

Can a spider web be too sticky? Tensile mechanics constrains the evolution of capture spiral stickiness in orb-weaving spiders

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Abstract

Orb-weaving spiders rely on sticky capture threads to retain prey long enough to be located and attacked. The evolution of viscid silk is associated with the high diversity of araneoid orb-weaving spiders, in part because it is cheaper to produce than the primitive dry cribellate fibrous adhesive used by deinopoid orb-weaving spiders. Unlike cribellate threads, viscid glue contributes little to the tensile strength of the capture spiral it decorates. However, viscid silk utilizes a unique suspension bridge mechanism, absent in cribellate silk, which increases total stickiness by recruiting the adhesion of multiple glue droplets. Here, we analyze the relationship between stickiness of viscid silk and various biomechanical and architectural features of webs that may influence its evolution, across a sample of 17 cribellate orb-weaving species. The force required to break capture spiral fibers is the single most important factor explaining about 90% of the variation in stickiness among orb spiders. Stickiness increases linearly with capture spiral strength, but with a significant safety factor because stickiness is always less than the force required to break the silk. Our results thus indicate that evolutionary changes in the stickiness of the capture spiral are largely constrained by the strength of the fiber the glue is placed on rather than by the chemistry of the glue itself. This implies that orb webs function optimally when threads are able to detach and adhere repeatedly to struggling prey.

Introduction

Architecturally elegant, spider orb webs are composed of regularly spaced elastic spirals of sticky capture silk laid down upon radial arrays of dry dragline silk. Orb-weaving spiders rely upon a combination of strength and stiffness from the dragline silk and stretchiness of the capture spiral to absorb the kinetic energy of flying insects that impact webs. The adhesiveness of the capture spiral then retains insects long enough to be located and captured by spiders (Eberhard, 1990; Opell, 1997*b*; Blackledge & Hayashi, 2006*a*; Blackledge & Zevenbergen, 2006; Blackledge & Eliason, 2007; Opell & Hendricks, 2007). The interplay between strength, stretchiness and stickiness of viscid silk capture threads therefore helps determine the type of prey that a spider can capture.

A major transition in orb web evolution occurred in the early Cretaceous in the common ancestor of 'modern orb weavers' (Araneoidea) (Selden, 1989). Ancestrally, spiders coated the capture spirals of orb webs with puffs of dry, adhesive cribellate fibrils, as still occurs in the extant deinopoid spiders (Opell, 1999; Opell & Bond, 2001). Cribellate adhesive silk works by physically entangling the setae

of an insect (Opell, 1994) and adhering to surfaces through van der Waal and hygroscopic forces (Hawthorn & Opell, 2002, 2003). However, cribellate fibrils were replaced by chemically adhesive viscid glue droplets in the modern orb weavers. Moreover, viscid glue coats capture spirals that are significantly stretchier than those in cribellate webs (Blackledge & Hayashi, 2006*b*). Araneoid spiders achieve greater stickiness per volume of glue (Opell, 1997*a,b*, 1998, 1999), in part due to a novel suspension bridge mechanism that recruits multiple glue droplets to simultaneously resist detachment (Opell & Hendricks, 2007). The transition to aqueous glue is associated with a dramatic increase in diversity of Araneoidea compared with its cribellate sister lineage Deinopoidea (Coddington & Levi, 1991; Bond & Opell, 1998; Opell & Bond, 2000).

Stickier glue is presumably beneficial to spiders because it should increase the ability of webs to retain prey (Opell, 1999; Opell & Bond, 2001). However, threads that adhere too strongly to prey may break, simultaneously damaging the web and freeing insects from it, thereby resulting in a potential tradeoff in selective pressures. Here we examine how stickiness varies across 17 species of orb weavers representing most major araneoid lineages, as well as

significant ranges of sizes and ecologies, to test the hypothesis that the tensile properties of silk constrained the evolution of capture spiral stickiness.

