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THE FEATURES OF CAPTURE THREADS AND ORB-WEBS PRODUCED BY UNFED *CYCLOSA TURBINATA* (ARANEAE: ARANEIDAE)

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ABSTRACT. Orb-webs constructed by members of the spider family Araneidae are composed of sticky and non-sticky threads deposited in a stereotypic fashion. This study examines how changes in a spider's nutritional condition affect the capture thread properties and architectural details of its web. It does so by characterizing the features of successive webs constructed by unfed spiders that were not allowed to recycle previous webs. The volume of a capture thread's viscous material and the threads' inferred stickiness decreases in successive webs, although the capture thread's extensibility does not change. The lengths of both capture thread and non-sticky thread decrease at similar rates in successive webs. The decreasing stickiness of capture threads reduces the stickiness per unit capture area. We did not detect asymmetry in the spacing of either spiral or radial threads of first and last webs, nor did we observe differences in the sizes of viscous droplets in outer and inner spiral turns. This suggested that these spiders assessed their silk resources before they initiated web construction and altered their behavior to produce a highly regular web of an appropriate size for their silk reserves.

Keywords: Nutrition, hunger, silk allocation, spider, thread extensibility, thread stickiness

Orb-webs constructed by members of the orbicularian subclade Araneoidea are highly integrated structures formed of the products of three spinning glands that independently draw their components from a common hemolymph pool (Foelix 1996). Non-sticky threads produced by ampullate glands form the web's anchor, frame, hub, and radial threads. The spirally arrayed, sticky prey capture thread is produced by two spinning glands. The flagelliform spigot on a posterior lateral spinneret produces a supporting axial fiber and the two adjacent aggregate spigots coat this fiber with a viscous aqueous solution. Material from the two posterior lateral spinnerets merge and the viscous solution coalesces into a series of droplets. These droplets are formed of a complex solution of organic and inorganic compounds, a variety of small proteins, and high molecular weight glycoproteins (Townley 1990; Vollrath et al. 1990; Townley et al. 1991; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast et al. 1993). Glycoprotein nodules form within each droplet and are thought to make the thread sticky (Vollrath et al. 1990; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast et al. 1993; Peters 1995). Hydrophilic compounds in the viscous material attract atmospheric moisture to maintain the thread's water content (Townley et al. 1991; Edmonds & Vollrath 1992), which accounts for about 80% of its volume (Gosline et al. 1986).

Non-sticky thread usually comprises the greater proportion of an orb-web's total thread length. Eberhard (1988a) estimates that sticky thread typically forms 36–54% of the total length of thread in an orb-web but that it is responsible for a greater percentage of an orb-web's mass because it has a greater volume per length than does non-sticky thread. This may suggest that supplies of capture thread precursors limit an orb-web's size. However, factors such as silk gland sizes, the efficiency with which glands extract precursors from the hemolymph, and the metabolic cost of producing threads affect a spider's ability to produce threads.

Orb-web architecture results from an interaction between the spider's innate web-building behavior, the environment, and the spider's silk resources. Web features such as capture area, number of radii, and spiral spacing exhibit intraspecific plasticity (Witt & Baum 1960; Eberhard 1988a). The effects of a spider's nutritional condition may contribute to this variability. Several studies report that as spiders became heavier the spiral spacing of their web increases (Witt & Baum 1960; Christiansen et al. 1963; Witt 1963).

Poor nutrition may affect web architecture in two ways. It may limit the supply of a spider's total silk protein, thereby reducing the lengths of all web elements, or it may also limit the length of all or some web elements by restricting one or more critical amino acids or other web compounds (Higgins & Rankin 1999).

Many spiders, including the species used in this study (pers. obs.), ingest silk and sticky droplets as they take down their webs and recycle this material in the new webs they construct (Carico 1986). This improves the economy of orb-web use; estimates of reuse of organic orb-web constituents range from 32–97% (Breed et al. 1964; Peakall 1971; Townley & Tillinghast 1988). Using the most conservative of these estimates, Opell (1998) concluded that web recycling reduced the cost of orb-web construction by about 32%. If web production is limited by certain amino acids and other compounds critical for web production, then web recycling may have even greater benefits.

A spider could accommodate diminishing supplies of thread precursors in two ways (Witt et al. 1968; Eberhard 1988a): 1. Evaluate silk supplies prior to web construction and alter the design of the entire web or 2. Respond to dwindling silk supplies as they are encountered during web construction. In the first case, if non-sticky silk reserves were low, a spider might construct a smaller outer frame that would reduce web area and minimize changes in the number of radii. If capture thread reserves were low, increased spiral spacing could maintain a uniform stickiness-per-web-capture-area ratio, but would alter the web's radius-to-spiral-turn ratio. In the second case, a severe reduction in non-sticky thread during frame construction might result in more widely spaced radii. If capture thread was being depleted, spiral spacing might increase in successive (more central) spiral turns or the size of the capture thread's viscous droplets might also decrease centrally.

