Klarenberg (1995) argued that the obligatory aerial dispersal might be a result of recent natural selection and be the reason behind the swift expansion of the species. New populations which are established during a period of expansion are always founded by individuals, which have ballooned.

If ballooning were a truly obligate phase, it would not only be important for natural selection but also be important for any rearing protocol for *A. bruennichi*. Allowing for ballooning in a rearing procedure might easily render laboratory breeding unfeasible as it could prove to be too time-consuming and laborious. However, an obligate ballooning phase has never been observed before, neither in other *Argiope* nor in the generally well studied *A. bruennichi*. Tolbert (1976, 1977) studied ballooning behavioral elements of *A. trifasciata* (Forskål, 1775) and *A. aurantia* Lucas, 1833. He concluded from field and laboratory observations that "it is unnecessary for spiderlings of either *Argiope* species to engage in aerial dispersal before building an orb web" (Tolbert 1977), which is an obvious discrepancy to Follner's and Klarenberg's (1995) claims. We here test the significance of ballooning for the construction of the first prey-capture web in the laboratory by comparing spiderlings reared under two experimental conditions, one with and one without ballooning.

Material & methods

We collected cocoons of *A. bruennichi* (*n*=6) in dry and semi-dry grasslands north-east of Halle (Saale) in late April 2002 (Germany, 160 m a.s.l., 51°33'31" N, 011°52'49" E). They were maintained in the lab in individual glass vials (9 cm diameter, 13 cm height, coated with fine gauze) at 23±2 °C and mist-sprayed with water every two days to avoid desiccation. The vial bottom was covered with initially wet cellulose wadding (1 cm). Second-instar spiderlings hatched from the cocoons in early May.

One day after hatching we simulated individual ballooning for 60 spiderlings (10 from each cocoon) by exposing the spiderling on a spatula to an air stream generated by a heat source and a fan (see Figs. 1-4 for details of the experimental design). We observed behavioral elements in the pre-ballooning phase in detail and noticed its mode. When the spiderling became airborne it was kept track of to retrieve the ballooner at the "landing strip" (Figs. 3, 4). The ballooning experiment was repeated immediately (re-ballooning) for each individual to satisfy a possible "ballooning drive" (see Tolbert 1977). The spiderlings had to actively participate in this experiment by showing the entire sequence of pre-ballooning and ballooning behavior (Figs. 1-4).



Figures 1-4. Design and course of the ballooning experiment. The spiderlings were placed on a spatula (sp) and exposed to a light air current by a fan (ve) and heat source (hs), which were placed at the left edge of a lab bench (240 cm). After cutting the drag line the spiderlings became airborne to land on the lab bench, which served as a landing strip (ls).

1, Pre-ballooning behavior: sp = spatula; ve = ventilator (light breeze); hs = heat source (25 Watt lamp, distance to spatula = 20 cm); sh = spiderling hanging from a dragline; bt = ballooning thread. 2, Initial ballooning phase. 3, Airborne spiderling: ls = "landing strip" (lab bench of 240 cm length). 4, Landing phase.

Following the experiments the "ballooners" were kept in the same unheated indoor room with windows admitting indirect natural light. They were housed in groups (*n*=20) in three gauze covered glass terraria (50x30x31 cm; 25±3 °C; 65±10% RH) and fed ad libitum 45-50 live *Drosophila melanogaster* once a day. Every two days we sprinkled the inside surfaces of the terraria with water. This prevented desiccation and allowed for normal drinking behavior of the spiderlings. The bottoms of the terraria were covered with a layer of commercial, pasteurized potting soil (3 cm) with grass tufts, some dry twigs and wooden skewers to enhance the number of potential attachment points for web building.

A control group of spiderlings (*n*=60) was treated in the same way, but without the ballooning procedure ("non-ballooners"). In both groups (ballooners vs. non-ballooners) spiderlings and orb webs were noted three times daily at 6 a.m., 12 p.m. and 6 p.m. to ensure individual based data sets. The rearing period was cut off after 19 days when all the surviving individuals successively had spun their first prey-capture orb-webs.

Voucher specimens are deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg (Zoological Institute), Germany (identification number 2568).

Results

The web-building activity of the spiderlings constantly increased in both the ballooners and the non-ballooners over time and reached 90±5% for ballooners (*n*=54, three terraria) and 95±5% for non-ballooners (*n*=57, three terraria) within a period of 19 d (Fig. 5). The differences in the web-building activity (Fig. 5) were not statistically significant between the two groups of spiderlings (Kruskal-Wallis test, *p*=0.7515; tested for daily built-first webs). The mean latency time for web-building (time from hatching from the cocoon to the construction of the first prey-capture web) was 8.61±4.28 days and 8.18±3.60 days for ballooners (*n*=54) and non-ballooners (*n*=57) respectively. This difference was not statistically significant (t-test, *p*=0.56).

Although mortality increased in the second half of the observation period (Fig. 6), it did not exceed 22% at the end of the experiment (ballooners:

21.7±2.89%, *n*=13, non-ballooners: 20.0±8.66%, *n*=12, difference not significant, t-test, *p*=0.77). The surviving animals caught prey in their orb webs and showed normal development with up to four moultings within the experimental time.

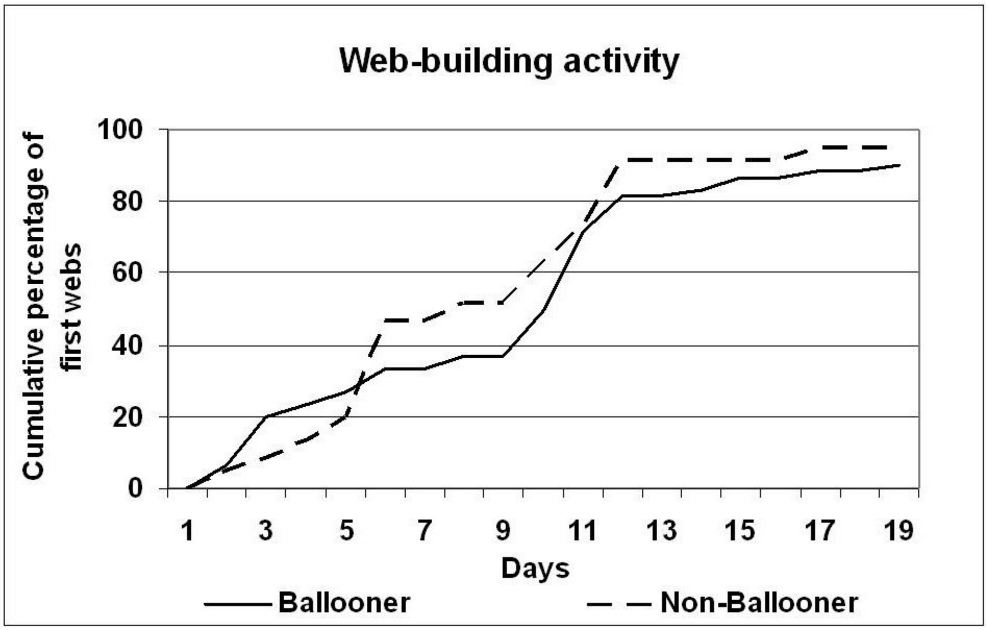


Figure 5. Web-building activity of the *A. bruennichi* spiderlings during laboratory rearing for both ballooners and non-ballooners.

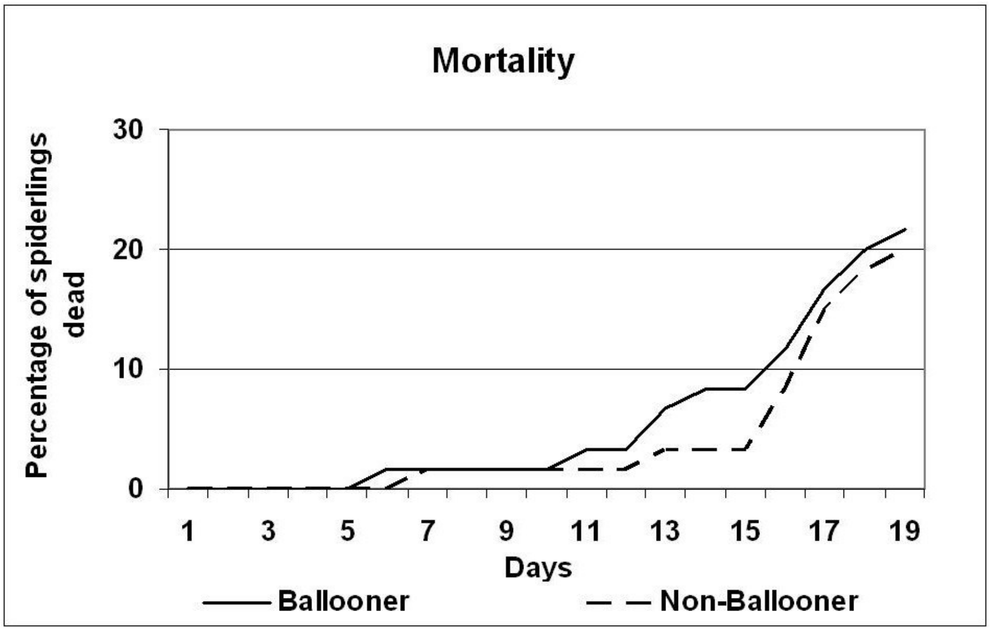


Figure 6. Mortality of the *A. bruennichi* spiderlings during laboratory rearing.

Using our protocol, we could initiate the full sequence of ballooning behavior promptly in every experiment. The *A. bruennichi* spiderlings always showed an identical sequence of pre-ballooning and ballooning behavior (Fig. 1-4). When exposed to the heat from the lamp, they displayed the "ballooning drive" behavior. Individuals walked to the margin of the spatula, spooled out a dragline and dropped down hanging from the line. While suspended and holding on to the drag line, they let out an additional line of 50-100 cm ballooning silk (Fig. 1). When this was lifted by the breeze generated by the fan and the heat source, the spiderlings cut the dragline and became airborne (Figs. 2, 3). After landing (Fig. 4) they hauled in the ballooning line, formed it with the legs into a silk blob and finally ate the silk, bringing the ballooning behavioral sequence to completion.

Discussion

Tolbert (1977) observed two modes of preparation for ballooning in sympatric field populations of *A. trifasciata* and *A. aurantia*. A spiderling attempting to become airborne climbs to the top of some blade of grass or other structures and adopts the typical "tip-toe" posture by depressing the cephalothorax and elevating the opisthosoma. Multiple silk lines are then exuded from the spinnerets. When moving air generates sufficient silk, the spiderling becomes a "ballooner" (Nielsen 1932; Richter 1970; Eberhard 1988). Alternatively, the spiderling can become airborne by dropping and hanging from a dragline, spinning a ballooning thread, which then gradually lifts and lengthens in the breeze. The ballooner cuts the dragline and floats off into the air (Nielsen 1932; Bristowe 1939).

Argiope bruennichi can display both pre-ballooning modes. But the drop and dragline mediated ballooning seems to be more frequent (Follner & Klarenberg 1995). In the field, second-instar spiderlings usually attach the draglines to tips of grass blades, or they use silk threads which connect the tips of grass haulms as attaching points (Follner & Klarenberg 1995). In our experiments, we offered individual spiderlings optimal starting conditions, and we never observed the tip-toe ballooning mode. Follner (1994) suggested that "tip-toe" might be a tactical alternative for individuals in unfavorable starting points (e.g., overcrowded tips of grass blades).

Our results show that it is not necessary for spiderlings of *A. bruennichi* to engage in aerial dispersal before building a prey-capture web. While ballooning is frequent in the field (Follner & Klarenberg 1995), it is clearly not an obligate part in the development of this species. In spite of the rapid expansion of the species over the past decades and the potential importance of aerial dispersal for colonizing new habitats, the role of ballooning in *A. bruennichi* does not differ from *A. trifasciata* and *A. aurantia* where this phase in life history is also not obligate (Tolbert 1977).