Materials and methods

Spiders and webs

We collected adult and penultimate female spiders at The University of Akron's Field Station at the Bath Nature Reserve, OH and nearby localities. *Nephila* were obtained from Gainesville, FL. Spiders were housed in cages that varied in size depending on the species. Most individuals were housed in 40 × 40 × 10 cm screen cages with removable plexiglass sides. The large *Nephila* spiders were housed in larger (80 × 80 × 20 cm), but otherwise identical cages. Small species (*Cyclosa*, *Mangora* and *Leucauge*) were housed in smaller circular wire cages of varying sizes covered with nylon screening. Finally, for species (*Gasteracantha*, *Micrathena*) or individuals (some *Nephila*, some *Cyclosa*) that rarely, or never, built webs in cages, individuals were released in a greenhouse. Spiders were misted with tap water regularly and humidifiers were used to keep humidity above 60% surrounding the cages. Webs were typically built within one or a few days of caging the spiders. Once webs were spun, we removed the spiders, weighed and measured them, and then preserved the spiders as vouchers (deposited at the University of Akron). Before sampling silk from the web, we photographed the web to later quantify web architecture. Sample sizes within species ranged from two to 35 webs (average 11.1 per species) with 14 out of the 17 species represented by four or more webs.

Silk testing

For each web, we collected four sets of capture silk from successively interior rows of capture silk, beginning at the bottom of the capture spiral. For each set, we collected four adjacent segments of silk from a single continuous row of capture spiral. First, we sampled capture spiral for tensile testing by gluing silk onto cardboard holders across either 10 or 16 mm gaps, depending upon the size of the web, using Elmer's[®] glue (Blackledge & Hayashi, 2006b). We then cut the silk from the web with a hot soldering iron. Second, we collected silk from the adjacent web sector directly to a glass slide to measure the diameters of the axial capture silk fibers, which became visible when the glue droplets spread out on the glass slide. Third, we sampled silk onto a second cardboard mount as described above to be used for stickiness testing. Fourth, we collected silk from the adjacent web sector onto a glass slide suspended upon 1.5-mm-thick wooden dowels that held the thread in air such that it maintained glue droplet shape. This allowed us to measure the volume and spacing of the glue droplets. We tested the tensile properties and stickiness of silk immediately after collection. Humidity in the tensile testing room ranged from 13 to 45%, with most of this variability occurring within the testing of individual species.

Tensile and stickiness tests were performed using a Nano Bionix test system (Agilent Technologies, TN, USA), previously described in Blackledge, Swindeman & Hayashi (2005). For each tensile sample, we measured force–extension curves of silk extended at a 10% s⁻¹ and calculated four mechanical or material properties. (1) Ultimate strength, or true breaking stress, was calculated as the amount of force required to break a fiber relative to the instantaneous cross-sectional area of the fiber. The instantaneous cross-sectional area of a fiber was calculated using an assumption of constant volume during extension (Vollrath, Madsen & Shao, 2001). (2) Extensibility, or true breaking strain. True breaking strain was calculated as the natural log of the breaking length divided by original length. The standard isovolumetric assumption was applied (Guinea *et al.*, 2006). (3) Breaking force was measured simply as the force applied when the silk broke. (4) Toughness, or the energy absorbed by a fiber before rupture, was calculated from the area under the stress–strain curve divided by sample volume.

For stickiness, we measured the force and extension required to pull the capture silk off of a standard surface. In the tensile tester, we pressed the glue covered capture spiral onto a 2-mm-wide strip of sandpaper (400-b grit silicon carbide) mounted on a small tack (Fig. 1). The sandpaper strip was replaced regularly so that each individual web was tested with a clean surface. We first lowered the silk sample until it first contacted the sandpaper, and then pressed the silk sample additional 2 mm to ensure firm contact. Finally, we pulled the silk away from the substrate at a rate of 1 mm s⁻¹. We measured stickiness directly as the force applied when the silk released from the substrate. We calculated the strain (σ_s) of the silk as

$$\sigma_s = (2 \times (\text{sqrt}(0.5l^2 + e^2)) - l)/l$$

where l was the initial length of the silk and e was the extension at release. We then calculated true strain (σ_{st}) as

$$\sigma_{st} = \ln(1 + \sigma_s)$$

Phylogeny

While a morphology-based phylogeny exists, containing many of the genera in this study, we chose to construct a molecular based phylogeny that would allow us to obtain estimates of branch lengths to be used in independent contrasts analyses. Our intent was not to conduct an exhaustive analysis of relationships among orb-weaving spiders (such analyses are underway in the lab of T. Blackledge), but rather to focus on the taxa in this study. We selected the cribellate orb-weavers *Deinopis spinosa* and *Uloborus diversus* as outgroups.

