



## Capture thread extensibility of orb-weaving spiders: testing punctuated and associative explanations of character evolution

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Spider orb-webs contain sticky prey capture threads and non-sticky support threads. Primitive orb-weavers of the Deinopoidea produce dry cribellar threads made of thousands of silk fibrils that surround supporting axial fibres, whereas the viscous threads of modern Araneoidea orb-weavers produce adhesive threads with an aqueous solution that coalesces as droplets around the axial fibres. We have previously shown that the greater diversity of the Araneoidea is phylogenetically significant and attributed this disparity to a number of advantages, considered key innovations, that adhesive thread has over cribellar thread. An important putative advantage of adhesive thread demonstrated by Köhler and Vollrath in their 1995 study is its greater extensibility, a feature that better adapts it to absorb the kinetic energy of a prey strike. However, this conclusion is based on a two-species comparison that does not take advantage of the modern comparative method that requires hypotheses to be tested in a phylogenetic context. Using a transformational analysis to examine threads produced by nine species, our study finds no support for the punctuated explanation that adhesive thread has a greater extensibility than cribellar thread. Instead, it strongly supports the associative null hypothesis that capture thread extensibility is tuned to spider mass and to architectural features of the web, including its capture area, capture spiral spacing, and capture area per radius.

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ADDITIONAL KEY WORDS:—capture thread – character evolution – orb-web–spider–transformational analysis.

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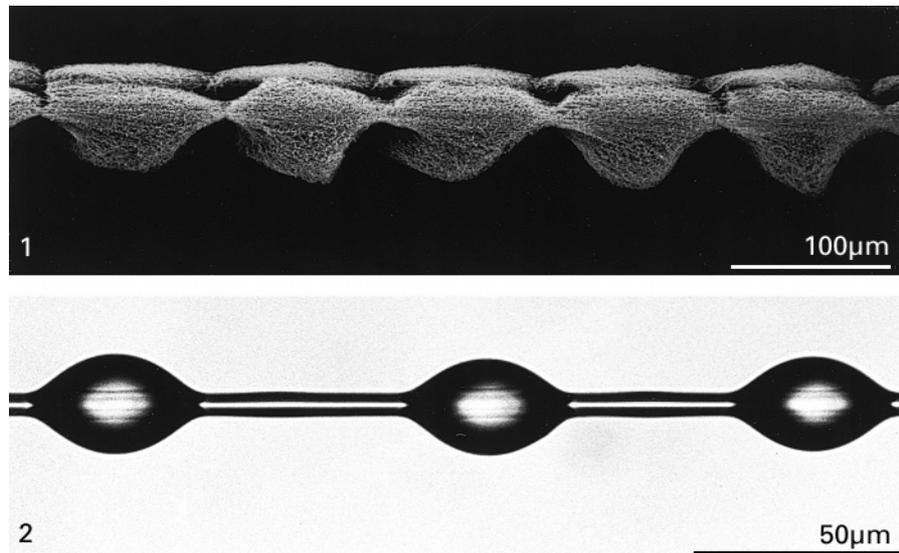
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## INTRODUCTION

Orb-webs contain two types of prey capture thread: the dry cribellar threads of the Deinopoidea (Fig. 1; Coddington, 1986; Eberhard & Pereira, 1993) and viscous adhesive threads of the Araneoidea (Fig. 2; Opell, 1997, 1998; Peters, 1986, 1995; Vollrath, 1992; Vollrath *et al.*, 1990). The transition from primitive horizontal orb-webs containing cribellar threads to the more modern vertical adhesive orb-webs containing adhesive thread coincided with a significant increase in species (Bond & Opell, 1998). In addition to a change in web orientation, changes in the spectral reflective properties, stickiness, and material cost of capture threads contributed to the success of modern orb-weaving spiders (see Bond & Opell, 1998 for a summary). Another putative adaptive feature of the adhesive capture thread is its enhanced extensibility and thus its greater potential for absorbing the force of a prey strike (Köhler & Vollrath, 1995). This is particularly advantageous for araneoids for which vertical orb-web orientation is synapomorphic (Bond & Opell, 1998).

