

ESTIMATING THE STICKINESS OF INDIVIDUAL ADHESIVE CAPTURE THREADS IN SPIDER ORB WEBS

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ABSTRACT. Sticky threads improve an orb web's ability to retain the insects that strike it, allowing a spider more time to subdue these insects before they can escape from the web. The adhesive capture threads found in most orb webs feature small droplets of aqueous material. Inside each droplet, glycoprotein granules coalesce to impart thread stickiness. An independent contrast analysis of threads produced by the adults of five species (*Leucauge venusta*, *Argiope trifasciata*, *Micrathena gracilis*, *Cyclosa conica*, *Araneus marmoreus*) and ontogenetic studies of the threads of two of these species show that the volume of material in a thread's droplets is directly related to its stickiness. Models based on these analyses predict thread stickiness to within an average of 11% of the mean measured values using measurements of droplet diameter and distribution that are easily made with a compound microscope. This approach will facilitate the inclusion of thread stickiness in studies that examine the properties and performance of spider orb-webs.

Keywords: Araneae, orb web, prey capture, spider thread, stickiness

The spirally-arrayed capture thread of a spider's orb web retains insects that strike the web, giving the spider more time to subdue these prey before they escape from the web (Chacón & Eberhard 1980; Eberhard 1986, 1989, 1990). Orb weaving spiders belong to the Orbicularia clade, which is comprised of two subclades: the Deinopoidea, whose members produce primitive cribellar capture threads, and the much larger Araneoidea, whose members produce viscous capture threads (Bond & Opell 1998; Coddington 1986, 1990a, 1990b; Coddington & Levi 1991; Griswold et al. 1998). Cribellar threads are dry fuzzy threads in which the outer surfaces are formed of thousands of fine, looped fibrils that are spun from the spigots of a spinning plate termed the cribellum and, in the Deinopoidea, are supported by a pair of inner axial fibers (Eberhard & Pereira 1993; Opell 1994a, 1994b, 1995, 1996, 1999a; Opell & Bond 2001). These cribellar fibrils snag on the setae and irregular surfaces of insects and adhere to smooth surfaces by van der Waals and hygroscopic forces (Opell 1994c; Hawthorn & Opell pers. obs.). In contrast, the viscous capture threads of araneoids are formed of a pair of supporting axial fibers overlain by a complex aqueous solution that coalesces into regularly spaced droplets (Vollrath 1992; Vollrath

et al. 1990). Within each droplet, a glycoprotein granule condenses and confers the thread's stickiness (Peters 1995; Tillinghast et al. 1993; Vollrath & Tillinghast 1991). Relative to both spider size and capture thread volume, viscous thread is stickier than cribellar thread (Opell 1997, 1998). Consequently, araneoids construct orb-webs with a greater stickiness per capture area than do deinopoids (Opell 1999b).

The stickiness of adhesive capture threads differs greatly among species and is related to both spider mass and web architecture (Opell 1997, 1998, 1999b). Although few in number, studies that have examined the effect of thread stickiness on orb web performance have found it to be significant. Using artificial orb web analogs, Chacón & Eberhard (1980) showed that increasing the amount of adhesive on the lines of these "webs" increased the number of prey that they retained. The observation that orb webs constructed by adult spiders retained prey for longer periods than those of conspecific juveniles was attributed to the putatively stickier threads produced by adults (Eberhard 1989), as was the greater size of prey captured by adults (Opell 1990). Using measurements of capture thread stickiness, capture thread length, and web capture area, Opell (1997, 1999b) computed and compared

the total stickiness and the stickiness per capture area of orb webs constructed by several species. However, ecological studies of orb web performance have never incorporated thread stickiness. This is because the techniques for measuring stickiness have only recently been developed and are rather laborious (Opell 1997, 1998).

Because glycoprotein granules condense from the material that forms a thread's droplets, I hypothesize that droplet volume is directly related to thread stickiness. Phylogenetic analysis of adhesive threads produced by five species and ontogenetic analyses of the threads produced by two of these species support this hypothesis. Formulas derived from these analyses make it possible to estimate accurately the stickiness of adhesive capture threads using a simple set of measurements made with a compound microscope. This procedure thus makes estimates of the stickiness of individual threads accessible to ecological and comparative studies.