The mortality of about 20% after 19 days in both experimental groups (difference statistically not significant) suggests that rearing of *A. bruennichi* spiderlings to adulthood may suffer from further mortality. Our rearing method based on a diet with *Drosophila melanogaster*, similar to Müller & Westheide (1993), worked fine for our purpose, where we only tested the effects of ballooning in second-instar spiderlings on their ability to make their first web.

At the average, more then eight days elapsed before *A. bruennichi* spiderlings begin to build their first prey-capture web. This appears to be a surprisingly long period, because the animals can only feed once the first web is built. We cannot exclude that this is a laboratory artifact, for example due to unattractive sites for web construction. However, the long latency did not interfere with the rearing regime. The animals appeared to be well adapted to temporary starvation because the mortality was low in this phase (Fig. 6). Also in the field, the spiderlings do not immediately start with prey-capture web construction (Follner & Klarenberg 1995) and endure extended periods of starvation. *Argiope* spiderlings easily survive several days nearby their cocoons, sometimes with communal meshworks of interlocking dragline threads ("communal tangles") (Tolbert 1976, 1977; Follner & Klarenberg 1995). Here they shelter until favorable weather or microclimate conditions allow for ballooning (Tolbert 1977; Follner & Klarenberg 1995; see also Suter 1999 for physics of ballooning).

Argiope spiderlings actively select suitable web sites by ballooning, re-ballooning or walking (Enders 1973; Tolbert 1977; Follner & Klarenberg 1995). Also in this non-predatory phase the spiderlings must resist starvation. Tolbert (1976) kept *A. aurantia* spiderlings in the laboratory without any food and water supply. Mortality remained moderate in these experiments for several days and only increased distinctly about two weeks after hatching.

The behavioral sequence could be easily triggered under artificial conditions in our study, suggesting that it will also occur in the field whenever environmental conditions allow. Therefore dispersal and population structure will be primarily driven by microclimatic conditions in the local habitats. The local persistence of non-emigrants (non-ballooners and short-distance ballooners) in *A. bruennichi* populations might facilitate aggregated dispersion patterns, just in weather phases which are unfavorable for aerial dispersal. Given ballooning is a less effective means of long-distance dispersal than previously thought (Roff 1981; Decae 1987; Wise 1993; Bonte et al. 2003), this could also explain the genetic differentiation among habitat patches in other *Argiope* species (Ramirez & Haakonsen 1999).

The role of natural selection in range expansion has recently been discussed for insects in the context of global warming (e.g., Pimm 2001; Thomas et al. 2001). However, improving environmental conditions at range margins can initiate range extensions purely on the basis of ecological, physiological and population-dynamic processes not requiring any evolutionary change (Thomas et al. 2001; see also Coope 1995; Williamson 1996). Our results are in line with these views and reject the hypothesis of Follner & Klarenberg (1995) that evolutionary processes have changed ballooning behavior in newly founded populations.

Chapter 4

‘Wrap attack’ activates web decorating behavior in *Argiope* spiders.

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Abstract. 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 three species which construct different types of web decorations: linear in *A. bruennichi*, irregular in *A. sector* and cruciate in *A. keyserlingi*. We show that depletion of aciniform silk has a stimulating effect on web decorating behavior in three 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 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*.

Introduction

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 evolutionary highly developed devices for prey capture (Nentwig & 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 & Robinson 1973; Scharff & Coddington 1997; Herberstein et al. 2000a). 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 & Li 2001; Li & Lee 2004; Cheng & Tso 2007).

Numerous proximate and ultimate explanations that account for web decorations have been proposed (review in Herberstein et al. 2000a; Bruce 2006; see also Robinson & Robinson 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 & Robinson 1970); to enhance the visibility of the web to non-prey species that might inadvertently damage the web (Horton 1980; Eisner

& Nowicki 1983; Kerr 1993) or to provide a molting platform (Robinson & Robinson 1973; Nentwig & 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 & 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 non-specific stress response (Nentwig and Rogg 1988) or simply a sign of a non-functional evolutionary relict behavior (Nentwig 1986). Since web decorations differ considerably in shape, size and the frequency of occurrence among various species of *Argiope* (Wiehle 1927; Nentwig & Heimer 1987; Herberstein et al. 2000a; Bruce & Herberstein 2005; Bruce 2006), they may well serve different (Herberstein et al. 2000a) 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, b; Blackledge and Wenzel 1999, 2001; Herberstein 2000; Craig et al. 2001; Seah & Li 2001; Bruce et al. 2001, 2005; Li & Lee 2004; Bruce & Herberstein 2006). The web decorations in this genus are constructed from fibrous silk produced by the aciniform glands (*glandulae aciniformes*) that are used for both the wrap attack and for constructing the typical zig-zag shaped decorations 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 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 following 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 quality of web decorations (Herberstein et al. 2000a; 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 the 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 two weeks. We also use a comparative approach with three species that express very different web decorating behavior to obtain greater taxonomic generality: (1) *A. bruennichi* with linear web decorations consisting of two zigzag bands, (2) *A. sector* with irregularly arranged zigzag bands, and (3) *A. keyserlingi* as a representative species with cruciate web decorations (similar to *A. aetheroides* used by Tso).

Material & methods

Study species and experimental design

Experiments were conducted on the Panpalearctic *A. bruennichi* (Scopoli, 1772), the North African *A. sector* (Forskål, 1775) and the Eastern Australian *A. keyserlingi* Karsch, 1878. All three species exhibit different basic web decoration types, constructing linear, irregular and cruciate forms respectively (Fig. 1). Egg sacs (*A. bruennichi* et *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*: West Pymble/Sydney, Australia) and brought to the laboratory (*A. bruennichi* and *A. sector*: Halle; *A. keyserlingi*: Melbourne). *A. bruennichi* and *A. sector* females were reared from the emergence from the egg sacs in environmentally controlled terraria (80x40x50 cm) with long day conditions (16h light/8h dark, at 26±1.5 °C, RH: 56±11.4%, see Walter et al. 2005 for details). One week prior to the tests, the experimental spiders were set on web-frames (wooden frames for *A. bruennichi* and *A. sector*: 35x35x7 cm; Perspex frames for *A. keyserlingi*: 58x58x15 cm) and kept under natural light conditions. Each spider was fed with a single prey item (one honeybee for *A. bruennichi*, one house cricket for *A. sector*, one 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.

Figure 1. Adult females of the three *Argiope* species and their web decorations in the laboratory: Left: *A. bruennichi* with linear shaped decoration; Middle: *A. sector* with cruciate-like (irregular) decoration; Right: *A. keyserlingi* with cruciate decoration pattern.

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 three honeybees (*Apis mellifera*) for *A. bruennichi* (*n*=11 spiders), three house crickets (*Acheta domesticus*) for *A. sector* (*n*=11 spiders) and four 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 control group had the same feeding regime with one prey item every second day. Because *Argiope* spiders typically construct a new capture web every day, we observed the decorating behavior on the day following 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 & 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±0.16 SE mm to 11.36±0.12 SE mm, *A. sector* (n=22) from 6.86±0.14 SE mm to 9.4±0.28 SE mm and *A. keyserlingi* (n=4) from 10.48±0.28 SE mm to 11.61±0.21 SE mm 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±57.62 SE cm² to 332.06±46.72 SE cm², n=11 and control: 280.18±38.66 SE cm² to 299.92±52.53 SE cm², n=11), and in *A. keyserlingi* web size increased over time, but similarly among the groups (treatment: from 657.66±68.69 SE cm² to 1479.57±61.38 SE cm², n=22 and control: 731.32±102.27 SE cm² to 1586.85±59.27 SE cm², 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±93.22 SE cm² to 323.08±47.71 SE cm², n=11 and control: 783.14±107.55 SE cm² to 599.36±66.92 SE cm², 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 three species. The proportion of decorating spiders was higher in the experimental than the control groups in all three species shortly after commencing the treatment and remained that way for the duration of the trial (Fig. 2). On average, the decorating frequency of treated *A. bruennichi* individuals was 66.33±5.93 SE % (n=11) compared with 46.22±7.05 SE % (n=11) in the control group, and similar differences were recorded in *A. sector* (treatment: 81.4±3.04 SE %, n=11 vs. control: 62.71±3.82 SE %, n=11) and *A. keyserlingi* (treatment: 78.37±2.78 SE %, n=22 vs. control: 62.14±1.82 SE %, n=22). The frequency of web decorating was significantly higher in silk removal than control groups in all three species (Chi²-test; *A. bruennichi*: χ^2=214.4, P<0.01, df=16; *A. sector*: χ^2=120.67, P<0.01, df=16; *A. keyserlingi*: χ^2=48.91, P<0.01, df=16).

The size of decorations was not consistently lower in the depletion than control treatment in any of the tested species (Fig. 2). There was no significant difference in the size of decorations between the two treatments in either *A. bruennichi* (17.14±3.52 SE mm² for the treatment group vs. 16.38±2.95 SE mm² for the control group, paired t-test: *t*=-0.26, *p*=0.8) or *A. sector* (43.6±3.84 SE mm² for the treatment group vs. 36.22±3.37 SE mm² 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±6.11 SE mm² for the treatment group vs. 56.97±4.38 SE mm² for the control group, paired t-test: *t*=-5.09, *p*<0.01).

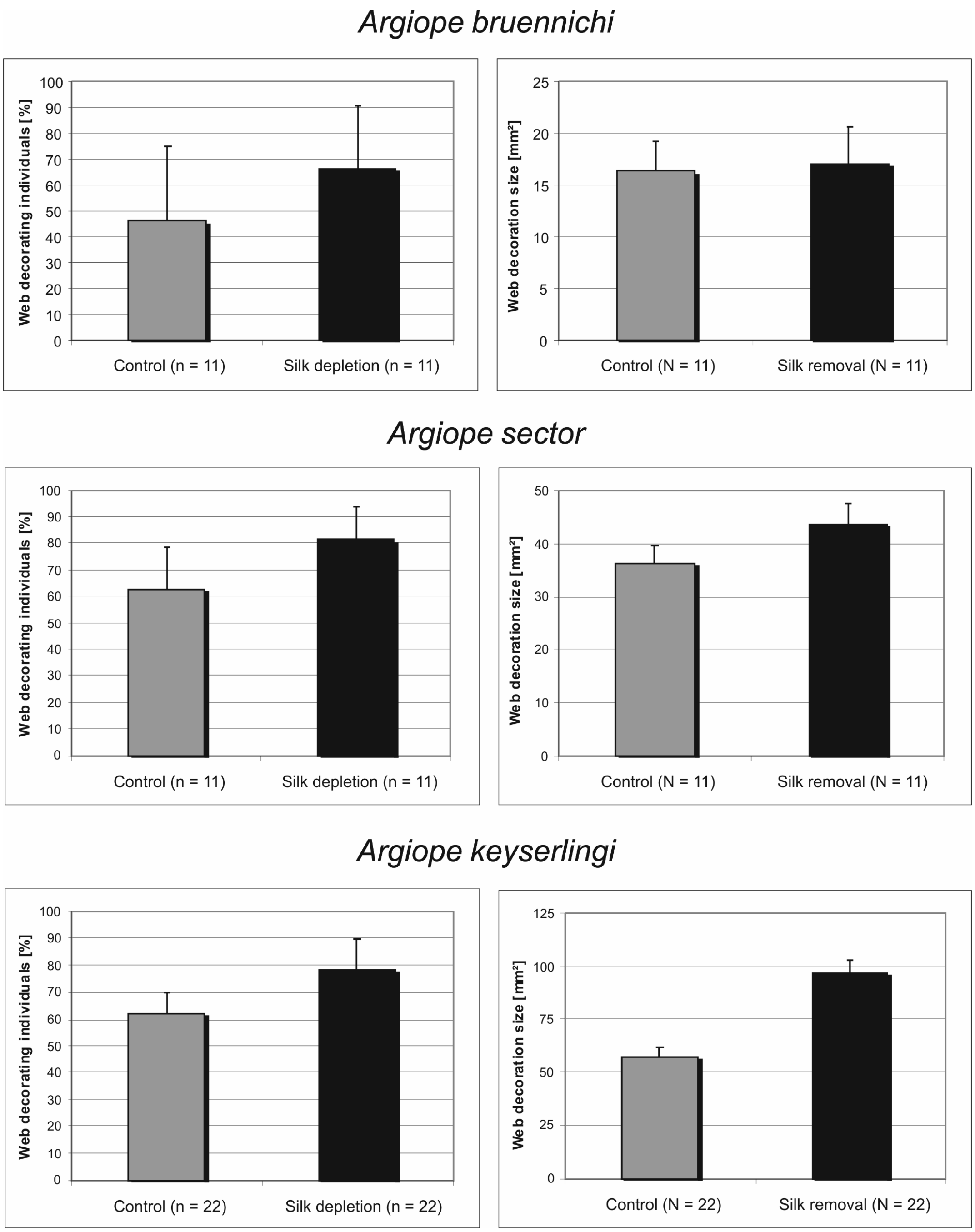

Figure 2. Average web decorating frequency (left chart) and web decoration size (right chart) over the observation period in all three tested *Argiope*-species. The frequency of web decorating behavior was significantly increased in the treatment group (Chi-square; *A. bruennichi*: χ^2=214.4, p<0.01, df=16; *A. sector*: χ^2=120.67, p<0.01, df=16; *A. keyserlingi*: χ^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).