Both cribellar and adhesive capture threads are supported by a pair of axial fibres that are spun from spigots that are presumed to be homologous (the flagelliform spigots on the posterior spinnerets; Foelix, 1996). Adhesive capture thread features a unique windlass mechanism that is initiated when the complex aqueous solution that coats the thread's supporting axial fibres coalesces into a series of regularly spaced viscous droplets. Each droplet reels in a sector of the axial lines, thereby



Figures 1, 2. Capture threads of orb-weaving spiders. Fig. 1. Scanning electron micrograph of the cribellar capture thread of *Waitkera waitakerensis*. Fig. 2. Light micrograph of the adhesive capture thread of *Argiope trifasciata*.

acting as a self-tensing mechanism (Vollrath & Edmonds, 1989) that serves to maintain web tension and probably helps dissipate the force of a prey strike (Lin, Edmonds & Vollrath, 1995). The extensibility of cribellar threads is due in part to the separation of the fine fibrils that form its surface and in part to the extensibility of its supporting axial fibres (Köhler & Vollrath, 1995).

In a detailed study of the functional properties of capture threads, Köhler & Vollrath (1995) showed that the extensibility of adhesive thread produced by immature araneids was 3.8 times greater than that of cribellar thread produced by mature uloborids of the same mass. They state that “The ecribellate capture silk is less time-consuming to build . . . more extensible, and hygroscopic . . . We assume these to be the main reasons why the aqueous viscid spiral of the ecribellate orb-weaving spiders should be more successful (i.e., used by more species, many of which are very common) than the hackled band of the cribellate orb weavers (used by few and rather rare species).” They hypothesize that the transition from cribellar to adhesive capture thread was associated with an increase in thread extensibility and indicated that this was one of the key adaptations that accounted for the disparity in clade size between the more diverse Araneoidea and the less diverse Deinopoidea.

Köhler & Vollrath’s 1995 study is important because it carefully examines and documents the material properties of capture threads. However, the critical question is whether an increase in extensibility characterized the divergence of the Araneoidea from the Deinopoidea or whether extensibility is functionally constrained within the Orbiculariae clade and changes in thread extensibility occurred at deeper phylogenetic levels. Our study tests the hypothesis posited by Köhler and Vollrath that this was an adaptive transition that occurred at the araneoid node and that the origin of adhesive capture thread was associated with an increase in thread extensibility. It does so by attempting to disprove the null, non-adaptive hypothesis that capture thread extensibility is determined principally by orb-web features and spider mass, an explanation that we consider to be an ‘associative explanation’ of morphological change. In contrast, Köhler & Vollrath (1995) predict that thread extensibility will be determined principally by the phylogenetic position of spiders, and, thus, attribute differences to what we term a ‘punctuated explanation’ of morphological change. By so doing, they follow the reasoning of Coddington (1988, 1990a, 1994) and Baum & Larson (1991) that defines an adaptation as an apomorphic character, in this case adhesive thread, that appears to have a positive selective value when compared to the plesiomorphic condition, cribellar thread.

Our null hypothesis assumes that orb-web features are constrained functionally rather than phylogenetically and predicts that the spacing of capture threads and the manner in which they are supported by non-sticky radial threads correlates with their extensibility. Capture threads that are more widely spaced and those that are supported at greater intervals by radii should have higher extensibilities to help them absorb locally some of the force of a prey strike as this force is being transferred to the web’s radii. Spider mass is correlated with both the capture area (Eberhard, 1988; Heiling & Herberstein, 1998; Opell, 1996, 1999) and the total stickiness of orb-webs (Opell, 1996, 1997, 1999) and may limit the amount of material that a spider can invest in a web’s capture thread (Eberhard, 1972, 1986, 1988; Peters, 1937; Witt *et al.*, 1968). Thus, it is probable that the extensibilities of capture threads produced by larger spiders are greater than those produced by smaller spiders. If these predictions are correct, then they will override any differences in extensibility

due simply to thread type and make it difficult to disprove the null hypothesis in a broader phylogenetic context.

In selected web features that should be associated with capture thread extensibility, we acknowledge that the orb-web operates as a unit and that many of its features are functionally linked. We do not argue that these web parameters are completely independent. However, they represent different avenues for examining the association between orb-web architecture and capture thread extensibility. If this association is strong, it should be supported by several indices. In summary, this study tests the hypothesis that greater thread extensibility is a property of the Araneoidea. In contrast, the null hypothesis attributes thread extensibility to differences in spider mass, web capture area, capture spiral spacing, and web capture area per radius.

