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Factors affecting the foraging success of the wasp-like spider *Argiope bruennichi* (Araneae): Role of web design

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Abstract: The adult wasp-like spider, *Argiope bruennichi* builds only linear stabilimenta for which several hypotheses have been suggested. Our field observations based on the foraging success and web design of both decorated and undecorated webs do not support the prey attractant hypothesis, because of similar amount of prey intercepted to any type of the orb-web. Web design (mesh height, capture thread length, web area) was affected by web height, but foraging success was not related to web height. The quantity of stabilimenta was negatively correlated with web area and web area was significantly related to the number of intercepted prey. We found a negative, but non-significant relationship between the quantity of stabilimenta and the number of prey intercepted to orb-webs. As predicted by foraging theory, higher investments in the spider's orb-web (capture thread length and web area) resulted in a higher foraging success. Our results indirectly support the non-foraging explanations for stabilimenta building. Moreover, the main prey of *Argiope* were orthopterans (> 40%), which are not attracted by the stabilimentum. We failed to find any differences in web design between decorated and undecorated webs. Other factors such as weather conditions were also briefly noted and discussed.

Key words: Araneae, stabilimentum, web decorations, foraging success, *Argiope bruennichi.*

Introduction

Several species of orb-weaving spiders insert ribbon-like silky structures called stabilimenta or web decorations to their orb-webs during web construction. Originally, E. Simon (cited by Robinson & Robinson, 1970) proposed a stabilizing (mechanical) function of stabilimenta. The function of these decorations is, however, still unclear and some alternative hypotheses were offered (for a detailed review see Herberstein et al., 2000a). Stabilimenta may stabilize and strengthen the web, advertise the web to birds, and avoid web damage or provide sunshield for the spider, protect spiders from parasitoid wasps or they can be a by-product of silk regulation. Recently, several studies have shown that stabilimenta reflected ultraviolet (UV) light (Craig & Bernard, 1990) and attracted insects (e.g. Hauber, 1998; Tso, 1996; Watanabe, 1999; Bruce et al., 2001). Moreover, the presence of stabilimentum may also attract predators (Seah & Li, 2001) and therefore, it is proposed that predator attraction is a cost for the higher foraging success of decorated webs (Bruce et al., 2001; Craig et al., 2001). Although the latest explanation seems to be convincing, serious arguments against the prey attractant hypothesis exist. First, Zschokke (2002) found no evidence of ultraviolet (UV) reflectance of stabilimenta of various orb-weaving spiders (but see Craig & Bernard, 1990). Thus, ultraviolet light cannot be an explanation for insect attraction to decorated webs. Second, Blackledge & Wenzel (1999) found that decorated webs of *Argiope aurantia* Lucas, 1833 females intercepted fewer insects than decorated webs. Moreover, spiders with decorated webs had higher survival (Blackledge & Wenzel, 2001) and the high conspicuousness of stabilimenta resulted in more web avoidance by prey, contradicting other studies. The aim of our study is to contribute to this debate using adult females of the wasp-like spider, *Argiope bruennichi* (Scopoli, 1772), as a model species that builds both decorated and undecorated orb-webs with linear stabilimenta (Malt, 1993). The main question addresses the prey attractant hypothesis, which predicts, that decorated webs should have greater foraging success than undecorated ones.

Material and methods

The study was conducted between July–September 2003 in grassland habitat (49°28′30″ N, 19°23′49″ E) in Slovakia, covered mostly by Poaceae. During the first survey, we individually marked all adult females found in the study plot using glue paint on the dorsal side of the opistosoma. All other spiders found in the study area throughout the season were also marked. We measured environmental factors that may affect foraging success. Because web design reflects spiders' behavioural and energetic investments in foraging, we also measured web area, capture thread length and mesh height of each orb-web observed. The spiders were located at 06:00 and web height (the distance from the ground to the hub of the web) and the distance of the web hub from the nearest flower, represented mainly by shamrock (*Trifolium* spp.) were recorded. If no flower was present in the 3 m radius around the orb-web ($n = 8$), the distance was not measured. This procedure was used because one would expect a higher abundance of pollinators such as flies and hymenopterans around flowers resulting in higher prey capture rates compared to the effects of other important factors such as the presence of the stabilimentum in the orb-web. The stabilimentum area was calculated as length × width of the stabilimentum (SEAH & LI, 2002). Capture thread length (CTL) was calculated following VENNER et al. (2001):

$$\mathrm{CTL} = \pi/16 \times (N_\mathrm{v} + N_\mathrm{h}) \times (D_\mathrm{ov} + D_\mathrm{iv} + D_\mathrm{oh} + D_\mathrm{ih})$$

whereby N_v = number of vertical spirals, N_h = number of horizontal spirals, D_ov = outermost vertical diameter, D_iv = innermost vertical diameter, D_oh = outermost horizontal diameter and D_ih = innermost horizontal diameter.

