Behav Ecol Sociobiol (2011) 65:1909–1915
DOI 10.1007/s00265-011-1200-8

ORIGINAL PAPER

Signals for damage control: web decorations in *Argiope keyserlingi* (Araneae: Araneidae)

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Received: 17 April 2011 / Revised: 17 April 2011 / Accepted: 3 May 2011 / Published online: 12 May 2011

Abstract Orb web spiders of the genus *Argiope* are permanently located at the hub of the orb web and are thus vulnerable to changing environmental conditions. Severe damage to the web by non-prey animals can have a significant impact on survival, through the cost of producing expensive silk and the loss of foraging opportunities. Thus, selection should favor web protection mechanisms, and the conspicuous web decorations, typical of *Argiope* spiders, may play a role. Decorated webs suffer less damage than undecorated webs, consistent with the view that they advertise the presence of the web to non-prey animals that may damage the web. However, whether spiders respond to web damage by increasing investment in web decorations has not been investigated. We subjected adult St. Andrew's Cross spider (*Argiope keyserlingi*) females to three levels of web damage and recorded their subsequent web-decorating behavior. Mild damage, similar to that caused by impacting prey, did not affect either web building or decorating behavior. However, spiders subjected to substantial web damage both reduced the size of subsequent webs and increased investment in web decoration size. These data are consistent with an advertising role of web decorations.

Keywords *Argiope* · Web decoration · Web protection · Prey attraction · Capture strategy · Visual signals · St. Andrew's cross spider

Communicated by J. Choe

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Introduction

The foraging behavior of animals is typically characterized by a balance between the benefits of acquiring appropriate nutrients against a suite of costs that may include the risk of predation, competition and, less commonly, parasitism (e.g., Stephens et al. 2007). The foraging strategy of many species of marine and terrestrial invertebrates involves the use of traps to capture prey (see Hansell 2005). Examples among terrestrial species include the conical pit traps of ant lions (e.g., Tusculescu et al. 1975; Scharf and Ovadia 2006), the sticky traps of fungus gnat (glow worm) larvae (Meyer-Rochow 2007), and several families of web-building spiders (e.g., Craig 2003). To be effective, a trap should be as inconspicuous as possible, and for species that utilize traps, the costs of foraging must include both the fabrication and maintenance of these constructions.

The orb-weaving spiders, including the Araneidae, Nephilidae, Tetragnathidae, and Uloboridae, construct a highly developed trap with which to capture prey (Nentwig and Heimer 1987). The orb web comprises a sticky spiral of silk threads that is suspended within a frame of non-sticky silk. The spider is bound to the fixed position of the web (Enders 1974; Olive 1982), and can respond to prey impacts by remaining either on the web or in nearby vegetation. As a consequence, these spiders are directly exposed to a changing environment, including microclimate and variation in prey and predator abundance. To protect themselves, several araneid species build retreats where they can hide, for example from predators or direct insolation (Foelix 1996; Thirunavukarasu et al. 1996; Pasquet et al. 2007). However, in some orb weavers such as *Argiope*, individuals do not build protective retreats but instead remain at the central hub of the web (Levi 1968; Scharff and Coddington 1997). The unintentional destruction of the web by non-prey organisms may result in some substantial costs, including the production of replacement silk (Craig 2003), lost foraging opportunities, and exposure to predators (e.g., Lubin et al. 1993).

Spiders in the genus *Argiope* are characterized by their construction of silk "decorations" (McCook 1889), zigzag-shaped bands of aciniform silk fibers that are attached to the orb web (Herberstein et al. 2000a; Bruce 2006). Web decorations create a highly conspicuous visual signal apparently contradicting the idea of an effective trap. While decorating behavior appears to be tightly linked to dwelling on the web (Blackledge and Wenzel 2001; Eberhard 2003), its functional significance remains unclear, and attempts to resolve this signaling paradox still generate a spirited debate (Herberstein et al. 2000a; Bruce 2006). Three explanations dominate this discussion: silk decorations may provide a signal for prey attraction (Craig and Bernard 1990; Tso 1998; Cheng et al. 2010), camouflage the spiders by concealing their outline (Edmunds 1986; Schoener and Spiller 1992; Blackledge 1998; Blackledge and Wenzel 2001), or alert non-prey animals to the presence of the web and thereby reduce unintentional damage (Horton 1980; Eisner and Nowicki 1983; Kerr 1993; Blackledge and Wenzel 1999). These explanations are not always clearly distinguishable: for example, the avoidance of webs by predatory birds may not only protect the integrity of webs but also the spider from being eaten (Horton 1980).