Genomic DNA was extracted from ethanol preserved spiders using Qiagen DNeasy Tissue Kits (Qiagen Inc. Valencia, CA, USA). We then sequenced partial fragments for two mitochondrial (16S, COI) and three nuclear (18S, 28S, H3) loci, providing roughly 4150 bp of data. Amplifications were performed using Techgene (Techne Inc. Burlington, NJ, USA) thermal cyclers. PCR reactions (50 μ L)

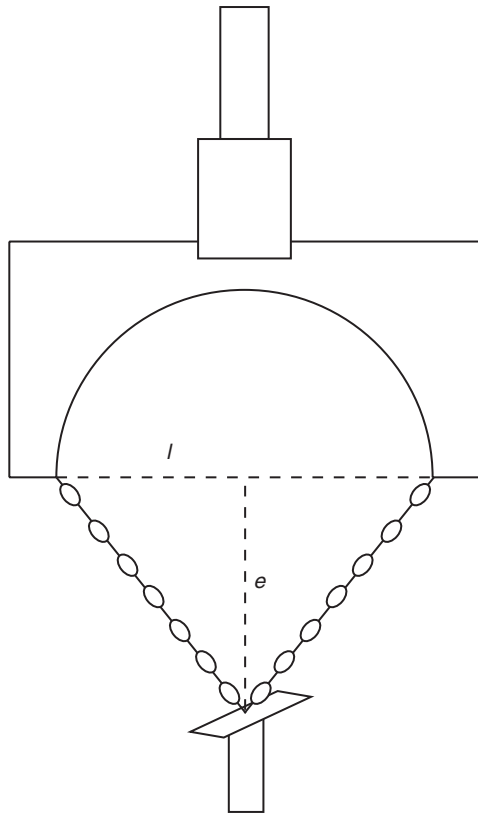


Figure 1 Experimental setup. The glue covered capture spiral was pressed onto 2-mm-wide strip of sandpaper mounted on a tack. The silk, of original length l , was then pulled away from the substrate at a rate of 1 mm s^{-1} . Stickiness was measured directly as the force applied when the silk released from the substrate at extension e .

included $0.5\text{--}1 \mu\text{L}$ genomic DNA, $1 \mu\text{L}$ dNTP mix, $0.5 \mu\text{L}$ of each primer, $\sim 0.25 \text{ U}$ *Taq* polymerase (Invitrogen), $6.5 \mu\text{L}$ of buffer and $41 \mu\text{L}$ of sdH_2O . PCR products were typically cleaned with Montage PCR filter units (Millipore Cidra Inc. Billerica, MA, USA) and then sequenced at the University of California, Riverside, Genomics Core Instrumentation Facility or sent to MacrogenUSA for cleaning and sequencing. DNA Vouchers are stored at the University of Akron.

Because no length variation occurred in the protein coding COI and H3 loci, the alignment of these markers was trivial. We used ClustalX to align ribosomal fragments (Thompson *et al.*, 1997), and then slightly edited the ends of the sequences in BioEdit (Hall, 1999). We used gap opening and extension costs of 8 and 4, with transitions weighted at 0.5. Gaps were treated as missing data in subsequent analyses. We chose not to focus on a detailed sensitivity analyses of the phylogenetic data here, however, analyses of larger datasets focusing on phylogenetic relationships of araneoid spiders and their relatives show that results are congruent across a variety of parameters such that the 8/4 alignment well represents the overall findings (T. Blackledge *et al.*, unpubl. data). We further show here that phylogenetic dependence is not an issue in the current study as statistical

results are closely similar whether analyzing the raw data, or using independent contrasts with two very different phylogenies, the one presented here, and the morphological phylogeny of Scharff & Coddington (1997). All sequences were deposited in GenBank (Table 1).

We performed a Bayesian analysis using MrBayes V3.1.2 (Huelsenbeck & Ronquist, 2001). We used Modeltest 3.6 (Posada & Crandall, 1998) to select from among 56 potential models of base substitutions. The best fitting model was GTR + γ + I for all loci. Each locus was modeled as an independent partition in the analysis and we further partitioned protein coding genes by codon position. Parameters were estimated independently for each data partition. Four Markov Chain Monte Carlo (MCMC) chains were run simultaneously for 10 000 000 generations and sampled every 1000 generations. We discarded the first 2000 000 generations as 'burn-in' and computed posterior probabilities from the majority rule consensus tree of the remaining post-burn-in trees.

