

THE PHYSICAL PROPERTIES OF SPIDER'S SILK AND THEIR ROLE IN THE DESIGN OF ORB-WEBS

By MARK DENNY*

Department of Zoology, Duke University, Durham, North Carolina

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SUMMARY

1. Determinations were made of several physical properties of the viscid and frame silks of the orb-webs built by the spider *Araneus sericatus* (Cl.).
2. Both types of silk show a breaking stress of approximately 1 GN/m² and an initial resilience of approximately 0.35.
3. The breaking extension ratio of viscid silk ($\lambda = 3.00$) is much greater than that of frame silk ($\lambda = 1.25$), and the viscid silk relaxes to a relatively greater extent.
4. These properties are correlated with the degree of crystallization of the protein from which the silk is made, this factor being controlled by the sequence of amino acids in the protein.
5. The physical properties of the viscid and frame silks allow them to function effectively as shock absorbers and structural elements, respectively; and allow the orb-web to function as an aerial filter with a minimum expenditure of material and energy.

INTRODUCTION

Distinct in their form and function among the great variety of the webs of spiders are the orb-webs, the spare and elegant constructions used as aerial filters by members of the *Argiopidae* and *Uloboridae*. Though utilizing different silks these two remotely related families (Kaston, 1964) build webs with the same basic structural features. This raises two basic questions concerning the design of orb-webs. First, does the orb-web represent the simplest way to build an aerial filter? Witt (1965), Witt, Reed & Peakall (1968), and Reed (1969) have provided a preliminary answer by presenting evidence that the orb-web structure is a simple and effective method of translating a limited set of anatomical and neurological parameters into a functioning food-gathering device. Second, does the orb-web design minimize the expenditure of material necessary to capture flying insects? In an attempt to answer this second question tests were performed to define some of the physical properties of the silks of the webs of a representative Argioid spider, *Araneus sericatus*.

* Present address: Department of Zoology, University of British Columbia, Vancouver, British Columbia.

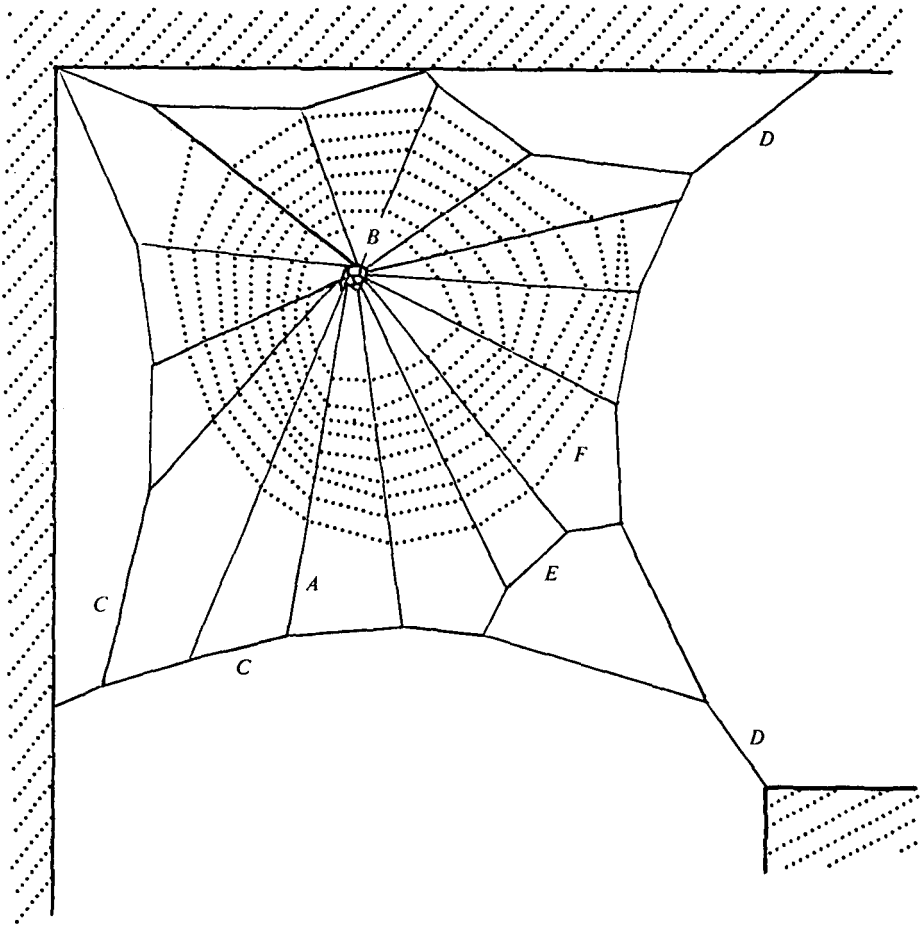


Fig. 1. A typical orb-web. Radii (*A*) diverge from an above-centre hub (*B*) to attach on the polygonal frame (*C*). The frame is held in position by the mooring or guy threads (*D*) tying the web to surrounding structures. Note that at (*E*) an addition to the frame, a cord, has been placed in order that the radii will not attach to the junction of the frame thread with a guy. Superimposed on this supporting framework is the viscid spiral (*F*).

Orb-web terminology

An orb-web is a planar net exhibiting the characteristic structures identified in Fig. 1. The frame, mooring guy and radial threads form the supporting framework for the completed web. A guy thread may simply be a continuation of a frame thread past its junction with another frame thread. Superimposed on the framework is the viscid spiral (in the *Argiopidae*) or the hackled band (in the *Uloboridae*). This spiral forms the sticky, catching component of the web.

An orb-weaving spider produces a number of distinct types of silk, each used for a specific function. In the genus *Araneus* the guys, frame and radii are derived from the large ampullate gland. Each element or thread may be composed of a number of parallel strands. One radial thread consists of two, or occasionally four, strands. Frame threads and guys may be compounded of 8–10 strands or more. The viscid spiral of *Araneus* is formed of a pair of strands derived from the flagelliform glands

(Sekiguchi, 1952) coated with a layer of viscid glue produced by the aggregate glands. This secretion gives the appearance under the microscope of glass beads strung upon the thread.

Definition of physical testing terms

A thread of initial length L_0 and initial cross-sectional area A_0 is clamped at both ends and held just taut, but with no force on the thread tending to stretch it. If the clamps holding the thread are moved apart the thread will be extended until it breaks. During this period of extension the thread will oppose the separation of the clamps with a force F .

The extension ratio, $\lambda = L/L_0$, defines for each new length, L , the elongation of the thread in proportion to its original length; and the extension rate, $d\lambda/dt = \dot{\lambda}$, the change in λ per unit time, t . Each value of λ is associated with a particular value of F . A graph of all the pairs (λ, F) forms a force-extension curve. The shape of the curve depends on a number of factors, among which are the extension rate, relative humidity and temperature.

If the volume of the thread remains constant throughout the test the cross-sectional area, A , at any given λ is equal to A_0/λ . The stress, σ , is defined as F/A .

A measure of stiffness, E , the Young's modulus of a material, is defined as $\sigma/(\lambda - 1)$. An alternative definition of Young's modulus, E_{tan} , the tangential modulus at a point, is equal to the slope of the line tangent to the stress-extension curve at that point.

Since the product of force \times distance = work = energy, the area under a force-extension curve is a measure of the energy required to extend a piece of material to its breaking point.

If the thread is extended to some λ and held at this length, the behaviour of F may be measured as a function of time. For many materials stress in such a stress relaxation experiment varies as a logarithmic function of time:

$$\ln \sigma_t = \ln \sigma_0 - t/\tau,$$

where τ (the stress relaxation time) is a constant fitting the equation to a particular material, σ_0 is the stress at time = 0, and σ_t is the stress at time = t .

If the thread is extended to some λ and then allowed to return to its original length, the energy derived from the return may be equal to or less than the energy expended in elongating the thread. Resilience, R , is the ratio of energy recovered per energy expended in an extension return cycle. Hysteresis, the proportional energy lost in such a cycle, is equal to $(1 - R)$.

MATERIALS AND METHODS

The silk samples used in the physical testing procedures of this study were obtained from the completed webs of adult female *Araneus sericatus* (Cl.). All spiders were housed in cages of approximately $50 \times 50 \times 10$ cm, a size sufficient for the building of full webs. The cages were kept in a controlled-environment chamber over winter at the beginning of the study and were later moved to greenhouses. Only webs that appeared normal in all respects were used.