In general, investigations of the function of a signal typically include records of its natural variation; the consequences of its differing strength and the response of the signaler to changing environmental circumstances. Numerous studies reveal both inter- and intraspecific variation in the web decoration patterns of *Argiope* spiders, under both field (Craig et al. 2001; Rao et al. 2007) and laboratory (Nentwig and Heimer 1987; Seah and Li 2002) conditions. Evidence that decorated webs suffer less damage than undecorated webs derived from observations of either the response of birds (Horton 1980; Blackledge and Wenzel 1999) or the damage suffered by webs with natural (Jaffé et al. 2005; Eberhard 2007) or experimentally manipulated (Eisner and Nowicki 1983; Blackledge and Wenzel 1999) variation in decorations. While these data are largely consistent with the view that decorations protect webs from damage by non-prey species, they provide little insight into the signaler's response. Importantly, these studies do not reveal whether spiders increase investment in web decorations in response to experiencing substantial web damage. This is a critical prediction, given the intraspecific variation in decorating behavior and the potentially negative impact of the conspicuous signal on foraging efficiency. Additionally, we do not know whether spiders distinguish between the damage generated by the regular impacts of prey (cf. Tso 1996) and the inadvertent damages by non-prey animals, and what degree of damage is necessary to trigger an increased investment in silk decorations. Here, we present a laboratory experiment in which we subjected orb web spiders *Argiope keyserlingi* with different levels of web damage and monitored their subsequent web-building and web-decorating behavior.

Methods

We collected adult females of *A. keyserlingi* from Ku-ring-gai Bicentennial Park (West Pymble, Sydney, Australia) where we found them between branches of various shrubs at heights of less than 2 m—the species' typical habitat (Rao et al. 2007). They were subsequently maintained in Perspex frames (58×58×15 cm) under natural light conditions in the laboratory at the University of Melbourne. Each day, individuals were fed with one blowfly (*Lucilia* spp.), and their webs moistened with a few sprays of water directed towards the surface of the web. The experimental treatment commenced after 1 week of acclimatization.

Spiders were assigned to one of two treatments: "mild" damage—where a quarter of all present radii were cut (Fig. 1a) to simulate damages usually caused by impacting prey animals and "heavy" damage—where the mild damage was augmented by cutting two diagonally opposite anchor threads (Fig. 1b), which caused the web to collapse, but the spider was still able to remain on the web. Spiders of the control group experienced no web damage. Twenty-two spiders were allocated to each group, and the treatment was repeated daily over 14 days.

We measured the following web parameters each day over the 14-day treatment period:

1. The capture area, following Tso (1999):
   Capture area = web area − hub area = $\pi \times [(\bar{x}R\mathrm{web})^2 - (\bar{x}R\mathrm{hub})^2]$, with $\bar{x}R\mathrm{web}$ being the mean web radius, measured from the center of the web to the outermost capture spiral and $\bar{x}R\mathrm{hub}$ being the mean radius of the web hub (calculated from measurements of vertical and horizontal diameters).
2. The mesh height, following Herberstein and Tso (2000):
   Average mesh height=$1/2((R_\mathrm{u}-H_\mathrm{ru})/(S_\mathrm{u}-1)+(R_\mathrm{l}-H_\mathrm{rl})/(S_\mathrm{l}-1))$, With R_u being the upper and R_l, the lower radius of the capture spiral; H_ru, the upper and H_rl, the lower radius of the web hub; and S_u, the number of capture spiral turns in the upper and S_l in the lower web half.
3. The pattern and the size of web decoration bands (following Tso 1999):
   Size of (each) silk decoration band = $(a + c) \times b/2$, because of their trapezium-shape with a being the