METHODS

Species studied.—I selected for study five species that represent major araneoid clades (Fig. 1), show considerable ecological diversity, and were abundant enough near Blacksburg (Montgomery County), Virginia to permit the sample sizes required by my studies. These species were identified using the systematic studies of Berman & Levi (1971) and Levi (1968, 1976, 1977, 1980, 1985). Voucher specimens are deposited in the Museum of Comparative Zoology, Harvard University. One value for droplet volume and one value for thread stickiness were computed from the threads produced by each spider. Interspecific comparisons are based on threads produced by adult females.

Leucauge venusta (Walckenaer 1841) is member of the family Tetragnathidae. Adult females have a mean body mass of 28.1 mg ($n = 26, SE = 2.3$), are typically found in shaded forest edges, and construct horizontal orb webs. The remaining species are members of the family Araneidae. *Argiope trifasciata* (Forskål 1775) is a large orb-weaver with a mean adult female body mass of 474.0 mg ($n = 25, SE = 51.6$). It is found on weedy vegetation, typically in exposed areas, where it constructs vertical orb webs with widely spaced capture spirals. *Micrathena gracilis*

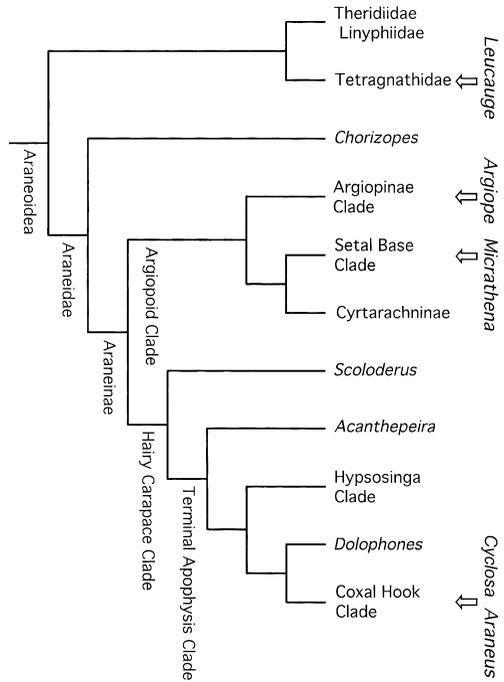


Figure 1.—An overview of araneoid phylogeny (summarized from fig. 82 in Scharff & Coddington 1997), showing the position of the five genera included in the current study.

(Walckenaer 1805) has a mean adult female body mass of 84.3 mg ($n = 21, SE = 5.0$). It occupies moist forests, where it constructs orb webs that have very closely spaced capture spirals and an orientation that ranges from nearly horizontal to vertical. *Cyclosa conica* (Pallas 1772) has a mean adult female body mass of 8.9 mg ($n = 23, SE = 0.8$), constructs vertical orb webs, and can be found on exposed shrubbery and on vegetation along forest edges. *Araneus marmoreus* Clerck 1757 has a mean adult female body mass of 677.1 mg ($n = 15, SE = 75.0$), constructs vertical orb webs on vegetation along forest edges, and uses a signal line to monitor its web from a retreat made of a curled leaf.

Thread collection and storage.—I collected some capture threads directly from orb webs on samplers made from microscope slides with raised, parallel, rectangular supports glued at 4.8 mm intervals to their upper surfaces. Doubled-sided tape atop these supports maintained the thread's native tension. In some cases, a sector of an orb web was first captured on an 18 cm diameter polished

aluminum ring with double-sided tape on its upper rim and thread samples were collected from this ring in the laboratory.

Threads were collected in the morning to ensure that they were fresh. However, it was not possible to determine precisely how old these threads were. Thread droplets were measured 2–4 h thereafter, and their stickiness was measured no more than 3 h later. Threads were maintained and measured at 23–25 °C and 60–62% RH (Table 1). Under these conditions, the hygroscopic properties of viscous threads maintain droplet volume (Townley et al. 1991). However, I did not attempt to measure the stability of droplet dimensions.