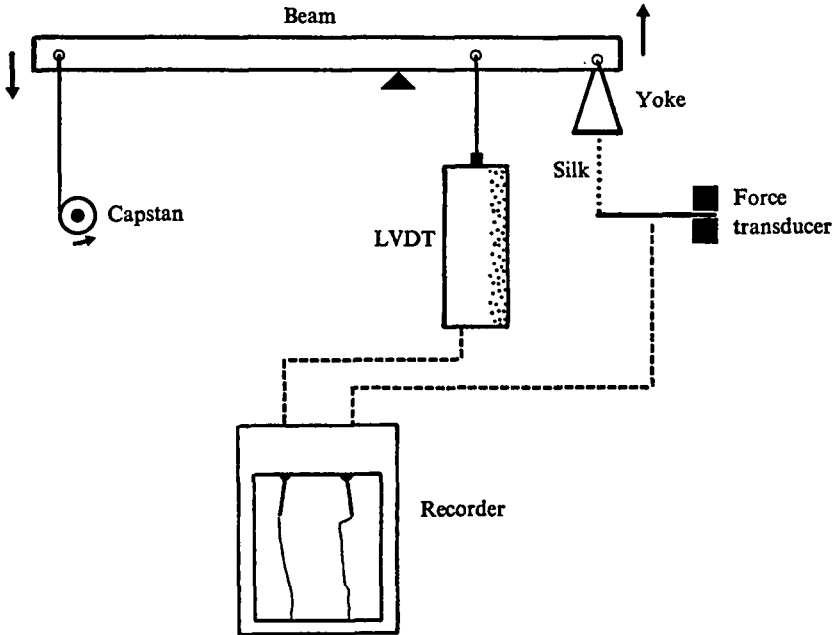


Fig. 2. A diagrammatic depiction of the rocking beam tester.
For a full explanation see the text.

Samples of silk were readily obtained from the webs. A Plexiglas frame in the shape of a U was positioned so that a thread approximately 2.5 cm long lay across the open end. The thread was pressed gently on to small tabs of double-sided sticky tape stuck to the arms of the U and then cut free from the web. The thread was neither unduly stretched nor allowed to relax during the process of removal.

Only samples appearing clean and undamaged when examined with a $40\times$ objective (N.A. 0.75, condenser N.A. 1.4) using green light (546 nm) were used. Using a Leitz filar micrometer (calibrated with a Leitz stage micrometer) the diameter of the threads was measured near the cut ends on the sticky tape. It was found that upon cutting a sample loose from the web the short section of thread outside the tape would inevitably double back to be stuck on the tape. The diameter of this portion of the thread was assumed to be the diameter under zero stress. By assuming strands to be of a circular cross-section (untested) these measurements of diameter provided a measure of the cross-sectional area of the strands.

Strands were typically 1–3 μm in diameter. An estimate of the error involved in these measurements of diameter was made by measuring the diameter of fine glass fibres (about 10 μm in diameter) with the light microscope and comparing the results with measurements made on the same fibres with a scanning electron microscope. The average error was found to be $\pm 7\%$.

Samples were taken only from webs that had been built on the day of sampling or the day before. In most cases the thread was tested on the day following sampling, and in no case did more than a week elapse between the time of sampling and the time of testing. Samples were stored at ambient temperature and humidity.

Tests were performed to determine the force–extension and stress relaxation charac-

teristics of both the viscid and frame silks of *A. sericatus*. The initial tests were carried out on a machine of my own design and construction (Fig. 2). A pivoted horizontal beam was attached by a string to a capstan driven by a small synchronous motor. From the other end of the beam were hung a yoke, to which the test thread could be glued, and the core of a linearly variable differential transformer (Schaevitz 500 HR-DC). The coil of the LVDT was held stationary directly below the beam by a clamp. The output from the LVDT was monitored by one channel of a Brush 220 chart recorder.

Mounted directly below the yoke and capable of being moved along three mutually perpendicular axes by a micromanipulator was a force transducer. This transducer consisted of a Bean type EA-06-500-BH-120 foil strain gauge glued to an approximately 4 cm long strip of 0.004-in spring steel. The strip was securely clamped at one end; to the other the test sample was glued. The change in resistance of the strain gauge was monitored and amplified by a Schaevitz DR-20 Wheatstone bridge and recorded on the second channel of the recorder.

The LVDT was calibrated by inserting the core into the coil with a micrometer. The force transducer was calibrated by hanging known weights from the free end of the steel strip. Both transducers gave linear responses for the ranges encountered during testing.

Tests were performed by gluing a silk thread between the yoke and the force transducer. Room-temperature-curing (RTC) epoxy cement was used to secure the thread in place. While the cement was hardening (24 h) the silk was held by the Plexiglas frame on which it was collected. The frame was then removed and the force transducer holding the bottom end of the silk raised until the thread was observed to go slack. The thread was maintained in this unstressed position for 15 min prior to the test. The force transducer was then carefully lowered while observing the sample with a dissecting microscope. When the sample was just taut its length (L_0) was measured with a set of vernier calipers and the transducer secured.

A force-extension test could then be performed by turning on the motor driving the capstan. The test was invalidated if the sample broke near the points of attachment. The angle through which the beam rocked in breaking a thread was small. Consequently any displacement of the test sample other than that due to the vertical movement of the beam was negligible.

From records of force and beam displacement force and stress *vs.* extension curves were calculated. As well as measuring the temperature in the laboratory at the time of the test, a measurement of the relative humidity was made with a Henson psychrometer.

Stress relaxation experiments employed the same apparatus and preparatory procedures. The test thread was elongated as before, but before the thread broke the capstan motor was turned off, thus maintaining the thread at a constant extension, and the force response with time was monitored.

Later force-extension, stress relaxation and cyclic loading tests were carried out on an Instron Universal testing machine. The Instron tester offered two primary advantages over my machine. (1) The force transducer and moving head of the Instron tester were equipped with clamps that obviated the necessity of gluing samples to the machine itself. This allowed several samples to be run on the same day, thereby

ensuring that temperature and humidity were uniform for the samples tested. (2) The Instron tester allowed a much larger range of extension rates. The primary disadvantage of the Instron tester was its relative insensitivity. Its maximum sensitivity, of 4 g full scale, was only marginally sufficient for measuring the properties of single threads of viscid silk, though it was adequate for frame silk. The force transducer of the Instron machine responded linearly for the range of forces encountered during testing. Each test was calibrated by hanging a known weight from the transducer before and after each test.

Samples for the Instron tests were prepared as above and attached to the machine according to a procedure suggested by R. A. Work of North Carolina State University. Samples were transferred from the Plexiglas frame to a caliper, being attached with double-sided sticky tape. The calipers were adjusted until the thread was judged to be at its resting length. The thread was then transferred to a piece of cardboard (1 × 3 in) that had a hole punched in it. The sample was placed across the hole and secured with double-sided tape before being fastened to the cardboard with RTC cement. The length of the glued sample was measured with vernier calipers. Samples of frame silk consisted of one thread but, in order to make a sample of viscid silk stout enough to be adequately detected by the Instron tester's force transducer, several threads were combined to make one sample. Such a sample usually consisted of 5–10 threads. Each sample was clamped into the machine, the strips on either side of the hole were cut, and the test conducted.

For cyclic loading tests the Instron tester was programmed to extend the sample by a set amount at a specific extension rate. Upon reaching the limiting extension the head reversed its direction and returned the sample to its original length at a rate equal to that of extension. A measure of the energy lost through one loading–unloading cycle was made by measuring the area within the resulting hysteresis curves with a Keuffel and Esser compensating polar planimeter.

RESULTS

Frame silk

The average diameter of a single strand of frame silk was 1.9 μm , with individual values ranging from 1.4 μm to 2.4 μm . No difference was found in the diameters of strands comprising radial, frame and mooring threads. The various components of the scaffolding thus differed only in the number of strands each contained.

The force–extension and stress–extension curves for the samples of frame silk revealed several consistent patterns. Table 1 contains a tabulation of the averaged results from four sets of tests composed of fifteen individual tests. Each set was performed on silk samples from a different spider.

The λ at breaking, λ_b , varied from 1.20–1.30 with a mean of 1.25. This variation in breaking extension ratio was not significantly correlated with the rate of elongation, or the relative humidity or temperature encountered during the tests. Experimental error in the measurement of the initial unstressed length of the sample and the retention of this length while installing the sample in the testing machine, estimated at $\pm 5\%$, is sufficient to account for this observed variation.