Data analysis

We used linear regression to compare the relationship between capture spiral stickiness, the morphology of glue droplets, web architecture and the tensile properties of capture threads. We used standard, forward and backward multiple linear regressions to determine which individual factors best explained stickiness variation. To account for non-independence of species due to phylogenetic relatedness, we also ran Independent Contrast analyses (Felsenstein, 1985) using the PDAP module (Midford, Garland & Maddison, 2008) of the evolutionary analysis package Mesquite v2.5 (Maddison & Maddison, 2008). As absolute values of the standardized phylogenetically independent contrasts were significantly correlated for some characters when using raw branch lengths, branch lengths were transformed before independent contrast analyses using the 'Branch Lengths Method of Nee' option. The analyses presented here were based upon our molecular phylogeny, however, none of the statistical conclusions differed from those obtained using a morphological phylogeny (Scharff & Coddington, 1997) and an assumption of equal branch lengths.

Results

Across the 17 species of spiders, stickiness ranged from 12.7 to $291.5 \mu\text{N}$ per 2 mm of thread. In comparison, the force required to break the capture spiral fibers during tensile tests (hereafter 'breaking load') ranged from 49.2 to $4025.4 \mu\text{N}$ (Table 2). Stickiness correlated positively with most measured aspects of web architecture and thread morphology (Table 2 summarizes results of web architecture, spider morphology and silk morphology and biomechanics, Table 3 summarizes statistical results). Because many aspects of thread morphology and web architecture scale strongly with spider size, we used standard, forward, and backward multiple linear regression analysis to determine which factors

Table 1 Taxon sample and Genbank accession numbers

Species	COI	16S	18S	28S	H3
<i>Araneus trifolium</i>	^a	^a	FJ525404	FJ525385	^a
<i>Araneus marmoreus</i>	FJ525333	FJ525366	FJ525403	FJ525384	FJ525348
<i>Argiope aurantia</i>	FJ525332	FJ525365	FJ525402	FJ525383	FJ525347
<i>Argiope trifasciata</i>	FJ525316	FJ525349	FJ525386	FJ525368	FJ525335
<i>Cyclosa conica</i>	FJ525319	FJ525352	FJ525389	FJ525371	FJ525338
<i>Eustala</i>	FJ525320	FJ525353	FJ525390	FJ525372	FJ525339
<i>Gasteracantha cancriformis</i>	FJ525321	FJ525354	FJ525391	FJ525373	FJ525340
<i>Larinioides cornutus</i>	FJ525322	FJ525355	FJ525392	^a	^a
<i>Leucauge venusta</i>	FJ525323	FJ525356	FJ525393	FJ525374	FJ525341
<i>Mangora gibberosa</i>	FJ525324	FJ525357	FJ525394	FJ525375	^a
<i>Metepeira labyrinthea</i>	FJ525325	FJ525358	FJ525395	FJ525376	FJ525342
<i>Micrathena gracilis</i>	FJ525326	FJ525359	FJ525396	FJ525377	FJ525343
<i>Neoscona arabesca</i>	FJ525330	^a	FJ525400	^a	^a
<i>Neoscona crucifera</i>	FJ525327	FJ525360	FJ525397	FJ525378	^a
<i>Nephila clavipes</i>	FJ525328	FJ525361	FJ525398	FJ525379	FJ525344
<i>Tetragnatha</i>	FJ525317	FJ525350	FJ525387	FJ525369	FJ525336
<i>Verrucosa arenata</i>	FJ525331	FJ525364	FJ525401	FJ525382	FJ525346
Outgroups					
<i>Deinopis spinosa</i>	FJ525318	FJ525351	FJ525388	FJ525370	FJ525337
<i>Uloborus diversus</i>	FJ525329	FJ525362	FJ525399	FJ525380	FJ525345

^aLocus not sequenced.

