

# Feeding mediated web-building plasticity in a cobweb spider

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## Abstract

Behavioral plasticity has been proposed as a means by which animals alter their phenotypes in response to changing conditions. Animals may display behavioral plasticity as a consequence of environmental variation. The detritus-based, bell-shaped cobweb spider *Campanicola campanulata* is an ideal model to study behavioral plasticity, because its web architecture is easy to be quantified, and the functions of different parts of the web are clear. Though the plasticity of cobweb architecture has been reported in a few species, retreats as important defensive structures have rarely been considered before because retreats in most cobwebs are relatively small compared with the web size. We studied the web-building behaviors of *C. campanulata* under different feeding regimes. We set up 3 spider treatments with different feeding conditions: marginally well fed, moderately well fed, and extremely well fed, and observed the differences in the web architecture among them. In addition, we measured the mechanical properties of anchor silk, and also calculated the foraging and defense investment of the spiders. The results showed that marginally well-fed spiders build cobwebs with significantly longer length of anchor silk, lower retreat to the ground, more number and longer gumfooted lines, and larger capture area, while extremely well-fed spiders build cobwebs with significantly bigger retreat volume and higher height of retreat to the ground. In addition, marginally well-fed spiders invest significantly less during cobweb construction. However, there was no significant difference between the breaking force and elongation at break in anchor silk among different treatments. These results demonstrated that marginally well-fed spiders invest more in foraging, and extremely well-fed spiders invest more in defense, and the spider made a balance between foraging and predator avoidance in response to changes in physiological state. Our study strengthens the current understanding of web construction in cobweb spiders, especially those facing high costs during retreat construction.

**Key words:** behavioral plasticity, *Campanicola campanulata*, cobweb spider, defense, foraging.

Animals with conflicts between foraging and defense may reconcile selective pressures from successful foraging and predator defense, either reducing foraging activity to reduce predation or taking risky actions to increase foraging efficiency (Lind and Cresswell 2005). Internal (e.g., shifts in energy requirements or states) and external changes (e.g., fluctuations in prey availability or predator density) affect whether defense or foraging is more important at different stages (Craig et al. 2001; Zhang et al. 2022). Behavioral plasticity provides a mechanism for explaining how animals adjust their behaviors as needed for defense or foraging (Rayor and Uetz 1990). Predators with plastic foraging strategies may have more selective advantages, which has been demonstrated in studies of trap predators such as ant lions and web-building spiders (Scharf et al. 2011). Animals can best adapt to changing environments by expressing different behaviors in different situations (Wong and Candolin

2015; Scharf 2016). Numerous studies of how state changes induced by prey availability influence foraging decisions have provided an important bridge for investigating behavioral plasticity and trade-offs between different behavioral investments (Blamires et al. 2011; Scharf et al. 2011).

In turn, any variables affecting the costs and benefits of behavioral choice will lead to behavior changes (Craig et al. 2001). In web-building spiders, many species decorate webs with silks (Herberstein et al. 2000; Wang et al. 2022) or construct retreats in their webs for defensive use (Eberhard et al. 2008). These defensive structures require a lot of energy and may decrease the energy that can be used in the construction of prey capture structures (Zevenbergen et al. 2008). Therefore, spiders may make a balance between constructing defensive structures and foraging structures under different prey abundance conditions (DiRienzo and Montiglio 2016). However, few studies have looked into this issue.

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Cobweb spider is an ideal model for studying how animals cope with selective pressures between foraging and defense because different parts of cobwebs function as different roles in foraging, predator defense, and reproduction (Eberhard et al. 2008; Zevenbergen et al. 2008; Higginson et al. 2015). In addition, the web architecture of cobwebs is easy to be quantified (Blackledge and Zevenbergen 2007). However, related reports are quite a few, especially about how cobweb spiders alter web construction behaviors in response to their environment, such as prey abundance. It has been reported in western black widow spider *Latrodectus hesperus* that the web architecture varied between starved and fed situations (Blackledge and Zevenbergen 2007; Zevenbergen et al. 2008). However, there are few reports that have taken retreats constructed by cobweb spiders into consideration, though they are widely used by many cobweb spiders (Eberhard et al. 2008). Benjamin and Zschokke (2003) demonstrated in theridiids that the spiders adjust their web architecture under foraging pressure. In addition, few studies have examined how the plasticity of web-building behavior relates to changes in the mechanical properties of web silk.

In Theridiidae, there is a group of spiders whose webs consist of anchor silk, a detritus-based bell-shaped retreat, and sticky gumfooted lines, mainly in the genus *Campanicola* and *Parasteatoda* (Henschel and Jocqué, 1994; Li et al. 2021; Figure 1). The retreat is made up of silk-coated sand grains, soil particles, prey remains, and plant debris, thus we call it detritus-based retreat. It functions to avoid predators (Manicom et al. 2008), and the gumfooted lines function as the primary prey capture elements as those in most cobwebs (Blackledge and Zevenbergen 2007). We observed in the field that the volumes of the retreat and the number of sticky gumfooted lines varied significantly in this species. It is often observed in the field that some retreats are so small or loose that part of the spider body is exposed directly to predators. Also, the height of retreat to the ground varied significantly; some are very close to the ground, but others are relatively higher. In theory, the spider would be more capable to avoid predators if its retreat is bigger and higher to the ground, and it would be more successful in foraging with more gumfooted lines and a lower retreat. Due to the energy consuming of constructing these 2 web structures (Blamires et al. 2014), we hypothesized that the spider may make a balance between constructing the retreat (i.e., for predator avoidance) and the gumfooted lines (i.e., for foraging), especially when the prey resources are scarce. To test our hypothesis, we investigated how *C. campanulata* distributed investment in constructing the retreat and the gumfooted lines in response to state changes induced by feeding regimes (marginally well fed vs. extremely well fed).