To examine the effect of nutritional deficit on orb-webs and their threads, we measured the features of successive threads and webs produced by unfed spiders. Our investigation expands an earlier study (Witt 1963) by examining a different species and by measuring the web and thread features of the same spiders over time, rather than comparing the features of one group of fed spiders and another group of starved spiders. To further limit a spider's silk resources, we also removed most of the silk from a web before it could be recycled. These procedures allowed us to test the hypothesis that the length of sticky thread declines more rapidly than non-sticky thread, and to examine the influence of diminishing nutritional resources on the volume, extensibility, and inferred stickiness of viscous thread. It also permitted us to further test the hypothesis (supported by Witt et al. 1968) that a spider assesses its silk resources before beginning web construction and uses this information to alter its silk allocation and web architecture, thereby maintaining uniform spacing of web elements and conserving critical elements of web design.

METHODS

Species studied.—We studied adult female *Cyclosa turbinata* (Walckenaer 1842), collected from June to August 1999 on the Virginia Polytechnic Institute and State University campus, and surrounding areas of Blacksburg, Montgomery County, Virginia (N 37.22874, W 80.42558). At the end of the study, spiders were preserved in 70% ethanol and identified using Levi (1977). Voucher specimens are deposited in the Museum of Comparative Zoology.

Experimental design.—Whenever possible, the stabilamentum was collected along with the spider and suspended from a support in the container in which the spider was housed, as this encouraged web building (Rovner 1976). Spiders were kept in 25 × 37 × 12 cm plastic boxes set upright on their longest sides. Wooden dowel rods 5 mm in diameter were glued around the perimeter of the box to serve as web attachment sites. The side of the box opposite the lid was removed and covered with plastic food wrap to allow easy access to the webs. The boxes provided ample space to accommodate the webs that *C. turbinata* produce under natural conditions. The boxes were kept in an environmental chamber with a 13:11 h dark-light cycle, a temperature of 25° C and a relative humidity of 80%.

We examined spiders daily and, after thread samples were collected or a web was photographed, we destroyed most of the web and removed most of its silk, leaving only the stabilamentum and a few framework lines and radii to encourage the spider to construct another web. After its web was destroyed, each spider was given an opportunity to drink by placing it on water-saturated cotton. If a spider did not make a web after 3 or 4 days, it was released.

Spiders were divided into two groups that were sampled on alternate days. Of the spiders we placed in boxes, eight produced enough webs to be included in comparisons of webs and ten produced enough webs to be included in thread comparisons. Every 48 hours, webs constructed by one group of spiders were dusted with corn starch (Carico 1977) and photographed. Uncontaminated capture threads were collected from webs produced by the other group of spiders. The webs constructed by spiders of each group were numbered sequentially. As many as 21 webs were made by individual spiders whose webs were dusted and as many as 30 webs by individual spiders whose threads were collected (mean numbers 12.4 and 13.8 respectively).

Web features.—Boxes containing dusted webs were elevated above a black cloth and the webs were photographed from a distance ~0.7 m. A reference measurement was recorded and, after printing enlarged photographs, used to compute an enlargement index for each web photograph. From these measurements, the lengths of sticky and nonsticky threads, spiral spacing, and the total area and capture area of webs were determined using the formulas given in Opell (1997).

We evaluated the regularity of spiral spacing and radial line distribution in the first and last webs constructed by the six spiders that produced the greatest number of webs. We measured the distance between the six outermost and between the six inner-most spirals along two radii in each web. From this, the mean inner and outer spiral spacing was computed. We measured (along the same spiral turn) the distance between each of three radii to the left and three radii to the right of these two reference radii and computed mean radius spacing.

Thread features.—The features of sticky thread samples taken from the outer- and inner-most 1–4 spiral turns of a web were measured. These samples were collected by carefully placing calipers whose tips were coated with double-sided tape against a thread and then cutting this portion from the web with small scissors. From each sample, we measured the lengths and widths of two droplets from each of two different thread segments and, from the same regions of the thread, the distance spanned by a series of droplets (mean number droplets = 17.5 droplets). When droplet size differed within a segment, we measured the dimensions of one of the smaller and one of the larger droplets. From these measurements, droplet volume (μm^3) per mm was calculated using the formulas given by Opell (1997). We evaluated the regularity of viscous droplet size and spacing in the first and last webs constructed by ten spiders that produced the greatest number of webs by comparing the droplet features of their outer and inner spiral turns.