Breaking stress was found to be a function of the rate of extension. For samples

Table 1. *Averaged values for some stress-extension properties of A. sericatus frame silk*

(Values averaged from 15 tests, samples from four spiders. Relative humidity varied from 48 to 52 %.)

	Extension rate (λ/min)		
	0.03	0.14	1.41
Average λ_f	1.24	1.24	1.27
Range of λ_f	1.21-1.27	1.20-1.27	1.21-1.30
Average σ_f (GN/m ²)	0.81	0.88	1.42
Range of σ_f (GN/m ²)	0.55-1.18	0.59-1.23	0.82-2.14
Average E_{initial} (GN/m ²)	9.81	8.62	20.50
Range of E_{initial} (GN/m ²)	5.19-11.80	4.60-15.20	6.54-50.30
Average E_{final} (GN/m ²)	3.52	3.72	4.07
Range of E_{final} (GN/m ²)	2.14-5.47	2.57-4.63	2.77-9.99
Average breaking energy (J/cm ²)	91.3	105.6	158.0
Range of breaking energy (J/cm ²)	62.3-122.9	59.2-131.9	99.2-211.9

Table 2. *Values for a single set of tests performed on the frame silk of A. sericatus as illustrated in Fig. 2*

(Temperature at testing 24 °C. relative humidity 48 %.)

	Extension rate (λ/min)		
	0.03	0.14	1.41
λ_f	1.26	1.25	1.28
σ_f (GN/m ²)	0.55	0.67	0.88
E_{initial} (GN/m ²)	12.40	5.56	6.07
E_{final} (GN/m ²)	2.14	2.70	3.10
Breaking energy (μJ)	4.49	6.48	14.56
Breaking energy/volume (J/cm ³)	63.0	59.2	94.0

taken from a single web the faster the sample was extended the more stress it was capable of sustaining without failure. However, the absolute value of breaking strength for each extension rate varied from one spider's web to another. The highest value of breaking strength, obtained at the highest rate of extension, for a sample from one web might be lower than the lowest value obtained from another web. These inter-web variations account for the broad ranges in the observed properties noted in Table 1. An insufficient number of tests were performed to tell whether this variation in breaking strength was due to some spiders producing stronger silk than others, or whether the variation was due to some other influence. Table 2 contains the results for a typical set of tests conducted on the silk of a single web.

The general shape of the stress-extension curves was consistent for all tests. Fig. 3 illustrates the results of the set of tests tabulated in Table 2. Three major features are held in common by the curves. Firstly, the initial Young's modulus ($\lambda < 1.01$) is the highest obtained during the extension of the sample. A similar result was obtained for a variety of different silks by Lucas, Shaw & Smith (1955) who attributed the high initial E to the stretching of weak cross bonds in the non-crystalline portion of the silk. Secondly, following the initial modulus, at $\lambda = 1.01-1.10$, E_{tan} decreases, reaching its lowest level at $\lambda = 1.05$. Thirdly, beyond $\lambda = 1.10$ the stress increases approximately linearly with increasing extension until failure occurs at $\lambda = 1.25$.

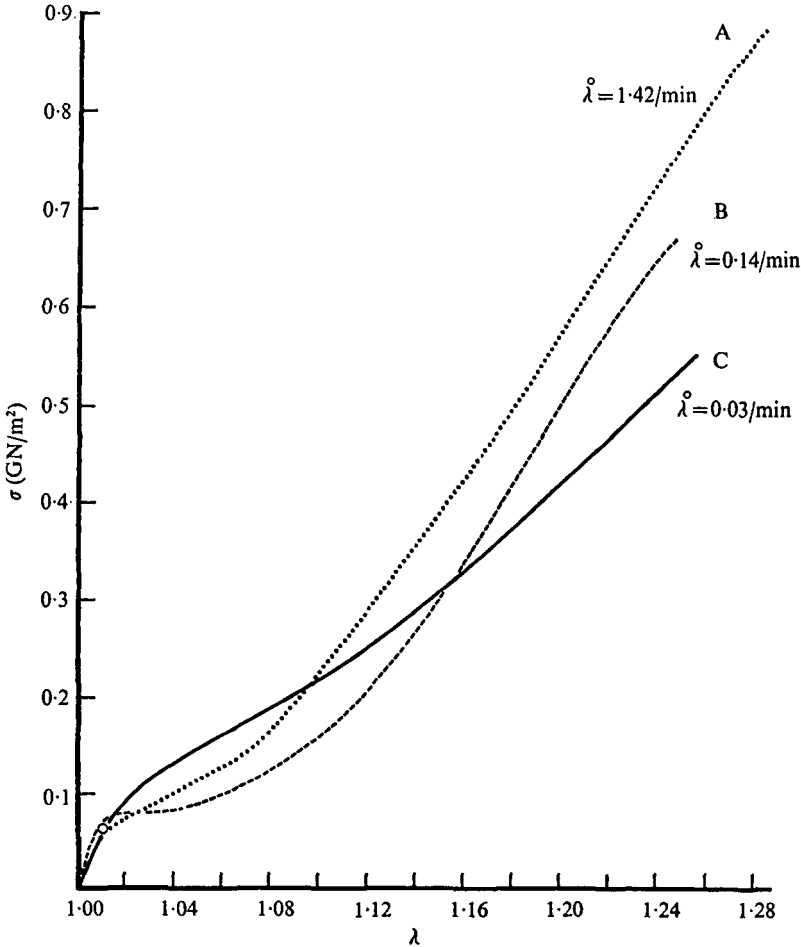


Fig. 3. Stress-extension ratio curves for the frame silk of *A. sericatus*. Samples were taken from one web and extended at three different rates. Note the pronounced plateau in (B) and the much less pronounced plateau in (C). The circle at lower left shows the approximate position on the curves of a thread in the web.

The plateau between $\lambda = 1.01$ and $\lambda = 1.10$ may be more or less pronounced from one sample to the next with no apparent correlation with extension rate, relative humidity or temperature. The results of these tests are consistent with those reported by DeWilde (1943), Lucas (1964) and Zemlin (1968).

In the same manner as breaking strength the Young's modulus at breaking extension, E_b , and in the final linear portion of the stress-extension curve is a function of extension rate; the higher $\dot{\lambda}$, the greater E . At $\lambda < 1.10$ no clear pattern is evident. The variability in the plateau and the low forces being encountered at low λ obscure any relationship between E , or E_{tan} , and $\dot{\lambda}$.

Inasmuch as the force required to extend a sample to a given λ increases with an increasing rate of extension, the energy required to break a thread of standard length and cross-sectional area (i.e. standard volume) is a function of $\dot{\lambda}$. Table 1 lists the averaged values of breaking energy for all tests, normalized to a sample volume of

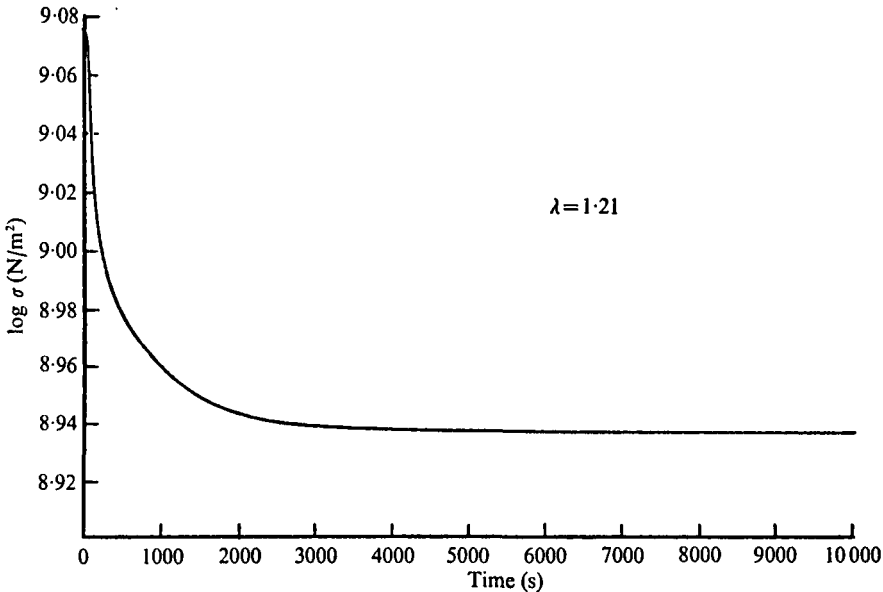


Fig. 4. A typical stress relaxation curve for the frame silk of *A. sericatus*. Equilibrium modulus is reached after approximately 5000 s.