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 three 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, 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 & Ushimaru 2004). Also, *Argiope* spiders can readjust web characteristics or change the web building frequency as a consequence of past capture experience (Heiling & Herberstein 1999; Herberstein et al. 2000b). 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 *A. trifasciata*. Nevertheless, our results with *A. bruennichi*, *A. sector* and *A. keyserlingi* are consistent with the prey attracting function of web decorations (Craig & 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 Prokop & Grygláková 2005; Blackledge & Wenzel 1999).

Blackledge (1998a) 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; Craig et al. 2001; Seah & Li 2002). Thus, sated spiders are better placed to take advantage of other benefits of web decorations, including camouflaging the spider (Schoener & Spiller 1992; Blackledge & Wenzel 2001; Eberhard 2003; Li et al. 2003) or protecting the web (Eisner & 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 *A. 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 *Argiope* 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.

Since *Argiope* 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 non-decorating spider *Araneus cavaticus* (Tillinghast & 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 *Argiope*, 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, since web decorating behavior varies profoundly within the genus *Argiope* (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 & 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 non-usage 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 feed back 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 & 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. Fig. 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 mechanism(s) 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.

Chapter 5

Moulting interferes with web decorating behaviour 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 zigzag 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* 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.

Introduction

Web decorating behavior 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. 2000a; 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* 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); non-visual values in terms of 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 zigzag 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. 2000a; Starks 2002; Bruce & Herberstein 2005; Rao et al. 2007). Most studies explore the adaptive significance of these structures (e.g., Blackledge 1998a, b; 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. 2000a; 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 on 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.

Materials & methods

Study species and experimental design

We chose the well known St Andrew's Cross spider, *Argiope keyserlingi* Karsch, 1878, to study the variation in web decoration under highly controlled laboratory conditions. This orb weaving species is distributed along the east coast of Australia (northern Queensland to Victoria in the south) building their webs between branches and leafs of bushes, e.g. in parks and gardens. *Argiope keyserlingi* is a well studied species concerning 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 (58x58x15 cm) in the laboratory, where they were kept under natural light conditions. Every other day, each spider was fed with one blowfly (*Lucilia* spp.). Since at this life stage the spiders are still of a similar size as the blowflies it has turned out in preliminary observations that this feeding regime is sufficient to keep spiders 'well-fed'. In the very same rhythm 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): $(a+c)/2xh$ (a and c = upper and lower width of zigzag bands, h = height of zigzag 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).

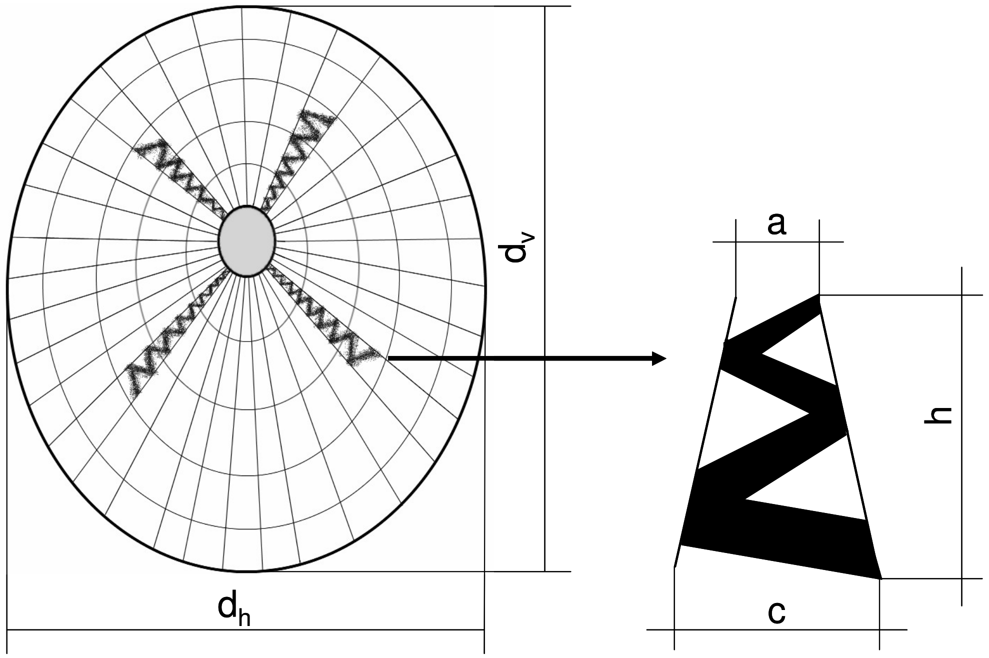

Figure 1. Web and decoration measurements from the webs of *A. keyserlingi*: Left: determination of the size of capture areas (incl. hub region), d_h=horizontal diameter, d_v=vertical diameter; Right: determination of decoration band sizes, a=upper width of the band, c=lower width of the band, h=length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

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^2-tests and t-test were used to detect differences in the proportion of decorated web parts and constructed decoration patterns. Web and web decorations 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 (in mean every 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 (in mean 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.

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 cm² (*n*=55) and mean size of the last measured web was 1630.61±21.99 SE cm² (*n*=55). Over the whole observation period, undecorated webs were significantly larger than decorated webs, ranging from 625.21±56.88 SE cm² to 646.54±70.57 SE cm² at the beginning of to the experiment to between 1563.21±42.56 SE cm² and 1700.50±37.42 SE cm² 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 mm² (*n*=55) at the beginning to 46.25±54.06 SE mm² (*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) zigzag bands were less frequent. In all partial cross shapes (one to three arms), the bands were significantly more often added to the lower web half (85.2% vs. 14.8%, n=50; Chi²-test, χ^2= 9.12, p<0.01). There 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%) twice, six individuals (10.51%) three times and three spiders (5.46%) four times. Only 19 spiders (with 34.55% significantly less, Chi²-test, χ^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).

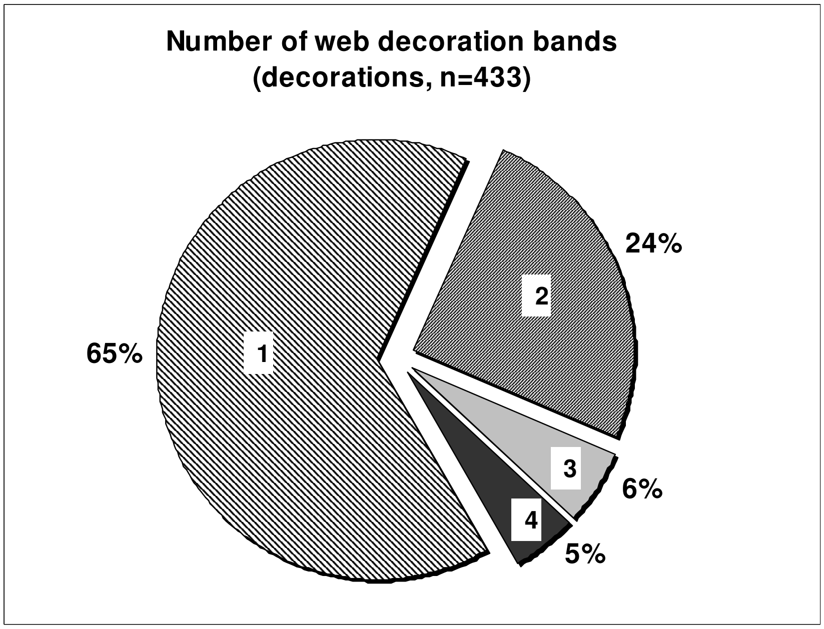

Figure 2. The variation in web decoration patterns of *A. keyserlingi* females under laboratory conditions. Partial cross shapes (one to three decoration bands = number 1-3 in the diagram) are more frequent than the typical cruciate shape (number 4).

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Web decorating behavior in 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: $F=14.36$, $p<0.01$).

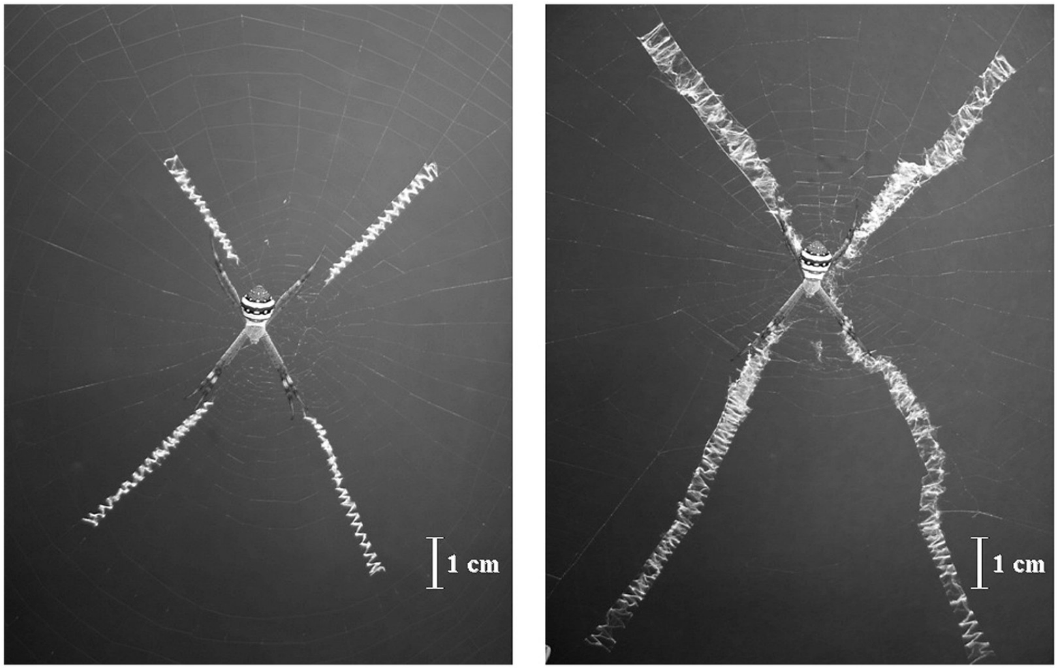

Figure 3. The ‘regular’ web decoration (left) and the ‘supersized’ web decoration (right) of *A. keyserlingi*.

The “supersized” decorations of the molting webs were characterized by a partial loss of the typical zigzag 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).

