

Behavioral Response of *Argiope trifasciata* to Recent Foraging Gain: A Manipulative Study

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ABSTRACT.—This study investigates how recent foraging gain affects the web-building behavior of the garden spider, *Argiope trifasciata*, especially stabilimentum-building. Adult female spiders in the field and in cages were randomly assigned to two groups, fed and unfed. Spiders in the fed group received three grasshoppers each day; spiders in the unfed group received no prey. The experiment was terminated after each *A. trifasciata* had built four consecutive webs; the number of days required by each spider was recorded. During the experiment I recorded silk length, catching area, mesh size and stabilimentum area of each web spun by test spiders. Continuously fed, field and caged spiders decreased silk output and web size, increased mesh size and increased the interval between successive foraging bouts. Unfed, caged spiders increased silk output and web size, maintained mesh size and shortened the interval between successive foraging bouts. Although unfed spiders in the field exhibited the same trend, changes in the web characteristics were not statistically significant. Stabilimentum size of fed caged spiders was greatly enhanced, but that of field spiders was unaffected. The size of stabilimenta built by unfed spiders in both field and cage was unaffected by the treatment. These results indicate that *Argiope trifasciata* do not alter size of stabilimenta in response to recent foraging gain alone, and factors other than food intake are involved.

INTRODUCTION

Many foraging studies of orb-weaving spiders examine how various web characteristics vary with food intake. Witt (1963) examined spiders' orb-building in various prey environments, and hypothesized that spiders build larger webs in response to higher prey intake. Higgins and Buskirk (1992) worked with giant wood spiders (*Nephila clavipes*) in various habitats, and found that spiders built larger orbs in habitats of lower prey availability. They proposed that larger orb size reflected spiders' increased foraging effort following previous low foraging success. Sherman (1994) artificially increased a nocturnal orb-weaving spider's (*Lariniodes cornutus*) prey intake and found a decrease in total length of silk produced and catching area of webs, but no change in size of web mesh. Higgins (1995) manipulated food intake of two species of *Nephila*, then examined the spiders' long-term response in orb size and weight gain. Spiders decreased orb size and weight gain when experiencing prolonged low food intake, and increased orb size and weight gain when experiencing prolonged high food intake. Based on the empirical evidence accumulated so far, orb-weaving spiders seem to change silk length and orb size in response to change in foraging gain.

In addition to silk output and orb size, recent studies have found that stabilimenta are important in the foraging of orb-weaving spiders. Stabilimenta are the silky structures on the webs of at least 19 genera of orb-weaving spiders (Eberhard, 1973; 1990; Levi, 1983; Tso pers. obs.), the function of which has been intensively studied over the past century. Stabilimenta had been hypothesized to adjust web tension, advertise the presence of the web,

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camouflage spiders and regulate spider's body temperature (see reviews in Edmunds, 1986; Nentwig and Heimer, 1987; Nentwig and Rogg, 1988; Craig and Bernard, 1990; Eberhard, 1990; Schoener and Spiller, 1992). Recently, several workers demonstrated that silk stabilimenta spun by various orb-weaving species greatly increased an orb's prey-interception ability. Craig and Bernard (1990) showed that web halves of *Argiope argentata* decorated with stabilimenta intercepted more prey than undecorated web halves. Decorated webs spun by *A. trifasciata* (Tso, 1996) and *A. appensa* (Hauber, 1998) intercepted more prey than undecorated webs. Even when stabilimenta were isolated from webs (spun by *A. aurantia*) and mounted on sticky traps, they were still capable of attracting insects (Tso, 1998a). Like the decorated webs of *Argiope* species, those spun by *Cyclosa conica* trapped more prey than undecorated ones (Tso, 1998b). These results suggest that stabilimenta may greatly affect the foraging success of spiders, and therefore should be seriously considered when studying the foraging ecology of orb-weavers building them.

The works by Higgins and Buskirk (1992), Sherman (1994) and Higgins (1995) lead me to hypothesize that past foraging gain, while greatly affecting silk length and orb size, may also affect stabilimentum size. Spiders may adjust stabilimentum-building, an effective foraging effort, according to various degrees of past foraging gain in the same way they adjust other web characteristics. I tested if manipulating food intake affected the size of stabilimenta and other foraging-associated web characteristics of webs spun by the garden spider, *Argiope trifasciata*.