1 cm^3 . The variation in E at low λ and the variability between sets of samples are particularly evident in this measurement of breaking energy, as exemplified by the wide range of values encountered. Table 2 lists the energies required to break the samples illustrated in Fig. 3, and these energies normalized to a volume of 1 cm^3 . Note the discrepancy in the increasing λ - increasing breaking energy correlation due to the variable development of the plateaux in the samples.

Figs. 4 and 5 illustrate the results of a typical stress relaxation test conducted on a sample of frame silk. The Young's modulus at time t after the start of the experiment, E_t , decreases rapidly during the initial few seconds after extension; the rate of decrease slowing until at $t \approx 5000 \text{ s}$ a plateau is reached. E_t at this equilibrium time is 0.75 of E_t at time zero. The curve cannot be fitted with any accuracy by a single value or a small set of values for τ . τ increases with increasing time. Measuring τ with respect to the equilibrium value of E_t , τ at $t = 1 \text{ s}$ is 0.566. At $t = 20 \text{ s}$, $\tau = 11.48$, and near the end of the test, with $t = 5000 \text{ s}$, τ has increased to 788.

Stress relaxation tests were carried out only at relatively high extensions, always above $\lambda = 1.10$. Below this extension, while the value of E_t at time zero was accurately measurable, the decay of E_t with time quickly brought the forces involved to a level too low for accurate measurement. For this reason it is not known whether these results for the stress relaxation behaviour of frame silk at high extensions hold for low extensions as well.

Four sets of tests of the cyclic loading behaviour of frame silk were carried out on samples taken from the webs of different spiders. Fig. 6 illustrates the results of one typical series of tests on a single thread, and in Table 3 these results are tabulated. The averaged results are tabulated in Table 4.

For each amount that a frame thread is extended, a certain portion of that extension

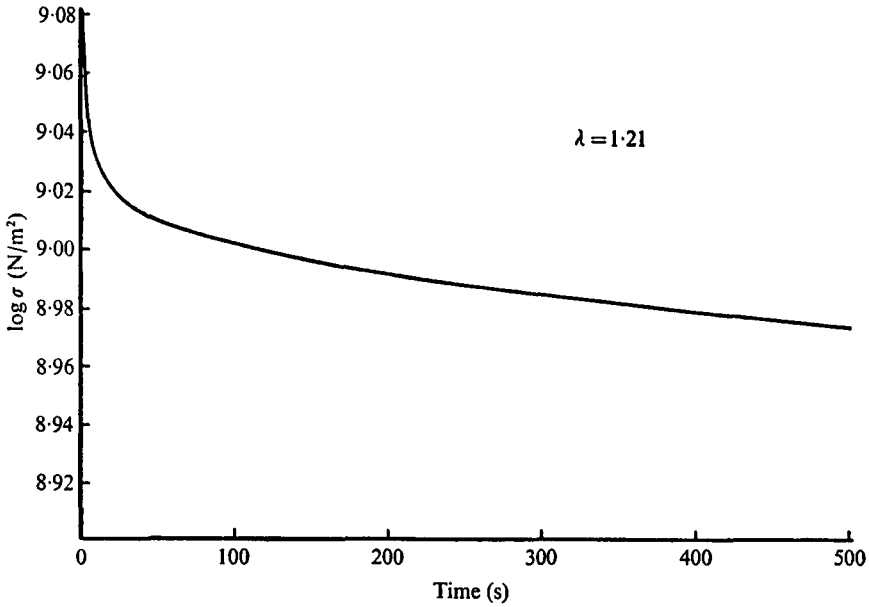


Fig. 5. A typical stress relaxation curve for *A. sericatus* frame silk; an expansion of the first few seconds of the graph shown in Fig. 3.

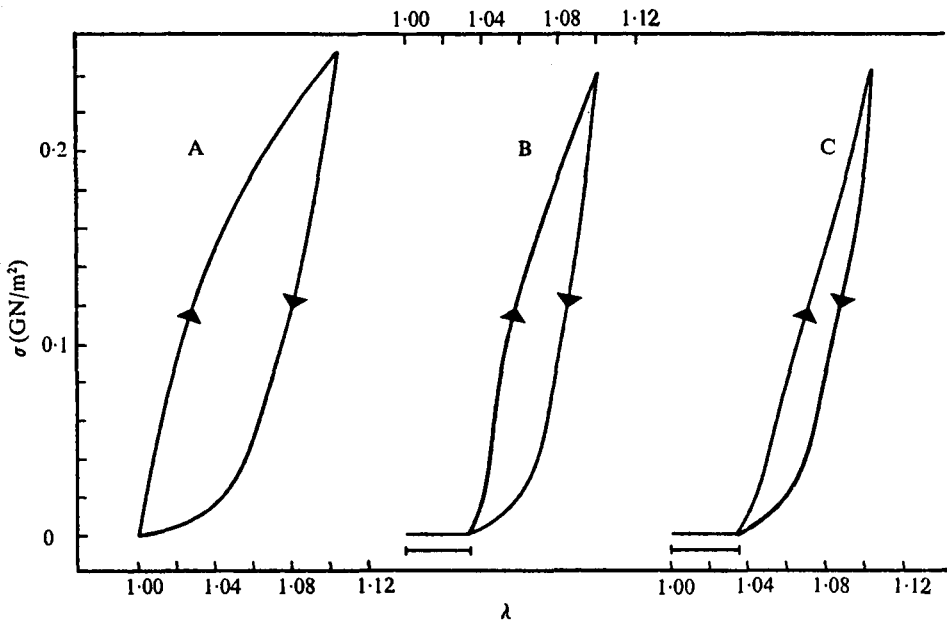


Fig. 6. A series of loading cycles on a single *A. sericatus* frame thread. Cycle (A) is the initial cycle in the series. $\dot{\lambda} = 6.99/\text{min}$. Cycle (B) is the fifth in the series. $\dot{\lambda} = 6.99/\text{min}$. Cycle (C) is the eighth in the series. $\dot{\lambda} = 0.70$. Bars show the extent of the non-recovered extension.

Table 3. Values for a single set of cyclic loading tests performed on the frame silk of *A. sericatus* as illustrated in Fig. 6

(Temperature at testing 24 °C, relative humidity 55%.)

	Extension rate (λ/min)		
	6.99 (A)	6.99 (B)	0.70 (C)
$\lambda_{\text{max}} = 1.11$			
Total energy of extension (μJ)	4.079	2.007	2.170
Energy lost (μJ)	2.562	0.914	1.028
Resilience	0.372	0.545	0.526

Table 4. Values for the hysteresis properties of *A. sericatus* frame silk

	Extension rate (λ/min)		
	0.08	3.89	14.36
Average λ	1.17	1.17	1.14
Average total energy, initial (μJ)	5.422	6.356	—
Range of initial energy (μJ)	3.965–6.878	4.079–7.887	—
Average total energy, subsequent (μJ)	2.895	3.971	5.742
Range of subsequent energy (μJ)	2.408–3.263	0.958–5.094	1.909–11.014
Average initial resilience	0.358	0.345	—
Range of initial resilience	0.264–0.453	0.327–0.372	—
Average subsequent resilience	0.523	0.539	0.699
Range of subsequent resilience	0.429–0.591	0.455–0.633	0.627–0.773

is only slowly recovered when the tension on the thread is removed. Though these tests were not designed to measure this slowly recoverable deformation accurately, it is estimated that the portion of slowly recoverable extension is about 50–55% of the total extension. This proportion of slowly recoverable extension did not vary with different λ , $\dot{\lambda}$, temperature or humidity. DeWilde (1943) noted this component of frame silk and measured it to be 50% of the total extension at high λ and somewhat greater than this at low extensions.

It was found that the rate of recovery of the slowly recoverable extension was temperature dependent. This effect was not extensively studied, but the results from one test provide a rough estimate of the phenomenon. A sample of frame silk extended to $\lambda = 1.20$ and returned to relaxed length required about 20 min to recover its original length at 25 °C. The recovery time at 40 °C was about 7 min, and at 60 °C about 4 min.

The results of a further test are shown in Fig. 7. The figures for the test are tabulated in Table 5. A sample was loaded through several cycles and the usual pattern of incomplete recovery noted. The sample, while unstressed, was then heated to an unspecified temperature by being exposed to an infra-red heat lamp for approximately 1 min. When loading was resumed the first cycle exhibited properties identical to those of the initial cycle of the series. This process was repeated several times with no change in the results. Further study will be necessary to completely define the nature of the slowly recoverable deformation of frame silk.