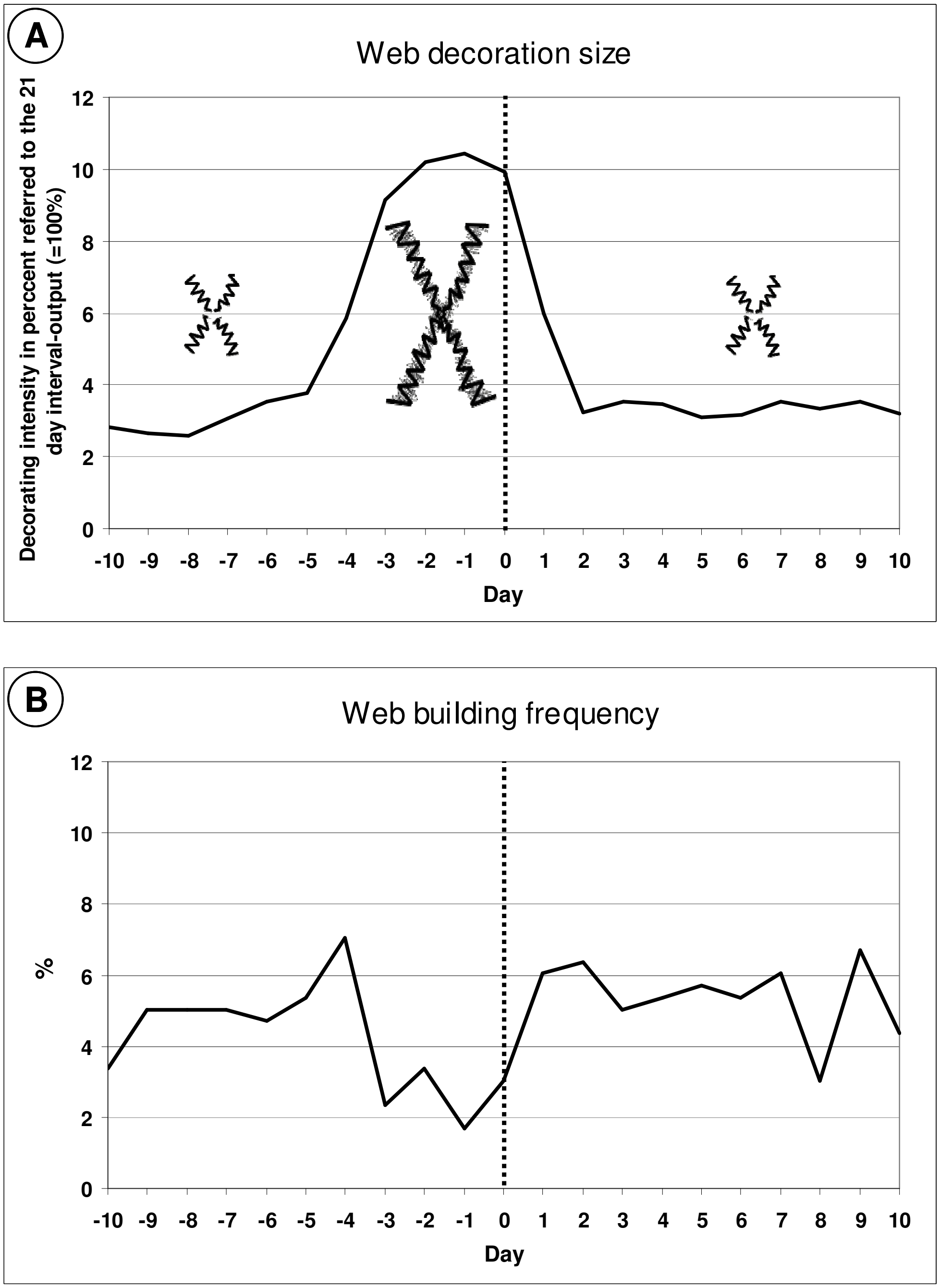

Figure 4. A, The size of the web decoration of *A. keyserlingi* dramatically increases prior to the maturation molt and then returns to the level prior to the molting event; B, Web building frequency decreases prior to the last molt; *dotted line*: day of molting (=day 0).

Discussion

Although individuals of *A. keyserlingi* usually build cruciate web decorations (Rao et al. 2007) consisting of up to four zigzag-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 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 described for *A. argentata* and *A. savignyi* Levi, 1968 in the laboratory (Nentwig & Heimer 1987). Moreover, Edmunds (1986) observed larger and denser decorations prior to moltings in wild populations 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 mostly in the context of prey attracting structures (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 with the sticky spiral that could interrupt the molting procedure by hindering individuals freeing 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 (Horton 1980; Eisner & Nowicki 1983; Kerr 1993) in preserving the integrity of the web during the molt. 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).

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 1999). 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 of 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. 2008a). 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 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.

Chapter 6

Are web stabilimenta attractive to praying mantids?

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Abstract. Certain species of orb-weavers add extra silk structures, termed a stabilimentum or web decoration, to their webs. In the genus *Argiope* stabilimenta are silken structures of densely woven zigzag ribbons. The adaptive value of these stabilimenta is still unclear and controversially discussed. In the course of time, many functional hypotheses have been proposed for silk stabilimenta. Because of their high visibility they are claimed to act as a visual signal for insects. So most recent hypotheses consider them as prey attractants although also predators (e.g. mantids) have been shown to be attracted by these structures. Bruce et al. (2001) reported that the praying mantid *Archimantis latistylus* was attracted to decorated webs of *Argiope keyserlingi* in a Y-maze choice test. In *Argiope*-species spiders construct different basic shapes of stabilimenta which can be cruciate, linear or discoid. The predator attraction hypothesis was supported by testing cruciate forms of *A. keyserlingi*. To test these predictions also for linearly shaped stabilimenta, the web decorations of the Palaearctic wasp spider *A. bruennichi* were tested in a laboratory experiment, adopting the Y-maze setup of Bruce et al. (2001) to make it comparable. Also a taxonomically similar predator was used for the test, *Mantis religiosa* (Mantodea: Mantidae). *M. religiosa* showed no preference for webs with stabilimenta, but only a very small number of individuals reached one of the both maze exits at all, rendering universally valid conclusions difficult. Generally, *Mantis* showed a scarce locomotor activity in the Y-maze apparatus and no signs of any predatory response, which indicates that the experimental design might be problematic for studying behavioural elements of praying mantids.

Introduction

Several araneid, uloborid and nephilid spiders add specific silk decorations, so-called stabilimenta (Simon 1895) to their webs (Hingston 1927; Robinson & Robinson 1973; Scharff & Coddington 1997; Blackledge 1998a). Stabilimenta can differ in shape from taxon to taxon (Eberhard 2003; Bruce & Herberstein 2006). In the genus *Argiope* (Araneidae) they consist of densely woven zigzag ribbons (Wiehle 1927; Robinson & Robinson 1973) built of numerous flimsy strands of aciniform silk (Peters 1993). These structures can vary largely in shape and size among *Argiope*-species, populations within species, but also among individuals within the same population (Herberstein et al. 2000a; Starks 2002; Bruce 2006; Bruce & Herberstein 2006). Stabilimentum building may be temporarily reduced or even ceased as observed in both field and laboratory studies (Robinson & Robinson 1974; Lubin 1975; Nentwig & Heimer 1987; Seah & Li 2002; Prokop & Grygláková 2005). Several, partly species-specific, stabilimentum types have been classified: e.g. linear, cruciate or irregular arranged silk bands between adjacent radii, discoid lines, or combined forms of hub-covering silk sheets and silken bands (Wiehle 1927; Nentwig & Heimer 1987; Bruce 2006; Bruce & Herberstein 2006).

The genus *Argiope* has become a model group in terms of testing hypotheses for possible functions of stabilimentum building behaviour (e.g. Edmunds 1986; Craig 1991; Kerr 1993; Tso 1996, 1998, 1999, 2004; Blackledge 1998a, b; Blackledge & Wenzel 1999, 2001; Herberstein 2000; Craig et al. 2001; Seah & Li 2001; Bruce et al. 2001, 2005; Li & Lee 2004; Bruce & Herberstein 2006). Yet, in spite of the rapidly growing literature on the stabilimentum phenomenon, the possible adaptive functions of these "web-decorations" remain unclear (see Herberstein et al. 2000a; Bruce 2006; see also Robinson & Robinson 1970). Initially thought to be strengthening or stabilising web structures (hence called "stabilimenta" by Simon 1895), a fair number of hypotheses have been proposed over the course of time to explain the ambiguous decoration phenomenon (reviews in Herberstein et al. 2000a; Bruce 2006). Some argue that stabilimenta act as camouflage devices to hide the exposed spider and its outline from visually hunting predators (Hingston 1927; Ewer 1972; Eberhard 1973; Lubin 1975; Tolbert 1975). Others suggest that the web decoration enhances the visibility to prevent damage by potential web destroyers like birds (Horton 1980; Eisner & Nowicki 1983; Kerr 1993). Furthermore, it has been argued that stabilimenta might form a moulting platform (Robinson & Robinson 1973; Nentwig & Heimer 1987), that they are a response to unspecific stress of the spider (Nentwig & Rogg 1988) or simply signs of a non-functional evolutionary relict behaviour (Nentwig 1986). Further hypotheses claim that the decoration should instead attract other animals such as prey insects to increase foraging success (Craig & Bernard 1990; Tso 1996, 1998; Hauber 1998; Bruce et al. 2001; Li 2005). This hypothesis is controversially discussed because there is evidence for the existence of a signal conflict. Bruce et al. (2001) state the conflict of attracting prey and predators alike.

Several personal observations and anecdotal statements report mantids preying upon spiders. This is in line with the intraguild predation model (see Holt & Polis 1997), according to which spiders cannot be excluded from mantids prey spectrum and vice versa. Since mantids prey recognition depends largely on prey movements (Reitze & Nentwig 1991), "[…] the most important interaction between mantids and other members of the broader generalist predator guild […] may be with cursorial spiders [vagrant web-spinners, crab spiders, wolf spiders]" (Hurd 1999; see also Hurd & Eisenberg 1990; Moran & Hurd 1994).

However, Bruce et al. (2001) observed three predatory strikes of *Archimantis latistylus* (Mantidae) to the cruciate stabilimentum building orb-web spider *Argiope keyserlingi* in the field. Inspired from these anecdotal events, they tested if silky web decorations could have functioned as visual cues which attract praying mantids. In a Y-maze choice test the authors found that, when the mantid was confronted with decorated vs. non-decorated orb webs of *A. keyserlingi*, they preferred the decorated web. Consequently, Bruce et al. (2001) suggested that *Argiope* has to manage a trade-off between the enhancement of foraging success and the risk of being preyed by mantids. Yet, only little has been published about vision-guided predation upon web-building spiders (Foelix 1996; Wise 1993). So Bruce et al. (2001) emphatically demanded comparative data for their result.

Here I test the supposed attractive function of stabilimenta in a comparable European intraguild system, using the common European mantid, *Mantis religiosa* Linnaeus, 1758 (Mantodea, Mantidae) and the wasp spider *Argiope bruennichi* (Scopoli, 1772), a common araneid spider with linear stabilimenta. For that purpose I adopted the experimental setup of Bruce et al. (2001) to ensure methodological comparability.

Material & methods

Study animals and rearing

Mantis religiosa is an up to 70 mm large southern European praying mantid (Reitze & Nentwig, 1991). This species has a light green, yellow or brownish colouration, probably adapted to its grassy habitats (Kral & Devetak 1999).

Individuals were raised in the lab after hatching from egg sacs which were originally sampled in Istria (Croatia). First juvenile stages were fed with *Drosophila melanogaster* ad libitum and later with stick insects (Phasmidae). Additionally, all individuals were sprayed with water in a two daily rhythm. Two months old juvenile mantids (5th-6th instar, body length 37.1±4.9 mm) were starved for two days (27±3 °C, 55±10% RH) before each trial (following Matsura & Inoue 1999).

In Europe the distribution of the Palaearctic wasp spider *A. bruennichi* was originally restricted to the Mediterranean region (Wiehle 1931). Its area expanded across central Europe during the last century (Sacher & Bliss 1990; Jonsson & Wilander 1999). *A. bruennichi* prefers open grassland habitats (Nyffeler & Benz 1989; Prokop & Grygláková 2005) and so can encounter *Mantis religiosa* in the Mediterranean region.

Juvenile spiders (6th and 7th instar) from a laboratory reared population were raised up in groups in a terrarium. Ten spiders were transferred to wooden frames

(35x35x5 cm) for orb web construction to ensure that at least two webs, one with and one without stabilimentum, would be available for each test. Only stabilimentum shapes with the typical linear decoration pattern consisting of two silken zigzag ribbons, one above and one beneath the hub, were used for the tests.