most correlated with variation in stickiness. In both the standard and the backward multiple regressions, breaking load of the capture spiral was the only significant factor (standard: $R^2 = 0.97$, $F = 29.5$, $P < 0.001$, breaking load $\beta = 1.06$; backward: $R^2 = 0.91$, $F = 154.1$, $P < 0.001$, breaking load $\beta = 0.96$). In the forward multiple regression, carapace width and ultimate stress of the capture spiral fiber were also significant ($R^2 = 0.96$, $F = 55.6$, $P < 0.001$, breaking load $\beta = 0.98$, carapace width $\beta = 0.44$, ultimate stress $\beta = -0.29$). Breaking load explained over 90% of the variation in stickiness (Fig. 2a) and capture threads released from substrates at ~20% of their breaking loads. For most species, capture spirals released from the substrate when they were extended to ~25% of their breaking length (Fig. 2b). Stickiness also correlated strongly with the stretchiness of the spiral fiber (Fig. 3).

Results were very similar after correcting for phylogenetic relatedness (Figs 2–4) among species using PDAP, which was not surprising considering that we intentionally sampled broadly from across the orb spider phylogeny. There were no qualitative differences in results whether using the phylogeny generated here, or the phylogeny of Scharff & Coddington (1997), for the independent contrast analyses.

Discussion

Orb-weaving spiders rely on sticky prey capture threads to retain prey long enough to be located and caught (Blackledge & Eliason, 2007). Yet, many insects escape quickly from orb webs, long before they are attacked by spiders (Rypstra, 1982; Blackledge & Zevenbergen, 2006). This suggests that spiders experience strong selective pressures

to increase the overall stickiness of the viscid glue droplets coating capture spirals. Indeed, a major event in orb web evolution is the transition from ancestral cribellate threads to viscid capture threads that increased relative stickiness of the capture spirals thereby allowing these spiders to maintain overall web stickiness at lower production costs (Opell, 1997b, 1998).

As an araneoid capture thread is pulled away from the substrate, individual glue droplets extend such that force is transferred from the edge of contact to successively interior droplets in what has been termed a 'suspension bridge model' (Opell & Hendricks, 2007). This prevents forces from concentrating at the edge of contact with the substrate, thereby allowing more surface area of the capture thread to contribute to adhesion. Thus, the stretchiness of glue droplets may act in part as a mechanism that increases adhesiveness. In addition, we find here that, stretchiness of araneoid capture threads is correlated with stickiness (Fig. 3).

However, the biomechanics of the core axial fibers of the capture spiral likely place significant limitations on the evolution of glue stickiness. Extreme stickiness is wasted if the glue is placed upon threads that break easily. We found that stickiness correlates strongly with the breaking force of the capture spiral, such that capture threads always release from the substrate at about 20% of the force required to break the fiber (Fig. 2a). The relatively smooth surface of the sandpaper used in our experiment (400 grit) provided a very consistent substrate across tests but also likely resulted in minimal estimates of stickiness. Opell & Schwend (2007), for example, found that capture spirals adhered with $3.5 \times$ more force to insect cuticle containing setae than to smooth surfaces. Extrapolating from our data threads might release

Table 2 Summary of measurements of spider size and web architecture, as well as silk and glue morphology and biomechanics

