The influence of prey on size, capture area and mesh height of the orb-web of the garden spider, *Argiope aemula* (Walckenaer, 1841) (Araneae: Araneidae)

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**ABSTRACT**

The orb-web garden spider *Argiope aemula* (Walckenaer, 1841) is a sit-and-wait predator. It is argued that it can anticipate its future prey environment by detecting the presence of prey and adjusting their web building behavior accordingly. Therefore this study therefore investigates the influence of the different prey sizes and density of the capture area and mesh height of the webs constructed by the spider. In the laboratory, the spiders were given prey with different size and densities to determine their influence on the web architecture. Results show that spider individuals can increase or decrease the sizes of webs, capture area, and mesh height in response to prey size and density. Starved spiders constructed significantly larger webs than well-fed spiders. In the absence of potential prey, the spiders constructed larger capture area. In the presence of small prey, spiders significantly constructed very narrow-meshed webs or tightly spaced capture spirals than the presence of larger prey but larger than in no prey regime. Similarly, the food deprived spiders spun small-spaced mesh height than well-fed spiders. The results of the present study demonstrate that spiders can manipulate their web architecture in response to different prey sizes and food availability (densities).

**Keywords**: *Argiope aemula* (Walckenaer, 1841), stabilimentum, web size, web capture area, web mesh height.

**INTRODUCTION**

All orb-web spiders are sit-and-wait predators. According to Murakami (1993), orb-webs must serve several functions and variation in design will influence prey capture success. These include web orientation (Eberhard, 1989), web tension (Craig *et al.*, 1985), silk strength (Craig 1987), web visibility or attractiveness to prey (Craig and Bernard, 1990) and web design (Eberhard, 1986). Once the web is built, it cannot be changed easily or quickly, and the quality of the trap and that the spider’s success in prey capture depends on the decisions made before the building. Herberstein *et al.* (2000) argue that the orb-web spiders employ flexibility in their foraging behavior. In response to periods of starvation, the web size is increased and the spider attack preys unselectively. Satiated spiders on the other hand, decrease the web size and reject less profitable prey. The web with a large mesh may be less efficient in keeping insects entangled than the web with smaller mesh. Specifically, this study aims to answer the following questions: (1) Does the prey body length variation results in the differences in web mesh height? (2) Does the variation in
foraging success influence the architecture of the web, hence, well-fed or satiated spiders build smaller web and absence of prey increases the web size and capture area?

**MATERIAL AND METHODS**

**Feeding Treatment.** Thirty seven (37) penultimate and adult females (Fig. 1) of *Argiope aemula* (Walckenaer, 1841) were collected and each was placed in a 13x9x9cm upturned plastic cup and watered through wet cotton and fed with one blue fly and brought to the laboratory. It was then starved for four days prior to experimentation to ensure that the spiders’ energetic status was uniform. Each spider was housed in a wooden cage 60 x 60 x 20 cm, covered with clean plastic sheeting on the top, front, and back. Screen sides provided ventilation. Only spiders (*N*=30) that spun webs on the next 24 hours were used in the experiment.

Spiders were subjected to three sequential feeding treatments. These were: (A) small-size prey; (B) large-size prey; and (C) no prey. Spiders in small-size prey regime were given fruit flies (*Drosophila* sp.; body size: 0.25-0.30 cm) *ad libitum* and one grasshopper (body size: 1.2-1.6 cm) was introduced directly into the webs to spiders in large-size prey regime. For the first three (1-3) consecutive days, spiders were given fruit flies *ad libitum*. For the next 3 days (day 4-6), spiders were given one grasshopper every day. For five (5) days (day 7-11) the spiders were fasted. The web architecture were observed every day in small and large prey regime, while in no prey regime, only webs spun in the final 3 days (day 9-11) were observed to ensure that the spiders were already starving. For the purpose of comparison, spiders in no prey feeding regime are categorized “starved” or “fasted” while in small-size prey and large prey regime are considered “poorly-fed” and “well-fed” respectively. The web architecture was observed and documented every day. The web was photographed with a ruler beside it (for calibration) and imported to UTHSCSA *Image Tool* software UTHSCSA *Image Tool* Version 3.00 where necessary measurements were done. The web capture area was determined by subtracting the area of the free zone (non-sticky spirals) from the size of the web while the mesh height is the average distance between sticky spirals of the web (Fig. 2).
The influence of prey on web size, capture area and mesh eight of the orb-web garden spider

Fig. 2: A schematic web of *Argiope aemula* demonstrating the web parameters measured. Free zone (white-color) is the area in the center of a web covered by non-sticky spirals and is present in both decorated and undecorated webs. Capture area (gray-color) is the rest of web area covered by sticky spirals. Mesh height/size/width is the distance between two consecutive sticky spirals. Stabilimentum, if present, may consist of one arm in the lower half or one arm on both the lower and upper halves, or two arms in both lower and upper halves of the webs. Sometimes stabilimenta may extend into the area covered by sticky spirals.