## Materials and Methods

### Study species

*Campanicola campanulata* (Araneae: Theridiidae) is widely distributed in South China, such as Hubei, Zhejiang, and Guizhou provinces (Chen 1993). It builds a web in cool but rain-proofed places such as concaves of rocks or earth walls, or under low overhanging branches (Figure 1A). It feeds mainly on ants, and usually lives in aggregation, building webs solitarily, with 1 spider per retreat (Figure 1B, C). The web consists of anchor silk, a bell-shaped retreat, and dozens of sticky gumfooted lines (Figure 1D). Anchor silks are usually made of strands of silk suspended from concave walls

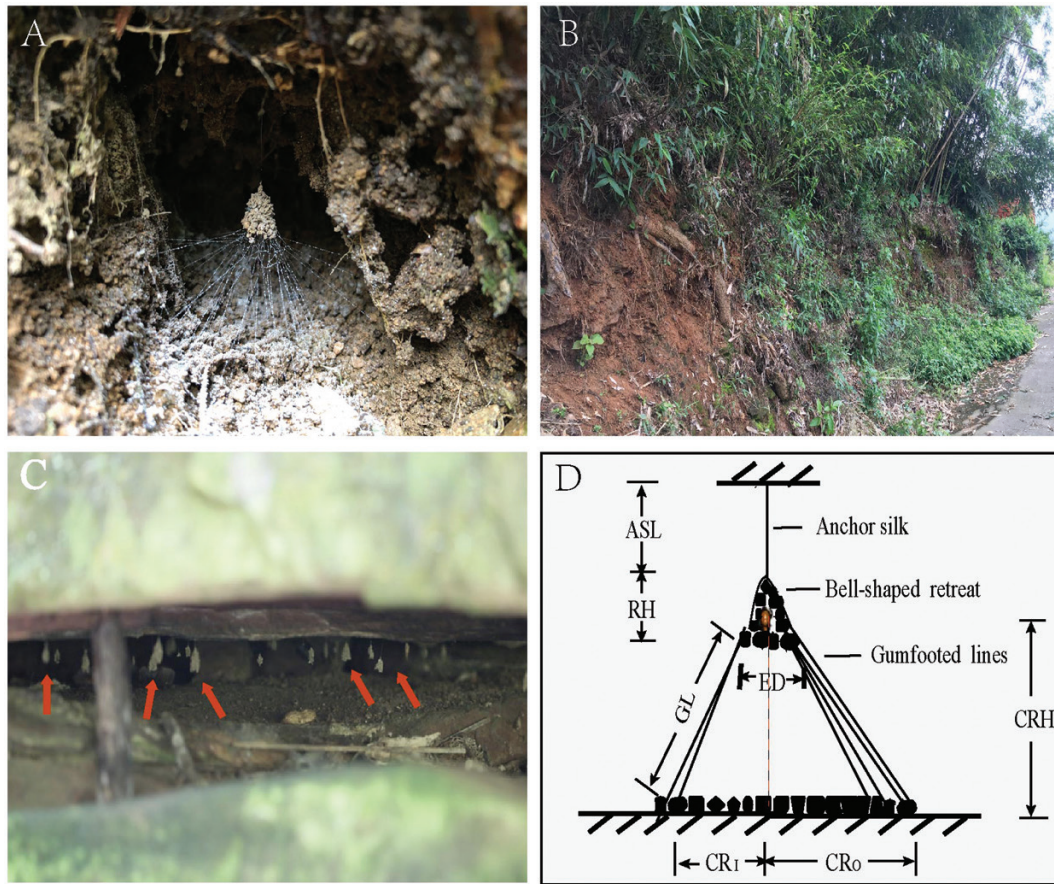
or tree roots. These structures prevent damage to the web by winds. The retreat is made of silk, sand, pebbles, debris, leaves, or shells, and has a small opening at the bottom. Its weight is usually 30–40 times the body weight of the spider. The gumfooted lines of the web emanate from the retreat edge and are fastened to coarse sand grains or fixed substrata, which are mainly used to form a capture web. When ants are intercepted by sticky gumfooted lines, the lines detach from the substrate and pull the prey up toward the retreat, making it difficult for the ants to gain the leverage needed for escape (Argintean et al. 2006). The configuration of the suspended retreat can significantly reduce the spider's vulnerability to enemies because there are silken tunnels inside the retreat (Henschel and Jocqué 1994), which the enemies cannot trespass into. In addition, the sticky gumfooted lines also more or less prevent the invasion of enemies, such as parasitic wasps.

### Spider and maintenance

From May to June 2019, we collected sub-adult (i.e., 1 molt before adulthood, ~2.4 mm in body length) *C. campanulata* from Hubei Dabie Mountain National Nature Reserve in Huanggang, Hubei Province, China (31°5'N, 115°48'E), and raised them to adulthood in the laboratory. The spiders were maintained individually in a plastic box (length × width × height: 10 cm × 5 cm × 10 cm) with bamboo sticks attached to their inner sides to allow them to build webs. The front and back sides of the box were made of removable transparent Perspex glass. All spiders were kept in the laboratory with controlled environmental conditions (temperature: 25 ± 1 °C; relative humidity: 80 ± 5%; photoperiod: 14 h: 10 h L:D). The bottom of the box was covered with a layer of sand for the spider to collect to build a retreat, and a piece of sponge with absorbed water was placed at the bottom of the box to provide water for the spider. We fed each spider with 2 ants (*Monomorium* sp., ~2.2mm in body length) every 2 days, and the developmental status (molting) of each spider was checked twice daily (09:00 and 21:00).

### Experimental design and procedure

Sixty newly matured female spiders (~2 days after maturity) were randomly divided into 3 treatments ( $N = 20$  in each group): marginally well fed, control (normal feeding, i.e., moderately well fed), and extremely well fed. The body size (carapace width, body length, and body weight) of each spider was measured before the experiment. We fed *Monomorium* ants to them for 6 days (each spider was fed every 2 days with 2 ants at each time). Then, we measured the morphological parameters of their webs and examined the mechanical properties of the anchor silks (i.e., threads underlying the axial fibers). These data were considered as pretreatment data. After collecting these data, we destroyed all the webs, and let the spiders build new webs in another 6 days, and during this period of time, the spiders were fed differently. According to our field dissection of the retreat of the spiders, we found that the most normally developed adult spiders generally consumed about 6 ants in a week. Therefore, in this study, for those spiders in control treatment (moderately well fed), they were fed every 2 days with 2 ants at each time (6 ants in total). For those spiders in marginally well-fed treatment, they were fed only once with 2 ants (2 ants in total). For those spiders in extremely well-fed treatment, they were fed every 2 days with 5 ants at each time (15 ants in total). We observed and recorded the consuming process to make sure the ants were



**Figure 1.** Web morphology, habitat, living pattern, and diagrammatic sketch of web architecture of spider *C. campanulata*: (A) a web situated in a soil concave; (B) spiders inhabit in soil slopes; (C) group living pattern; (D) main parameters of web architectures measured in this study.

consumed. After these 6 days of different feedings, we measured the morphological parameters of the webs and examined the mechanical properties of the anchor silks again in each group. These data were considered as posttreatment data.