Species	N	Carapace width (mm)	Spiral diameter (μm)	Spiral true stress (MPa)	Spiral true strain (mm/mm)	Spiral toughness (MPa)	Spiral breaking load (mN)	Glue release load (mN)	Glue volume (μm ³)	Droplets/mm	Mesh width (cm)
<i>Araneus marmoreus</i>	3	5.17 ± 0.61	3.75 ± 1.03	885.12 ± 160.10	1.45 ± 0.03	155.18 ± 31.02	2168.53 ± 759.13	291.54 ± 136.04	206472 ± 173962	6.27 ± 1.39	0.27 ± 0.02
<i>Araneus trifolium</i>	7	5.01 ± 0.31	4.11 ± 0.27	1142.81 ± 63.97	1.72 ± 0.05	210.43 ± 17.13	2863.69 ± 425.00	279.69 ± 89.24	94588.37 ± 24920.31	7.03 ± 0.64	0.47 ± 0.03
<i>Argiope aurantia</i>	16	4.65 ± 0.16	4.83 ± 0.38	1039.92 ± 88.58	1.59 ± 0.06	212.41 ± 25.56	4025.36 ± 544.75	471.28 ± 89.43	23669.84 ± 4912.99	12.08 ± 0.68	0.48 ± 0.02
<i>Argiope trifasciata</i>	15	3.25 ± 0.15	2.71 ± 0.23	882.31 ± 70.36	1.45 ± 0.04	170.16 ± 15.01	1274.05 ± 218.11	82.71 ± 22.35	5466.80 ± 1652.27	20.02 ± 2.50	0.29 ± 0.03
<i>Cyclosa conica</i>	2	1.35 ± 0.25	0.71 ± 0.04	308.03 ± 57.98	0.87 ± 0.11	54.16 ± 8.74	49.17 ± 1.56	12.68 ± n/a	255.23 ± n/a	23.76 ± n/a	0.16 ± n/a
<i>Eustala</i>	3	1.82 ± 0.09	1.07 ± 0.17	757.16 ± 104.54	1.01 ± 0.13	126.96 ± 20.43	233.56 ± 37.01	47.71 ± 11.49	529.49 ± 229.18	40.78 ± 6.25	0.35 ± 0.02
<i>Gasteracantha cancriformis</i>	11	2.56 ± 0.06	1.10 ± 0.08	985.87 ± 85.64	0.96 ± 0.03	145.43 ± 14.02	331.24 ± 23.08	56.14 ± 16.32	3876.55 ± 737.23	17.34 ± 0.80	0.27 ± 0.02
<i>Larinioides cornutus</i>	26	3.65 ± 0.14	2.56 ± 0.13	1141.19 ± 69.22	1.25 ± 0.04	209.26 ± 14.85	1669.80 ± 155.24	270.40 ± 35.53	5278.31 ± 895.35	21.61 ± 2.55	0.56 ± 0.04
<i>Lecauge venusta</i>	12	1.82 ± 0.07	0.93 ± 0.07	886.50 ± 126.05	0.89 ± 0.04	147.91 ± 21.36	232.44 ± 35.90	20.23 ± 3.54	715.54 ± 193.9	45.21 ± 7.41	0.25 ± 0.02
<i>Mangora maculata</i>	9	1.28 ± 0.04	0.77 ± 0.05	250.04 ± 57.06	0.87 ± 0.10	53.02 ± 13.80	52.44 ± 16.04	15.58 ± 5.59	76.93 ± 30.62	63.51 ± 12.02	0.09 ± 0.01
<i>Metepira labyrinthea</i>	9	2.20 ± 0.09	1.51 ± 0.14	777.80 ± 94.45	1.03 ± 0.03	123.41 ± 15.87	464.96 ± 56.47	72.00 ± 28.45	3039.77 ± 517.88	18.70 ± 2.61	0.23 ± 0.02
<i>Micrathena gracilis</i>	16	2.16 ± 0.07	1.26 ± 0.08	269.04 ± 32.28	0.90 ± 0.05	51.28 ± 6.07	136.97 ± 23.49	44.70 ± 9.42	5752.56 ± 1728.31	14.98 ± 1.92	0.14 ± 0.01
<i>Neoscona arabiesca</i>	35	1.99 ± 0.07	1.38 ± 0.08	536.86 ± 47.54	1.13 ± 0.03	101.67 ± 10.55	274.90 ± 36.48	48.84 ± 9.33	1664.98 ± 369.62	32.82 ± 3.02	0.28 ± 0.01
<i>Neoscona crucifera</i>	5	4.98 ± 0.19	2.98 ± 0.53	1095.29 ± 171.52	1.48 ± 0.08	252.12 ± 44.11	1742.78 ± 420.25	254.44 ± 64.81	11481.33 ± 3074.66	13.46 ± 2.24	0.36 ± 0.04
<i>Nephila clavipes</i>	12	4.90 ± 0.16	4.17 ± 0.34	234.80 ± 22.85	1.52 ± 0.07	39.93 ± 4.01	644.92 ± 61.20	126.55 ± 22.71	15887.62 ± 3648.69	9.04 ± 0.98	0.32 ± 0.02
<i>Tetragnatha</i>	4	1.77 ± 0.09	1.85 ± 0.64	763.54 ± 173.76	1.07 ± 0.19	126.82 ± 30.67	859.98 ± 544.40	104.45 ± 55.06	4487.19 ± 3839.39	20.84 ± 5.49	0.41 ± 0.06
<i>Verrucosa arenata</i>	4	2.67 ± 0.05	1.35 ± 0.26	1396.51 ± 56.37	1.16 ± 0.17	296.69 ± 30.98	606.36 ± 135.67	72.80 ± 33.97	3333.49 ± 615.99	13.38 ± 2.45	0.50 ± 0.01

Numbers represent averages (n = number of individual spiders/webs tested) ± standard error.