The stickiness of an adhesive capture thread can be estimated from the volume of the thread's droplets (Opell 2002). This volume is computed from measurements of droplet length, width, and distribution (Fig. 2 & Formulas 1–4 in Opell 2002). The thread measurements used to compute this volume are shown in Figure 2 of Opell (2002). We used the data from this earlier study to develop a formula to estimate the stickiness of capture threads produced by adult *C. turbinata*. This was done by regressing the volume of thread droplets per mm of thread length against thread stickiness to obtain the significant ($n = 17$, $F = 11.16$, $P = 0.0041$, $R^2 = 0.41$) formula:

$$\begin{aligned}&\text{Stickiness } (\mu\text{N/mm thread contact})\\&\quad = \text{droplet volume } (\mu\text{m}^3) \text{ per mm}\\&\qquad \times 0.000221\\&\qquad + 4.87.\end{aligned}$$

Table 1.—Comparison of thread features. L_B = thread length at breaking, L_I = initial thread length. Values are reported as mean ± 1 standard error. The mean number of webs in each of the three categories is presented in the first row. The *P* values of repeated ANOVA's are given for the complete model and separately for the three web orders and the ten spiders whose values were included. An * denotes features that we consider to show change by virtue of significant model and order (web sequence) *P* values and consistently increasing or decreasing mean values.

	Webs 1–3 $n = 15$, $\bar{X} = 1.9 \pm 0.3$	Webs 4–7 $n = 12$, $\bar{X} = 5.6 \pm 0.3$	Webs 8–30 $n = 26$, $\bar{X} = 13.9 \pm 1.1$	ANOVA *P* Values (Model, Order, Spider)
Droplet Diameter (μm)	9.68 ± 1.00	7.17 ± 0.40	5.68 ± 0.31	* 0.000, 0.000, 0.035
Droplets per mm	38.7 ± 2.9	42.0 ± 3.6	55.5 ± 3.4	* 0.008, 0.001, 0.139
Total Droplet Volume (μm^3 / mm × 10^3)	17.52 ± 4.28	9.17 ± 1.79	6.71 ± 1.47	* 0.047, 0.000, 0.241
Extensibility (L_B / L_I)	4.14 ± 0.38	3.26 ± 0.34	3.86 ± 0.32	0.048, 0.563, 0.039

We then computed estimated stickiness values for each of the undusted web samples of the current study and regressed these stickiness values against the sequential numbers of the webs from which these threads were taken to obtain the significant ($n = 51$, $F = 15.26$, $P = 0.0003$, $R^2 = 0.23$) formula:

$$\text{Stickiness } (\mu\text{N/mm thread contact}) = -1.2742 \text{ natural log web number} + 9.4346.$$

Using this formula, we assigned a stickiness value to the threads in each of the dusted webs. As these were the webs for which we measured thread lengths, this permitted us to estimate the total stickiness of the webs' capture threads and the stickiness per web capture area.

After the droplets on the threads were measured, the thread was placed on the tips of digital calipers covered with double sided tape and opened to a distance of 2.5 mm. A motor separated the tips of the calipers at a rate of 17 μm per second. When the thread broke, the motor was stopped and the distance the calipers had spread was recorded. Extensibility was then computed as a ratio of the breaking length of a thread to its initial length.

Statistical analyses.—We included in our analyses of threads only spiders that constructed at least 9 webs (mean number of webs = 13.3) and in our analysis of webs only spiders that constructed at least 7 webs (mean number of webs = 10.3). We divide webs into three sequential groups (e.g., for thread features: Webs 1–3, Webs 4–7, and Webs 8–30) and used a repeated measures analysis of variance (RMANOVA) test to examine differences among the values of thread and web features. Spiders could (and did) make more than 1 web in each of the three web groupings that we used, which is one reason we used the RMANOVA and also accounts for sample sizes being greater than the total number of spiders used. The RMANOVA model included two components: web sequence and spider. The former accounted for changes in nutritional condition and the latter for inter-individual variability. We consider as significant only those values whose increase or decrease was marked by the following: 1. a significant ($P \leq 0.05$) overall model; 2. a significant web sequence model component; and 3. a consistent (non-oscillating) change in the value in question. If, for example, the first two requirements were met but an index showed a reduction in the Webs 4–7 sequence but an increase in the Webs 8–30, we attributed this oscillation to a cause other than declining nutritional condition. Paired t-tests were used to compare spiral and radial spacing and capture thread droplet features. Statistical tests were performed with SAS for the Power Macintosh computer (SAS Institute, Cary, North Carolina).