### Web architecture and behavioral investments

For each web, we measured 8 kinds of web parameters, including the length of anchor silk (ASL), the height of retreat (RH), the number of gumfooted lines (GLN), the height of the retreat center from the ground (CRH), the diameter of retreat entrance (ED), the length of each gumfooted line (GL), the lengths of inner and outer capture radii ( $CR_1$  and  $CR_0$ ), and the weight of the retreat (RW) (Figure 1D). The projection of gumfooted lines on the ground is irregular, some gumfooted lines are near to the center, and the others are far to the center, so we used  $(CR_1 + CR_0)/2$  to calculate the average radius to estimate the capture area. The weight of the retreat was measured after the other 7 web architecture parameters were measured. We cut the retreat off from the web and measured its weight to the nearest 0.01 mg using an electronic balance (FA1004N type, HANGPING). Because the capture area is an important indicator for prey capture and the volume of retreat is an important indicator of predator avoidance, spiders with bigger capture area may have higher foraging success and spiders with larger retreats may offer better protection from predation (Manicom et al. 2008), we calculated the CA of the cobweb and the RV with the following formula:

$$\text{Capture area} = \pi \times CR^2$$

$$\text{Retreat volume} = \frac{1}{3}\pi \times \left(\frac{1}{2}ED\right)^2 \times RH$$

where

$$CR = (CR_1 \times CR_0)/2$$

We also quantified the behavioral investments: foraging investment (material cost, i.e., total length of gumfooted lines, GTL) and defense investment (DI) during web building with the following formula:

$$\begin{aligned} \text{Total length of gumfooted lines} \\ = \sum GL_1 + GL_2 + GL_3 + \dots + GL_n \end{aligned}$$

$$\text{Defense investment} = RW \times CRH \times g$$

where,  $GL_1, GL_2, \dots, GL_n$  are the length of each gumfooted line.  $\pi$  is 3.14 and  $g$  is 9.8  $m/s^2$ .

We selected the GTL to quantify foraging investment because gumfooted lines are the primary foraging tool of cobweb spiders (DiRienzo and Montiglio 2016), including *C. campanulata*.

### Anchor silk mechanical properties

In web-building spiders, the silks at the anchoring point are glue-like cement consisting of aligned nanofibrils, lipid enclosures, and a dense, isotropic boundary layer, which are used to strongly fasten to substrates (Wolff et al. 2015). Anchor silk is essential for maintaining the integrity of the

cobweb because it is used to hang the whole web (Wolff et al. 2020; Figure 1D). To examine the impact of the feeding regime, we tested and compared the mechanical properties of anchor silks between pretreatment and posttreatment groups. We made U-shaped cardboards (width  $\times$  depth: 10 mm  $\times$  10 mm), and used a pair of them to collect the anchor silks by crossing and adhering them to the 2 arms of 1 piece and locked up by the other piece. Two kinds of mechanical properties were examined: the breaking force (BF) (i.e., loading force when the silk breaks) and elongation at break (EB).

The mechanical properties of anchor silks were measured in accordance with British Standard BSEN13895:2003, following the methods of Zhao et al. (2019). Specifically, a paper was cut into a 3 cm  $\times$  4 cm rectangle, from which a 1 cm  $\times$  2 cm rectangle was cut from the center. The anchor silk was put upright on a piece of paper and fixed from the upper and lower ends of the paper with scotch tape to ensure that the distance between the 2o ends of the anchor silk was 10 mm (Remadevi et al. 2017). The tensile properties, including breaking force (BF) and elongation at break (EB) of treated anchor silks, were recorded by a universal material testing machine (INSTRON-3365, Instron, USA) by pulling the silk lengthwise. Each treatment was repeated 18 times (pretreatment:  $N = 18$ , posttreatment:  $N = 18$ , respectively) under the same testing condition to obtain reliable representative data, and only 1 anchor silk sample was taken from each web. Pretension was used to remove the stress to maintain the standard testing condition for all silk samples. The pretension of silk was given as  $0.5 \pm 0.05$  cN/tex, the gauge length was  $10 \pm 0.2$  mm, and the stretching speed was  $5 \pm 0.1$  mm/min (standard testing environment:  $20 \pm 2$  °C, relative humidity  $65 \pm 3\%$ ) (Shofner et al. 1991; Yu et al. 2003).

## Statistical analysis

We checked the data for the normality and homogeneity of variance using Shapiro–Wilk and Levene tests, respectively. Since the data were not normally distributed, we used the Kruskal–Wallis test to compare the differences in web architecture, mechanical properties of anchor silk, foraging, and DI between treatments. If there was a significant difference in the results, a pairwise comparative analysis was used to compare the results between any 2 groups. Wilcoxon’s signed-rank test for matched pairs to compare the pretreatment and posttreatment results in each treatment. We performed all statistical analyses using R 4.3.0 (R Core Team 2022). All tests were 2-tailed, and the  $P$ -value for significance was set at  $<0.05$ .

## Results

There were no significant differences between the body size (carapace width, body length, and body weight) of the spiders among the 3 treatments (marginally, moderately, and extremely well fed; Table 1). In the measurement of web morphology, a total of 117 webs were measured (pretreatment:  $N = 20$  for each of the marginally, moderately, and extremely well fed; posttreatment:  $N = 17, 20,$  and  $20$  for marginally, moderately, and extremely well fed, respectively). In the test of mechanical property of anchor silk, 39 anchor silks were successfully sampled and measured (pretreatment:  $N = 8, 4,$  and  $9$  for marginally, moderately, and extremely well fed, respectively; posttreatment:  $N = 7, 4,$  and  $7$  for marginally, moderately, and extremely well fed, respectively).