Table 3 Regressions between stickiness and various aspects of spider size, thread morphology and web architecture done individually

Variable	Standard	IC
Carapace width (mm)	$R^2 = 0.78^{**}$	$R^2 = 0.69^{**}$
Spiral diameter (μm)	$R^2 = 0.76^{**}$	$R^2 = 0.71^{**}$
Spiral true stress (MPa)	$R^2 = 0.33^*$	$R^2 = 0.35^*$
Spiral true strain (mm/mm)	$R^2 = 0.74^{**}$	$R^2 = 0.59^{**}$
Spiral toughness (MPa)	$R^2 = 0.36^*$	$R^2 = 0.35^*$
Breaking load (log mN)	$R^2 = 0.91^{**}$	$R^2 = 0.88^{**}$
Glue volume (μm ³)	$R^2 = 0.24^*$	$R^2 = 0.10$
Droplets/mm	$R^2 = 0.50^{**}$	$R^2 = 0.52^{**}$
Mesh width (mm)	$R^2 = 0.54^{**}$	$R^2 = 0.49^{**}$

All are significant using standard regression, and all but glue volume using Independent Contrasts (IC) (*0.05–0.01, ** < 0.001). All regressions are positive, except the number of droplets per mm. Standard and backward multiple regressions identify breaking load of the capture spiral as the only significant factor, explaining about 90% of variation in stickiness.

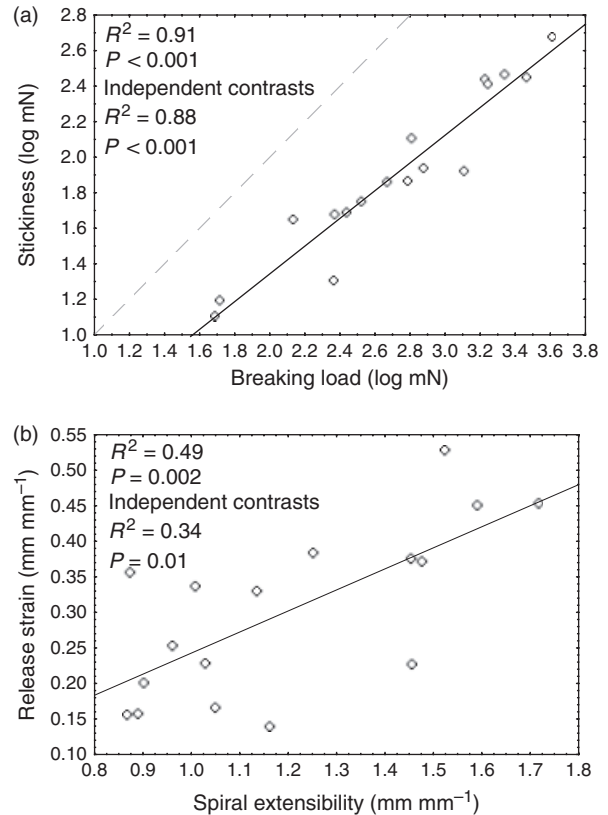


Figure 2 Relationship between tensile performance and adhesion of capture spirals. (a) The maximum sticky force is highly correlated with breaking load. Dashed gray line indicates one to one correlation. (b) The total extensibility is also highly correlated with the maximum extension of fibers when the glue releases.

from insects with setose cuticle at about 60–70% of the force required to break the fiber. A consistent release at 20–70% force suggests that capture spiral stickiness exhibits a significant safety factor that minimizes the probability of threads breaking under most circumstances.

The efficacy of the initial interception of an insect by an orb web is determined by the web's overall capacity to dissipate kinetic energy, which is transferred throughout the capture spiral and radial threads. However, subsequent retention of insects is affected primarily by how individual segments of threads resist breaking and by their stickiness. If an entangled insect pulls free from a capture spiral then the insect may escape, but it is also likely to contact nearby rows of capture spiral or even that same thread. By detaching instead of breaking, a segment of capture thread may repeatedly adhere to an insect and continue to disrupt its struggles.