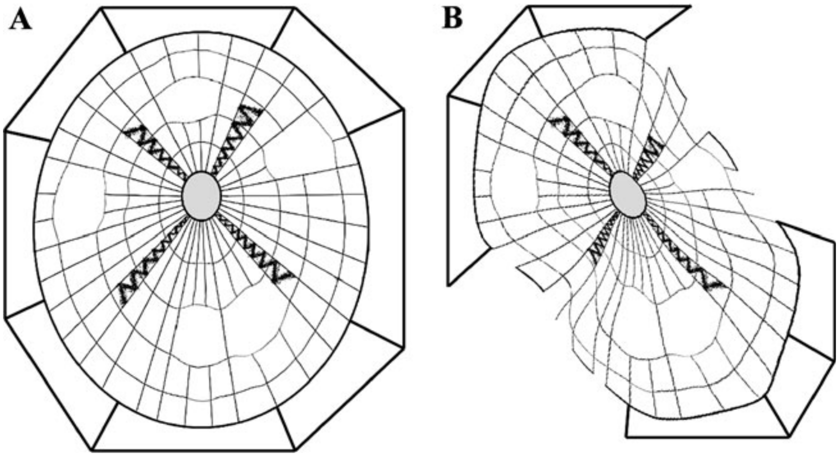

Fig. 1 Illustration of the two levels of artificial damages applied to webs of *A. keyserlingi* females; **a** "mild" damage, cutting a quarter of all present radii to create holes similar to those appearing after prey impacts; **b** "heavy" damage, cutting a quarter of all present radii plus two diagonally opposite anchor threads to eliminate the web's tension without completely destroying the web

inner width, *c* the outer width, and *b* the length of the decoration band.

Statistical analyses

For statistical analyses, we used STATISTICA (version 7.0) including *t* tests for the evaluation of differences in mean sizes of webs and web decorations between the first and the last day of the experiment within each treatment. Differences in the number of individuals that built a web decoration (web-decorating frequency) throughout the observation period were calculated using a Kruskal–Wallis ANOVA. We tested the web sizes, average mesh heights, and web decoration sizes for normal distribution using the Kolmogorov–Smirnov test. Temporal changes in the size of the web were then analyzed with repeated measures ANOVAs using days as repeats. Since measures of web decoration size were not normally distributed, we compared the groups with a Friedman ANOVA.

Results

Web-building behavior

The size of the capture area of the webs did not change during the observation period in either the control (+4.4%, from 1,636.38±187.73 cm^2 at the beginning to 1,708.57±130.36 cm^2 at the end of observation; $t_{22}=-1.47$, $p=0.15$) or the mild damage treatments (+1.4%, 1,510.62±252.46 cm^2 from the beginning to 1,531.37±185.62 cm^2 at the end of observation; $t_{22}=-0.38$, $p=0.71$). However, spiders that experienced the heavy damage treatment significantly reduced the size of their webs by 12.8%, from 1,743.20±163.53 cm^2 at the beginning to 1,518.87±242.73 cm^2 at the end of the observation (*t* test, $t_{22}=3.21$, $p<0.0023$). Throughout the duration of the treatment, spiders that experienced heavy web damage significantly reduced the size of their webs in comparison to spiders that experienced mild or no web damage (repeated measures ANOVA, $F_{2,845}=531.75$, $p<0.001$; Fig. 2). The average mesh height was not affected by the treatment (from 5.11±0.72 mm at the beginning to 5.53±0.74 mm at the end of observation). Moreover, there was no significant difference among groups (control, from 5.39±0.6 mm at the beginning to 5.32±0.89 mm at the end of observation; mild damage, from 5.47±0.55 mm at the beginning to 5.37±0.71 mm at the end of observation; repeated measures ANOVA, $F_{2,845}=1.09$, $p=0.33$).