MATERIALS AND METHODS

The spider and spider web.—This study was conducted between 1 August and 15 September 1995 in the University of Michigan Matthaei Botanical Gardens in Ann Arbor, Michigan. Banded garden spiders, *Argiope trifasciata* Forskål 1775 (see Levi 1968 for taxonomic information), were abundant in the prairie located at the Gardens. Only adult female spiders were included in the experiment, because mature male spiders do not build large webs with a foraging function. Webs of *A. trifasciata* are typically composed of radii, concentric spirals and supporting frames. A fourth component, stabilimenta, is sometimes present on either the lower half or both lower and upper halves of webs. The central hub of the web, on which the spider rests, is covered with nonsticky spirals. The rest of the web, the catching area, is constructed of sticky spirals (Fig. 1).

Field experiment.—Web sites of 37 *Argiope trifasciata* were located in the field, and spiders were marked by applying enamel paint on the dorsal opistosoma. To prevent spiders from receiving food other than that offered, nylon screens (40×40 cm²) were erected on bamboo sticks 10 cm away from a web on both sides paralleling the web. Spiders in the field might have various levels of past foraging success, which would lead to various initial hunger levels among test spiders. To unify spiders' initial hunger level, after the erection of screens (Day 1), spiders were given a grasshopper (body length between 10 and 15 mm) and were given nothing for the next two days (Day 2 and Day 3). On the beginning of Day 4, after measuring web characteristics (web 1), I randomly divided 37 test spiders into two groups and gave them different food treatments. Spiders in the first group ($n = 14$) were fed and those in the second group ($n = 23$) were unfed. Spiders in the first group were given three grasshoppers (body length between 10 and 15 mm, caught from the study site) each day until each built three more webs (webs 2, 3, and 4). Spiders in the second group were kept unfed until each built three more webs. Since *A. trifasciata* in the study site did not produce egg sacs until early to mid-October (Tso, pers. obs.), I assumed that the reproductive status and the effect of egg development on foraging response were approximately the same among test spiders. The number of days spiders took to build four consecutive webs after

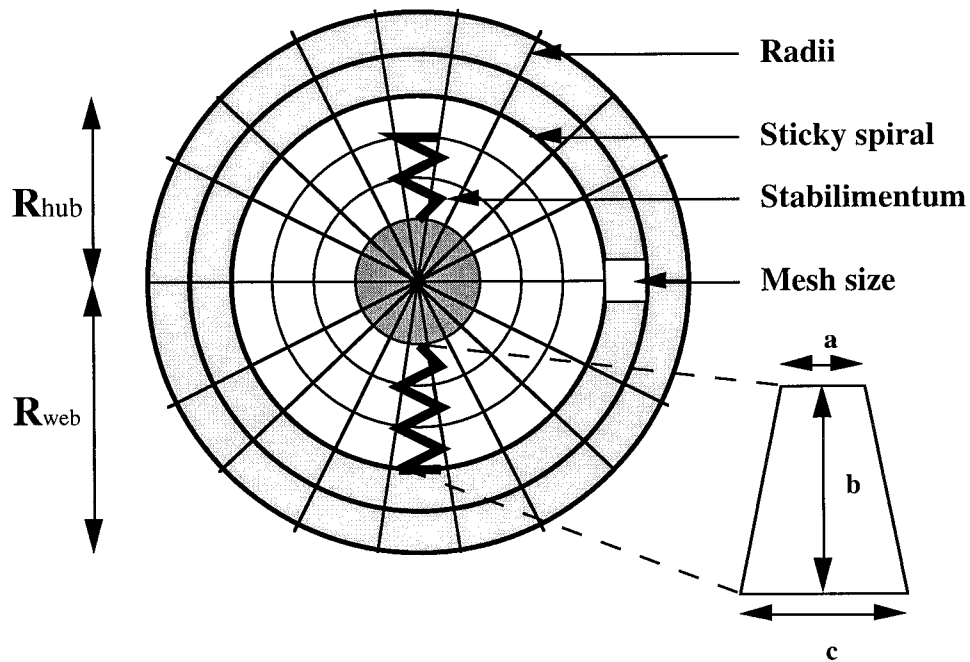


FIG. 1.—A schematic web of *Argiope trifasciata* illustrating the web characteristics measured. Area of stabilimenta is calculated as $(a + c)b/2$

preexperiment feeding was recorded. The building of a new web represents initiation of a new foraging bout (Higgins and Buskirk, 1992). Normally, most orb-weavers build a new web each day (Carico, 1986), which equals one foraging bout per day. The use of old webs represents an increase in the interval between two consecutive foraging bouts, which indicates a decrease in foraging efforts. Therefore, the number of days a spider took to build four consecutive webs was used as another estimate of foraging effort.