The first time a sample was stretched to a certain extension ratio its resilience upon the release of tension was low, energy being lost as a consequence of the incomplete recovery of the material in the time span of a single cycle. Repeated extensions to the

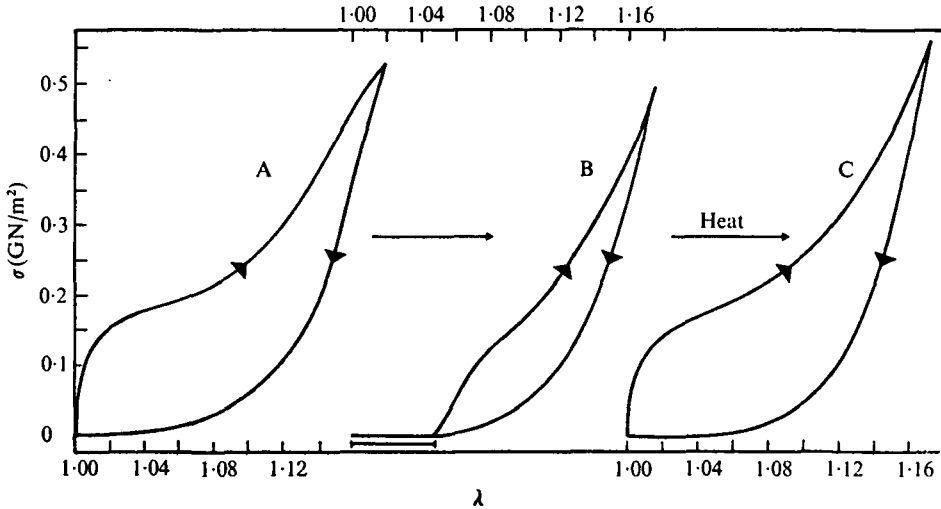


Fig. 7. The recovery of frame silk upon heating. Cycle (A) is the initial cycle; cycle (B) a subsequent cycle exhibiting non-recovered extension. After being heated the silk returns to its initial properties in cycle (C).

Table 5. Values for a test showing the slowly recoverable deformation of *A. sericatus* frame silk and its effect on cyclic loading

	Designation in Fig. 7		
	(A)	(B)	(C)
$\lambda = 1.18, \dot{\lambda} = 3.85/\text{min}$			
Total energy (μJ)	6.484	3.857	6.596
Total energy lost (μJ)	4.367	1.892	4.281
Resilience	0.327	0.509	0.351

same λ , however, show a higher and constant resilience, and no further non-recovered deformation. The force necessary to extend a thread initially to a given extension was a function of $\dot{\lambda}$ consistent with the results of the simple force-extension experiments. Further extensions to the same λ , however, were extension-rate-independent within the accuracy of the testing procedure.

This exact correlation between the rate-dependent force of extension and the slowly recoverable component of λ implies that this component accounts for the viscosity of the material.

As with the tests in simple non-cyclic extension, the force and energy necessary to extend a thread to a given λ varied from one spider's web to the next with no apparent pattern. This variation leads to the broad ranges in the energy figures cited in Table 3. When comparing each sample with itself, as in the computation of resilience, there is much less variability. The Instron tester was programmed in a manner that precluded the accurate recording of the initial loading cycle at high rates of extension.

In summary, the frame silk of *A. sericatus* may be characterized as a visco-elastic material. A high breaking stress, in the range of 1 GN/m^2 , coupled with a relatively low breaking λ of 1.25 yield a high E_f of approximately 4 GN/m^2 . Breaking strength, and consequently E_f , vary with λ , and this rate-dependent or viscous behaviour is a result of a slowly recoverable component of extension. The time necessary for the

Table 6. Stress-extension properties of the viscid silk of *A. sericatus*

	Extension rate (λ/min)			
	0.07	0.32	3.98	30.36
Average σ_f (GN/m ²)	1.11	1.27	0.76	0.92
S.D. σ_f ($\times 10^9$)	0.34	0.29	0.17	0.37
Average E_{final} (GN/m ²)	0.56	0.56	0.49	0.55
S.D. E_{final} ($\times 10^9$)	0.14	0.04	0.12	0.15
Average λ_f	2.90	3.29	3.03	2.85
S.D. λ_f	0.21	0.32	0.41	0.13
Breaking energy (J/cm ²)	95.6	150.4	142.0	—
S.D. of breaking energy	14.8	57.2	36.5	—

Values averaged from 41 samples from four spiders. Relative humidity varied from 31% to 56%. Mechanical noise at low λ did not allow measurement of extension energy at the highest extension rate.

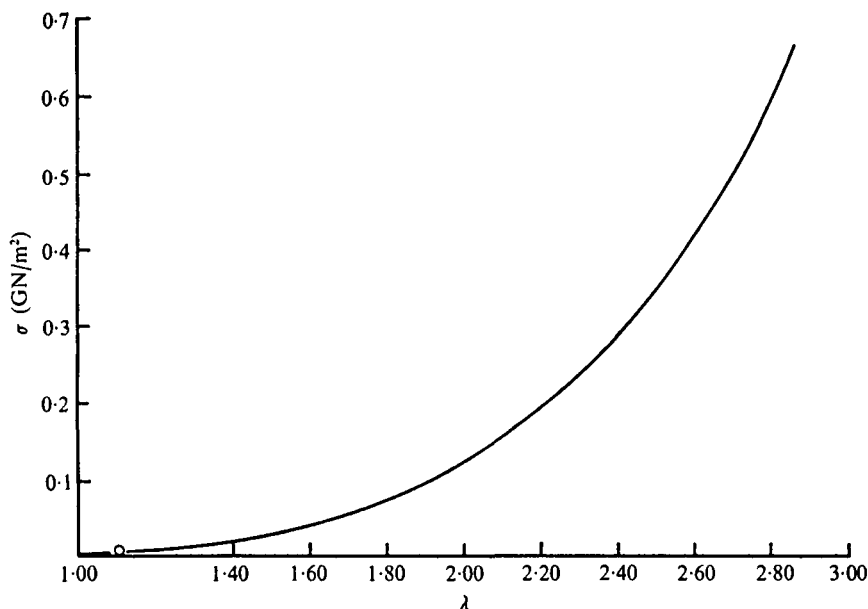


Fig. 8. A typical stress-extension ratio curve for the viscid silk of *A. sericatus*. The circle at lower left shows the approximate position on the curve of the silk in the web.

complete recovery of this component is inversely proportional to temperature. The silk exhibits a low resilience (approximately 0.35) upon initial extension, and a higher subsequent resilience (approximately 0.50). The silk stress relaxes to equilibrium in a short period of time E_t at equilibrium being equal to approximately 0.75 of E_t at time zero.

Viscid silk

The average diameter of a single strand of viscid silk was measured to be $1.5 \mu\text{m}$ with values ranging from $1.0 \mu\text{m}$ to $1.9 \mu\text{m}$.

Though many of the force-extension and stress-extension properties of the viscid silk appear to be identical to those of the frame silk, some differ considerably. The most apparent of the differences is the much higher breaking λ of the spiral material

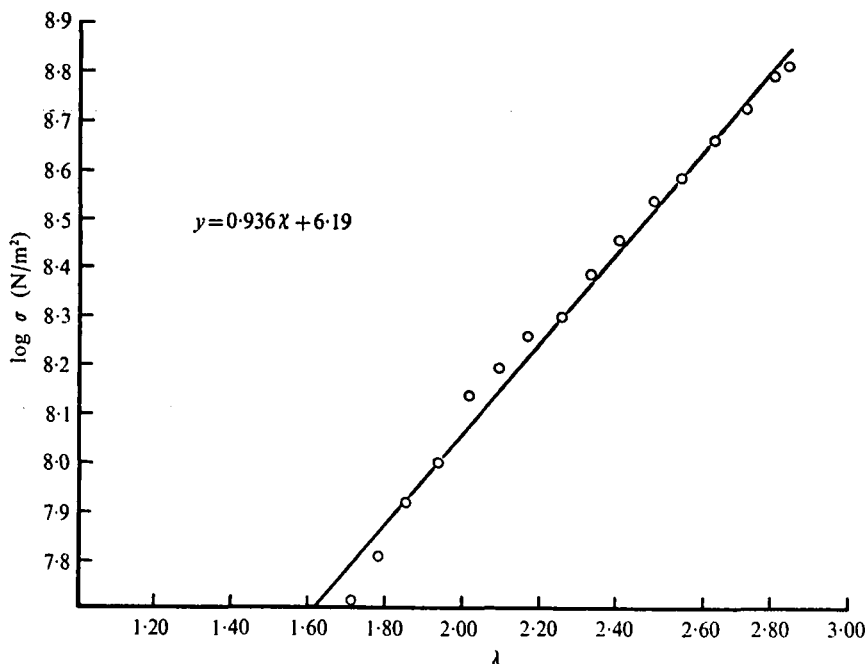


Fig. 9. A typical stress-extension ratio curve for the viscoid silk of *A. sericatus*; Fig. 8 replotted as the log of stress.