The thread properties of each species probably perform optimally under the environmental conditions typical for that species. However, Townley et al. (1991) show that the size of viscous thread droplets can change as they take up the atmospheric water and that this is influenced by ambient humidity. Thus, temperature and humidity differences among habitats probably influence droplet volume and this feature may change over the course of a day. By maintaining threads under stable and fairly uniform temperature and humidity conditions, I believe that this fluctuation was minimized and that I established conditions that were acceptable for the broad comparisons made in this study.

Droplet volume.—I first examined a thread under a dissecting microscope to ensure that it was not damaged. Its droplets were then measured at 500 X under a compound microscope. Both the repeatability and resolution of measurement of droplet diameters were about 0.4 μm (Opell 1997). I determined thread volume from measurements (Fig. 2) of the distance (D) spanned by a series of droplets (N) and the lengths (L, dimension parallel to thread length) and widths (W) of two droplets. Droplet length influenced the number of droplets included in a series as shown in Table 1. Two thread sectors were measured for each spider's web (subscripts 1 and 2). When droplet size was not uniform, I measured representatives of the larger and smaller droplets. Table 1 gives the mean intra-sample range of droplet length and width for each species. Increasing the number of droplets and thread sectors measured increases the accuracy with which thread volume can be computed. All measurements were in μm . I used the follow-

ing formulas to compute the volume (μm^3) of viscous material in the droplets of a 1-mm length of adhesive thread.

Mean Droplet Radius (MDR)

$$= (\text{Grand Mean of L and W})/2. \quad (1)$$

Droplet Volume (DV)

$$= 4 \times \pi \times \text{MDR}^3/3. \quad (2)$$

Droplets per mm (DPMM)

$$= ((N_1 + N_2)/(D_1 + D_2)) \times 1000. \quad (3)$$

Droplet Volume per mm (DVPMM)

$$= \text{DV} \times \text{DPMM}. \quad (4)$$

Interdroplet volume was not included in these calculations, as it is small and does not appear to contribute to glycoprotein granule formation (Opell 1997). Values of droplet volume include the volume of the supporting axial fibers that run through the droplets. I did not attempt to factor out this volume for two reasons. First, for the species studied axial fiber diameters are small, ranging from 1.03–5.37 μm (Opell & Bond 2001); and fibrils comprise only a small part (0.07–0.75%, mean 0.35%) of a droplet's volume. Second, the objective of this study was to devise a simple method for estimating thread stickiness. Axial fiber diameter is difficult and time-consuming to measure (Opell & Bond 2001) and its inclusion is inconsistent with this objective.

Thread stickiness.—Thread stickiness is reported as the force (μN) required to overcome the stickiness of a 1 mm length of thread. As described in more detail by Opell (1997), this was determined by first pressing a 2 mm wide piece of 320 grit, 3M waterproof silicon carbide sandpaper against a thread with a standard force. The force required to pull the contact plate from the thread was then measured with a strain gauge made from a stainless steel needle. The particles on the surface of these sandpaper plates were of uniform size and distribution (Opell 1993) and these plates registered the same stickiness for adhesive threads as did contact plates made from fleshfly wings (Opell 1997). Thus, the stickiness values obtained by this method were similar to those registered by a representative insect surface.

Phylogenetic analyses.—Features of species that are evolutionarily related are not, in

Table 1.—Droplet measurements and thread stickiness values and the conditions under which threads were stored and measured (mean ± 1 standard error). The mean intra-sample range of droplet length and width is given in parentheses.