Laboratory experiment.—Several factors affect the acquisition and interpretation of field experiment data. Spiders will leave the web site for reasons such as low prey abundance (Olive, 1982; Janetos, 1986) or vegetation complexity (Enders, 1976; 1977). When spiders are attacked by predators or when webs are destroyed by various environmental factors (wind, rain, etc.), sample size will be seriously reduced. Finally, vegetation complexity of web sites greatly affects web characteristics. The space available at a certain web site limits the expansion of a spider's web. These factors make interpretation of food treatment effect difficult. Therefore, I repeated the same experiment in the laboratory at Matthaei Botanical Gardens to better control the factors described above. I built 20 cages ($40 \times 40 \times 20$ cm³) out of foam board and nylon screen, and introduced one adult female *Argiope trifasciata* into each cage. After these caged spiders received preexperiment feeding (identical to that received by field spiders), I randomly assigned half of them to be fed and the others to be unfed. When all caged spiders had built three more webs, the whole procedure was repeated again using another 20 spiders collected from the field. Data collected from two sets of laboratory experiments were pooled for the analysis.

Measurement of web characteristics.—Beginning with web 1, I recorded the following var-

ables from webs built by spiders in the field and cages: (1) number of radii (#radii), (2) area of stabilimenta (stab. area), (3) mean hub radius ($\bar{x}R_{\text{hub}}$), (4) mean web radius ($\bar{x}R_{\text{web}}$) and (5) mean number of sticky spirals ($\bar{x}\#\text{spiral}$) (Fig. 1). Except for the number of radii and area of stabilimenta, the other variables were averaged from measurements from four cardinal points of the webs. I estimated mean mesh size, total silk length and catching area by equations provided by Sherman (1994), and parameters were calculated as follows:

$$\text{Mean mesh size} = \frac{\text{Mean web radius} - \text{mean hub radius}}{\text{Mean number of meshes in catching area}} = \frac{\bar{x}R_{\text{web}} - \bar{x}R_{\text{hub}}}{\bar{x}\#\text{spiral} - 1};$$

$$\begin{aligned} \text{Total silk length} &= \text{total spiral length} + \text{total radii length} \\ &= [(\bar{x}R_{\text{web}} + \bar{x}R_{\text{hub}}) \times \bar{x}\#\text{spiral} \times \pi] + [(\bar{x}R_{\text{web}} - \bar{x}R_{\text{hub}}) \times \#\text{radii}]; \end{aligned}$$

$$\text{Catching area} = \text{web area} - \text{hub area} = \pi \times [(\bar{x}R_{\text{web}})^2 - (\bar{x}R_{\text{hub}})^2].$$

Each day after measuring the web variables, I made a small hole in the upper right corner of the web. Since *Argiope* spiders do not repair their webs during the day (Tso, pers. obs.), the absence of the hole on the web indicated that a new web was built. I also marked stabilimenta with enamel paint to tell if the stabilimentum observed was newly built or left over from the previous web. Since a newly-built web indicated initiation of a new foraging bout, the web variables were only measured from newly built webs. For all the webs recorded throughout the study, when spiders built a new web, they built a new stabilimentum.

Data analysis.—I used Multivariate Analysis of Variance (MANOVA) tests to simultaneously examine various foraging responses of *Argiope trifasciata*. The web characteristics recorded from web 1 were used as the foraging effort before treatment, and those recorded from web 4 were used as the foraging effort after treatment. Web characteristics examined in MANOVA tests were total silk length, catching area, mesh size and stabilimentum area. A total of four MANOVA tests were performed to assess the web characteristic changes of (1) field-fed spiders, (2) caged-fed spiders, (3) field-unfed spiders and (4) caged-unfed spiders. I used two Mann-Whitney *U* tests to compare the number of days spiders took to build four consecutive webs after pre-experiment treatment between fed and unfed spiders in the field and cages.

RESULTS

Complete data for fed spiders was collected from 13 (out of 14) spiders in the field and 13 (out of 20) spiders in cages, while complete data for unfed spiders was collected from 12 (out of 23) spiders in the field and 13 (out of 20) spiders in cages. Two reasons were responsible for the low data-retrieval rate of caged spiders. First, some introduced spiders did not build any functional orb-webs in the cages. Second, field spiders tended to consume all the grasshoppers provided, but some caged spiders did not consume all the grasshoppers provided. To ensure that field and caged fed spiders received the same level of feeding so their performance could be compared, I excluded from the analyses data recorded from caged spiders failing to consume all the grasshoppers provided.