(see Table 6). The breaking extension of the viscoid silk was consistently close to 3.00 compared to 1.25 for frame silk. Breaking strength, however, was quite similar to that of frame silk. The average for the entire 41 samples was 1.1 GN/m², compared to values ranging from 0.8 GN/m² to 1.4 GN/m² for frame silk. As a consequence of the much higher breaking extension of the viscoid silk the value of E_f is relatively low, averaging 0.6 GN/m².

Neither breaking stress nor breaking extension, and consequently E_f , was found to vary with elongation rate. The temperature and relative-humidity variations encountered during testing appeared to have no effect on the tests.

The general shape of the stress relaxation curve for the viscoid silk is in sharp contrast to that of the frame silk (see Fig. 8). A high initial modulus is either absent or the forces too small to have been measured by the instruments used for the tests. Thus, from a low initial E_{tan} the curve slopes upward with an ever-increasing E_{tan} . When log σ is plotted against extension ratio the resulting graph approximates a straight line (see Fig. 9). The shape of the curve was not found to vary with extension rate, relative humidity or temperature.

The energy required to break the viscoid silk, normalized to a standard volume of 1 cm³, averaged 1.2×10^2 Joules/cm³, very close to the figure obtained for frame silk. Breaking energy did not vary significantly with extension rate, relative humidity or temperature.

Figs. 10 and 11 illustrate a typical stress relaxation curve for a sample of viscoid silk. The curve is similar to that typical of frame silk. E_t decays very rapidly in the first few seconds after extension, the rate of decay decreasing with passing time. An equilibrium

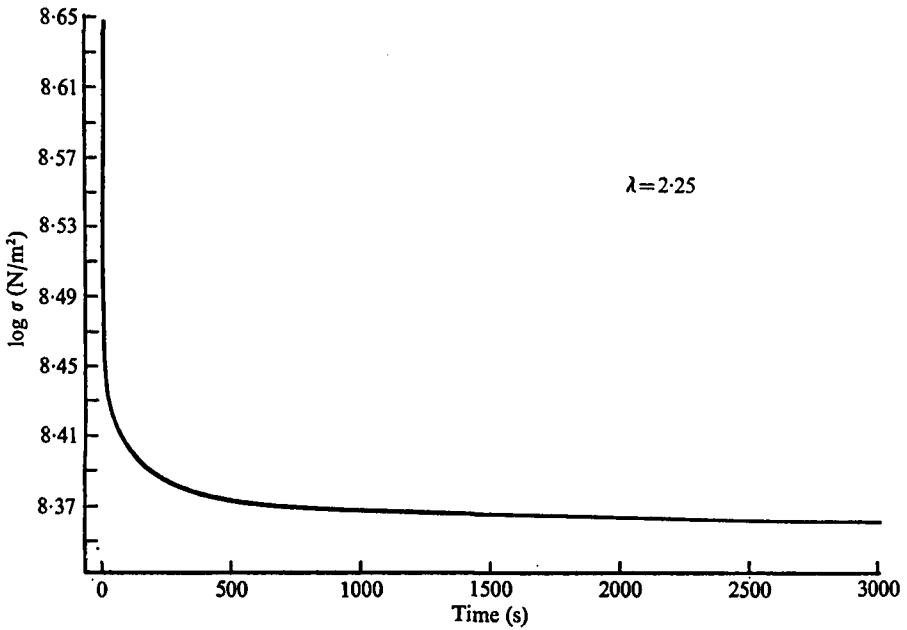


Fig. 10. A typical stress relaxation curve for the viscid silk of *A. sericatus*. Equilibrium modulus is reached at approximately 2300 s after extension.

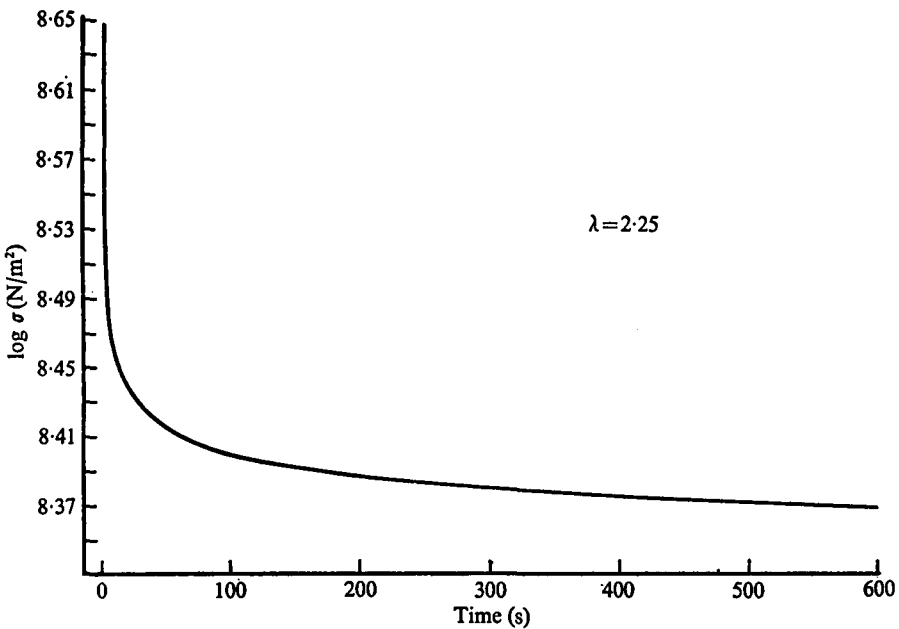


Fig. 11. A typical stress relaxation curve for the viscid silk of *A. sericatus*; an expansion of the first few seconds of Fig. 10.

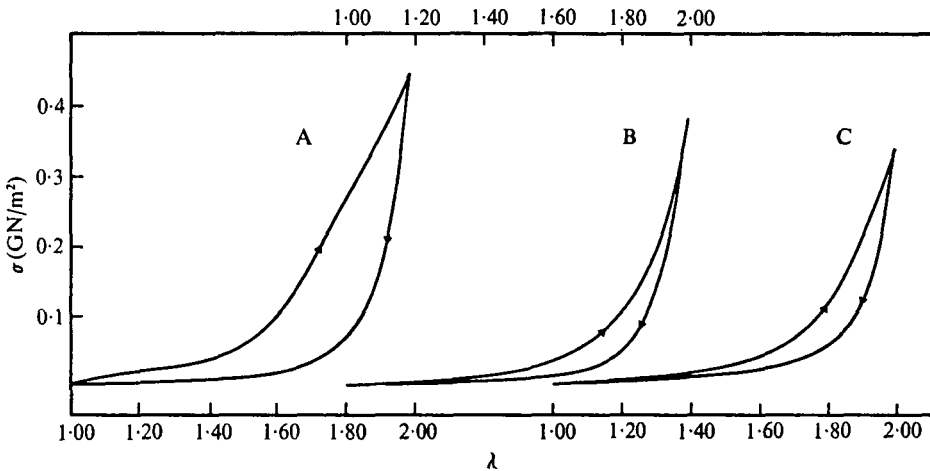


Fig. 12. A series of loading cycles on the viscoid silk of *A. sericatus*. Cycle (A) is the initial cycle of the series. $\dot{\lambda} = 17.37/\text{min}$. Cycle (B) is the second cycle in the series. $\dot{\lambda} = 17.37/\text{min}$. Cycle (C) is the seventh in the series. $\dot{\lambda} = 2.64/\text{min}$.