Web area was calculated following BLACKLEDGE & GILLEPSIE (2002) as

$$(D_\mathrm{ov}/2) \times (D_\mathrm{oh}/2) \times \pi - (D_\mathrm{iv}/2)^2 \times \pi.$$

The mesh height (average distance between spirals) was calculated for the vertical diameter of the orb web as $D_\mathrm{ov} - D_\mathrm{iv}/(N_\mathrm{v} - 2)$.

Prey capture success was estimated by surveying each spider's web every 30 min, from 06:00 to 12:00. All prey items entangled in the web, or eaten by the spider were carefully removed, fixed in formaldehyde (8%) and later measured under a binocular microscope. To avoid starvation of the observed spiders that may significantly affect web design and web decorating behaviour (e.g. HERBERSTEIN et al., 2000b), we used only non-consecutive days for our observations. Thus, the spider's food intake was left intact for several days to improve normal food intake. Only adult *Argiope* females were included in the investigation.

Weather conditions were divided using a scale, whereby Level 1 was clear days, cloudy days were noted as Level 2 and rainy days as Level 3.

Statistical analysis. The data were inspected for normal distribution using the Kolmogorov-Smirnov test or alternatively the Shapiro-Wilk test and log-transformed if necessary. In accordance to data distribution, parametric or nonparametric tests were used. All the statistical tests were two-tailed. The reported values are means ± SD.

Results

Effects of web placement on web design

Web height significantly correlated with the number of spirals ($r_s = 0.359$, $P < 0.01$, $n = 119$), with CTL ($r_s = 0.415$, $P < 0.01$, $n = 119$) and also with web area ($r_s = 0.405$, $P < 0.01$, $n = 119$). Mesh height was marginally correlated with web height ($r_s = 0.178$, $P = 0.052$, $n = 119$), but no correlation was found between mesh height and CTL ($r_s = -0.129$, $P = 0.162$, $n = 119$), nor web area ($r = 0.106$, $P = 0.252$, $n = 119$). Moreover, the distance from the nearest flower did not correlate with web height ($r_s = 0.016$, $P = 0.864$, $n = 111$). No relationship between flower distance and mesh height was detected ($r_s = -0.126$, $P = 0.188$, $n = 111$).

Most of the orb webs observed contained stabilimentum (89 of 119). We did not find any differences in web design between webs with and without stabilimentum (Tab. 1).

After excluding undecorated webs, we found that the quantity of stabilimenta (percentage of stabilimentum area covering the web to the web area) correlated negatively, but significantly with web area ($r_s = -0.585$, $P < 0.001$, $n = 75$, see Fig. 1). The distance from the nearest flower was similar in decorated (109.047 ± 74.61) ($n = 85$) and undecorated webs (94.346 ± 74.88) ($n = 26$) ($U = 978.50$, $P = 0.78$).

Web height tended to be lower in those webs that contain stabilimentum (28.101 ± 6.168, $n = 30$) in comparison with undecorated webs (31.700 ± 7.804, $n = 89$), but this difference was not significant (U-test, $U = 1039.0$, $P = 0.069$).

The effect of weather conditions on web design

We found a significant effect of weather conditions on CTL, stabilimentum area and the web area (Tab. 2). The effect on other variables, such as mesh height, web height, and the quantity of stabilimenta remained nonsignificant.

Factors affecting foraging success

Web area clearly correlated with the number of insects trapped in the orb web ($r_s = 0.319$, $P < 0.01$, $n = 119$, Fig. 2) and, similarly, CTL ($r_s = 0.249$, $P = 0.006$, $n = 119$) and mesh height ($r_s = 0.201$, $P = 0.029$, $n = 119$) also significantly correlated with prey number. In contrast, web height ($n = 119$) and distance from the

Table 1. Differences in web design between decorated and undecorated webs.

Orb-webs	CTL (cm)	Web area (cm^2)	Mesh height (cm)
Decorated ($n = 89$)	1015.06 ± 586.14	378.64 ± 258.99	0.22 ± 0.06
Undecorated ($n = 30$)	1055.46 ± 493.75	383.46 ± 184.55	0.22 ± 0.01
Mann-Whitney U'	1205.0	1181.0	1197.5
P	0.426	0.346	0.400

Table 2. The effect of weather conditions on web design (one-way ANOVA or Kruskal-Wallis ANOVA was performed).