Total silk length.—*Argiope trifasciata* in field and cages responded similarly to the fed treatment but differently to the unfed treatment. After feeding, the total length of silk produced in web 4 was reduced significantly for both field (58.6% less, Table 1a) (MANOVA: $df = 1$, $F = 36.065$, $P < 0.001$) and caged spiders (40.8% less, Table 1b) (MANOVA: $df = 1$, $F = 31.000$, $P < 0.010$) when compared to web 1. Food deprivation significantly increased silk production of spiders in cages (63.5% more, Table 2b) (MANOVA: $df = 1$, $F = 17.410$, $P < 0.001$). However, silk length recorded from web 4 of spiders in the field

TABLE 1.—Mean (\pm SE) of silk length (Silk, cm), catching area (Area, cm²), mesh size (Mesh, mm), stabilimentum area (Stab. area, mm²) and percentage of spiders building stabilimenta (% Build stab.) before and after fed treatments recorded from *Argiope trifasciata* in both the field and cages

	Silk	Area	Mesh	Stab. area	% Build stab.
(a) Field spiders:					
Web 1	1656.0 \pm 117.9	387.7 \pm 51.2	2.8 \pm 0.2	66.5 \pm 35.7	61.5%
Web 4	686.6 \pm 110.2	184.5 \pm 33.1	3.7 \pm 0.2	62.6 \pm 17.7	61.5%
(b) Caged spiders:					
Web 1	1529.3 \pm 85.4	402.3 \pm 27.3	3.4 \pm 0.2	106.2 \pm 14.9	92.3%
Web 4	905.3 \pm 72.5	276.7 \pm 27.6	4.2 \pm 0.2	174.7 \pm 20.7	92.3%

was not significantly higher than that of web 1 (Table 2a) (MANOVA: df = 1, F = 0.003, P > 0.050).

Catching area.—Feeding significantly reduced the catching area of webs built by *A. trifasciata* in the field (52.5% smaller, Table 1a) (MANOVA: df = 1, F = 11.101, P < 0.010) and in cages (31.3% smaller, Tables 1b) (MANOVA: df = 1, F = 10.478, P < 0.010). Web 4, spun by unfed *A. trifasciata* in cages, was significantly larger (46.4% larger, Table 2b) than web 1 (MANOVA: df = 1, F = 8.481, P < 0.010). But under the same treatment the catching area of web 4 built by *A. trifasciata* in the field did not statistically differ from that of web 1 (Table 2a) (MANOVA: df = 1, F = 0.010, P > 0.050).

Mesh size.—Previous studies of orb weavers suggested that mesh size tends to remain constant under various foraging conditions. However, in this study *A. trifasciata* altered mesh size in response to increased foraging gain. Feeding significantly increased mesh size of web 4 built by spiders in the field (32.1% larger, Table 1a) (MANOVA: df = 1, F = 10.980, P < 0.010) and in cages (23.5% larger, Table 1b) (MANOVA: df = 1, F = 9.551, P < 0.010). In contrast, mesh size of web 4 did not differ statistically from that of web 1 for unfed spiders in the field (Table 2a, MANOVA: df = 1, F = 0.293, P > 0.050) and in cages (Table 2b, MANOVA: df = 1, F = 2.501, P > 0.050).

Stabilimentum area.—Although food treatments used in this study significantly affected the aforementioned web characteristics, their influence on the size of stabilimentum was not as distinct. Feeding did not significantly affect stabilimentum area of web 4 built by spiders in the field (Tables 1a, MANOVA: df = 1, F = 0.010, P > 0.050), nor did it alter the proportion of spiders building decorated webs (Table 1a). In contrast to what was

TABLE 2.—Mean (\pm SE) of silk length (Silk, cm), catching area (Area, cm²), mesh size (Mesh, mm), stabilimentum area (Stab. area, mm²) and percentage of spiders building stabilimenta (% Build stab.) before and after unfed treatments recorded from *Argiope trifasciata* in both the field and cages