Table 7. Values for a typical cyclic loading test on the spiral silk of *A. sericatus*

	Designation in Fig. 12		
	(A)	(B)	(C)
$\lambda_{\text{max}} = 1.98$			
Extension rate (λ/min)	17.37	17.37	2.64
Total energy (μJ)	8.441	4.058	4.172
Energy lost (μJ)	5.605	1.672	1.851
Resilience	0.337	0.588	0.556

E_t is reached at $t = 2500$ s. No small set of relaxation times accurately describes this relaxation behaviour. τ , calculated with respect to equilibrium E_t , increases with time after extension. At $t = 1.2$ s, $\tau = 3.96$, at $t = 20$ s, $\tau = 40.59$, and with the sample approaching equilibrium at $t = 2300$ s, $\tau = 3.4 \times 10^4$. E_t at equilibrium is approximately 51% of E_t at time zero.

As with the frame silk tests, stress relaxation experiments could only be performed on the viscoid silk at high extension ratios ($\lambda > 1.80$). These results, then, represent the stress relaxation behaviour associated with only a certain portion of the stress-extension curve, and their comparability to situations of lower λ is not known. No effects of temperature or relative humidity were noted.

Successful cyclic loading tests were performed on two, multi-thread samples of viscoid silk. Fig. 12 illustrates a typical series of loading cycles conducted on a sample of viscoid silk, and the results are tabulated in Table 7. Several features are held in common with the equivalent curves for frame silk. The initial extension to a certain λ is accompanied by a relatively high total expenditure of energy and a low resilience. The average resilience for initial loading cycles was 0.38. From these tests it was not possible to say whether this loss of retrievable energy was due to a portion of the samples' extension not being recovered. The force involved when extending a sample the first few per cent was so small that accurate measurement of the border between a

tension existing in the thread and the sample lying slack was impossible with the instruments used.

Further extensions to the same λ involve a smaller expenditure of total energy and a higher resilience. The resilience encountered in non-initial loading cycles averaged 0.59. The number of tests was insufficient to detect any possible variation in resilience with extension rate. It was noted, however, that after a series of cycles at a certain extension ratio, if the sample were allowed to stand unstressed for a period of 5 min and then cycled again, the first cycle following the rest period was characteristic of an initial cycle with a high total expenditure of energy and a low resilience. This procedure was repeated several times, with the same result obtained each time. These results suggest a time-reversible component in viscid silk analogous to that of frame silk.

In summary, the viscid silk of *A. sericatus* may be characterized as an elastic material with a possible slowly recoverable component of extension. A breaking stress of 1.1 GN/m², coupled with a large breaking λ of 3.00, yields an E_f of approximately 0.6 GN/m². The silk exhibits a low initial resilience (approximately 0.38) and a higher subsequent resilience (approximately 0.59). The silk stress relaxes to equilibrium in a short period of time, E_t at equilibrium equal to approximately 0.50 of E_t at time zero.

DISCUSSION

Physical properties

On the basis of information existing in the literature an hypothesis may be formulated concerning the molecular structure responsible for the physical properties of spider's silk.

The molecular characteristics of frame silk appear to be typical of silks in general. The frame silk of *Araneus diadematus*, a close relative of *A. sericatus*, consists largely of small side-chain amino acids (Andersen, 1970; Lucas, 1964; Peakall, 1964, 1968) and is highly bi-refrangent (Zemlin, 1968). X-ray diffraction analyses show this silk to be a partially crystalline substance (Lucas, 1964; Warwicker, 1960). It appears likely, then, that the molecular configuration of frame silk is similar to that of *Bombyx mori* silk, the amino acids of the fibroin sequenced such that long segments of the polypeptide chains consist solely of residues with small side groups packed into a β -pleated sheet-crystalline formation, with the bulky side-chain amino acids confined to non-crystalline regions (Lucas, 1964).

The amino acid composition of the base strands of *A. diadematus* viscid silk does not differ substantially from that of frame silk (Andersen, 1970). No report is to be found of an X-ray diffraction analysis of viscid silk. It is noted, however, that viscid silk is only weakly, if at all, bi-refrangent (personal observation), making it unlikely that this silk contains crystals of the size found in frame silk. The difference can be accounted for if a different amino acid sequence exists in viscid silk; if the bulky side-chain amino acids, rather than being grouped together, are scattered throughout the polypeptide chains, the small side-group amino acids may be prevented from forming stable crystals.

Such a difference in crystallinity between frame and viscid silks may account for the primary difference in their physical properties, the greater extensibility of viscid

silk. The vast majority of amino acid links in the polypeptide chains of viscid silk, rather than being bound up in highly oriented and inextensible crystals, would be free to participate in the extension of the material, a situation more typical of a rubber than a silk. The physical properties of frame silk will be dominated by the interaction of the crystalline and amorphous regions to yield a stiffer, less extensible material. However, since the strength of both silks will be limited by the strength of the non-crystalline portion of the polypeptide chains, their breaking stresses should be the same, and are.

Web design

The physical properties of the silks of an orb-web are of interest not only for the clues they provide concerning the molecular structure of silk, but also for the role they play in the design of the web. The hypothesis to be examined here is that the orb-web is designed to use the minimum amount of material necessary to provide the spider with a functional prey-catching device.

The synthesis of silk to be used in web construction is the major energy drain on the orb-weaving spider (Lubin, 1973). The minimization of the volume of silk necessary for web building will thus minimize the total energy expenditure of the spider and maximize the energy gained (in the form of food) per energy expended. The maximization of this ratio is of ecological and evolutionary advantage to the spider.

Several aspects of web design show adaptations for volume minimization. Firstly, the construction of the orb in a single plane allows the spider to 'aim' the web. By building a web in a vertical plane the spider minimizes the chance of accidental destruction by falling objects while maintaining a large projected area with which to intercept prey, which fly with a primarily horizontal motion. Szlep (1958) has experimentally confirmed for *A. diadematus* that Argioid orb-weavers build their webs vertically. The advantages will be decreased when a strong wind blows and both prey and non-prey objects travel with a horizontal component of motion. Witt (1965) notes that on windy days Argioid spiders do not spin webs.

Within the constraint of an overall planar construction the individual elements of an orb-web could be arranged in a myriad different ways. Of these possible arrangements only a very few are found in nature, and these closely resemble each other and Fig. 1. Witt (1965) proposes explanations for some of the advantages offered by this configuration, noting that it allows the spider positioned at the hub, or attached to it by a silk line, to detect and locate vibrations originating anywhere on the web. This arrangement also allows for rapid movement to the point of impact. The arrangement of guys and frame provides a structure to which the radii may attach, while allowing the shape of the web to be largely independent of the shapes of surrounding objects.

Further explanations for the configuration of the web involve the mechanics of web function and the manner in which the physical properties of spider's silk are suited to this function. DeWilde (1943), Savory (1952) and others have noted a distribution of the numbers of strands found in threads forming different parts of the scaffolding of orb-webs. For *A. sericatus* the radii typically contain 2 strands; frame threads, 4-8 strands; and guys, 8-10 strands.

This ordered partitioning of the number of strands and thereby the cross-sectional areas of the threads found in different elements suggests the application of a theory of

Table 8. Values of tension and stress in the elements of a web of *A. sericatus*

	Radius	Frame	Guy
Number of elements in web	16	23	7
Average number of strands	2	4	5.3
Range of number of strands	—	—	4-8
Average tension ($N \times 10^{-4}$)	1.646	6.624	8.110
Range of tensions ($N \times 10^{-4}$)	0.418-3.385	1.080-15.770	2.546-17.449
Average cross-sectional area ($cm^2 \times 10^{-7}$)	0.63	1.26	1.67
Average stress (MN/m^2)	26	53	49
Range of stress (MN/m^2)	8-54	9-125	15-105

minimum volume design known as Maxwell's lemma (Parkes, 1965) which states that if every member of a structure built of one substance is under tension such that the *stress in all members is equal* and equal to the breaking stress of the material, the structure is built with the minimum volume necessary to resist the forces causing the tensions in the members. Essentially the theory states that if a structure is designed such that, when loaded to the breaking point, every member breaks at once, the material from which the structure is built is being used to its maximum capacity and the least amount of material is needed.

To determine the possible applicability of Maxwell's lemma to orb-webs the cross-sectional areas of, and the stresses in, the elements of the scaffolding of an *A. sericatus* web were determined. A typical web was chosen and the tension in one guy measured. The web was photographed and the angles between web elements measured. Orb-webs are constructed such that nowhere in the supporting framework (the hub excepted) do more than three elements meet at a junction. Consequently it was possible to calculate the tensions in all web elements. Samples were then taken from the framework and the number and cross-sectional areas of the strands noted. The results appear in Table 8.