## MATERIAL AND METHODS

### *Species studied*

We measured the extensibility of cribellar capture threads produced by three species of the Uloboridae, five species of Araneidae, and one species of Tetragnathidae (Table 1). Only adult females were used in this study. The relationship of these species and a description their web orientations and habitats are given in Figure 3. The individuals whose thread extensibilities were measured were taken from the same populations as those for which web parameters were measured in previous studies (Opell, 1997, 1999). Although we did not measure the extensibility of the threads of *Siratoba referena*, features of this species' web were included in the analysis of spider mass and capture area per radius. The spiral spacing and capture area values for *Neoscona hentzii* were inferred from those of *Araneus marmoreus*.

### *Extensibility measurements*

It is important to note that previous studies (Craig, 1987; Köhler & Vollrath, 1995) have measured the extensibility of resting capture thread (which we term fundamental extensibility) by shortening a capture thread until its tension was reduced to zero prior to beginning measurements. As capture thread extensibility has presumably been selected in the context of a functioning web, we believe that it is instructive and consistent with the definition of adaptation presented above to compare the extensibilities of cribellar and adhesive threads under their actual loadings in an orb-web. By comparing these realized thread extensibilities, we hoped to rigorously test the null hypothesis and present a clearer picture of the functional differences between the primitive and advanced capture threads of orb-webs.

We collected entire orb-webs or large sectors of orb-webs on 18 cm diameter polished aluminium rings with double-sided tape on their upper rims. In the laboratory we examined these samples under a dissecting microscope to determine that their threads were intact and unstretched. Single capture thread strands were then transferred to the tips of two rivets whose heads were glued to a microscope slide so that their tips were 2 cm apart. These threads were re-examined to ensure that they were not damaged during transfer. Double-sided tape on the rivet tips

TABLE 1. Spider masses, conditions under which extensibility was measured, extensibility, repeatability of extensibility measurements, and capture area per number of radii (mean,  $\pm 1$  SE, and sample size in parentheses). Ancestral values are given in brackets; those for capture area per radius were computed with a phylogeny that included *S. referena*. Species are identified by superscripts that correspond to the numbered points in Figures 4 and 5

Family species	Weight mg	Temperature °C	Percent relative humidity	Extensibility (% original length)	Repeatability (% mean extensibility)	Capture area per radius (cm <sup>2</sup> )
Araneidae:						
<i>Araneus marmoreus</i> <sup>1</sup> Clerck	692.10 $\pm 85.45(10)$ [490.14]	23.0 $\pm 0(10)$	59.60 $\pm 0.16(10)$	1039 $\pm 86(10)$ [958]	16.30%	20.83 $\pm 0.76(13)$ [11.17]
<i>Neoscona hentzi</i> <sup>2</sup> (Keyserling)	557.21 $\pm 43.54(19)$ [490.14]	23.37 $\pm 0.11(19)$	59.79 $\pm 0.10(19)$	997 $\pm 35(19)$ [958]	8.61%	—
<i>Cyclosa conica</i> <sup>3</sup> (Pallas)	7.42 $\pm 0.34(20)$ [221.11]	24.55 $\pm 0.27(20)$	61.50 $\pm 0.22(20)$	749 $\pm 55(14)$ [837]	19.09%	1.97 $\pm 0.10(17)$ [11.17]
<i>Argiope trifasciata</i> <sup>4</sup> (Forsk.)	315.43 $\pm 27.29(21)$ [193.42]	22.62 $\pm 0.12(21)$	59.57 $\pm 0.11(21)$	1100 $\pm 47(21)$ [920]	13.02%	24.78 $\pm 2.01(22)$ [13.00]
<i>Micrathena gracilis</i> <sup>5</sup> (Walckenaer)	99.06 $\pm 6.36(21)$ [193.42]	24.14 $\pm 0.10(21)$	59.71 $\pm 0.16(19)$	857 $\pm 44(20)$ [920]	16.69%	3.52 $\pm 0.22(20)$ [13.00]
Tetragnathidae:						
<i>Leucauge venusta</i> <sup>6</sup> (Walckenaer)	28.37 $\pm 2.89(15)$ [82.79]	24.73 $\pm 0.18(15)$	60.27 $\pm 0.62(15)$	586 $\pm 61(15)$ [656]	14.73%	6.35 $\pm 0.44(16)$ [7.97]
Uloboridae:						
<i>Octonoba sinensis</i> <sup>7</sup> (Simon)	12.61 $\pm 1.79(18)$ [15.04]	22.61 $\pm 0.14(18)$	60.72 $\pm 0.45(18)$	753 $\pm 53(22)$ [618]	24.97%	8.55 $\pm 0.61(23)$ [6.80]
<i>Uloborus glomus</i> <sup>8</sup> (Walckenaer)	6.86 $\pm 0.41(28)$ [15.04]	24.04 $\pm 0.16(28)$	61.61 $\pm 0.33(28)$	604 $\pm 36(23)$ [618]	15.83%	6.13 $\pm 0.30(26)$ [6.80]
<i>Waitkera waitakerensis</i> <sup>9</sup> (Chamberlain)	7.72 $\pm 0.47(24)$ [25.66]	25.04 $\pm 0.28(24)$	70.00 $\pm 1.20(24)$	299 $\pm 18(24)$ [498]	14.69%	3.18 $\pm 0.21(25)$ [3.49]
<i>Siratoba referena</i> <sup>10</sup> (Muma & Gertsch)	—	—	—	—	—	1.57 $\pm 0.15(22)$ 3.49