	Silk	Area	Mesh	Stab. area	% Build stab.
(a) Field spiders:					
Web 1	1740.2 \pm 161.4	409.7 \pm 61.2	2.8 \pm 0.2	39.6 \pm 13.3	58.3%
Web 4	1754.4 \pm 166.3	418.3 \pm 56.4	2.9 \pm 0.2	60.4 \pm 14.4	61.5%
(b) Caged spiders:					
Web 1	1141.2 \pm 129.8	336.2 \pm 43.3	3.7 \pm 0.3	108.5 \pm 16.4	92.3%
Web 4	1865.8 \pm 115.4	492.5 \pm 31.7	3.3 \pm 0.1	117.9 \pm 18.3	92.3%

predicted, feeding increased stabilimentum size of caged spiders (64.2% larger, Tables 1b) (MANOVA: $df = 1$, $F = 7.186$, $P < 0.050$), although it did not generate a significant effect on the proportion of spiders building decorated webs (Table 1b). Whereas food deprivation significantly affected other web characteristics of caged spiders, this treatment neither increased nor decreased stabilimentum area of field (Tables 2a, MANOVA: $df = 1$, $F = 1.124$, $P > 0.050$) or caged spiders (Tables 2b, MANOVA: $df = 1$, $F = 0.148$, $P > 0.050$), or the proportion of spiders building decorated webs (Table 2a, 2b).

Foraging bouts.—Fed spiders in the field took significantly longer to build four consecutive webs after pre-experiment feedings (5.1 ± 0.2 vs 4 ± 0.0 days, Mann-Whitney $U = 132$, $P < 0.010$), as did fed spiders in cages (5.4 ± 0.2 vs 4.5 ± 0.2 days, Mann-Whitney $U = 128$, $P < 0.050$).

DISCUSSION

Although food treatments used in this study affected web characteristics such as silk length, catching area and mesh size, they did not affect size of stabilimenta as predicted. When *Argiope trifasciata* experienced high food intake they reduced foraging effort by lowering silk production, reducing orb size, increasing mesh size and lengthening the intervals between successive foraging bouts. When *A. trifasciata* experienced low foraging success they increased both foraging effort by producing more silk and building larger orbs, while maintaining mesh size and the interval between successive foraging bouts. However, feeding did not reduce but increase the size of stabilimenta of caged spiders. Whereas feeding treatment generated contradictory results, food deprivation failed to generate significant effects on the area of stabilimenta. These results indicate that, although stabilimenta can be considered one of *Argiope* spiders' foraging efforts, the control of its construction is far more complicated than that of other web characteristics examined in this and previous studies. Since the field and laboratory feeding experiments in this study, and the laboratory feeding experiment conducted by Nentwig and Rogg (1988) both failed to generate a predictable influence on the size of stabilimenta, food intake is not the sole controlling factor.

The differential effect of food treatments on orb silk and stabilimentum silk output may result from a difference in utilization patterns of glands producing these silks. Peters (1993) found that aciniform glands were responsible for production of stabilimentum silk. However, aciniform glands' secretion is also used in prey wrapping (Foelix, 1982). *Argiope* spiders use prey-wrapping in subduing their prey (Harwood, 1973; Olive 1980), and this practice requires much silk. For instance, an adult *Argiope aurantia* needs to spend an average of 20 to 30 sec of wrapping time to subdue an orthopteran (Harwood, 1973). Moreover, the catching success of *Argiope* spiders is low (20% to 50%, Olive, 1980; Pasquet and Leborgne, 1990). When an *Argiope* spider tries laboriously to subdue a prey but fails to consume it, the subduing act may greatly deplete the spider's aciniform glands while providing little nutrient supplement. When this occurs, the size of stabilimenta would be greatly reduced in the next foraging bout. Perhaps *Argiope* spiders always decorate their webs whenever possible, and the amount of silk available in the aciniform gland determines the size of stabilimenta. Whereas aciniform glands are used both before (building stabilimenta) and during foraging bouts (wrapping prey), the glands producing other orb silk (*e.g.*, aggregates and flagelliformes glands) are mostly used once before each foraging bout. Because *Argiope* spiders usually build one orb each day, and do not repair web damages, *Argiope* spiders' orb silk production is likely to be relatively free from contributing factors other than past foraging gain. This explains why food treatments of this study generate predicted effects on orb silk production.