Web-decorating behavior

The proportion of individual spiders that built web decorations increased significantly in all three treatments over the course of the experiment (control, from 28.6% to 54.6%; Fisher's exact: $p<0.016$, mild damage, from 18.2% to 52.4%; Fisher's exact: $p<0.013$, heavy damage, from 28.6% to 81.8%; Fisher's exact $p<0.001$). While the decorating frequency of spiders in the mild damage treatment did not significantly differ from that in the control, the percentage of decorating individuals was significantly higher in the heavy damage treatment compared with the control (Kruskal–Wallis, $H=8.23$; $p=0.016$).

The size of web decorations varied among the individuals in each treatment. Nevertheless, all of the spiders significantly increased the size of their web decorations during the observation time (control, from 20.3±54.4 mm^2 to 98.8±190.5 mm^2; *t* test, $t_{22}=-2.95$, $p<0.0052$; mild damage, from 14.6±35.9 mm^2 to 113±127.7 mm^2; *t* test, $t_{22}=-3.48$, $p<0.0012$; heavy damage, from 21.86±34.7 mm^2 to 207.8±117 mm^2; *t* test, $t_{22}=-4.35$, $p=8.9\text{E-}05$). This increase in decoration investment did not differ between the control and the mild damage treatments, but the increase in decoration size was significantly greater among the heavy damage treatment (Friedman ANOVA, $\chi^2=18.43$, $p=9.96\text{E-}05$; Fig. 3).

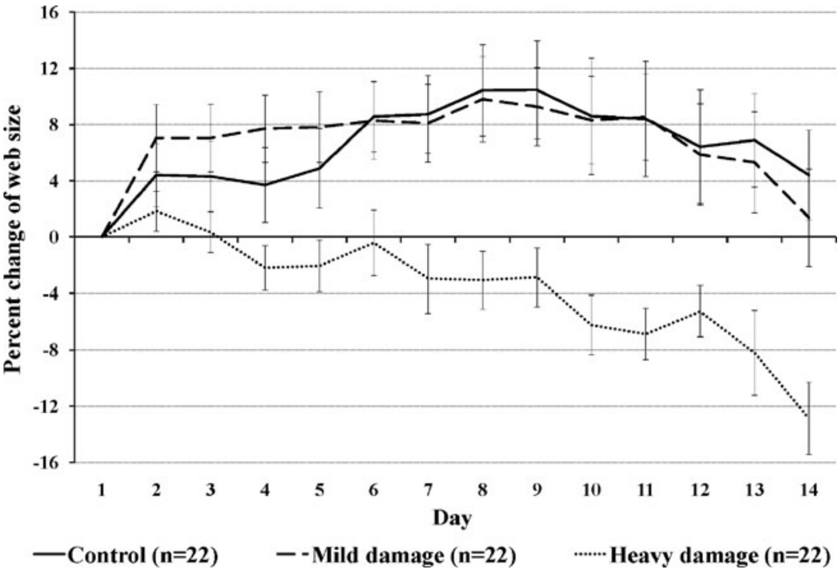

Fig. 2 Percent change of the web sizes in the three spider groups during the 14-day observation period. Heavy damage treatment caused a significant decrease of web size in *A. keyserlingi*

Discussion

Our experiments revealed that *A. keyserlingi* spiders adjust their web-building and web-decorating behavior according to their experience of web damage. In contrast to studies observing the consequences of web decoration, these results provide experimental support for a tactical use of web decorations for advertising the web, thereby providing protection against inadvertent destruction by non-prey animals such as birds (Horton 1980; Kerr 1993), mammals, or very large insects that are not typically arrested by the silk. Web damage may include ruptures of the frame and anchor threads leading to a collapse of the web's tension or even to the complete disintegration of the web. Spiders suffering substantial damage to their web reduced the size of the capture area of subsequent webs, and built more and larger web decorations. In contrast, spiders suffering mild web damage, similar to that associated with prey-capture events, did not change their investment in either the size of the web or web decorations.