**Statistical Analyses.** Linear Regression, Kruskal-Wallis Test and One-way ANOVA were used to compare between treatments in terms of web size, web capture area and mesh heights. Statistical Analysis was performed using the Paleontological Statistics (PAST) Software.

**RESULTS AND DISCUSSION**

Table (1) shows that the prey treatment had a confound effect on the web size (ANOVA: $F=43.5$; $df=2$; $p<0.001$), web capture area ($F=30.08$; $df=2$; $p<0.001$) and web mesh height ($F=34.79$; $df=2$; $p=0.001$). The web size was significantly different between the three treatments (Figure 2 and Table 1). Starved spiders spun significantly larger webs than well-fed spiders (NP=$2078.3\pm457.3$ cm$^2$ vs. LP=$1250\pm466.0$ cm$^2$; Turkey’s Pairwise Test: $Q=7.645$, $p<0.001$). Similarly, spiders in small-prey regime constructed larger webs than spiders in large prey regime (SP=$1607.8\pm497.5$ cm$^2$ vs. LP=$1250\pm466.0$ cm$^2$, $p<0.001$).

Table 1: Mean ($\pm$SD) web parameters for No Prey (NP), Small-size Prey (SP), and Large-size Prey (LP) *A. aemula*.

<table>
<thead>
<tr>
<th>Parameters (cm$^2$)</th>
<th>No Prey</th>
<th>Small-Size Prey</th>
<th>Large-size Prey</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Web Size</td>
<td>2078.3±457.3; $n=50$</td>
<td>1607.8±497.5; $n=65$</td>
<td>1250±466.0; $n=67$</td>
<td>3.1E-13*</td>
</tr>
<tr>
<td>Capture Area</td>
<td>2009.7±404.5; $n=48$</td>
<td>1594.6±484.3; $n=53$</td>
<td>1216.6±456.7; $n=31$</td>
<td>1.9E-11*</td>
</tr>
<tr>
<td>Mesh Height (cm)</td>
<td>0.43±0.06; $n=46$</td>
<td>0.36±0.08; $n=60$</td>
<td>0.49±0.09; $n=44$</td>
<td>4.3E-13*</td>
</tr>
</tbody>
</table>

*P values are from Kruskal Wallis and ANOVA (*) Tests comparing the treatments (comparing means) and $n$ is the number of webs measured in each parameter.

In the absence of potential prey, spiders not only increased the web size but also the capture area. A significant difference in web capture area was observed among spiders in different feeding treatments ($p<0.001$). The no prey spiders constructed significantly larger capture area than in the presence of small prey.
This result further shows that fasted or starved spiders constructed the largest web capture area than those poorly-fed and well-fed spiders.

In the presence of small prey, spiders significantly constructed very narrow-meshed webs or tightly spaced capture spirals than the presence of larger prey (SP = 0.36 ± 0.08 cm vs. LP = 0.49 ± 0.09 cm; Q = 11.46, p < 0.001). Moreover, in the absence of prey, spiders constructed significantly narrower-meshed (0.43 ± 0.06 cm; N = 46) compared to spiders in the presence of large prey (NP = 0.43 ± 0.06 vs. LP = 0.49 ± 0.09; Q = 5.03, p < 0.001). Our results demonstrate that spiders are capable to manipulate web mesh height in response to different prey sizes. Spiders in small-size prey regime decrease the mesh height to improve retention of smaller prey because more silk can adhere to the prey. A potential for undertaking prey-specific web adjustments requires that the spider can classify prey types and respond to a change in prey types by altering features of the web in an adaptive way (Sandoval, 1994). The results of the present study show that in addition to facultative decorating their webs A. aemula adjust their web size and design based upon previous foraging history and success. A. aemula significantly increase or decrease their web size, web capture area and mesh height in response to changing prey size and density. It has been suggested that the ability of web-building spiders to function as predators is intimately linked to the construction of webs, such that, they manipulate the sizes (Sherman, 1994) and design (Craig, 1987) of webs as either evolutionary or behavioral responses to changes in prey density or type.