Family Species (individuals)	Temp. (°C)	Percent relative humidity	Mean droplets per series	Droplet length (μm)	Droplet width (μm)	Droplets per mm	Droplet volume (μm ³ /mm × 10 ³)	Thread stickiness (μN/mm)
Tetragnathidae	25 ± 0.1	61 ± 0.5						
<i>Leucauge venusta</i> (25)			8	12.5 ± 0.51 (2.2)	10.1 ± 0.42 (2.1)	41.4 ± 2.1	31.3 ± 2.6	19.3 ± 1.3
Araneidae	23 ± 0.3	60 ± 0.5						
<i>Argiope trifasciata</i> (33)			13	43.0 ± 2.1 (21.0)	29.3 ± 1.3 (18.8)	9.4 ± 0.56	257.7 ± 31.4	28.2 ± 1.9
<i>Micrathena gracilis</i> (17)	23. ± 0.2	62 ± 0.4	4	24.9 ± 1.0 (5.3)	19.8 ± 0.72 (6.2)	20.2 ± 0.92	117.2 ± 9.3	26.4 ± 1.6
<i>Cyclosa conica</i> (18)	24 ± 0.1	61 ± 0.5	6	11.8 ± 0.64 (3.9)	9.6 ± 0.56 (3.9)	34.0 ± 2.4	21.3 ± 2.2	9.6 ± 0.76
<i>Araneus marmoreus</i> (21)	23 ± 0.2	61 ± 0.2	9	59.6 ± 3.6 (23.2)	46.9 ± 3.1 (21.5)	6.9 ± 0.80	480.2 ± 55.7	32.0 ± 2.7

a strict sense, independent and, therefore, violate the assumptions of parametric statistics (Felsenstein 1985; Harvey & Pagel 1991). Therefore, I employed the independent contrast (IC) method of Felsenstein (1985) to determine if the droplet volume and stickiness of threads produced by adult female spiders were related. This method accounts for the influence of phylogeny on continuous characters by analyzing differences in the values expressed by sister taxa (both extant taxa and their inferred ancestors). These differences are then normalized and relationships among the resulting independent contrast values are analyzed with regression statistics. I used the Comparative Analysis of Independent Contrasts program of Purvis & Rambaut (1995) to compute normally distributed independent contrast values and the S.A.S statistical package (S.A.S. Institute Inc., Cary, North Carolina) to perform this and the other statistical tests reported in this study.

Ontogenetic analyses.—I examined developmental changes in the droplet volume per mm and the thread stickiness per mm of threads produced by *A. trifasciata* and *M. gracilis*. I selected these species because threads produced by adult females have similar stickiness values but differ greatly in the size and distribution of their droplets (Table 1). *Argiope trifasciata* produces threads with much greater droplet volume but only half as many droplets per mm as threads of *M. gracilis*.

I collected threads from the field rather than from spiderlings reared in the laboratory to reduce the possibility that spider diet would unnaturally affect the results of this study. I collected threads from *A. trifasciata* from early June to late October at a site where the previous year I observed a large number of adult females of this species and only one individual of the sympatric species, *A. argentata* Lucas. I collected threads of *M. gracilis* from early June to late August at a site where, for two years, this was the only species of this genus that I observed. As spiderlings do not emerge synchronously from egg sacs and as it was not possible to permanently mark spiderlings, I was unable to determine precisely the age of individuals included in each developmental series. My approach was, therefore, to sample these populations regularly to obtain threads produced by immatures of increasing size and, eventually, by adult spiders, thereby obtaining capture threads from each species that had droplets of increasing size.

RESULTS

Phylogenetic analysis.—Droplet volume ranged from 21–480 × 10³ μm³ per mm length

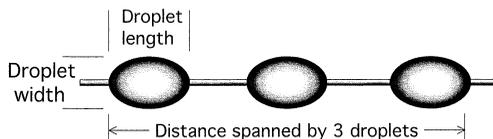


Figure 2.—Measurements used to compute droplet volume.

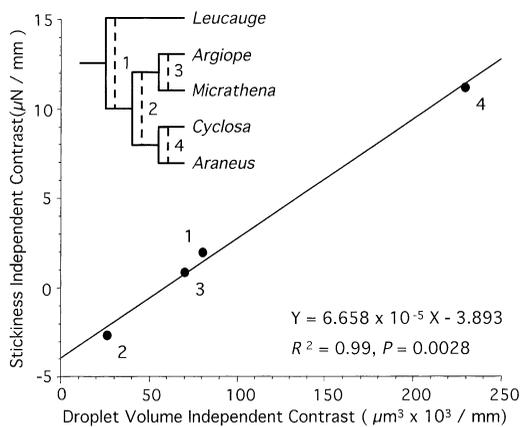


Figure 3.—Relationship between change in droplet volume per mm and thread stickiness, as determined by an independent contrast analysis. Numbers refer to independent contrast values between the sister taxa identified in the pruned phylogeny.

of capture thread and stickiness ranged from 9.6–32.0 μN per mm of thread length (Table 1). IC analysis supports the hypothesized association between droplet volume and thread stickiness by showing that the IC values for droplet volume and thread stickiness are directly related (Fig. 3; $n = 4$, $F = 356.64$, $P = 0.0028$, $R^2 = 0.99$).