RESULTS

Thread features.—Mean droplet diameter decreased and mean droplet number per mm increased in subsequent webs (Table 1). The net result was a decrease in droplet volume per mm of thread, with the mean value for webs in the last group being only 38% that of the webs in the first group. In contrast, thread

Table 2.—Comparison of web features. Values are reported as mean ± 1 standard error. The mean number of webs in each of the three categories is presented in the first row. When the sample size differs from that reported immediately under each of the three web sequences, this number is reported in brackets. The *P* values of repeated ANOVA's are given for the complete model and separately for the three web orders and the ten spiders whose values were included. An * denotes features that we consider to show change by virtue of significant model and order (web sequence) *P* values and consistently increasing or decreasing mean values.

	Webs 1–3 $n = 9$, $\overline{X} = 2.1 \pm 0.3$	Webs 4–6 $n = 8$, $\overline{X} = 4.9 \pm 0.2$	Webs 7–21 $n = 20$, $\overline{X} = 11.6 \pm 1.1$	ANOVA *P* Values (Model, Order, Spider)
Frame Length (cm)	552.3 ± 39.9 [8]	491.4 ± 22.0 [7]	409.9 ± 20.7 [18]	0.026, 0.065, 0.329
Radii Length (cm)	2027.0 ± 250.6 [8]	1797.1 ± 117.3 [7]	1287.1 ± 94.3 [18]	* 0.000, 0.014, 0.011
Non-capture Length (cm)	2579.3 ± 277.5 [8]	2288.6 ± 106.2 [7]	1697.0 ± 111.5 [18]	* 0.001, 0.012, 0.019
Capture Length (cm)	2026.4 ± 216.2 [8]	1662.6 ± 96.1	1273.6 ± 84.1	* 0.003, 0.006, 0.113
Total Thread Length (cm)	4684.5 ± 488.5 [8]	3958.2 ± 195.7 [7]	2937.1 ± 195.4 [18]	* 0.001, 0.007, 0.054
Radii Length/Frame Length	3.64 ± 0.4 [8]	3.73 ± 0.4 [7]	3.10 ± 0.1 [18]	0.033, 0.434, 0.047
Non-capture/Capture Length	1.24 ± 0.05 [8]	1.39 ± 0.08 [7]	1.40 ± 0.05 [18]	0.013, 0.080, 0.015
Radii Length/Capture Length	0.96 ± 0.05 [8]	1.08 ± 0.06 [7]	1.05 ± 0.04 [18]	0.003, 0.072, 0.003
Spiral Turns	25.2 ± 1.4	21.9 ± 1.2	18.9 ± 0.7	* 0.002, 0.004, 0.126
Spiral Spacing (mm)	1.73 ± 0.06	2.01 ± 0.01	2.11 ± 0.07	0.000, 0.085, 0.000
Number of Radii	45.5 ± 3.3 [8]	42.1 ± 1.3 [7]	34.4 ± 1.5 [19]	0.000, 0.073, 0.005
Radii per Spiral Turn	1.77 ± 0.09 [8]	1.97 ± 0.11 [7]	1.83 ± 0.05 [19]	0.001, 0.016, 0.000
Total Web Area (cm^2)	109.6 ± 14.3	106.0 ± 10.0	87.2 ± 7.6	0.147, 0.116, 0.171
Capture Area (cm^2)	101.2 ± 13.4	98.0 ± 9.8	80.9 ± 7.1	0.130, 0.111, 0.143
Total Stickiness (mN)	17562 ± 2116	12341 ± 702	8191 ± 588	* 0.000, 0.000, 0.111
Stickiness per Area ($\mu N / cm^2$)	179.5 ± 10.4	130.5 ± 7.6	108.8 ± 7.5	* 0.000, 0.000, 0.004

Table 3.—Indices of web regularity. The mean number of webs in each of the two categories is presented in the first row. Values are reported as mean ± 1 standard error. *P* values are for paired t-tests.

	First Web *n* = 6, $\overline{X}$ = 2.0 ± 0.6	Last Web *n* = 6, $\overline{X}$ = 11.8 ± 2.2
Radii Spacing:		
Right (mm)	7.93 ± 0.47	7.13 ± 0.56
Left (mm)	8.42 ± 0.40	7.31 ± 0.72
P	0.099	0.637
Spiral Spacing:		
Outer (mm)	1.95 ± 0.20	2.08 ± 0.13
Inner (mm)	1.95 ± 0.16	2.00 ± 0.14
P	0.928	0.177

Table 4.—Indices of droplet regularity. The mean number of webs in each of the two categories is presented in the first row. Values are reported as mean ± 1 standard error. *P* values are for paired t-tests.