Our experimental data support a web integrity protection explanation for the adaptive value of web decorations in *Argiope* spiders (see reviews in Herberstein et al. 2000a; Eberhard 2003; Bruce 2006). Previous studies suggesting a protective effect of web decorations are based on either observations of the persistence of the web's integrity, or on the response of potential destructors to silk-decorated webs (Horton 1980; Eisner and Nowicki 1983; see also Kerr 1993). For example, the silken decorations are visible to birds (Bruce et al. 2005), who avoid contacting the sticky

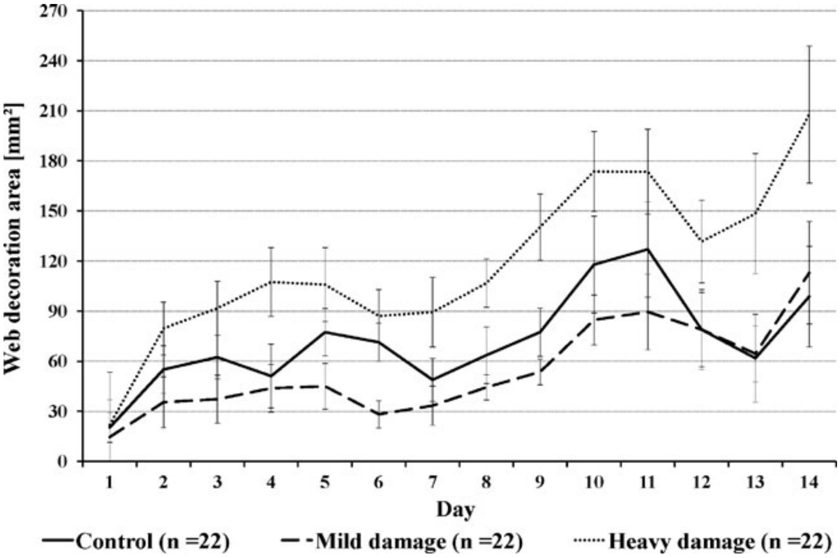

Fig. 3 Change of decoration size in the three spider groups during the 14-day observation period. Heavy damage treatment caused a significant increase of decoration investment in *A. keyserlingi*

web using the decoration as a cue (Horton 1980; Blackledge and Wenzel 1999). Thus, decorated webs remain undamaged for longer than undecorated ones (Eisner and Nowicki 1983). The present study provides evidence of facultative adjustment of decorating behavior in response to web damage: spiders of *A. keyserlingi* invest more in web decorations when faced with the costs of chronic web damages. This result is consistent with previous studies suggesting decorations protect the webs against inadvertent destruction by non-prey animals (Eisner and Nowicki 1983) that may include birds, mammals, and large invertebrates that cannot be arrested by the web. For example, birds and mammals that share the same habitat with the shrub-dwelling *A. keyserlingi* (Herberstein et al. 2000b; Rao et al. 2007) may utilize the visual impression of the decoration as a cue to avoid the web. Predatory birds may avoid decorated webs (Horton 1980), so the increased decorating investment may further protect the spider from predation consistent with other reports on the defensive functions of web decorations (e.g., Schoener and Spiller 1992; Blackledge 1998). In this context, Nakata (2009) observed an increased decoration investment in *Cyclosa argenteoalba* spiders after exposure to vibratory stimuli mimicking insect predators. However, as the web damage treatment did not convey any vibrations in our study, the observed response of *A. keyserlingi* spiders did not conform to this explanation.