Ontogenetic analysis.—For threads of both *A. trifasciata* and *M. gracilis* with droplets of increasing size, droplet volume per mm was directly related to thread stickiness per mm (Fig. 4; $n = 94$, $F = 33.25$, $P = 0.0001$, $R^2 = 0.27$ and $n = 67$, $F = 69.25$, $P = 0.0001$, $R^2 = 0.52$, respectively). When \log_n droplet volume per mm was used, a better fit for *A. trifasciata* was obtained and the fit for *M. gracilis* did not change appreciably ($F = 83.44$, $P = 0.0001$, $R^2 = 0.48$ and $F = 67.90$, $P = 0.0001$, $R^2 = 0.51$, respectively). An analysis of covariance test showed that slopes of the regression lines for \log_n droplet volume per mm and thread stickiness did not differ ($F = 0.20$, $P = 0.65$) and a comparison of the intercepts of the two species regression lines showed that they also did not differ ($F = 1.41$, $P = 0.24$). Thus, a single regression line satisfactorily describes developmental changes in \log_n droplet volume per mm and the stickiness of these two species' capture threads (Fig. 4).

Characteristics of threads produced by adult females.—The IC analysis documented that there is a direct relationship between

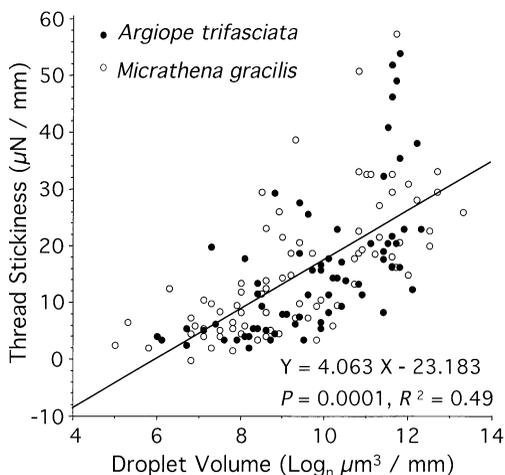


Figure 4.—Developmental changes in droplet volume and thread stickiness of *Argiopo trifasciata* and *Micrathena gracilis*. A common regression line is shown, as the slopes and intercepts of the two species' regression lines do not differ.

droplet volume and thread stickiness (Fig. 3). However, as IC values are derived values, they do not depict the actual relationship between these features. Therefore, I employed traditional regression analysis to describe the relationship between droplet volume per mm of thread length and thread stickiness. In one analysis I used the pooled values of adult females from the five species (Fig. 5; $n = 113$, $F = 58.26$, $P = 0.0001$, $R^2 = 0.34$) and in another the mean values of each of the five

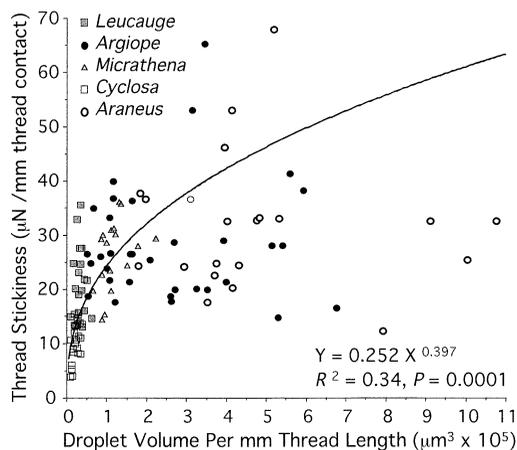


Figure 5.—Relationship between droplet volume per mm of thread and thread stickiness for adults of five araneoid species.