maintained the original tension of a thread as it was transferred to the instrument used to measure extensibility. This instrument incorporated a digital caliper with an accuracy of 0.01 mm. The caliper's jaws were opened to a width of 2.50 mm and a strand of thread was captured on a 7–9 mm wide span of doubled-sided tape affixed to each of the caliper's jaws. A switch activated the motorized advancement mechanism that opened the jaws of the caliper. When the thread broke, the switch was immediately released, stopping the motor. The final span of the jaws was divided by the initial span to yield thread extensibility. We measured the extensibility of three capture thread strands from each individual's web and used the mean of these values at this individual's value. The repeatability of the extensibility measurements of an individual spider's threads is computed as the standard error of the mean of its three values. This value is placed in perspective when it is expressed as a percent of the individual's mean thread extensibility. In Table 1 we report the mean percent repeatability of the extensibility measurements for each species.

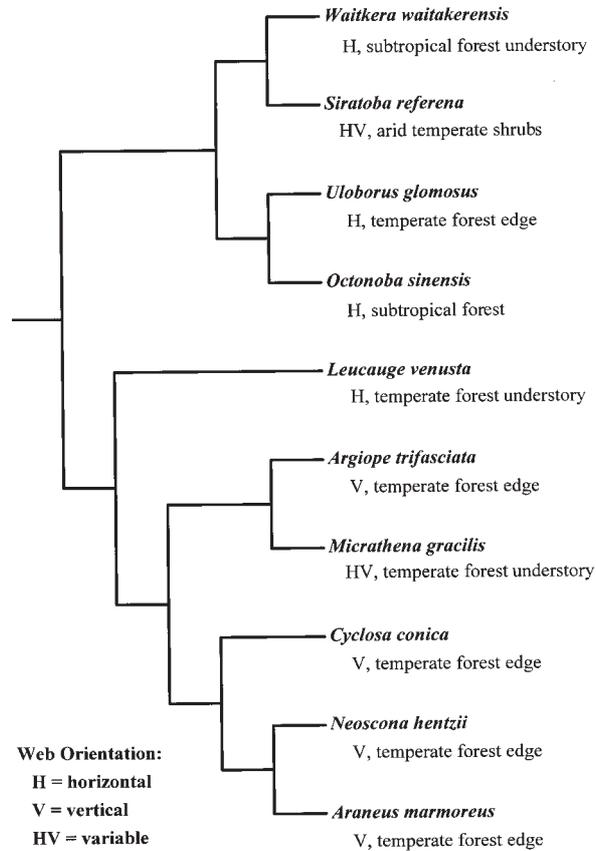


Figure 3. Phylogeny of the species included in this study (from Coddington, 1990b; Scharff & Coddington, 1997) and their orb-web orientations and habitats.

The tape on the caliper's jaws was changed frequently and we believe that its extreme adhesiveness, combined with the 7–9 mm length thread contact, insured that threads did not slip as force was applied to them. When we began these studies, we observed threads under a dissecting microscope as they were stretched and saw no evidence of slippage. The viscous nature of adhesive threads makes slippage more likely in these threads than in dry cribellar threads. Consequently, if slippage did occur it makes it easier to disprove the null hypothesis, because it would have the effect of increasing the extensibility of adhesive threads. If slippage occurred in one type of thread and not the other, this should be reflected by consistently different standard errors of extensibility and percentages of repeatability for the two thread types and there is no evidence for this (Table 1). The mean standard errors of the extensibility of adhesive and cribellar threads, expressed as a percent of the species' mean, are 6.5% and 8.3%, respectively and the mean repeatabilities are 14.68% and 18.50%, respectively.