	Level 1 ($n = 62$)	Level 2 ($n = 45$)	Level 3 ($n = 12$)	Test statistics	P
CTL	853.07 ± 393.93	1365.04 (542.22)	839.21 ± 387.29	$F_{2,16} = 17.847$	< 0.01
Stabilimentum area	1.74 ± 2.38	2.32 ± 1.75	1.12 ± 1.29	$H'_2 = 6.410$	0.041
Web area	335.35 ± 150.75	520.26 ± 240.97	322.16 ± 151.56	$H'_2 = 21.240$	< 0.001

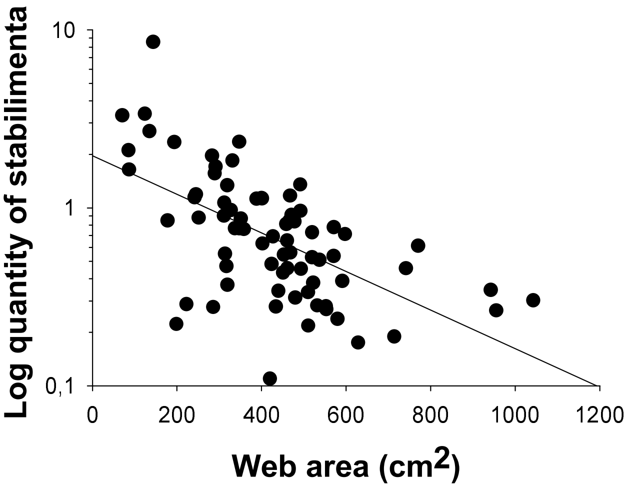

Fig. 1. Negative relationship between quantity of stabilimenta and area of web.

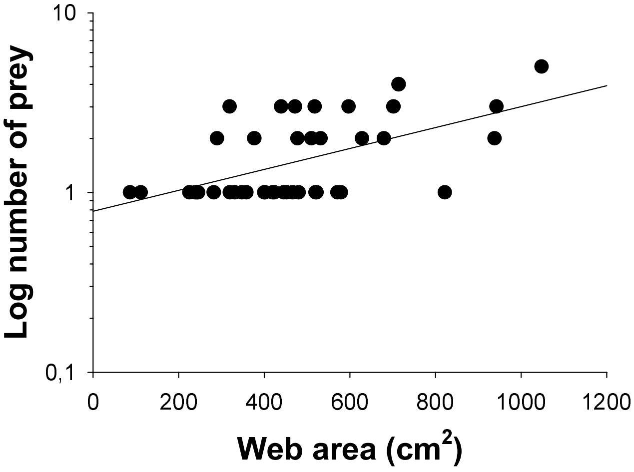

Fig. 2. The relationship between web area and the number of prey intercepted.

nearest flower ($n = 111$) did not affect foraging success ($P > 0.111$, respectively). Weather conditions, surprisingly, showed no effect on prey capture rate (Kruskal–Wallis $H' = 0.186$, df = 2, $P = 0.911$). We did not find any difference between the number of insects captured in decorated ($n = 89$) or undecorated ($n = 30$) orb-webs (Mann-Whitney $U = 1219.500$, $P = 0.409$) even when excluding those webs that did not intercept any prey (31 vs 12, Mann-Whitney $U = 139.500$, $P = 0.167$). Similarly, there was no difference in average prey length between decorated (15.146 ± 5.747 mm, $n = 29$) and undecorated webs (14.963 ± 6.961 mm, $n = 12$)) (t-test, $t = 0.87$, df = 39, $P = 0.931$). Because the quantity of stabilimenta correlated significantly with web area (see above), we used residuals from stabilimentum area and web area (as independent variable) and number of prey (dependent variable) in a linear regression. We found a negative although not clearly significant relationship between these variables ($r = -0.161$, $P = 0.080$).

More than 40% (decorated webs: 45%, undecorated: 43%) of captured insect specimens were orthopterans. Using a χ^2 test, there was no difference between the proportion of flying (decorated = 18, undecorated = 11) and jumping insects (24 vs 12), in decorated and undecorated webs ($\chi^2 = 0.15$, $P = 0.70$).

We used logistic regression analysis for comparison between successful (i.e. those webs that caught at least one prey) and unsuccessful webs (webs that did not contain any prey). Mesh height, distance from the nearest flower and web height was not significantly different. However, successful orb-webs had a significantly greater web area (475.15 ± 212.71 vs 366.22 ± 200.23, logistic regression, $\chi^2 = 7.21$, df = 1, $P = 0.007$) and CTL (1182.91 ± 497.83 vs 973.08 ± 517.52, $\chi^2 = 4.42$, df = 1, $P = 0.039$) than unsuccessful webs.