The Y-maze apparatus

I used a Y-maze apparatus following that of Bruce et al. (2001) for the choice tests (Fig. 1). All walls of the maze were lined with non-reflective black foil. The top of the maze was covered with Perspex panes. Two fluorescent tubes (20 W) with natural light spectrum above the apparatus illuminated the interior of the Y-maze as well as the webs in front of the two exits. The two test webs (one with and one without stabilimentum) with the spiders at the hub were placed eight cm from the end of each of the two maze-arms. The opisthosoma of the spiders, directly located on the web hub, were placed at the same height as was the centre of the 'exit-hole'. A black cardboard was placed behind the webs to ensure a maximum contrast for the recognition of stabilimenta by *Mantis*. Using a fan (20 W) that was placed at a distance of 25 cm from the open entrance of the maze, I stimulated each mantid to move by allowing an air current (fan stage one) to pass through the maze.

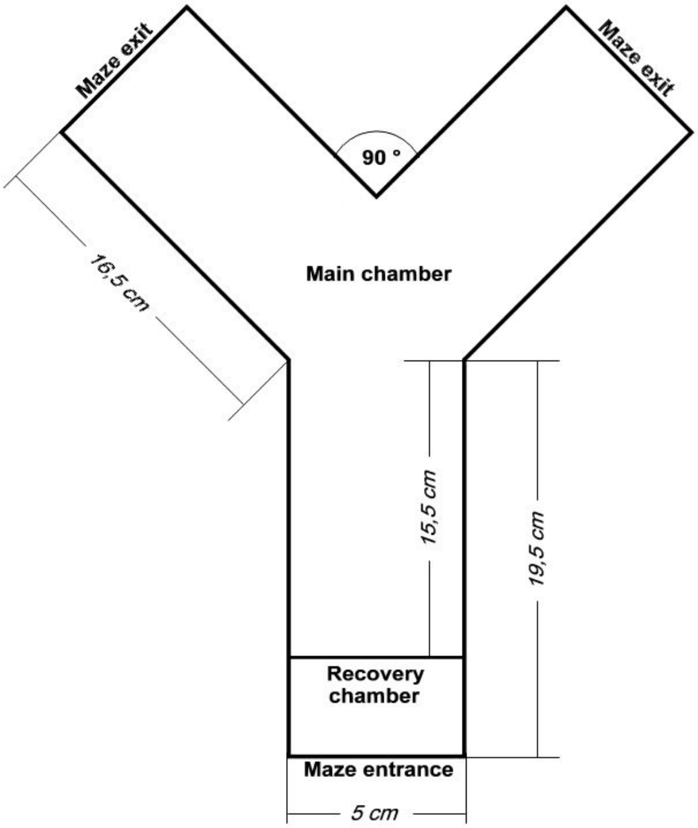

Figure 1. Schematic diagram of the Y-maze apparatus for the choice experiments (reconstruction, following Bruce et al. 2001).

The test scheme

I conducted 25 trials in all. In each trial both web types were randomly assigned to either the left or the right exit of the maze. The orb webs were used more than once but the mantids were exchanged for every trial to eliminate any effect of individual learning that might affect the testing. Naïve juvenile *M. religiosa* were placed individually into the Y-maze recovery chamber. After two minutes of recovering I opened the slide separating this part from the main chamber. The trials started as soon as a mantid was released, and finished after an individual had reached an exit, or at a maximum time of 60 minutes. After each trial the maze was washed out with ethanol (70%) to eliminate potential olfactory cues which might interfere with subsequent tests.

I recorded the elapsed time the mantids needed to get from the starting point to a maze exit. I further observed the behaviour of the animals to identify possible elements of prey recognition or prey capture behaviour.

Results

Inside the Y-maze apparatus the individual locomotor behaviour differed widely. All 25 trials were included in the calculation. Nine mantids showed no locomotor activity at all and did not leave the recovery chamber within the observation period of 60 min. The remaining 16 animals (64%, n=25) started to move towards the bifurcation of the main chamber. Eleven of them walked on approaching an exit, and will be hereafter referred as "approachers". "Non-approachers" (n=14) comprised non-locomotory (n=9) mantids and mantids that stopped in the main chamber (n=5) (Fig. 2).

Within the "approachers"-group no preference for stabilimenta was recordable. Five mantids chose the exit with decorated web and six the exit with undecorated webs (Fig. 2). The difference is not statistically significant from an equal distribution (Chi²-test, χ^2=0.763, p>0.05). On average stabilimentum-choosing mantids needed 30.63±3.66 min to reach the exit and mantids which approached the maze exit without stabilimentum 24.81±3.84 min, respectively. Concerning this time lapse there was no statistically significant difference between both groups (t-test, p=0.31).

In all cases no behavioural elements could be observed that indicated either a predatory response or even an attack sequence.

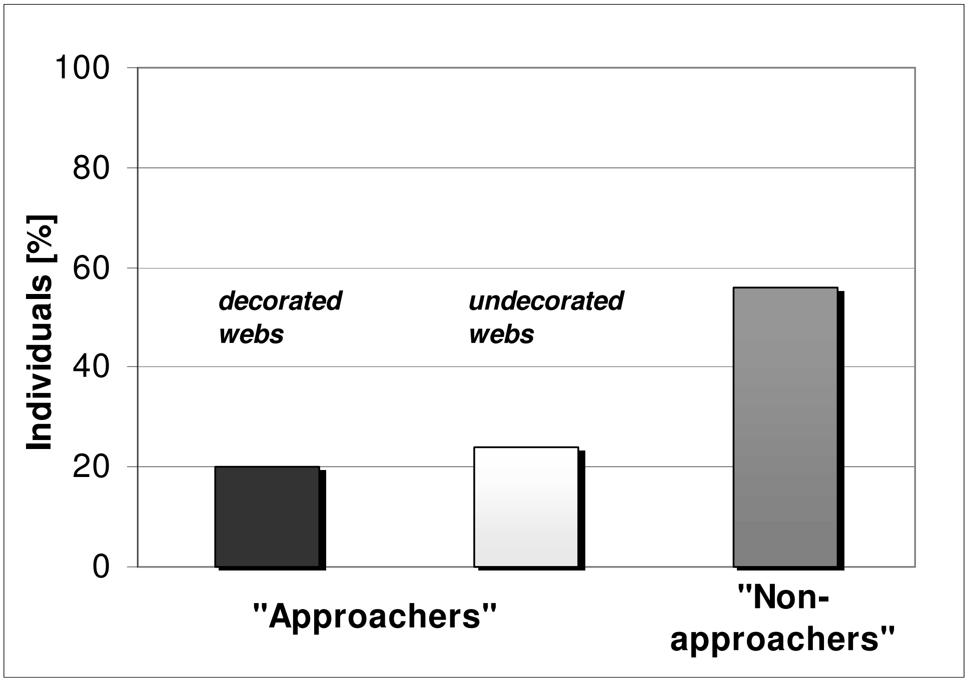

Figure 2. Response of *M. religiosa* individuals (*n*=25) to decorated (*n*=5) vs. undecorated (*n*=6) *A. bruennichi* webs (Y-maze choice test). Approachers: individuals approaching decorated or undecorated webs.

Discussion

In this study I tested a possible attracting function of web stabilimenta of *Argiope bruennichi* to a potential predator, *Mantis religiosa*, using a Y-maze choice test. Bruce et al. (2001) examined this hypothesis using a similar test in *Argiope keyserlingi* and *Archimantis latistylus* system. They found *Archimantis* choosing significantly more often the maze exit with stabilimentum containing webs indicating an attractant function of web-decorations for putative predators. However, my results are not consistent with the results of Bruce et al. (2001). More than half (56%) of all tested mantids did not show any evaluable movement inside the Y-maze during the observation period. Remaining 11, exit-reaching individuals eventually showed no preference for webs with a stabilimentum. This may result from species-specific differences between the two tested systems. Apart from that, the small sample size could also conceal differences in mantid's preference in my experiment. But even the large number of non-locomotory individuals imply possible methodological insufficiencies to detect different responses by the predator.

The latter is possibly responsible for not having observed any behavioural sequence of prey recognition, which is actually typical for praying mantids when foraging (Prete 1999). This may be due to two reasons. One is the distance from the bifurcation to the webs behind one of the exits of the Y-box. The most important prerequisite for prey recognition is spotting a target. This visual stimulus has to be at a minimum distance for detection by praying mantis. Depending on the species (regarding foreleg-length, see Maldonado et al. 1967) and nutritional status this distance has been proved to be only few centimetres (Charnov 1976). Since the webs were approximately 24 cm apart from the point of decision making (bifurcation) in the maze, the attracting cue might be beyond the visual recognition field of *M. religiosa* (Fig. 1). A second reason arises from the hunting strategy of mantids as such. Praying mantids usually are considered as ambush predators which mainly react on movements of potential prey (Reitze & Nentwig 1991). Regarding this characteristic of mantids, the problem can be solved by starvation prior to the test. Under unfavourable conditions like starvation or low prey densities mantids can change form their normally performed ambush strategy into an active seeking behaviour (Inoue & Matsura 1983). This might explain the generally stronger pronounced locomotor behaviour of *Archimantis* individuals in the study of Bruce et al. (2001). They used laboratory raised mantids, but no information about the dietary status prior to test was given. In my experiment mantids were starved for two days (following Matsura & Inoue 1999) before starting trials in the Y-maze in order to elicit moving and seeking behaviour. However, this could not trigger movements sufficiently. Unfortunately, Bruce et al. (2001) did not present an "approachers"-"non-approachers"-ratio, probably because tested individuals were repeatedly placed in the maze after 24 h when remaining motionless within the observation period.

Finally, in case that an individual reached an exit of the maze, no attack sequence (see Corrette 1990; Reitze & Nentwig 1991) was recordable. In regard to an ambush foraging strategy of mantids, orb web spiders, like *Argiope*, are vulnerable to be preyed only when moving. So spiders would be at higher risk when relocating web site (Lubin et al. 1993), rebuilding their webs or while courtship and mating (Herberstein & Fleisch 2003). Neither of these behaviours occurred during the experiment. Consequently, it is not surprising that *Mantis* did not show any typical prey capture sequence when reaching the maze-exit. The motionless impression of the spider and its web should be uninteresting.

Bruce et al. (2001) suggested that the tested mantids did not react on movements but on a visual cue represented by the reflectance (including UV-spectrum) of the stabilimentum of *A. keyserlingi*. Although the authors cannot explain the stimulating effect in detail, it is thoroughly possible. Mantids are known to be "opportunistic predators that will eat a wide range of prey, including very large arthropods and even small vertebrates" (Prete et al. 1999). But also non-predatory ingestive behaviours are reported (Prete et al. 1992), including ingestion of plant parts, like fruits, as well as water droplets. UV-reflectance, for instance by stabilimentum silk, therefore, may be falsely interpret as water drops. If true, spiders, which attached stabilimenta to their webs, were indeed at a higher risk to be preyed by mantids. In my study *Mantis* individuals did not experience any water shortage, hence they were unlikely to forage for water sources. This could explain the sparely expressed mantid locomotor behaviour compared with the findings of Bruce et al. (2001). These explanations remain yet speculative due to the lack of information about the individual stage in their study.

Conclusions

A potential signal conflict between prey and predator attraction by web decorations is controversially discussed (Bruce et al. 2001 vs. Eberhard 2003). It is postulated that such a conflict may have favoured the evolution of the highly variable stabilimentum building behaviour in the genus *Argiope*. Different stabilimentum patterns (Blackledge 1998b; Craig et al. 2001; Starks 2002; Bruce & Herberstein 2006) might aggravate the conditioning towards a particular shape in both prey and predator.

In contrast to the study of Bruce et al. (2001), my results do not support the predator attracting hypothesis. But the small sample size possibly does not allow for universally valid conclusions in this case. However, the large number of non-locomotory mantids and the lack of predatory behaviour indicate that the apparatus used is too oversimplified to test the predator attraction hypothesis appropriately and can not account for both the complexity of prey recognition behaviour in mantids (Prete 1999) and the supposed high plasticity among (intraguild) prey-predator system at the genus level.