As higher extension rates cause spider threads to become stiffer and stronger (Denny, 1976), we extended threads at 0.017 mm per second. This slow rate of extension increases the accuracy with which the breaking distance is recorded. For example, for *W. waitakerensis*, which has the lowest extensibility at 299%, an initial

TABLE 2. Mean values of web features (from Opell, 1999); ancestral values computed for these analyses reported in brackets

Species	Spiral Spacing (mm)	Area (cm <sup>2</sup> )
<i>Araneus marmoreus</i> (n = 15)	3.10 [2.85]	600.00 [504.96]
<i>Neoscona hentzi</i>	3.10 [2.85]	600.00 [504.96]
<i>Cyclosa conica</i> (n = 23)	1.60 [2.34]	92.00 [314.89]
<i>Argiope trifasciata</i> (n = 25)	3.90 [2.59]	848.00 [465.57]
<i>Micrathena gracilis</i> (n = 21)	1.30 [2.59]	201.00 [465.57]
<i>Leucague venusta</i> (n = 18)	2.40 [2.80]	209.00 [262.69]
<i>Octonoba sinensis</i> (n = 24)	5.50 [5.08]	426.00 [276.67]
<i>Uloborus glomosus</i> (n = 27)	5.70 [5.08]	204.00 [276.67]
<i>Waitkera waitakerensis</i> (n = 27)	3.60 [4.03]	92.00 [200.01]

thread length of 2.5 mm and a very slow reaction time of 2 s would exaggerate thread extensibility by only 0.45%.

#### *Web features*

Table 2 gives values for web features used in this study. The capture area of an orb-web is the area inscribed by its inner- and outer-most capture thread spiral. These values and mean capture spiral spacing are taken from Opell (1999) and capture area per radius indices are computed from this data set. Low values of this index indicate that the capture threads of a web are well supported by radii.

#### *Phylogenetic analysis*

To examine relationships between cribellar thread extensibility and spider mass and web features we employed a phylogeny (Fig. 3) based on Coddington (1990b) and Scharff & Coddington (1997) and the ancestor-reconstruction method described by Huey & Bennett (1986, 1987) and summarized by Harvey & Pagel (1991). This approach seeks evidence for a functional relationship between two characters by examining transformations in their states. Two features that evolve in concert, as demonstrated by a significant regression between the changes in their states are considered to be functionally related. We first determined the probable ancestral values of each species' features using the rooted minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison, 1992). We chose this method of reconstruction over linear parsimony reconstruction because squared change reconstruction spreads

change more evenly over the tree (Maddison & Maddison, 1992). This method seems more appropriate because the taxa used in this study are distantly related and are a small subset of the total taxonomic diversity of the Orbiculariae. We then calculated the changes from each species' most immediate ancestral value to its expressed value and examined the relationships between these changes using regression techniques. Tables 1 and 2 give the inferred ancestral values used in these analyses. This approach attempts to factor in the effect of species interrelationships for statistical tests because species taken from a phylogeny are "manifestly non-independent" (Felsenstein, 1985) rendering the basic assumptions of statistical tests invalid. In all instances, changes in values were normally distributed (Shapiro–Wilk–W–Statistic  $P > 0.05$ ). For all statistical analyses, we used programs of the SAS Institute, Inc.

#### RESULTS

In all instances but two, the masses of individuals whose thread extensibilities were measured (this study) and whose web parameters were measured (Opell, 1997, 1999) did not differ ( $t$ -test:  $P = 0.08$ – $0.90$ ).  $T$ -tests showed that the mean mass of *A. trifasciata* females whose threads were measured was 33% smaller than that of individuals whose web parameters were measured ( $N$  for extensibility = 21,  $N$  for web features = 25,  $t = 2.571$ ,  $P = 0.014$ ) and that the mean mass of *L. venusta* females whose threads were measured was 38% greater than that of individuals whose web parameters were measured ( $N$  for extensibility = 15,  $N$  for web features = 18,  $N = t = 2.413$ ,  $P = 0.022$ ).

Table 1 gives the extensibility values for the capture threads of nine species and their computed ancestral values. Table 2 gives values for web features. The greatest extensibility was measured for the thread of an adhesive orb-weaver and the smallest extensibility for the thread of a cribellate orb-weaver. However, a  $t$ -test shows that the mean of each group was not different ( $t = 1.851$ ,  $P = 0.107$ ).