## Web architecture

There were no significant differences in web architecture, behavioral investments, and anchor silk properties between the pre- and posttreatment for the control group (Table 2),

**Table 1.** Mean ( $\pm$ SE) of the body size of spider in the experiment ( $N = 20$  in each treatment)

Parameters	Marginally well fed	Control (moderately well fed)	Extremely well fed	$\chi^2$	$df$	$P$
Carapace width (mm)	$0.917 \pm 0.074$	$0.908 \pm 0.059$	$0.948 \pm 0.072$	1.506	2	0.461
Body length (mm)	$2.449 \pm 0.162$	$2.446 \pm 0.220$	$2.507 \pm 0.213$	0.830	2	0.660
Body weight (mg)	$3.501 \pm 0.969$	$3.658 \pm 1.086$	$3.648 \pm 1.074$	0.893	2	0.640

**Table 2.** Mean ( $\pm$ SE) of web architectures, mechanical properties of anchor silk, foraging and behavioral investment measured in pre- and posttreatment in control (moderately well fed) treatment

Parameters		Pretreatment	Posttreatment	$V$	$P$
Web architecture	ASL (mm)	$14.98 \pm 5.46$	$14.40 \pm 5.72$	83	0.644
	RH (mm)	$11.05 \pm 3.02$	$11.50 \pm 3.10$	138	0.225
	ED (mm)	$6.44 \pm 0.91$	$6.48 \pm 0.93$	107	0.642
	CRH (mm)	$49.50 \pm 5.28$	$49.85 \pm 5.40$	100	0.867
	RW (mg)	$111.13 \pm 29.35$	$111.37 \pm 28.60$	106	0.985
	GLN	$16.10 \pm 3.32$	$16.40 \pm 3.60$	116	0.686
	CA (cm <sup>2</sup> )	$14.70 \pm 4.90$	$14.85 \pm 4.24$	209	0.382
Anchor silk properties	BF (cN)	$4.19 \pm 1.29$	$3.26 \pm 1.46$	3	0.625
	EB (%)	$25.29 \pm 9.43$	$28.21 \pm 6.02$	7	0.625
Behavioral investment	GTL (mm)	$791.25 \pm 185.22$	$804.53 \pm 178.73$	71	0.216
	DI (10 <sup>-6</sup> J)	$5.41 \pm 1.60$	$5.43 \pm 1.47$	66.5	0.156

ASL: the length of anchor silk; RH: the height of retreat; ED: the diameter of retreat entrance; CRH: the height of retreat center from the ground; RW: the weight of retreat; GLN: the number of gumfooted line; RV: the volume of retreat; CA: capture area of the web; GTL: the total length of gumfooted line; DI: the defense investment during web-building; BF: breaking force; EB: elongation at break.

indicating that web-building frequency did not affect the web-building behaviors of the spider.

In pretreatment, there were no significant differences in any measured parameter of web architectures among the 3 treatments (Table A1, Figure 2), indicating that the web architecture of the different treatments in pretreatment was not significantly varied. However, in posttreatment, there were significant differences among all these parameters among the 3 treatments (ASL:  $\chi^2 = 21.88$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2A; RH:  $\chi^2 = 29.91$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2B; GLN:  $\chi^2 = 26.13$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2C; CA:  $\chi^2 = 21.88$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2D; RV:  $\chi^2 = 32.21$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2E; CRH:  $\chi^2 = 28.35$ ,  $df = 2$ ,  $P < 0.001$ , Figure 2F; ED:  $\chi^2 = 26.01$ ,  $df = 2$ ,  $P < 0.001$ ; RW:  $\chi^2 = 22.26$ ,  $df = 2$ ,  $P < 0.001$ ) (Table A1), suggesting that web architecture can be significantly affected by different feedings.

In posttreatment, comparing with webs built by spiders in control (moderately well fed) and extremely well-fed treatment, the webs built by those in marginally well-fed treatment have significantly longer length of anchor silk (ASL) ( $V = 152$ ,  $P < 0.001$ ) and lower retreat (RH) ( $V = 0$ ,  $P < 0.001$ ). Because the longer length of anchor silk and lower retreat mean that the spiders would be faster to reach entangled ants, but more vulnerable to predators; thus, these results together

with results that webs built by spiders in marginally well-fed treatment have more number of gumfooted lines (GLN) ( $V = 150$ ,  $P < 0.001$ ) and a bigger capture area (CA) ( $V = 153$ ,  $P < 0.001$ ), indicating that marginally well-fed spiders invested more in web structures for prey capture. In turn, webs built by those in extremely well-fed treatment group have a bigger volume of retreat (RV) ( $V = 201$ ,  $P < 0.001$ ), and a higher height of retreat to the ground (CRH) ( $V = 194$ ,  $P < 0.001$ ) (Figure 2, Table A2), indicating that extremely well-fed spiders invest more in predator avoidance rather than in prey capture.