So the results of Bruce et al. (2001) on *Archimantis latistylus* may be interpreted alternatively as "an escape rather than a predatory response" (Eberhard 2003). However, I argue that if stabilimenta have an attracting effect to potential predators, like mantids, it is not yet satisfyingly demonstrated. More sophisticated experiments, considering species-specific characteristics with improved experimental designs and a larger sample size, are needed to test whether stabilimenta may act as visual cues for mantids and other predatory animals.

Chapter 7

Argiope bruennichi shows a drinking like behaviour in web hub decorations (Araneae, Araneidae).

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Abstract: As stationary predators, araneid spiders that lack protective retreats are especially vulnerable to abiotic influences. Species of the genus *Argiope* permanently remain at the hub of their orb webs, and are thereby exposed to desiccating circumstances. Like other land arthropods, spiders must balance their hygric status. Beside desiccation avoidance behaviours, they can manage this balance by water gain through either liquefied prey items or direct ingestions of free water. Drinking-like behaviours are sparely documented for araneids. We observed *Argiope bruennichi* ingesting accumulated water droplets from the silk-overstitched web hub, a part of the web decoration, and subsequently tested whether this behaviour is a regular feature of this species. In fifty percent of our observations, spiders that had been sprayed with water actively searched the hub decoration for water droplets and ingested them. The behavioural elements were very stereotype among the tested individuals. Significantly, *A. bruennichi* females only searched the covered web hubs for water, even though the entire web was moistened. These data suggest that hub decorations of *A. bruennichi* might have an adaptive significance by helping to maintain a balance of water metabolism, adding yet another element to the spirited debate about the functional significance of web decorations.

Introduction

Spiders, like all terrestrial animals, constantly lose water by evaporation (e.g. through respiration; Davies & Edney 1952) and have to balance their hygric status by active water intake (Pulz 1987). Two basic mechanisms are known to balance water metabolism: indirectly by ingestion of liquefied prey (Edney 1977; Pollard 1988; Seibt & Wickler 1990), or by direct intake of free water (see review of Pulz 1987) similar to "drinking behaviour" in other animals. Investigations into the behavioural ecology of spiders typically focus on prey capture behaviour and prey composition (Nyffeler & Benz 1981; Olive 1981a, b; Nentwig 1983; Malt et al. 1990; Champion de Crespigny et al. 2001), although laboratory studies typically incorporate water spraying as a component of spider husbandry (e.g. Herberstein & Fleisch 2003; Zschokke & Herberstein 2005; see also Jackson 1974). Nevertheless, to our knowledge, drinking-like behaviour of araneids has never been addressed.

Web building spiders are stationary predators due to the fixed position of the web (Enders 1974; Olive 1982). Orb web spiders are directly exposed to abiotic microclimatic variation, including wind and sun radiation enhancing water evaporation. Several species of the araneid genus *Argiope* occupy dry habitats (Enders 1973, 1974; Olive 1980; Edmunds 1986) making them vulnerable to water loss during dry seasons. The lack of protective retreats (Levi 1968; Scharff & Coddington 1997) further aggravates dry-stress situations (Ramirez et al. 2003), compared with orb weaving species which can take cover in hideouts (Foelix 1996).

The avoidance of desiccation, the physiological counterpart of water gain, has been studied in some detail in orb weavers that show a strong correlation between body temperature and solar radiation (Robinson & Robinson 1973, 1979; Biere & Uetz 1981). Since overheating of the spider body results in higher water losses (Davis & Edney 1952; DeVito & Formanowicz Jr. 2003), various behavioural traits reducing sun exposure will reduce or prevent water evaporation (Tolbert 1979; Humphreys 1993). These traits include the selection of microhabitats for appropriate web sites, the orientation of the web itself and the position of the spider in the web (Higgins & Ezcurra 1996), and the incorporation of web-based retreats (e.g. Thirunavukarasu et al. 1996). All these behavioural elements can reduce the direct sun radiation to the spider body and thus are passive mechanisms to avoid desiccation. In this context, web attachments may also be important: for example, the silken 'mats' (Bruce 2006) covering web hubs of several orb weavers may act as sun shields (Robinson & Robinson 1973; Humphreys 1992, 1993).

Web structures may also function as water collecting devices. Edmonds & Vollrath (1992) showed that atmospheric water can accumulate in the sticky drops of the capture spiral of *Araneus diadematus*. If web components can act as water collectors, then the silk 'stabilimenta' (Simon 1895) of *Argiope* might also be useful for obtaining water from atmospheric origin. These web decorations (McCook 1889; Marples 1969) consist of densely woven silken bands (Peters 1993) and vary largely in shape and size among species, populations within species, and among individuals within the same population (Herberstein et al. 2000a; Starks 2002; Bruce & Herberstein 2006; Bruce 2006). Several decoration types have been classified: linear, cruciate or irregular arranged zigzag-bands between adjacent radii; discoid lines; irregular silk mats covering the hub of the web or combined forms of hub-covering silk sheets; and silken bands (Robinson & Robinson 1970; Nentwig & Heimer 1987; Humphreys 1992; Herberstein et al. 2000a; Bruce & Herberstein 2006; Bruce 2006).

Olive (1980) noticed that droplets can accumulate in web decorations of *A. trifasciata* when the webs were sprayed with water. One individual was observed taking in accumulated water droplets directly out of the zigzag-bands. Although this was only a single event, Olive (1980) suggested that *Argiope* can catch water from rain or dew and web decorations may be involved in the regulation of water-supply. We investigated whether this drinking-like behaviour is typical of these spiders by observing the behaviour of *A. bruennichi* spiders under laboratory conditions.

Material & methods

Like Olive (1980), we serendipitously observed water ingestions in the wasp spider, *Argiope bruennichi* (Scopoli, 1772). While periodically spraying the webs, some individuals ingested water droplets that were accumulated in a fine meshwork overlaying the web hub. The 'overstitching' (Robinson & Robinson 1973) of the hub of the orb web with a fine mat of silk is an almost invariant part of the web decorating behaviour in *A. bruennichi*, even under laboratory conditions (Wiehle 1931; Becker 1983).

We examined whether the observed drinking-like behaviour is a stereotype behavioural sequence in *A. bruennichi*, by spraying water in the orb webs and observing the spiders' response to this stimulus. We also observed the capacity of the webs to accumulate and retain sprayed water.

Following our preliminary observations, we only tested adult *A. bruennichi* females (one month after maturity moult). These animals typically reduce the web decorating behaviour to hub overstitching (Peters 1953; Edmunds 1986; Nentwig & Heimer 1987) and do not built the conspicuous zigzag-bands.

All females were reared from the emergence from the egg sac in environmentally controlled terraria (80x40x50 cm) with long day conditions (16h light/8h dark, at 26±1.5°C, RH: 56±11.4%, following Walter et al. 2005). All spiders were fed with one grasshopper every other day. Due to the limited space for web building only two equally sized adult *A. bruennichi* females (16.3±0.4 SE mm) were assigned to one terrarium. In five terraria the webs of ten adult females were misted by 15 successive spray shots of water at a distance of 30 cm (using a standard water sprayer for misting pot plants) one day after every feeding. This treatment allowed for a complete misting of the webs. All individuals were observed over a period of 21 days, and a total of 110 individual observations were performed. All behavioural responses after spraying were recorded.

Results

In 34 cases, the spiders had not constructed a new web on the test day, leaving a total of 76 assessable observations in which spiders built a web with hub decorations. After spraying the webs, the water formed droplets in most regions of the web, including the covered hub and the viscid capture spiral (Fig. 1).

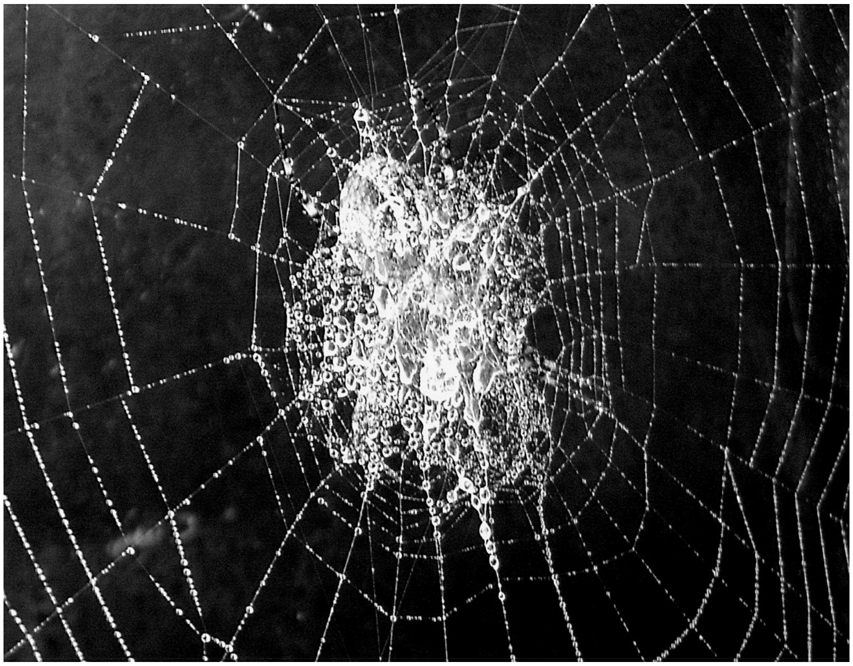

Figure 1. Accumulated water droplets in the covered hub and sticky spiral of the web of *Argiope bruennichi* after spraying (spider hidden behind the hub).

As a first reaction towards the water spray, spiders slightly elevated their body and spread the first two leg pairs over the web level (88%, *n*=67 observations). Excess water ran down over the body and the legs, finally dripping down. Five spiders at first absconded the web hub after being sprayed, and left the hub area by roping down or running towards an edge of the web ("fleeing"-behaviour). However, in every case the animals quickly returned within a few seconds.

In most of the cases spiders engaged in cleaning behaviour directly after the water spray treatment (91%, *n*=69 observations), although the timing and duration of this behaviour was highly variable (see below). Spiders mostly wiped or shook off adhering excess water droplets. Rarely (7%, *n*=5 observations) were some water droplets ingested. After the self-cleaning phase, a behavioural sequence of active water intake followed in half of all observations (49%, *n*=37). The females gave up the typical resting posture in the web and actively searched the hub cover for water droplets with their pedipalps. Once a droplet was discovered, the spiders moved their mouthparts directly towards the surface of the covered hub to actively suck the water (Fig. 2). Afterwards they continued their search, and all ten spiders exclusively searched within the hub decoration for water (100%, *n*=37 observations) but never in other parts of the web, although water droplets were present throughout the web. The five individuals that initially “fled” after the web was misted had the opportunity to imbibe water from other web parts, since they temporarily left the hub. However, these spiders never searched for water or ingested droplets from other parts of the web.

The elapsed time between self-cleaning behaviour and searching for water droplets was 135±25 SE s, and was not significantly different between observations of “fleeing“ and “non-fleeing” spiders (t-test; *p*=0.21, *n*=37). In seven observations only did spiders commence searching and ingesting water without the self-cleaning phase. The average duration of this sequence varied from five seconds to ten minutes (Fig. 3) with mean of 122±22 SE sec. The duration of searching and drinking was highly variable among individuals for which we obtained several observations (for example, one female recorded times of 20 s to 620 s, cf. Fig. 3).

Figure 2. Adult female of *A. bruennichi*; Left: with typical resting posture, Right: while taking up a water droplet from its covered web hub.

Every female showed the stereotype hub-searching and droplet-sucking behaviour at least once within the observation period (Fig. 3), indicating the regularity of the behavioural sequence as a drinking-like behaviour. As soon as spiders finished water ingestions, they adopted the resting posture again and did not resume any of the described behavioural elements.