For the nine species, change in thread extensibility and change in spider mass were directly related (Fig. 4A). Change in the capture areas, capture spiral spacing, and capture area per radius of webs produced by these nine species were also directly related to change in thread extensibility (Fig. 4B–D).

These relationships remain significant when *N. hentzii*, whose web parameters were inferred for those of *A. marmoreus*, was excluded from the analysis. Change in extensibility was directly related to change in capture area ( $F = 19.231$ ,  $P = 0.005$ ,  $r^2 = 0.76$ ,  $Y = 0.0053 X - 0.0007$ ), capture spiral spacing ( $F = 9.732$ ,  $P = 0.0206$ ,  $r^2 = 0.62$ ,  $Y = 1.2726 X + 0.0016$ ), and capture area per radius ( $F = 11.962$ ,  $P = 0.0135$ ,  $r^2 = 0.67$ ,  $Y = 0.8907 X$ ).

These relationships were also seen when analyses were restricted to orb-weavers that produce adhesive capture threads. Change in extensibility was directly related to change in spider mass ( $F = 9.937$ ,  $P = 0.0344$ ,  $r^2 = 0.71$ ,  $Y = 0.0062 X + 0.0017$ ), capture area ( $F = 19.288$ ,  $P = 0.0118$ ,  $r^2 = 0.83$ ,  $Y = 0.0043 X + 0.0017$ ), capture spiral spacing ( $F = 8.072$ ,  $P = 0.0468$ ,  $r^2 = 0.67$ ,  $Y = 1.0495 X + 0.0017$ ), and capture area per radius ( $F = 15.152$ ,  $P = 0.0177$ ,  $r^2 = 0.79$ ,  $Y = 0.1274 X + 0.0017$ ).

For the nine species for which capture area per radius is available, change in capture area per radius was directly related to change in spider mass (Fig. 5). There

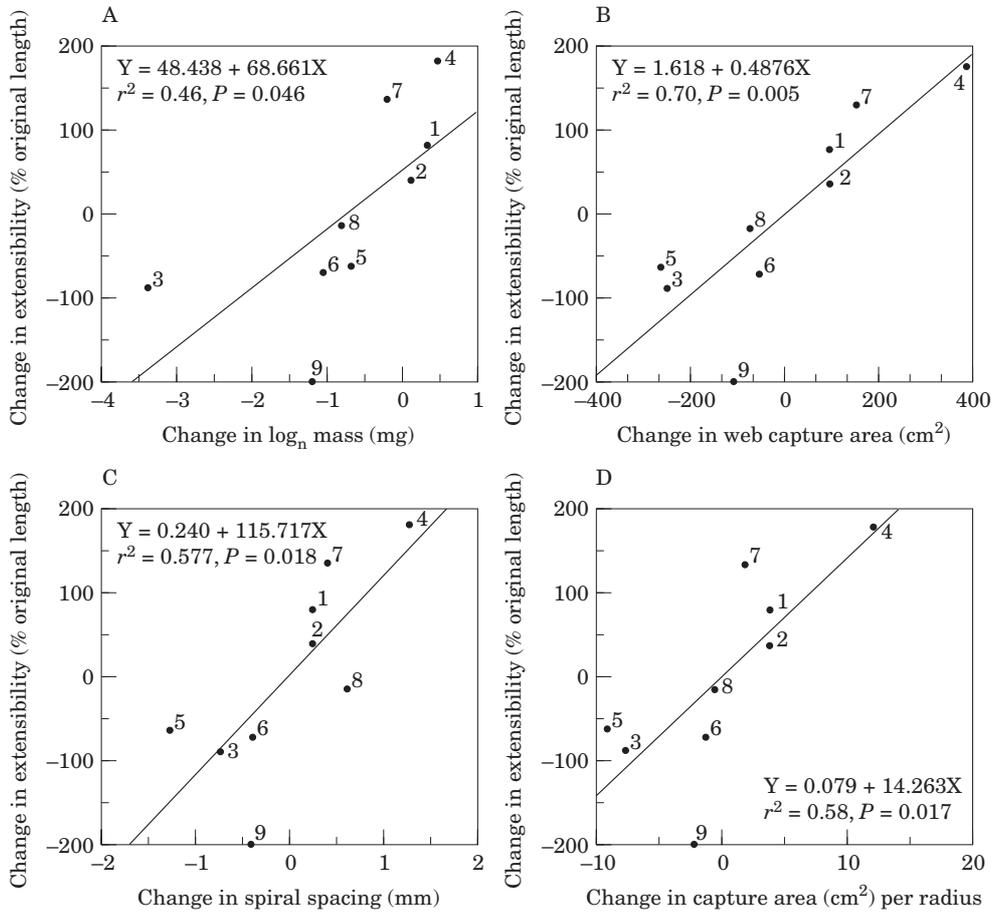


Figure 4. Relationships between changes in the following factors and thread extensibility: (A) spider mass; (B) web capture area; (C) web capture spiral spacing; (D) web capture area per radius.