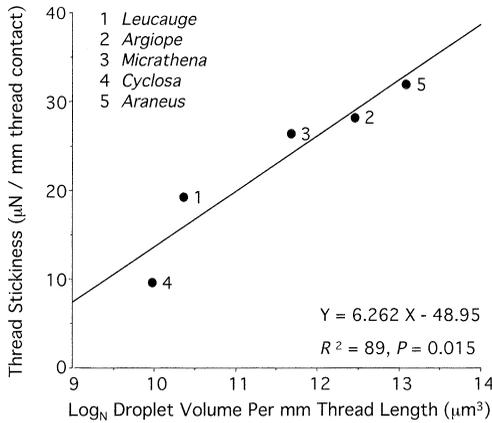


Figure 6.—Relationship between the mean adult values of droplet volume per mm of thread and thread stickiness for five araneoid species.

species (Fig. 6; $n = 5$, $F = 25.03$, $P = 0.015$, $R^2 = 0.89$). In both analyses droplet volume was directly related to thread stickiness and in both this relationship was curvilinear. That is, stickiness increased at a slower rate than did droplet volume. Consequently this relationship was best explained by formulas that used log values of droplet volume (Figs. 5, 6). The plot of all values (Fig. 5) shows that as a thread's droplet volume increases, so too does the variance of its measured stickiness.

Only for the threads produced by adult female *C. conica* was there a direct relationship between droplet volume per mm thread length and thread stickiness ($n = 18$, $F = 11.71$, $P = 0.0041$, $R^2 = 0.41$, stickiness ($\mu\text{N}/\text{mm}$) = 0.00022 thread volume ($\mu\text{m}^3/\text{mm}$) + 4.860). In the other four species this relationship was not significant ($0.13 < P < 0.94$). When \log_n droplet volume per mm thread length was used, the relationship for *C. conica* remained significant ($n = 18$, $F = 12.29$, $P = 0.0029$, $R^2 = 0.43$, stickiness ($\mu\text{N}/\text{mm}$) = $4.370 \log_n$ thread volume ($\mu\text{m}^3/\text{mm}$) - 33.53) and for the other four species it was insignificant ($0.08 < P < 0.84$).

Modeling thread stickiness.—I developed and evaluated three models to predict the stickiness of adhesive threads (Fig. 7): one based on adult thread features, one based on ontogenetic data, and one based on a trial-and-error empirical examination of droplet values. Because phylogenetic analyses demonstrate a direct relationship between droplet volume per mm and thread stickiness, I based the first

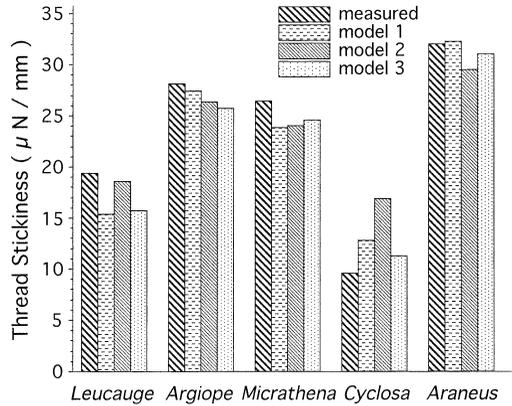


Figure 7.—Comparison of measured stickiness (S) and the values predicted by three models. Model 1 is based on the regression of mean adult values and has the formula: $S = \text{Log}_n$ droplet volume per mm $\times 6.262 - 48.95$. Model 2 is based on the ontogenetic regression and has the formula: $S = \text{Log}_n$ droplet volume per mm $\times 4.063 - 23.183$. Model 3 is an empirical model and has the formula: $S = \text{Log}_n$ (droplet width \times droplet length \times droplets per mm) $\times 13.184 - 96.288$.

model on a regression of the mean adult values of these variables (Fig. 6). The second model uses the common ontogenetic regression formula shown in Fig. 4 to predict stickiness. The third model is based on the observation that the product of droplet length (DL), droplet width (DW), and the number of droplets per mm (DPMM) successfully predicted thread stickiness ($F = 40.24$, $P = 0.008$, $R^2 = 0.93$) according to the following formula:

$$\begin{aligned} \text{Thread Stickiness} \\ = \log_n(\text{DL} \times \text{DW} \times \text{DPMM}) \times 13.184 \\ - 96.288. \end{aligned} \tag{5}$$

Figure 7 compares the performance of these three models. For model 1 the mean absolute difference between each of the five species' measured and predicted stickiness values was 13.23%, for model 2 it was 20.52%, and for model 3 it was 10.76%.