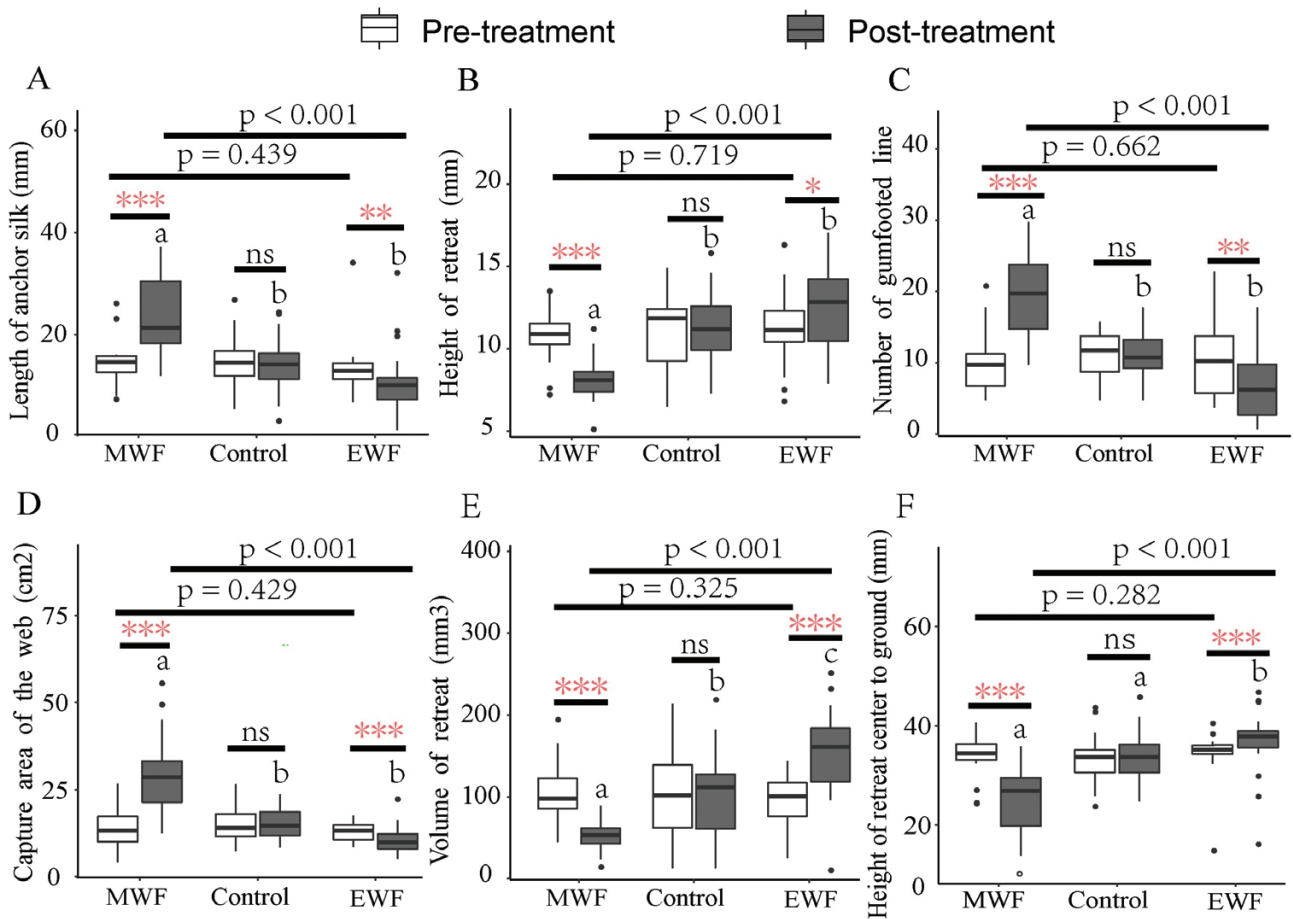
### Anchor silk properties

In pretreatment, there were no significant differences in breaking force (BF) ( $\chi^2 = 1.19$ ,  $df = 2$ ,  $P = 0.535$ ) (Figure 3A) or elongation at break (EB) ( $\chi^2 = 1.25$ ,  $df = 2$ ,  $P = 0.535$ ) (Figure 3B) of anchor silk among the 3 treatments. Also, there were no significant differences in BF ( $\chi^2 = 0.35$ ,  $df = 2$ ,  $P = 0.839$ ) (Figure 3A) or EB ( $\chi^2 = 0.32$ ,  $df = 2$ ,  $P = 0.850$ ) (Figure 3B) in anchor silk among the 3 treatments in posttreatment (Figure S1). In addition, there was no significant difference in either BF or EB of anchor silk between pre- and posttreatment in all marginally, moderately, and extremely well-fed treatment groups. These results suggested that the construction of anchor silk was not affected by feeding conditions.

**Table A1.** Mean ( $\pm SE$ ) of web architectures, anchor silk properties, foraging and behavioral investments measured in pre- and posttreatment for all treatments

Treatment	Parameters	Marginally well fed	Control (moderately well fed)	Extremely well fed	$\chi^2$	$df$	$P$	
Pretreatment	ASL (mm)	15.30 $\pm$ 1.16	15.14 $\pm$ 1.21	14.56 $\pm$ 1.35	1.65	2	0.439	
	RH (mm)	10.81 $\pm$ 0.37	11.27 $\pm$ 0.62	10.93 $\pm$ 0.53	0.66	2	0.719	
	ED (mm)	6.36 $\pm$ 0.17	6.45 $\pm$ 0.20	6.87 $\pm$ 0.12	6.50	2	0.059	
	CRH (mm)	50.31 $\pm$ 1.04	50.19 $\pm$ 1.20	50.67 $\pm$ 1.22	2.53	2	0.282	
	RW (mg)	116.93 $\pm$ 4.97	111.59 $\pm$ 6.49	114.05 $\pm$ 5.96	0.42	2	0.809	
	GLN	16.45 $\pm$ 1.22	16.25 $\pm$ 0.74	16.10 $\pm$ 1.37	0.82	2	0.662	
	RV (mm <sup>3</sup> )	117.40 $\pm$ 8.39	127.86 $\pm$ 12.26	136.35 $\pm$ 8.08	2.25	2	0.325	
	CA (cm <sup>2</sup> )	13.71 $\pm$ 1.32	14.76 $\pm$ 1.10	12.63 $\pm$ 0.60	1.69	2	0.429	
	BF ( $\mu$ N)	4.27 $\pm$ 1.57	4.19 $\pm$ 1.29	5.23 $\pm$ 1.42	0.35	2	0.839	
	EB (%)	26.32 $\pm$ 5.93	25.29 $\pm$ 9.43	32.95 $\pm$ 7.04	0.32	2	0.850	
	GTL (mm)	809.26 $\pm$ 64.72	804.04 $\pm$ 41.46	802.30 $\pm$ 75.06	0.48	2	0.788	
	DI (10 <sup>-6</sup> J)	57.60 $\pm$ 3.19	56.85 $\pm$ 3.57	58.77 $\pm$ 3.62	0.39	2	0.822	
	Posttreatment	ASL (mm)	24.96 $\pm$ 2.64a	14.71 $\pm$ 1.28b	11.03 $\pm$ 1.62b	21.88	2	<0.001
		RH (mm)	8.14 $\pm$ 0.35a	11.78 $\pm$ 0.69b	12.79 $\pm$ 0.66b	25.29	2	<0.001
ED (mm)		5.68 $\pm$ 0.13a	6.48 $\pm$ 0.21a	7.65 $\pm$ 0.28b	29.80	2	<0.001	
CRH (mm)		40.47 $\pm$ 2.36a	50.265 $\pm$ 1.20a	53.340 $\pm$ 1.528b	23.35	2	<0.001	
RW (mg)		87.55 $\pm$ 4.69a	111.37 $\pm$ 6.40b	126.93 $\pm$ 4.67c	19.44	2	<0.001	
GLN		22.82 $\pm$ 1.46a	16.40 $\pm$ 0.81b	12.75 $\pm$ 1.27b	21.94	2	<0.001	
RV (mm <sup>3</sup> )		69.67 $\pm$ 4.51a	134.20 $\pm$ 12.98b	203.89 $\pm$ 17.06c	30.77	2	<0.001	
CA (cm <sup>2</sup> )		32.18 $\pm$ 4.21a	14.85 $\pm$ 0.95b	11.07 $\pm$ 1.00b	31.30	2	<0.001	
BF ( $\mu$ N)		6.23 $\pm$ 1.62	3.26 $\pm$ 1.46	5.38 $\pm$ 1.29	1.19	2	0.551	
EB (%)		37.44 $\pm$ 5.94	28.21 $\pm$ 6.02	35.56 $\pm$ 2.78	1.25	2	0.535	
GTL (mm)		1091.52 $\pm$ 71.55a	804.54 $\pm$ 39.97b	652.23 $\pm$ 75.65b	17.05	2	<0.001	
DI (10 <sup>-6</sup> J)		36.57 $\pm$ 3.15a	56.58 $\pm$ 3.32b	68.93 $\pm$ 3.84b	25.86	2	<0.001	