	First Web *n* = 10, $\overline{X}$ = 1.2 ± 0.1	Last Web *n* = 10, $\overline{X}$ = 13.3 ± 1.4
Droplet Diameter:		
Outer (μm)	11.13 ± 1.04	5.43 ± 0.39
Inner (μm)	10.69 ± 2.39	4.56 ± 0.45
P	0.853	0.066
Droplets per mm:		
Outer	28.33 ± 3.51	51.09 ± 4.14
Inner	43.17 ± 5.88	76.35 ± 9.80
P	0.070	0.012

extensibility did not change in successive webs (Table 1).

Web features.—Although frame thread length declined during the study this difference was not significant (Table 2). However, the lengths of all other web elements diminished by 34–37% in subsequent webs (Table 2). The surprising uniformity of this decline is also documented by the failure of web order to explain differences in the ratios of radii thread to frame thread lengths, non-capture to capture thread lengths, and radii to capture thread lengths. The decline in capture thread length was reflected in a decreased number of spiral turns, although this was not accompanied by an increase in spiral spacing. The number of radii did not diminish. Total web capture area did not decrease. However, as a consequence of declining capture thread volume per mm of thread length (Table 1), total estimated web stickiness decreased by 47%. This was associated with a 32% decrease in the estimated stickiness per cm^2 of web capture area.

The spacing of radii and capture spirals showed no irregularity in first or last webs (Table 3) and, therefore, provided no evidence of diminishing intra-web silk resources. Outer spirals tended to have larger droplets that were more closely spaced than inner spirals (Table 4). However, the only significant difference was in the droplet distribution of the last webs constructed.

DISCUSSION

Cyclosa turbinata exhibited a surprising ability to continue constructing orb-webs in the absence of both new resources and recycled material from previous webs. Reduced metabolic rate induced by starvation (Anderson 1974) and the elimination of bouts of prey capture may help extend a spider's resources. The lengths of both capture threads and non-sticky threads decreased in subsequent webs, but we found no support for the hypothesis that capture thread length decreased more quickly than non-sticky thread length. It is possible that frame thread length did not decrease significantly because, when leaving web remnants to encourage spiders to re-build their webs, we may have left proportionately more non-sticky threads than sticky threads. Due to the subjectivity of this procedure, we are unable to assess this possibility. However, we believe that we left so little silk that it had a minimal effect. The maintenance of a fairly stable ratio of these two thread types may be explained by the decrease in the volume of viscous material covering the capture threads. Rather than compensating for diminishing capture thread reserves only by reducing capture thread length, *C. turbinata* reduces both capture thread length and capture thread volume. This may help explain why the observed decrease in web capture area was not significant. In contrast, in studies using *Araneus* spp., Witt (1963) found that web diameter decreased and spiral spacing increased after 10 and 17 days of starvation. The regularity of radii and capture spirals in *C. turbinata* webs supports the hypothesis that a spider can assess its silk resources before constructing a web and, even as these resources decline, construct a web that has a regular architecture. This agrees with Witt's (1963) observations on *Araneus diadematus* Clerck, 1757. Evidence for memory based, compensatory web construction behavior has been noted in orb-web temporary spiral construction in other species (Eberhard 1988b).

The nutritional independence of the capture thread's inner axial lines and their viscous covering is shown by the thread's unchanging extensibility (attributed to its axial lines) in the face of its decreasing viscous volume (Table 1). Changes in the size and distribution of the thread's viscous droplets may result from changes in the chemical composition of this material or smaller amounts of viscous material may alter the dynamics of droplet formation. Changes in the diameters of axial fibers may also influence droplet size. As the thread's viscous material has both high water content (Gosline et al. 1986) and hydrophilic capabilities (Townley et al. 1991), a spider's hydration and the humidity of its environment may affect the features of its capture thread. We attempted to control for these factors by providing spiders with regular access to water and maintaining them and measuring their threads under uniform conditions.

Although we attribute the changes in threads and webs that we observed to the declining nutritional states of the spiders, we cannot entirely rule out the effect of aging. However, we judge the aging effects to be relatively minor as our study ended in August, and at this locality, *C. turbinata* adult females build webs until mid October. Additionally, the webs we observed were judged symmetrical by our indices and showed none of the characteristics of ''senile webs'' that are sometimes built by orb-weaving spiders near the end of their lives (Eberhard 1971).

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