Increasing evidence suggests that orb spiders depend upon the capture of especially large prey for survival and reproduction (Venner & Casas, 2005; Blackledge & Eliason, 2007). However, these prey likely place the greatest demands upon the retention capacities of webs. We found a remark-

ably consistent relationship between stickiness and breaking load for capture threads across a phylogenetically broad survey of spiders. These included representatives of three different families (Tetragnathidae, Nephilidae and Araneidae) that spin architecturally diverse webs. The generality of this pattern argues that capture thread biomechanics act as a fundamental constraint upon the evolvability of the stickiness of capture spirals. One important mechanism by which spiders can therefore manipulate the overall stickiness of webs is through changes in architecture. By spacing spirals of silk closer together, a spider can substantially increase the retention times of many prey (Blackledge & Zevenbergen, 2006) and gain access to the crucial but difficult to capture large, rare prey (Blackledge & Eliason, 2007).

In summary, the stickiness of viscid glue in orb webs closely correlates with the strength of the capture spiral across diverse species of spiders. This suggests that silk tensile mechanics act as an evolutionary constraint on stickiness that minimizes the probability of capture spiral threads breaking during prey capture. We hypothesize that this both prevents web damage, and increases the overall retention of prey by allowing capture threads to repeatedly adhere to struggling insects.

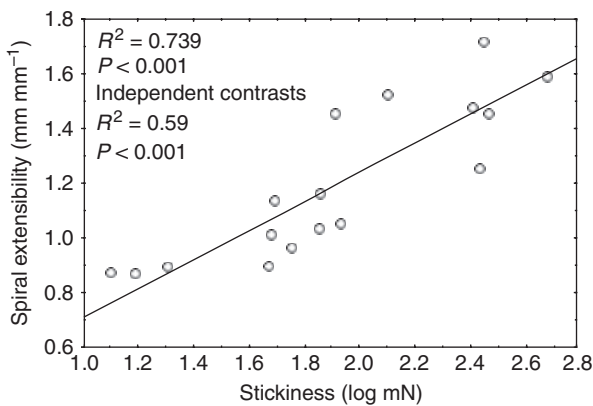


Figure 3 Correlation between stretchiness and stickiness of the capture spirals for 17 species of orb-weaving spiders.

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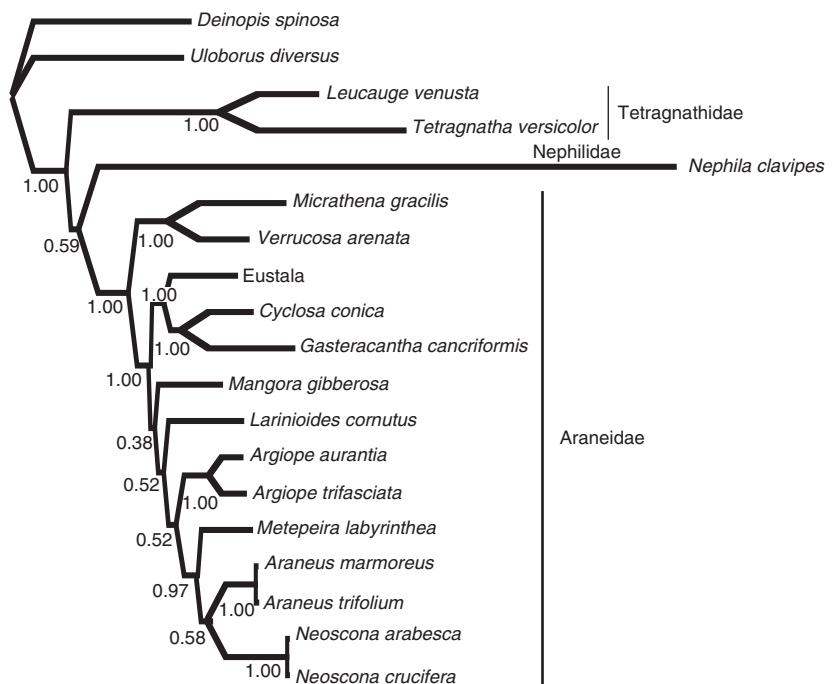


Figure 4 Relationships among taxa in this study, based upon Bayesian analysis of five molecular loci. Branch lengths are proportional and numbers indicate posterior probabilities.

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