ASL: the length of anchor silk; RH: the height of retreat; ED: the diameter of retreat entrance; CRH: the height of retreat center from the ground; RW: the weight of retreat; GLN: the number of gumfooted line; RV: the volume of retreat; CA: capture area of the web; GTL: the total length of gumfooted line; DI: the defense investment during web-building; BF: breaking force; EB: elongation at break.



**Figure 2.** Boxplots of the web architecture in pretreatment ( $N = 20$  for each of treatment) and posttreatment ( $N = 17, 20,$  and  $20$  for marginally, moderately, and extremely well-fed treatments, respectively) for female *C. campanulata* in different feeding treatments: (A) length of anchor silk (ASL); (B) height of retreat (RH); (C) number of gumfooted line (GLN); (D) capture area of the web (CA); (E) volume of retreat (RV); (F) height of retreat center to ground (CRH). Boxplots show the median (central line), first and third quartiles (box), and different lower case letters indicate significant difference between treatments. Ns, no significant difference. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . MWF, marginally well fed; Control, moderately well fed; EWF, extremely well fed.

### Behavioral investment

There were no significant differences in the total length of gumfooted lines (GTL) ( $\chi^2 = 0.48$ ,  $df = 2$ ,  $P = 0.535$ ) and the DI during web building (EE) ( $\chi^2 = 0.39$ ,  $df = 2$ ,  $P = 0.822$ ) of the spider among the 3 treatments in pretreatment. However, they showed significant difference among treatments in post-treatment (GTL:  $\chi^2 = 17.05$ ,  $df = 2$ ,  $P < 0.001$ ; EE:  $\chi^2 = 25.86$ ,  $df = 2$ ,  $P < 0.001$ ) (Figure 3C, Table A1), in which GTL and EE showed no significant difference between control treatment and well-fed treatment. However, GTL was significantly increased in marginally well-fed treatment compared with that in control (moderately well fed) treatment and extremely well-fed treatment (Figure 3C), and EE was significantly decreased in marginally well-fed treatment compared with that in control (moderately well fed) treatment and extremely well-fed treatment (Figure 3D). These results suggested that starvation can significantly affect foraging investment and DI. Under the starvation situation, spiders invested more in foraging structures rather than in defense structures.

### Discussion

Blackledge et al. (2011) pointed out that there are 3 energetic costs associated with web building, the metabolic costs

of synthesizing silk proteins, the caloric energy contained in the silk itself, and the behavioral costs of assembly. In our current study, the parameters of spider webs we measured can be categorized as behavioral costs. We studied the plasticity of material investment of cobweb spider *C. campanulata* in response to different feeding regimes. The result showed that the web-building behavior of this spider can be significantly affected by different feeding conditions. Specifically, marginally well-fed spiders invest more in constructing web structures for prey capture, such as gumfooted lines and capture area, while extremely satiated spiders invest more in constructing web structures for predator avoidance, such as retreat volume and retreat height. This result suggested that the parameters of the web architectures were good proxies for differentiating the “investments” of spiders under different feeding regimes, though we actually did not measure specific energetics. Also, this result is consistent with previous report in *L. hesperus* that starved spiders spun webs with more sticky gumfooted threads compared with those spun by fed spiders (Blackledge and Zevenbergen 2007). However, in the present study, we do not know exactly what threshold of feeding frequency and quantity in this species is starving, though the manipulation already has shown differences among different treatment groups. We may study how spider builds webs under starving condition.