DISCUSSION

Phylogenetic and ontogenetic analyses support the hypothesis that the volume of material in an adhesive thread's droplets is directly related to its stickiness. Models based on these comparisons provide good estimates of the

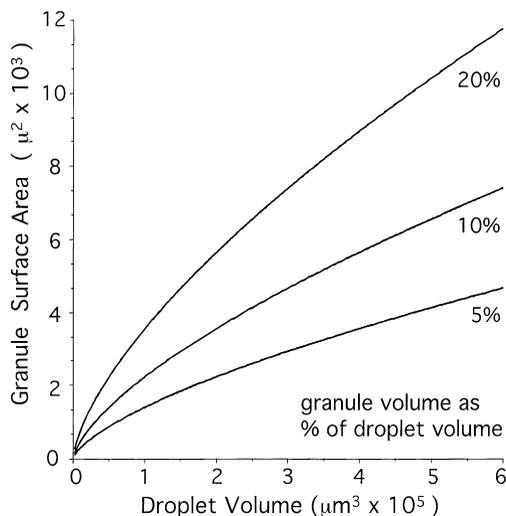


Figure 8.—Relationship between the volume of a viscous droplet and the surface areas of its glycoprotein granule, with granule volume being computed as 5%, 10%, and 20% of droplet volume.

stickiness of adhesive threads that have a wide range of droplet size and distribution patterns and that are produced by spiders of greatly different masses. The simplicity and accessibility of this approach will facilitate the inclusion of thread stickiness in studies that examine the properties and performance of spider orb webs. However, it is important to remember that these models are based on the threads of only five species from the temperate region of North America that belong to two families and that they represent only a small part of araneoid diversity. Additionally, variance in the stickiness predicted by the droplet volume of threads (Fig. 5), particularly the threads of large araneoids, such as *A. trifasciata* and *A. marmoreus*, requires that the capture threads of many individuals be measured to usefully estimate the stickiness of a species' threads.

The curvilinear relationship between droplet volume per mm of thread length and thread stickiness (Figs. 4, 5) is most easily explained by the relationship between the volume of a viscous droplet and the surface area of the glycoprotein granule that lies within it. If contact between a thread's granules and an object is responsible for thread stickiness, then the surface areas of granules should be directly related to thread stickiness. The model presented in Fig. 8 shows that as granule size

increases relative to droplet volume, granule area and, presumably, thread stickiness increases. However, this model also shows that when granule volume is a constant percent of a droplet, granule surface area increases more slowly than does droplet volume. Thus, it appears that the benefits (in terms increased thread stickiness) of producing capture threads with larger adhesive droplets diminish unless there is also an increase in granule volume relative to droplet volume. Similarities in the shapes of the curves in Figs. 5 & 8 suggest that no such compensatory increase in granule volume has occurred in the species that were studied. However, the similarity of these curves may be coincidental and the shape of the curve in Fig. 5 may instead reflect interspecific differences in the composition and concentration of glycoproteins and hydroscopic compounds in the droplets of these species.

The ability of an orb web to intercept prey is related to its capture area (the area between the inner- and outer-most capture spiral of the web), whereas the web's ability to retain prey is related to its stickiness per capture area (Opell 1999b). The origin of modern adhesive orb webs like those treated in this study was associated with an increase in the stickiness per capture area (Opell 1999b). However, there were differences in the stickiness per capture area among the five adhesive orb webs examined by Opell (1999b). The methods described in this study make it easier to examine the consequences of these differences in web design. For example, do larger spiders tend to construct webs characterized by a greater capture area and a smaller stickiness per capture area because they are better equipped to subdue larger prey than are smaller spiders? Are the running and response speeds of a spider associated with the capture area and stickiness per area of its orb web? Are horizontal orb webs characterized by a greater capture areas and smaller stickiness per capture area because they tend to capture smaller, more erratically flying insects (Craig 1987)? Does the stickiness per capture area of an orb web influence the guild of insects that it captures? These and other questions can be addressed by estimating and considering capture thread stickiness.

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