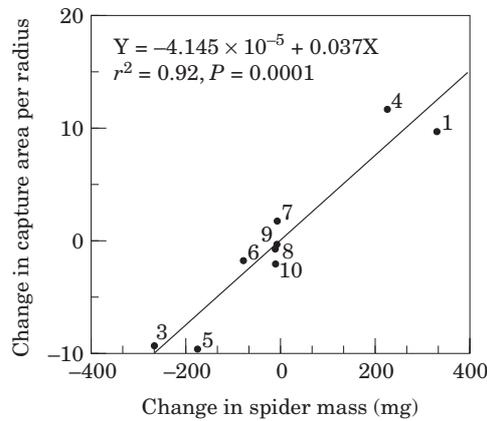


Figure 5. Relationship between change in spider mass and change in web capture area per radius.

was no difference in the slopes of the regression lines for cribellate and adhesive orb-weavers ( $F=0.81$ ,  $P=0.41$ ) and an ANCOVA showed that their intercepts did not differ ( $F=0.00$ ,  $P=0.98$ ). Thus, the relationship shown in Figure 5 is common to all the orb-weavers studied.

#### DISCUSSION

We agree with Felsenstein (1985) that “phylogenies are fundamental to comparative biology; there is no doing it without taking them into account.” The results of this study exemplify the ability of the contemporary comparative method, which uses phylogeny, to discriminate between punctuated and associative explanations of character differences. Contrary to Köhler & Vollrath (1995), our analysis provides no support for the hypothesis that adhesive thread has a greater extensibility than cribellar thread. Instead, it strongly supports the null hypothesis that differences in capture thread extensibilities are satisfactorily explained by differences in orb-web features and in spider mass. Major differences in the extensibility of capture threads are explained by changes in spider size, web area, number of radii per web capture area, and spiral spacing (Fig. 4A–D).

By measuring the extensibilities of capture threads that were under their natural web tensions, our study should yield smaller values than those that first relaxed thread tension. However, the slower rates of thread extension that we used should maximize thread extensibility. The more rapidly a thread is extended, the stiffer and stronger it becomes (Denny, 1976). Our extension rate of 0.017 mm/s was much slower than the 15 mm/s used by Craig (1987) and the 0.6 mm/s used by Köhler & Vollrath (1995). Differences in all of these experimental variables make comparisons of the extensibility values from different studies difficult.

This study measured the capture thread extensibility of representatives of only three deinopoid genera and five araneoid genera. This includes only a small part of the diversity of these orbicularian lineages and it is possible that the inclusion of additional species with different orb-web architectures might change our results and the conclusions that we draw from them. However, the fact that the included species show significant relationships between capture thread extensibility, spider mass, and orb-web features suggests that these relationships are real and have been shaped by the functional requirements of orb-web design. Our results show only that a common model can explain the extensibility of deinopoid and araneoid capture threads. Had the number of deinopoid species been greater, it would have been instructive to compare these relationships between the two lineages. However, an examination of these data does not suggest a pattern that contradicts the conclusion that the extensibility of adhesive capture thread does not exceed that of cribellar thread. In fact, the distribution of deinopoid values in Figure 4A (points 7, 8, and 9) may indicate that, relative to spider size, the extensibility of cribellar thread exceeds that of adhesive thread, as a line drawn between these points has a greater slope than the line for all included species.