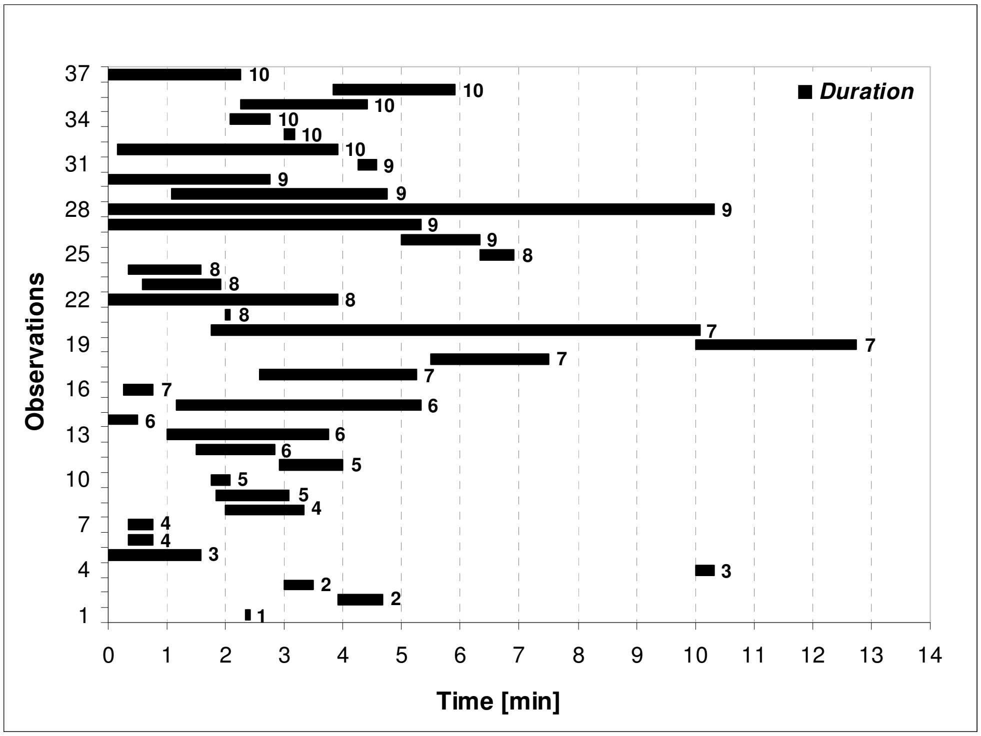

Figure 3. Start and duration of observed drinking behaviour of adult females of *A. bruennichi* in the laboratory (numbers next to the bars: No. of female).

Discussion

Our observations reveal that *Argiope bruennichi* shows a regular water searching and water ingesting behaviour on its covered web hub when sprayed with water. Since ingested water droplets were not subsequently discarded, this behavioural sequence can be considered as drinking behaviour. Although the whole web was misted, *A. bruennichi* exclusively searched the overstitched web hub for water droplets. Apart from ingesting water while self-cleaning, the spiders only take up droplets out of this part of the web decoration.

Spiders rarely absconded the web hub after it was misted with water and this behaviour is most likely an artefact of the treatment, since web bouncing is a more typical defence or avoidance response in *Argiope* (Wiehle 1931; Tolbert 1975; Jackson et al. 1993). All of the fleeing spiders returned to their web hubs a few seconds later, and this behaviour did not interfere with the following sequence of searching for and drinking water. Rather, most spiders spent some time self-cleaning, the duration of which was highly variable and probably depended upon the moisture of the spider's body parts or sensitive organs (e.g. trichobothria).

The systematic search for water and the water ingestions of *A. bruennichi* spiders from covered web hubs followed a stereotyped behavioural pattern of drinking. Since several spiders belonging to the genus *Argiope* occur in dry habitats (Enders 1974; Olive 1980; Edmunds 1986), this behavioural repertoire might allow for the compensation of water loss. Catching dew in early morning is often the only source of moisture in such habitats. Whenever the amount of water gained by liquefied prey is insufficient to compensate losses by evaporation, direct water ingestion will be crucial for survival (see Seibt & Wickler 1990). Thus, the silk mats covering the hub, which form part of the web decoration of *A. bruennichi*, may serve as devices to collect and hold water from atmospheric origin, since spiders are exclusively searching for water in web hubs.

Other silk types are already known for their capacity to absorb and store water (Gosline et al. 1999; Vollrath & Knight 2001). Edmonds & Vollrath (1992) argue that consuming all threads before rebuilding the web may therefore contribute to the water intake of *A. diadematus*. But so far, silken hub covers had been discussed only in the context of acting as physical sun shields (Robinson & Robinson 1973; Humphreys 1992, 1993) to decrease both body temperature and water loss (see Edney 1977). Drinking behaviour in web building spiders in general confined to a few, anecdotal reports. Berry (1987) for example, observed juvenile spiders of the semi-social tropical orb weaver *Cyrtophora moluccensis* ingesting small droplets of water that had accumulated in threads of their community-web. Suter (1985) noticed that individuals of the linyphiid spider *Frontinella pyramitela* drink dew or rain drops from their webs. In contrast, drinking behaviour in *A. bruennichi* seems to be more closely associated with a specifically designed web structure. This behaviour has also been observed in the zigzag-bands of *Argiope* spiders. Olive (1980) reports on the water-accumulating effect of the silken zigzag-bands of web decorations in *Argiope trifasciata* and on one spider which ingested water from this structure.

Using the hub cover as a structure to facilitate drinking adds a new hypothesis to the ongoing discussion about the possible adaptive value of web decorations in *Argiope* spiders (see review of Bruce 2006). A sit-and-wait predator like *Argiope* (Olive 1982), which is permanently exposed to sun and desiccation stress (Tolbert 1979; Ramirez et al. 2003), must rely on a variety of mechanisms to minimise water loss and efficient mechanisms to gain water. The spiders in our study were not water or food deprived, yet all spiders showed the same stereotype behavioural elements of water search and drinking in the hub cover, suggesting that this web decoration might be of adaptive significance for *A. bruennichi*. Nevertheless, further studies might focus on the intensity of the drinking and hub decorating behaviour among individuals that vary in their hygric status. Moreover, it remains to be seen whether different decorations in other *Argiope* species are used in a similar fashion, and thus whether water collection is a more widespread function of web decorations.

Chapter 8

Synthesis

The debate about the adaptive value of web decorations in *Argiope* spiders has been lasting over many decades and has become very controversially. A large suite of possible functional explanations arose and recently the major focus of the discussion lies on the incompatibility of different hypotheses. Most authors are focusing on a single and unique function for web decorations and only few synthesize the different opinions and findings in arguing a concurrent validity of various hypotheses, stating web decorations to be multifunctional. The present study provides new insights to the possible proximate mechanisms standing behind the web decorating behaviour, keeping the possible ultimate effects of the decorations in mind.

The comparison of the effect of aciniform silk removal in three different *Argiope*-species indicates that there is a link to the physiology of the spiders (chapter 4). The depletion of the aciniform glands leads to an increase of the web decorating activity indicating an overcompensated silk production in these glands. Perhaps the material used for the decoration construction originates from the regulation of the activity of the aciniform glands. This might be especially important for *Argiope*'s wrap attack, since the aciniform silk is also used for prey wrapping (Peters 1993; Tso 2004). For the wrap attack the spiders repeatedly need large amounts of this type of silk. The web decoration behaviour might be important for activating the aciniform glands to ensure a sufficient supply of wrapping silk. In this way, the outsourcing of aciniform silk in form of large decorations shortly before a moult (chapter 5) may facilitate resuming the wrap attack after the moult. During the moulting phase spiders cease prey capturing for several days and must swiftly compensate this deficit. Since the aciniform glands might be not completely effective shortly after the moult (see Townley et al. 2006) the recycling of the decoration bands may provide the spiders with the most needed amino acids to ease resuming the silk production. Nevertheless, the increase of the web decorating activity prior to moultings can be also explained with ultimate factors, like web protection (Eisner & Nowicki 1983; Kerr 1993) or camouflaging the spider (Blackledge & Wenzel 2001; Eberhard 2003).

Regardless of the proximate causes that enable spiders to spare the aciniform silk not only for wrapping but also for decorating the web, evolutionary, the visual characteristics of this silk may have generated quite ultimate values for *Argiope* when it is integrated in the capture web. Hence, the arrangement of the specific zigzag-shaped decoration bands might represent the result of a selection concerning the pattern in which “regulative silk” can be outsourced. In this way, it is further possible that web decorations fulfil several (species-specific) ultimate functions depending on a broad range of influencing factors like genetic setup, occupied habitat, prey composition, risk of predation, weather conditions etc. In fact, the high individual variability of the web decorating behaviour in *A. bruennichi* (chapter 2) and *A. keyserlingi* (chapter 5) indicates that these structures may truly act as multifunctional tools in their webs. Even within a short time span of only four days *A. bruennichi* alters the decoration pattern up to three times. If web decorations would serve a single function than a higher consistency of patterns must be expected. Thus, it might well be that web decorations are used in different ways, possibly in context of an conditional strategy (Starks 2002).

The fact that web decorations are also involved in the drinking behaviour (chapter 7) demonstrates that ultimate effects are not inevitably based on the visual traits of the silk. *A. bruennichi* regularly ingests water droplets from its covered web hub and uses this decoration part quite directly based on its structural characteristics. This observation does not unambiguously explain the occurrence or the pattern of web decorations, but it clearly supports the idea of a multifunctional tool.

The Y-maze choice test of the predator attraction hypothesis reveals that results from single experiments do not directly allow for generalised conclusions on the significance of the web decorating behaviour (chapter 6). Although Y-maze choice tests were repeatedly used for attraction tests combined with orb webs (Craig &

Bernard 1990; Bruce et al. 2001; Bjorkman-Chiswell et al. 2004) this apparatus turned out to be not suitable for testing the predator attraction hypothesis, at least when a mantid is used. But based on this methodology Bruce et al. (2001) stated an attracting effect of web decorations of *A. keyserlingi* on *Archimantis latistylus*. Contrary, in my experiment *Mantis religiosa* showed neither an interest for web decorations of *A. bruennichi* nor any predatory behaviour inside the maze. Apart from not excludable species-specific differences this result rather indicates that the Y-maze was inappropriate.

In the future there is still no other option but further proving existing hypotheses on the particular species of interest, including the critical reassessment of an alleged established methodology. In this context field studies and laboratory experiments must be combined to reliably reveal the ecological relevance of collected data. In an initial experiment in this thesis I could show that the ballooning is not an obligate life history phase in *A. bruennichi* (chapter 3) as it was previously claimed (Follner & Klarenberg 1995). Without an elaborate ballooning simulation the rearing protocol is clearly facilitated, allowing to raise large numbers of individuals with a similar constitution and history for comparative experiments.

Conclusion

At first the detection of a potential physiological background of the web decorating behaviour in *Argiope* spiders anew extends the research field. But it also offers the opportunity to get closer to the solution of the riddle of this conspicuous behaviour. Further studies not only have to question how web decorations may function but also where the silk for these structures does come from? This study is meant to be a starting point and shall help to extend the researcher's view to not only rely on single experiments but rather combining (often neglected) observations with experimental studies including a suit of different approaches and comparisons of different species within and, maybe, beyond the genus *Argiope*. It might be helpful to reduce the number of ultimate hypotheses by testing potentially contradictory results (possibly deriving from unsuitable approaches?). And for concretising the suggestion of proximate silk regulation processes standing behind the web decoration it will be necessary to combine behavioural investigations with those on the physiology of the spiders. In particular, we need more investigations on influences of the wrap attack behaviour on the decorating activity of the spiders, more information about the link between decorating behaviour and moultings (e.g. in juveniles) and an extended knowledge on regulatory processes in the aciniform silk glands.

After all, I conclude that the material used for web decorations of *Argiope* originally derive from a regulatory process of the aciniform silk production. The outsourcing of precious silk is combined with the risk of the loss of this material. It is comprehensible that using the deposited silk in a secondary way would balance this risk by benefiting from other positive values (e.g. due to visual traits of the silk). Given that such trade-off exists, the pattern in which spiders arrange the aciniform silk in their webs has been underlying evolutionary processes selecting for ultimate effects of web decorations. Due to these processes the silken decorations of *Argiope* spiders have turned out to be adaptive, maybe in several ways, acting as multifunctional tools in the orb web. In this means, web decorations in *Argiope* represent an example for the variable silk use in spiders that nicely demonstrate the significance of silk for the adaptation on a steadily changing environment.