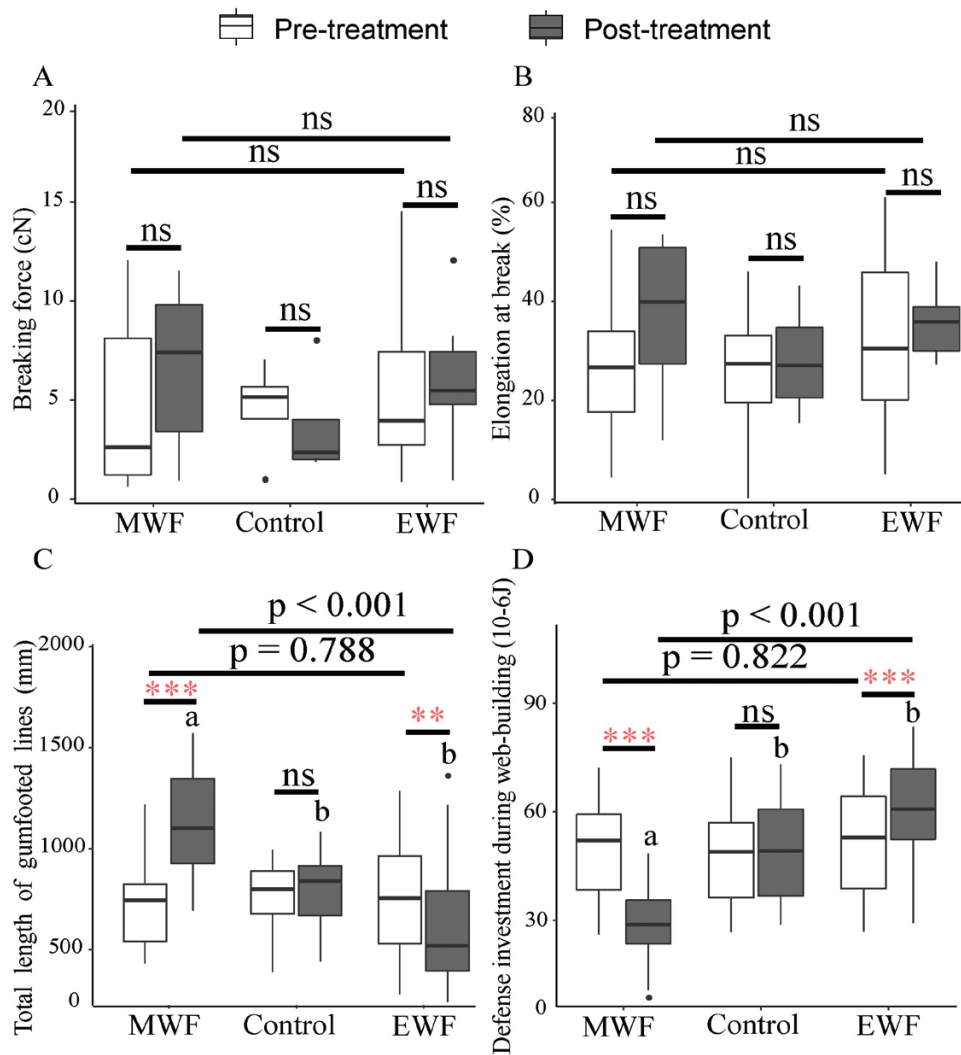
**Table A2.** Mean ( $\pm SE$ ) of web architectures, anchor silk properties, foraging and behavioral investments measured for all groups

Group	Parameters	Treatment		V	P
		Pretreatment	Posttreatment		
MWF	ASL (mm)	15.30 $\pm$ 1.16	24.96 $\pm$ 2.64	152	<0.001
	RH (mm)	10.810 $\pm$ 0.367	8.135 $\pm$ 0.347	1	<0.001
	ED (mm)	6.36 $\pm$ 0.17	5.68 $\pm$ 0.13	11	0.002
	CRH (mm)	50.31 $\pm$ 1.04	40.47 $\pm$ 2.36	0	<0.001
	RW (mg)	116.93 $\pm$ 4.97	87.55 $\pm$ 4.69	0	<0.001
	GLN	16.45 $\pm$ 1.22	22.82 $\pm$ 1.46	150	<0.001
	RV (mm <sup>3</sup> )	117.40 $\pm$ 8.39	69.67 $\pm$ 4.51	0	<0.001
	CA (cm <sup>2</sup> )	13.71 $\pm$ 1.32	32.18 $\pm$ 4.21	153	<0.001
	BF ( $\mu$ N)	4.27 $\pm$ 1.57	6.23 $\pm$ 1.62	22	0.219
	EB (%)	26.32 $\pm$ 5.93	37.44 $\pm$ 5.94	25	0.078
	GTL (mm)	809.26 $\pm$ 64.72	1091.52 $\pm$ 71.55	143	<0.001
	DI (10 <sup>-6</sup> J)	57.60 $\pm$ 3.19	36.57 $\pm$ 3.15	0	<0.001
	Control	ASL (mm)	15.14 $\pm$ 1.21	14.71 $\pm$ 1.28	83
RH (mm)		11.27 $\pm$ 0.62	11.78 $\pm$ 0.69	138	0.225
ED (mm)		6.45 $\pm$ 0.20	6.48 $\pm$ 0.21	107	0.642
CRH (mm)		50.19 $\pm$ 1.20	50.27 $\pm$ 1.20	100	0.867
RW (mg)		111.59 $\pm$ 6.49	111.37 $\pm$ 6.40	106	0.985
GLN		16.25 $\pm$ 0.74	16.40 $\pm$ 0.81	116	0.686
RV (mm <sup>3</sup> )		127.87 $\pm$ 12.26	134.20 $\pm$ 12.98	139.5	0.204
CA (cm <sup>2</sup> )		14.76 $\pm$ 1.10	14.85 $\pm$ 0.95	209	0.382
BF ( $\mu$ N)		4.19 $\pm$ 1.29	3.26 $\pm$ 1.46	3	0.625
EB (%)		25.29 $\pm$ 9.43	28.21 $\pm$ 6.02	7	0.625
GTL (mm)		804.04 $\pm$ 41.46	804.54 $\pm$ 39.97	71	0.216
DI (10 <sup>-6</sup> J)		56.85 $\pm$ 3.57	56.58 $\pm$ 3.32	66.5	0.156
EWF		ASL (mm)	14.59 $\pm$ 1.35	11.03 $\pm$ 1.62	29
	RH (mm)	10.93 $\pm$ 0.53	12.79 $\pm$ 0.66	174	0.011
	ED (mm)	6.87 $\pm$ 0.12	7.65 $\pm$ 0.28	112.5	0.793
	CRH (mm)	50.67 $\pm$ 1.22	53.34 $\pm$ 1.53	194	<0.001
	RW (mg)	114.05 $\pm$ 5.96	126.93 $\pm$ 4.67	201	<0.001
	GLN	16.10 $\pm$ 1.37	12.75 $\pm$ 1.27	28	0.007
	RV (mm <sup>3</sup> )	136.35 $\pm$ 8.08	203.89 $\pm$ 17.06	201	<0.001
	CA (cm <sup>2</sup> )	12.63 $\pm$ 0.60	11.07 $\pm$ 1.00	210	<0.001
	BF ( $\mu$ N)	5.23 $\pm$ 1.42	5.38 $\pm$ 1.29	13	0.938
	EB (%)	32.95 $\pm$ 7.04	35.56 $\pm$ 2.78	13	0.938
	GTL (mm)	802.30 $\pm$ 75.06	652.23 $\pm$ 75.65	37	0.009
	DI (10 <sup>-6</sup> J)	58.77 $\pm$ 3.62	68.93 $\pm$ 3.84	204	<0.001