If an orb-web is to function as an effective aerial snare, it must successfully absorb and dissipate the kinetic energy generated by a prey strike (Craig, 1987; Denny, 1976; Eberhard, 1981). Our understanding of exactly how this is done has recently changed. Among the Araneoidea, Craig (1987) recognized two extremes in orb-web

performance based on their ability to absorb the force of a prey strike: high energy absorbing webs and low energy absorbing webs. High energy absorbing webs are typically taut webs that have many radii per spiral turn and that absorb kinetic energy by relying more on superior tensile strength than elasticity. In contrast, low energy absorbing webs have fewer radii per spiral turn, are under less tension, and absorb energy primarily by being displaced. Horizontal orb-webs are typically low energy absorbing webs. However, when Lin *et al.* (1995) combined computer modelling and empirical data to describe the performance of *Araneus diadematus* orb-webs as they intercepted objects, a more elaborate picture emerged. The web of this species is a classical, high energy absorbing orb, yet it absorbs a significant amount of force through aerodynamic dampening, which requires the web to be displaced into an air column so that energy is absorbed through friction with the air. Thus orb-webs that differ in their abilities to absorb the force of prey strikes may differ not in the mechanism they employ to absorb kinetic energy, but in the degree to which they rely on each mechanism.

The extensibility of orb web capture threads can be explained at two levels: functional tuning and scaling. Functional tuning relates thread extensibility to details of web architecture whereas scaling relates spider size and web capture area to thread extensibility. Webs that have higher values of spiral spacing, or capture area per radii, are webs whose capture threads must individually or collectively absorb greater amounts of the kinetic energy of prey impact as they transfer force to the radii. *Argiope trifasciata* has spirals that are 63% more widely spaced and a capture area per number of radii ratio that is 86% greater than *Micrathena gracilis* and, consequently, has capture threads that are 28% more extensible.

A direct relationship has been established between spider mass and capture area for both cribellate and adhesive orb weavers (Opell, 1999). This study demonstrates that spider mass is also directly related to capture thread extensibility. As the studies of Craig (1992, 1997) point out, the functional properties of spider threads are linked to their molecular structure. In *Escherichia coli* the energetic cost of synthesis differs greatly among amino acids (Craig & Weber, 1998). Likewise, differences in the amino acid composition of spider dragline silk suggest that both their production costs and properties differ among taxa (Craig *et al.*, 1999). Thus, the cost and supply of the amino acids that form a spider's capture threads may limit thread extensibility.

Although there is no absolute difference in the extensibility of the adhesive and cribellar capture threads, there appear to be still other advantages of adhesive threads (summarized by Bond & Opell, 1998). Both cribellar and adhesive capture threads have substantial extensibilities, although their overall elastic properties appear to differ considerably and this affects their performance within an orb-web. Unlike adhesive thread, stretched cribellar threads cannot return to their original lengths and conformations. The self-tensing mechanism of an adhesive thread returns it to its initial length after stress is relieved and apparently fully restores the thread's elastic properties. This property helps modern orb-webs remain taut as they respond to wind currents and reduces the likelihood that adjacent capture threads will come into contact. These features are particularly important in vertical orb-webs where capture threads that sag are likely to stick to threads beneath them. In contrast, the stressed outer fibril sheath of a cribellar thread cannot be restored and the thread neither returns fully to its initial length nor reestablishes its ability to dissipate force through stretching.

A major difference between cribellar thread and adhesive thread is that cribellar

thread is dry, whereas both the adhesiveness and extensibility mechanisms of adhesive thread operate within an aquatic environment established by the aqueous solution that coats the thread and coalesces into droplets (Vollrath *et al.*, 1990). The windlass mechanism of adhesive thread requires this aquatic environment (Vollrath & Edmonds, 1989), as does the stickiness that results from the glycoproteins within each of its droplets (Peters, 1995; Tillinghast *et al.*, 1993; Vollrath & Tillinghast 1991). Hydrosopic agents in this solution maintain the adhesive thread's water content (Townley *et al.*, 1991), thereby insuring its stickiness and allowing its extensibility to be fully realized. This change in the nature of capture thread could have been driven by selection favouring either enhanced thread extensibility or enhanced thread stickiness.

There is evidence that the mechanism by which adhesive threads achieve their stickiness is superior to that of cribellar threads. Comparisons of capture thread stickiness show that adhesive capture thread achieves its stickiness at a lower material cost than does cribellar thread (Opell, 1998). This increased economy enables an adhesive orb-weaver to construct, at no additional material cost, a web that has a greater total stickiness (Opell, 1997) and a greater stickiness per capture area (Opell, 1999) than that made by a cribellate orb-weaver of similar mass. By showing that there is no difference in the extensibility of cribellar and adhesive thread, this study suggests that selection for enhanced stickiness may have been the leading force behind the transition from cribellar to adhesive thread.

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