In the present study, the spiders were fed first with large-size prey (body size: 1.2-1.6 cm) and then allowed to starve, where the former built smaller webs than the latter. The increase in the web size could have been due to foraging success but not due to prey size since spider in no prey treatment built the largest web than those in small-prey and large-prey treatments. The prey used in the experiment strongly differed in weight and body size (prey size: 0.25 cm vs. 1.2-1.6 cm; Figure 3). These differences in prey size and weight might have affected the web size and web capture area obtained after prey digestion due to the differences in satiation between treatments rather than the effect of experience with different types of prey.

The starved spiders were also observed to be able to manipulate their web size (LP: 1250±466.0 vs. NP: 2078.3±457.3) probably to increase the prey interception rates. Although, the effect of web design on prey capture rates was not directly tested in the present study, several studies show that these web variations can directly influence the length, number and types of prey entangled (Miyashita & Shinkai, 1995; Herberstein, and Elgar 1994; Craig, 1987). Manipulation of investment in webs as means to alter foraging web area will reflect in a higher prey interception, hence, higher prey capture rate (Herberstein & Elgar 1994); a greater number of radii enable the web to absorb more kinetic energy and thus retain heavier and faster flying prey (Craig, 1987). In the absence of potential prey, spiders (starved) not only increased the web size but also the capture area. The no prey spiders constructed larger capture area than those in the presence of small prey and large prey.

Our present study also indicates a short-term response of mesh height to the type of prey. In the presence of small prey (body size: 0.25-0.30 cm; weight: 0.0011-0.0018g), spiders significantly constructed very narrow-meshed webs or tightly spaced capture spirals compared to the presence of larger prey (body weight: 1.20-1.60 cm; weight: 0.1309±0.071g) probably to efficiently intercept and capture the detected small-sized prey. The spiders were fed first with small-size prey, as the prey
was replaced with large-sized prey, the spiders adjusted (increased) the distances between the web sticky spirals. This suggests that spiders in different feeding groups adopted different foraging strategies (e.g. narrow-spaced or larger-spaced mesh height) based upon an assessment of their previous foraging success (presence of small-prey or large-prey or interception and consumption of small-prey and large prey). This further suggests that starved or food-deprived spiders increased their foraging effort in terms of silk investment by spinning more tightly spaced sticky spirals compared to satiated or well-fed spiders. Furthermore, in the absence of prey, spiders constructed narrower-meshed compared to spiders in the presence of large prey but larger than in the presence of small-size prey. This is probably because spiders were unable to detect presence of any prey type or cannot know why they are not catching prey, so spider in no prey treatment made a compromise between increasing and decreasing the mesh height to accommodate both small-size and large-size prey.

In the present study, the food-deprived spiders did not only increase the web size and capture area but also increased the number of spiral turns while decreasing the distances between spirals turns. Suggesting that starved spiders should increase their web construction effort (increased investment on web spirals) to efficiently increase their foraging effort. In addition, the increasing web construction effort could be ultimately directed to increasing prey capture rates thus increase foraging success which has a significant implication to spiders’ survival. According to Chacon and Eberhard (1980) and Herberstein et al. (2000), a larger capture area results in higher prey interception and by increasing the distance between sticky spirals spiders may enlarge over-all capture area without greater energy expenditure. Hence, the food-deprived spiders commonly increase web area to enhance prey encounter. Similarly, based on the study conducted by Eberhard (1986) and Peakall and Witt (1976), a large web intercepts more insects but at the same time more expensive to construct than small web of the same design, not only in terms of material but also because of a higher construction effort.

Finally, the observed differences in web mesh height is due to the differences in prey body length (prey size: 0.25cm vs. 1.2-1.6 cm) and prey kinetic energy (Prokop, 2006). The effects of web architecture, especially on mesh height, are interesting in light of mixed and contradicting results from other studies (Heiling and Herberstein, 1998; McReynolds & Polis, 1987, Herberstein & Elgar 1994; Eberhard, 1986; Nentwig, 1983; Vollrath 1992a,b; Murakami, 1983, Uetz et al. 1978; Blackledge and Zevenbergen, 2006, and Prokop, 2006). Murakami (1983) and Uetz et al. (1978) argued that a lower mesh height will target prey items with a smaller body length that otherwise fly through a web. Blackledge and Zevenbergen (2006) found out that increased mesh width of *Argiope aurantia* orb-webs resulted in a general reduction in the retention times of insects, though the retention times for different taxa of insects were not predicted by any specific morphological or flight characteristics. The retention times of insects are very complex, but their results suggest that mesh width can act to selectively capture a certain taxa of insects over others. The findings of their study may help to explain the variation in web architectures (mesh height) spun by *A. aemula* spiders in response to prey size variation. Our results on mesh height, however, contradicts the findings of Witt (1963), that when prey conditions were bad, thread production decreased and both web area and mesh height increased when spiders were starved.
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