Chapter 9

Zusammenfassung

Der adaptive Wert von Netzdekorationen (Stabilimenten) bei Spinnen der Gattung *Argiope* wird seit mehreren Dekaden kontrovers diskutiert. Heute findet sich in der Literatur ein breites Spektrum an möglichen Funktionshypothesen, deren teilweise Gegensätzlichkeit derzeit im Fokus der Diskussion steht. Die meisten Autoren beschreiben die Bedeutung der Stabilimente zumeist nur in Verbindung mit einer einzigen, alleingültigen Funktion. Nur wenige vertreten alternativ auch die Ansicht, dass verschiedene Funktionen gleichzeitig realisiert sein könnten und Stabilimente damit als „Multifunktionswerkzeuge“ dienen. Die vorliegende Arbeit liefert neue Erkenntnisse über mögliche Mechanismen, die dem Stabilimentbau von *Argiope*-Arten zugrunde liegen, ohne die adaptiven Effekte, die diese Strukturen letztlich im Netz der Spinnen erzielen, zu vernachlässigen.

Der im Kapitel 4 beschriebene Einfluss des aciniformen Seidenentzuges auf das Stabilimentbauverhalten dreier *Argiope*-Arten verdeutlicht, dass zwischen beiden Aspekten möglicherweise ein physiologischer Zusammenhang besteht: Die Verstärkung des Stabilimentbaus nach dem Entzug der Seide deutet auf eine Überkompensation der Produktion in den aciniformen Spinndrüsen (Glandulae aciniformes) hin. Da aciniforme Seide von den Spinnen nicht nur für die Anfertigung der Stabilimente, sondern auch für das Einwickeln von Beutetieren verwendet wird (Peters 1993; Tso 2004), liegt die Schlussfolgerung nahe, dass die Stabilimentseide ursprünglich aus einer Regulation der Aktivität der Glandulae aciniformes entspringt. Für *Argiope*'s typische „wrap attack“ (das schnelle Überwältigen der Beute durch ‚Überwerfen’ mit breiten Fadenbändern) benötigen die Spinnen eine große Menge an Einwickelseide. Daher könnte das Stabilimentbauverhalten einer Aktivierung der aciniformen Spinndrüsen dienen, wodurch dann für einen wiederholten Beutefang ausreichend Einwickelseide zur Verfügung steht. Ein ähnlicher Zusammenhang kann auch die Beobachtung des verstärkten Stabilimentbaus von *A. keyserlingi* vor der Reifehäutung erklären (Kapitel 5): Da während der Häutungsphase der Beutefang für einige Tage unterbrochen ist, ermöglicht das Ablegen von Spinnenseide in Form von

Stabilimenten womöglich eine schnelle Wiederaufnahme des Beutefangs nach der Häutung. Aufgrund verschiedener Umstrukturierungen im Spinnapparat während dieser Phase (Townley et al. 2006) sind auch die Glandulae aciniformes unter Umständen kurz nach der Häutung noch nicht wieder voll funktionsfähig (vgl. Townley et al. 2006). Das Recyceln der Stabilimente könnte daher den Spinnen kurzfristig als wichtige Eiweißquelle für die Wiederaufnahme der aciniformen Seidenproduktion dienen. Dennoch kann die Verstärkung des Stabilimentbaus vor der Häutung auch mit direkten (ultimaten) Effekten der Netzdekorationen erklärt werden: Die Spinnen schützen so möglicherweise auch das Netz durch Schaffung eines Warnsignals für potenzielle Netzzerstörer (vgl. Eisner & Nowicki 1983; Kerr 1993) oder tarnen sich vor potenziellen Prädatoren (vgl. Blackledge & Wenzel 2001; Eberhard 2003).

Abgesehen von der Frage, wodurch es den Spinnen möglich ist, aciniforme Seide sowohl für das Einwickeln von Beute als auch für die Anfertigung der Stabilimente zu nutzen, können die visuellen Eigenschaften dieser Strukturen im Laufe der Evolution ganz unmittelbare Bedeutung in den Radnetzen von *Argiope* erlangt haben. In welcher Weise die „ausgelagerte“ Seide in Form der zickzack-förmigen Stabilimentbänder im Netz arrangiert wird, unterläge dann der Selektion. So ist es auch durchaus vorstellbar, dass Stabilimente (heute) verschiedene Funktionen erfüllen; abhängig von der Art, dem genetischen Inventar, vom bewohnten Habitat, von der Beutezusammensetzung, vom Prädationsrisiko, von den Wetterbedingungen etc. Tatsächlich deutet die hohe Formenvariation der Stabilimente von *A. bruennichi* (Kapitel 2) und *A. keyserlingi* (Kapitel 5) auf eine multifunktionelle Relevanz hin. Selbst innerhalb eines kurzen Zeitraumes von nur vier Tagen ändert *A. bruennichi* die Form der Stabilimente bis zu dreimal. Dienten Stabilimente nur einer einzigen Funktion, würde man eine höhere Stetigkeit der Form erwarten. Demzufolge ist es wahrscheinlich, dass Stabilimente den Spinnen auf verschiedene Weisen dienen, möglicherweise sogar im Rahmen einer konditionalen Strategie (Starks 2002).

Die Tatsache, dass Stabilimente in auch Beziehung zum Trinkverhalten der Spinnen stehen (Kapitel 7) belegt, dass der adaptive Wert dieser Strukturen im Radnetz der Spinnen nicht zwangsläufig mit den visuellen Eigenschaften der Seide verknüpft sein muss. *A. bruennichi* nimmt regelmäßig gesammelte Wassertropfen aus den Stabilimenten auf und nutz auf diese Weise die Netzdekoration direkt, basierend auf den strukturellen Eigenschaften des Seidengeflechts. Auch diese Beobachtung stützt die These einer multifunktionalen Bedeutung der Stabilimente.

In Kapitel 6 wurde die anlockende Wirkung der Stabilimente auf Prädatoren in einem Y-förmigen Labyrinth untersucht. Die Ergebnisse verdeutlichen, dass verallgemeinernde Schlussfolgerungen aus Einzelexperimenten nicht möglich sind. Obwohl derartige Y-Boxen immer wieder in Attraktions-Versuchen zur Anwendung kommen (Craig & Bernard 1990; Bruce et al. 2001; Bjorkman-Chiswell et al. 2004), war schnell ersichtlich, dass diese Apparatur für den Test besagter Hypothese ungeeignet ist, zumindest wenn Gottesanbeterinnen (Mantodea: Mantidae) als Prädatoren verwendet werden. Zwar stellten Bruce et al. (2001) mit diesem Test eine anlockende Wirkung der Stabilimente von *A. keyserlingi* auf *Archimantis latistylus* fest, jedoch konnte ich dieses Ergebnis mit einem ähnlich Artenpaar (*A. bruennichi* vs. *Mantis religiosa*) nicht bestätigen: Die Europäische Gottesanbeterin (*M. religiosa*) zeigte im Labyrinth weder ein Interesse für die Stabilimente von *A. bruennichi*, noch irgendein Verhalten, welches Beutesuche oder gar Beutefang signalisiert. Beim Vergleich beider Experimente kann natürlich nicht ausgeschlossen werden, dass konträre Ergebnisse auf artspezifische Unterschiede zurückzuführen sind. Allerdings ist es wahrscheinlicher, dass die verwendete Apparatur für Lauerjäger wie Gottesanbeterinnen ungeeignet ist, um ein aktives Beutefangverhalten auszulösen und beobachten zu können.

Auch bei zukünftigen Untersuchungen zum Stabilimentbau von *Argiope*-Arten wird es letztlich unumgänglich sein, bereits existierende Funktionshypothesen mit der jeweiligen zu untersuchenden Art zu überprüfen und dabei auch die vermeintlich etablierte Methodik kritisch zu hinterfragen. So galt beispielsweise das

„Ballooning“ (Windverdriftung mittels Fadenfloß) bei *A. bruennichi* als obligater Lebensabschnitt bei den Jungspinnen, ohne das die Tiere nicht zum Netzbau übergehen würden (Follner & Klarenberg 1995). Zu Beginn meiner Untersuchungen konnte ich jedoch zeigen, dass ein fehlendes Ballooning die weitere Entwicklung der Spinnen keineswegs beeinflusst. Dieses Ergebnis war immens wichtig für die Aufzucht von *A. bruennichi*, da nun auf eine aufwendige Simulation der Windverdriftung verzichtet werden konnte.

Die Erkenntnis, dass der Stabilimentbau bei *Argiope*-Arten auf fundamentale physiologische Ursachen zurückzuführen sein könnte, erweitert zunächst erneut das Forschungsfeld. Sie bietet aber andererseits auch die Chance, der Lösung des Rätsels deutlich näher zu kommen. Zukünftige Untersuchungen sollten daher nicht nur darauf abzielen, die ultimate Funktion der Stabilimente im Radnetz der Spinnen zu beschreiben, sondern zu klären, welche Umstände es den Spinnen überhaupt ermöglichen, zusätzliche Seide für Stabilimente zu verwenden? Meine Arbeit sehe ich daher als ein Startpunkt für die zukünftige „Stabilimentforschung“, die verschiedene methodologische Ansätze kombinieren und auch klassische Beobachtungen nicht ausschließen sollte. Wir benötigen zudem weitere Vergleichsstudien an verschiedenen radnetzbauenden Spinnen, innerhalb und außerhalb der Gattung *Argiope*, nicht zuletzt, um die immer unübersichtlicher werdende Anzahl an Funktionshypothesen weiter zu minimieren. In Bezug auf den möglichen regulatorischen Zusammenhang zwischen der Aktivität der Glandulae aciniformes und der Intensität des Stabilimentbaus steht die Forschung noch am Anfang. Ohne ein näheres Verständnis der Drüsenphysiologie stoßen reine Verhaltensuntersuchungen bald an ihre Grenzen.

Abschließend schlussfolgere ich aus den von mir gewonnenen Ergebnissen, dass das Material, das Spinnen der Gattung *Argiope* in ihren Stabilimenten verbauen, einer Regulationstätigkeit der aciniformen Spinndrüsen entspringt. Das Auslagern wertvoller Seide ist immer auch mit dem Risiko verbunden, dieses Material zu verlieren. Es ist durchaus nachvollziehbar, dass eine Zweitverwendung der deponierten Seide im Radnetz dieses Risiko zumindest teilweise aufwiegen kann. Dann wiederum ist die letztendliche Form, in der die aciniforme Seide ins Netz eingewoben wird, selektiv. Durch visuelle und strukturelle Eigenschaften der Stabilimentseide erfüllen die zickzack-förmigen Seidenbänder von *Argiope* heute wahrscheinlich verschiedene Funktionen im Radnetz der Spinnen. Auf diese Art und Weise repräsentiert das Phänomen Stabilimentbau sehr gut die Fähigkeiten der Spinnen, sich mithilfe der Seide an ständig verändernde Umweltbedingungen anzupassen.

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Appendix

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Curriculum vitae

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PhD thesis: „The adaptive value of web decorations for *Argiope* spiders (Arachnida, Araneae)”
PhD student at the Department of Zoology, Martin-Luther-University Halle-Wittenberg, funded by grants from the Federal State of Saxony-Anhalt, Ministry for Science and Culture, and the Deutsche Forschungsgemeinschaft (DFG)

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Erklärung

Hiermit erkläre ich, dass diese Arbeit von mir bisher weder der Mathematisch-Naturwissenschaftlich-Technischen Fakultät der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht wurde. Ich erkläre, dass ich mich bisher noch nicht um den Doktorgrad beworben habe. Ferner erkläre ich, dass ich diese Arbeit selbständig und nur unter Zuhilfenahme der angegebenen Hilfsmittel und Literatur angefertigt habe.

Halle (Saale), den 20.03.2008

A. Walter

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André Walter