Discussion

Our results do not support the prey attractant hypothesis (e.g. CRAIG & BERNARD, 1990; TSO, 1996; HAUBER, 1998; HERBERSTEIN, 2000), because both the decorated and undecorated webs caught a similar number of prey. Moreover, there were no qualitative differences between the proportion of flying and jumping insects captured, so the prediction that flying insects (mainly pollinators) are attracted to decorated webs (e.g. TSO, 1996; WATANABE, 1999; BRUCE et al., 2001) cannot be supported. However, these results should be interpreted cautiously because they are based on simple observations rather than a direct choice experiment.

As the web area of spiders increased, the proportion of stabilimentum area decreased and number of prey caught increased. A negative relationship between stabilimentum area and web area has been also found by SEAH & LI (2002), can be explained as a foraging strategy. Because higher investment in sticky spirals leads to higher prey capture which is important mainly for starved spiders (e.g. HERBERSTEIN et al., 2000b), spiders may compensate energetic costs associated with this investment by building smaller stabilimenta. However, our results are more consistent with Blackledge & Wenzel (1999, 2000), who found that spiders include stabilimenta in their webs with a cost of prey capture, because the high visibility of stabilimenta increases prey avoidance of decorated webs. The reason why we did not find clear evidence for this suggestion may be caused by the high proportion of jumping insects, which do not respond to the presence of stabilimenta (Tso, 1998).

We found that grasshoppers constituted more than 40% of prey of the *Argiope*. Because grasshoppers are, at least in our study, generally bigger and thus energetically more profitable than flies or hymenopterans, we suggest that capturing such big prey would be more beneficial than capturing pollinators. This is also confirmed either by (i) higher prey capture success of *Argiope* capturing grasshoppers in comparison with flying, rapidly escaping insects (Olive, 1980) and/or (ii) by inhabiting lower stratum of the vegetation by this species where the probability of capturing jumping insects is higher (e.g. Olive, 1980). Moreover, (iii) the likelihood of being attacked by parasitoid wasps correlates positively with web height (Blackledge & Wenzel, 2001). Thus, stabilimentum building would be beneficial in grasshopper-poor habitats where flies constitute a greater part of spiders' prey. In addition, we did not detect the effect of the nearest flower distance on spider's prey intake (but see McReynolds, 2000), which suggests that flying insects were not an important part of spiders' diet in the study area. We suggest that web decorations, at least in grasshoppers-rich habitats, probably serve a function other than prey attraction.

Spiders alter investment in orb-webs according to the energetic costs associated with web building behaviour (e.g. Venner et al., 2003). Food deprived spiders tend to invest more in sticky spirals, increase the web area and decrease stabilimentum building (Herberstein et al., 2000b; Seah & Li, 2002) which can increase their rate of prey encounter (Chacón & Eberhard, 1980; Higgins & Buskirk, 1992). Our study clearly supports this prediction, because bigger webs captured more prey. The high frequency of stabilimenta occurrence in our study could be caused either by a high level of food satiation, which is not unusual in the orb-weaving spiders (see Wise, 1979) and/or by the high abundance of parasitoids (Blackledge & Wenzel, 2001). Since we did not study the effect of parasitoids in our study, further studies of whether stabilimenta may have an anti-predator defense mechanism are needed. Surprisingly, mesh height was also significantly related to number of prey intercepted. First, it can be explained by the lower visibility of these webs which had greater mesh height, because they reflect less light than small mesh, and thus they have higher prey interception success (Rypstra, 1982; Craig & Freeman, 1991). Second, this result could be a simple byproduct of the correlation between web area and mesh height.

One of the main functions of the spider web is prey capture. Thus, the quality of the orb-web significantly affects a spider's foraging success (Craig, 1989). There are few studies examining the effect of weather conditions, especially wind and light (e.g. Vollrath et al., 1997; Herberstein & Fleisch, 2003) on spider's web geometry. We showed that orb-web design, mainly web area, capture thread length and stabilimentum area was significantly affected by weather conditions, particularly by rain. In agreement with other abiotic effects, we suggest, that reduced web area may reduce web damage by rain. Weather, such as rain, wind and temperature affects insect mobility, but we did not detect any effect of weather on prey capture rate. However, our observations of weather conditions were very simple and we did not gain enough data for webs built on rainy days. Thus, further research is needed to examine abiotic factors on spider foraging behaviour.

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