Considering aciniform gland content as one of the regulating factors of stabilimentum size can help interpret the observed results. Food-deprivation does not affect stabilimentum size of either field or caged *Argiope trifasciata*. Since unfed spiders did not use their wrapping silk and thus did not deplete their aciniform gland, an unaltered stabilimentum size was a reasonable consequence. Fed spiders in the field also did not significantly alter their stabilimentum area, which may result from a trade-off between excessive use of wrapping silk and increased silk secretion due to excessive feeding. The amount of food received by fed spiders greatly exceeds the daily foraging intake of *A. trifasciata* (around 0.2 ± 0.4 grasshopper per day) in the study site as estimated by Tso (1996), and that huge increase of nutrients will considerably increase the activity of the aciniform gland. The significant increase of caged spiders' stabilimentum size may result from those spiders' high food intake and low aciniform gland output. In contrast to field spiders' quick response to prey and active prey-wrapping, caged spiders tended to barely notice the introduction of grasshoppers. Moreover, the remains of consumed grasshoppers dropped by caged spiders were usually only slightly wrapped. The slight use of wrapping silk, plus increased silk production resulting from excessive food consumption, should be responsible for caged spiders' increased stabilimentum size.

While caged unfed *Argiope trifasciata* greatly increased silk output and catching area, unfed spiders in the field did not exhibit similar responses. Differential responses of field and caged spiders to food deprivation may result from the following reasons. First, unfed spiders in the field might have received some undetected prey. Although unfed spiders in the field were frequently monitored in the day time to remove any insect accidentally caught by the web, when researchers were absent, spiders sometimes received a small amount of prey. In contrast, the food intake of caged spiders was effectively controlled. Thus, receiving uncontrolled prey would result in a smaller increase of foraging effort. Second, in the spider's natural habitat the extent to which web dimensions could be altered is very limited. In the field, while the reduction of web size was less affected by the dense vegetation pattern, the small amount of space available to *A. trifasciata* would prevent the spiders from greatly expanding the sizes of their webs. However, caged spiders were provided with a larger-than-normal web site, thus the building of large webs was made possible. So, the dense vegetation pattern in the field should be partially responsible for the difference in the extent of web enlargement between caged and field unfed spiders.

Although this study fails to demonstrate that *Argiope* spiders alter stabilimentum size according to past foraging gain, some of the spiders' responses provide interesting insights about foraging strategies of orb-weaving spiders. First, this study demonstrated that spiders increase mesh size when receiving ample food. The size of the mesh is suggested to determine the lower size limit of prey that can be intercepted by the web (Uetz *et al.*, 1978; Chacón and Eberhard, 1980; Murakami, 1983). The increase of mesh size will lead to a reduced size range of prey (a reduced diet breadth), which indicates that spiders become more choosy about prey as they experience high recent foraging gain.

Second, maintaining the mesh size by unfed spiders during food deprivation indicates that there is a proportional, instead of diminishing, return for orb-weaver's foraging effort. Rypstra (1982) suggested that spiders' increased foraging output will lead to a diminishing return. Because, as a spider increases foraging effort by increasing thread density of its web, both prey-retaining ability and web visibility increase. Efforts made by the predator to retain prey better would make the web more visible to prey, thus generating a diminishing return. However, results from this study indicate that spiders can increase foraging effort without increasing web visibility. *Argiope trifasciata* did not increase its effort by increasing both density of thread (decreasing mesh size) and size of orb. Instead, it increased silk output

but maintained mesh size. In this way, a spider's chance of intercepting prey can be increased, but not at the cost of increasing web visibility. Therefore, *A. trifasciata*'s increase in foraging effort will lead to a proportional return instead of a diminishing return. If this is the case, the energy reserve of spiders becomes the limiting factor for the expansion of orb size.

Finally, the prompt increase of *Argiope trifasciata*'s silk output and catching area in response to food deprivation suggests that orb-weavers' short-term and long-term responses to low foraging success differ. Higgins (1995) demonstrated that orb weavers follow a small-orb-size, low-weight-gain strategy when prey intake is continuously low. However, silk output and catching area of caged *A. trifasciata* under food deprivation increased considerably. Some of the test spiders significantly increased their orb size in web 2 or web 3. This phenomenon indicates that prompt and extensive increase in foraging effort is the initial response of orb-weavers when experiencing low foraging success. If continuously receiving low prey intake, orb-weavers then will gradually reduce their foraging output, as was demonstrated by Higgins (1995). Therefore, the short-term response of orb-weavers to low prey intake should be a prompt and extensive increase of foraging effort, and the long-term response a reduced foraging output reflected by smaller orb size.

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