ASL: the length of anchor silk; RH: the height of retreat; ED: the diameter of retreat entrance; CRH: the height of retreat center from the ground; RW: the weight of retreat; GLN: the number of gumfooted line; RV: the volume of retreat; CA: capture area of the web; GTL: the total length of gumfooted line; DI: defense investment during web-building; BF: breaking force; EB: elongation at break. MWF: marginally well-fed; Control: moderately well-fed; EWF: extremely well-fed.

According to optimal foraging theory, trap-building predators make decisions based on their physical condition and the costs and benefits of adopting a specific behavior to maximize fitness (Scharf et al. 2011). In our study, the spider showed different web-building strategies according to different feeding conditions. Marginally well-fed spiders build webs with more gumfooted lines and a bigger capture area, increasing the chance to capture and retain the prey. Also, they built retreats lower, which improves the feeding

efficiency by reducing prey wrapping time and reducing the cost of carrying prey back to the retreat, but in turn increases the risk of being attacked by dangerous prey, such as some species of ants. Many ants are armed with strong stingers, mandibles, and formic acid, and can carry out an effective collective attack (Líznarová and Pekár 2013). Extremely well-fed spiders prefer to build retreats higher, reducing the likelihood of direct confrontations with these dangerous ants.



**Figure 3.** Boxplots of the mechanical properties of anchor silk (pretreatment:  $N = 8, 4,$  and  $9$  for marginally, moderately, and extremely well-fed treatments, respectively; posttreatment:  $N = 7, 4,$  and  $7$  for marginally, moderately, and extremely well-fed treatments, respectively), the foraging and behavioral investments in pretreatment ( $N = 20$  for each of treatment) and posttreatment ( $N = 17, 20,$  and  $20$  for marginally, moderately, and extremely well-fed treatments, respectively) for female *C. campanulata* in different feeding treatments: (A) breaking force (BF); (B) elongation at break (EB); (C) total length of gumfooted line (GTL); (D) defense investment during web building (DI). Boxplots show the median (central line), first and third quartiles (box), and different lower case letters indicate significant difference between treatments. Ns, no significant difference. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . MWF, marginally well fed; Control, moderately well fed; EWF, extremely well fed.

The cost of retreat construction in *C. campanulata* is high because the spider has to spend a lot of energy to pick up the grains of sands, pull them up into the air, and using sticky silk to conglutinate them together (Henschel and Jocqué, 1994). Thus, a starved spider may not afford to build a big retreat. In our study, we observed that marginally well-fed spiders build a smaller retreat probably due to the pressure of both foraging and physical conditions, making the spiders easy to be detected and attacked by predators. In addition, our result showed that the DI for constructing the cobwebs is significantly lower in marginally well-fed spiders. These adjustments to the web-building behaviors imply a state-dependent change in web-building strategies that made a balance between foraging and predator avoidance.

We confirmed and expanded on previous studies showing that spiders use various prey cues and internal states to adjust web architecture and silk properties to improve their fitness. Sherman (1994) reported that in *Larinioides*

*cornutus*, hungry spiders invest more efforts into foraging, and satiated spiders reallocate energy from continued foraging to egg production. Mayntz et al. (2009) found that prey-limited *Zygiella x-notata* increased the total capture area of its web. Blamires et al. (2017) revealed that *Argiope keyserlingi* adjusted the chemical properties of silks according to their nutritional history, and the spider with low-protein diets spun stickier threads to enhance foraging. These results are consistent with the results in our study. However, we did not test the impact of egg production and hatching on web architecture in different feeding groups. It has been reported in the cobweb spider *L. hasselti*, adult females alter web structure when they are in possession of an egg sac at a cost to safety and foraging (DiRienzo and Aonuma 2018). In addition, we did not test the chemical component and mechanical properties of the gumfooted silks to explore whether they can be affected by different feeding conditions. We may investigate these potential factors in the future.



Blackledge and Zevenbergen (2007) found that the material properties of silk spun by the fed and fasted *L. hesperus* spider were not varied significantly. This is consistent with our result in the mechanical property test of the anchor silk of *C. campanulata*, which showed that the breaking force and elongation at the break of the anchor silks were not significantly affected by different feeding regimes. Currently, it is unknown whether the mechanical property of the anchor silk is mainly correlated with the spider body size, or has any correlation with the spigot size of the spinneret where the silk was extruded, and we may investigate these in the future. One possible reason for the lack of significant changes in the mechanical property of the anchor silk is that the spider almost always fed on gasters of the *Monomorium* ants (Zhang personal observation), which contain more lipids than proteins (Pekár et al. 2010), and enhancing silk properties requires a large intake of protein (Blamires et al. 2014). In future, we may test the mechanical properties of anchor silk of spiders that feed on different ant species.

In summary, we first tested the web-building plasticity in a retreat-made cobweb spider *C. campanulata* under different feeding conditions. The results showed that marginally well-fed spider invested more in foraging, and extremely well-fed spider invested more in defense. This behavior is probably an adaptive strategy that has evolved to respond to pressures of foraging and predation.

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## Author Contributions

H.Z., J.L., J.C., and S.Z. conceived and designed the study. J.L., H.Z., J.C., and C.L. collected the spider in the field. J.L., H.Z., Z. Z., G.L., and C.L. conducted experiments and collected data. J.L., H.Z., and S.Z. analyzed the data and wrote the manuscript. All authors gave final approval for publication.

## Conflict of Interest Statement

The authors declared that they had no competing interests related to this work.

## Data Availability Statement

All the data supporting the results can be archived at <https://doi.org/10.5061/dryad.9kd51c5kh>.

## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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