Spiders that sustain chronic damage to their web may, in addition to changing its size and visibility, move the web to a new location. Chmiel et al. (2000) showed experimentally that spiders of *A. keyserlingi* suffering chronic damage to one side of the web, thereby compromising web tension, relocated the web a small distance in the opposite direction. In the present experiment, spiders were maintained in frames that provided no opportunity to alter the web site. Nevertheless, abandoning the web is energetically costly and increases the risk of predation (Lubin et al. 1993). An alternative solution is to reduce the size of the web, and spiders of *A. keyserlingi* reduced the size of the web by 13% over a 14-day period of substantial damage. This response to damage may occur in other contexts. Spiders anticipating a molt build smaller webs than expected for their body size (Higgins 1990; Walter et al. 2008), which might reduce the risk of web damage at a time when the spider is defenseless, unable to move, and particularly vulnerable to disturbance (Robinson and Robinson 1973; Baba and Miyashita 2006).

Interestingly, all spiders in our study significantly increased their decoration investment over the course of the experiment. Since the control and the mild damage treatments did not significantly vary from each other, this is most likely an overall effect of the captive conditions. All individuals were collected in the field, so their previous feeding regimes were unknown. However, *Argiope* spiders increase their web decorating activity when they are well-fed (Herberstein 2000; Craig et al. 2001). The feeding regime of *A. keyserlingi* in the present study may have similarly resulted in well-fed individuals, who could thus invest more in decorations.

One of the most widely discussed explanations of the adaptive value of web decorations is that they provide a visual sign that attracts prey insects (Craig and Bernard 1990; Tso 1996, 1998; Herberstein 2000; Bruce et al. 2001; Li et al. 2004). In this context, Hauber (1998) found a strong correlation between the presence of web decorations and the size of orb webs in *Argiope appensa*. The construction of either large webs without, or small webs with decorations may achieve similar capture success in this species, suggesting a trade-off between the productions of different types of silk. Accordingly, it is possible that the response of *A. keyserlingi* to the heavy damage treatment in our experiment was principally a reduction in the size of the web. The subsequent potential decrease in foraging success arising through a reduction in capture area is then offset by increasing investment in web decorations that would attract more prey. We are unable to confirm such a trade-off since the different types of silk threads in an orb web are synthesized by different silk glands that require different amounts of specific amino acids (see overview in Vollrath and Knight 2001). Nevertheless, we wonder whether an optional substitution of different silks is possible. Finally, the potential trade-off between web size and web decoration investment has been attributed to different prey availabilities (Tso 1996). This explanation is not applicable for the present study because the feeding regime was the same for all treatment groups.

The reduction in the size of the web following heavy damage may represent a mechanism of reinforcing the tension of the web, by either increasing the concentration of the capture spiral to a smaller area or the thickness of used silk threads, in response to an increase in the frequency of failed captures of larger prey. Nakata (2010) reports that *Cyclosa argenteoalba* spiders increase the tension of the web by pulling particular radii towards the central hub, thereby improving detection of impacting prey. Alternatively, the reduction in web size may reflect an adjustment in web characteristics in response to a perceived encounter with high-energy prey impacts, rather than damage caused by non-prey individuals. *Nephila pilipes* spiders that catch large prey insects increase the diameter of silk threads, apparently to increase the stiffness of the web and thus withstand the high-energy impacts of these larger preys (Tso et al. 2007, see also Vollrath and Köhler 1996). We cannot test this possibility as we did not measure silk thread thickness, but we did not observe a reduction in the average mesh height that may indicate a change in web tension, nor any changes in the posture of *A. keyserlingi*.

Our experiments provide a relatively novel approach to investigating the adaptive significance of signal design, namely the response of the signaler to variable environmental conditions. This approach, which takes a signaler's perspective, provides more compelling support for a signaling function of web decorations directed toward potentially destructive, non-prey organisms. However, as our findings potentially match the prey-attraction hypothesis, we cannot completely exclude other functional explanations. Teasing apart different explanations requires increasingly sophisticated experimental designs. Tests of how a signaler changes the strength of its signal in response to a changing environment will clarify the importance of other explanations, perhaps revealing that web decorations provide a range of benefits (see also Herberstein et al. 2000a; Starks 2002) that are both species-specific and context-dependent.

Acknowledgments We thank Mariella Herberstein for her help in collecting spiders, Todd Blackledge and an anonymous referee for their helpful comments, and DFG for the financial support (to AW).

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