The web does not strictly meet the criteria of Maxwell's lemma. While all the members of the web are in tension, the stress varies between the elements. The differences in stress, however, are much less than the differences in tension. To the extent to which the stresses are made equal the web approximates a minimum volume structure under Maxwell's lemma. Witt (1965) points out that orb-weavers neither run out of silk while building a web, nor at the end of construction have a large amount of silk left over. Thus, working with a set volume of material, the spider apportions this material at close to its maximum advantage.

A further minimization of the volume of material used per web is achieved in the orb-webs of *A. sericatus* by the use of exceedingly fine fibres. For a web containing 10 m of thread (about 30 m of single strand) the volume of the web is about 10^{-6} cm³. In order that the web may be constructed with such a small volume the silk must be designed to be capable of sustaining the stresses imposed by the functioning of the web.

In light of the physical properties of spider's silk the manner in which this silk is suited to this task may be examined. Firstly, both the frame and viscid silks exhibit a very high breaking stress. Lucas (1964) compares the strength of frame silk of *A.*

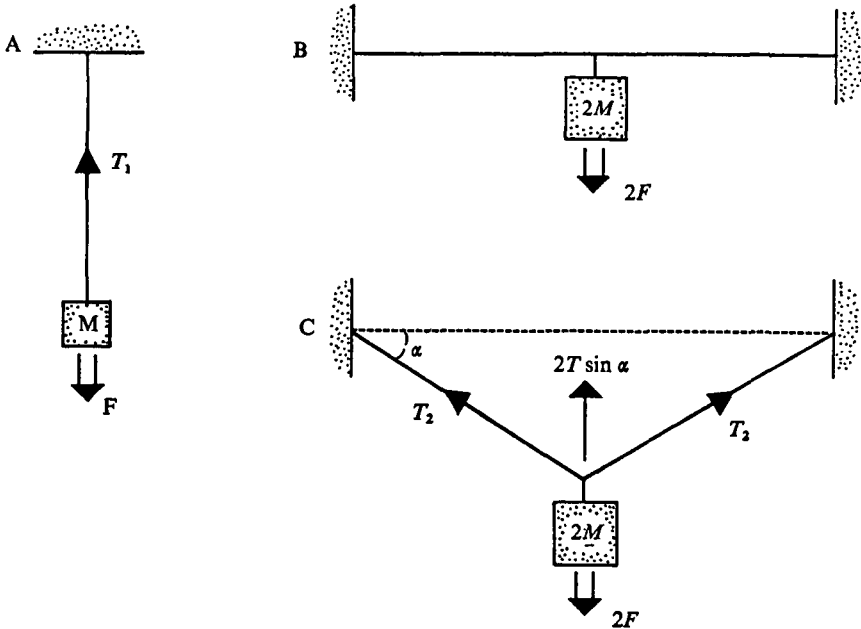


Fig. 13. An illustration of the forces acting when a thread is stretched.

diadematus with several materials and finds the spider's silk compares favourably with both steel and high-tenacity nylon.

Other aspects of the suitability of silks to web construction are less obvious. Consider the situation shown in Fig. 13A. A fibre supports a mass M which exerts a force F . If the mass is stationary, the force in the fibre opposing F , tension T_1 , must equal F . Now consider Fig. 13B. Two fibres identical to that in Fig. 13A are each fixed at one end and hold between them a mass equal to $2M$ exerting a force equal to $2F$ perpendicular to the axis of the fibres, a situation analogous to a captured insect or the spider itself being supported by an element of an orb-web.

The system will deform to the equilibrium situation shown in Fig. 13C. Again there must be a force acting on the weight equal and opposite to $2F$. This force is provided by the tension in the fibres, $T_2 = F/\sin \alpha$. When $\alpha = 90^\circ$ the situation is the same as that in Fig. 13A, and when α is $< 90^\circ$ T_2 will become very large. Due to this fact a guitarist can snap a string of high-tensile-strength steel, and it would seem that an insect, regardless of the high strength of silk, could break through the fibres of a web.

It is in this aspect of web design that the more subtle physical properties of spiders' silk are of importance. The tension T_2 in Fig. 13C is a function of α , and α in turn is a function of the elastic modulus and extensibility of the fibre. For fibres of a given breaking strength the maximum force they can resist without breaking when loaded as in Fig. 13C is a function of the maximum λ , λ_f , they can sustain:

$$F_{\max} = \sigma_f \cdot \frac{A_0}{\lambda_f} \cdot \sin \alpha,$$

$$F_{\max} = \sigma_f \cdot \frac{A_0}{\lambda_f} \cdot \frac{(\lambda_f^2 - 1)^{\frac{1}{2}}}{\lambda_f}.$$

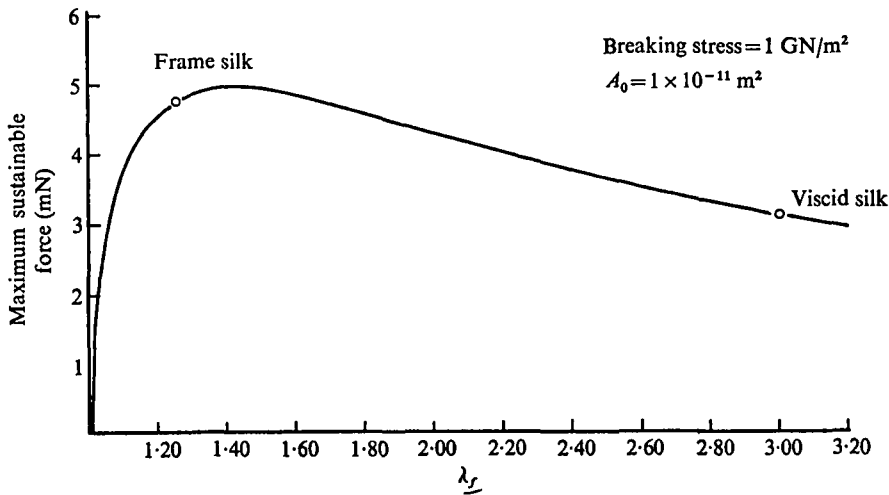


Fig. 14. The theoretical maximum sustainable force for a fibre of given σ_b and cross-sectional area as a function of λ_f .

This function reaches a maximum at $\lambda_f = 1.42$ (see Fig. 14). Fibres with maximum extensions much less than 1.2 are relatively weak under such a loading regime, as are fibres with λ_f much beyond 2.0. The maximum extension of frame silk at 1.25 is close to the theoretical maximum. In this respect the frame silk is well adapted to its function as a scaffolding material, being maximally strong in the resistance of static loads.

Viscid silk with a λ_f of 3.0 is well beyond the point of maximum strength shown in Fig. 14. The function of the highly extensible viscid silk becomes apparent when the dynamic load represented by a moving object is considered. In order for a moving object to be trapped by the web its velocity must be brought to zero. The magnitude of deceleration the object must undergo in being stopped is a function of the distance over which the deceleration is accomplished; the smaller the distance the higher the deceleration. For an object of mass M , a force equal to Ma (where a is the rate of deceleration) must be applied by the silk to the object, and this force will be greater the shorter the distance allowed in which to bring the object to a halt. The great extensibility of the spiral thread allows the impacting object to be slowed over a distance that is large relative to that offered by the frame silk, thereby decreasing the force impinging on the web at impact. Further, an insect trying to struggle free from a web will be held by the sticky, highly extensible spiral thread. In the web these threads lie in the initial portion of their stress-extension range where E_{tan} is low (see Fig. 8). Thus any thrust by an insect with leg or wing will be met, not with an elastic force that would provide something to push against, but rather with the near-forceless stretching of the thread to no advantage. Thus the physical properties of the two silks of the orb-web suit these materials to their function within the net.

It may well be asked at this point what sort of prey a spider's web is capable of catching. A mass M moving at velocity V has a kinetic energy of $MV^2/2$. In stopping this object this energy is transferred to the entrapping web. The spiral silk of *A. sericatus* was found to absorb $1.2 \times 10^2 \text{ J/cm}^3$ before breaking. Four threads of two

Table 9. *Estimated maximum velocities of flight and kinetic energy for some representative insects*

Maximum velocity (cm/s) = $2.5 \times$ wing length (cm) \times beat frequency (Hz). Wing length, beat frequency and weight data taken from Greenwalt (1962).

Species	Common name	Wing length (cm)	Beat frequency (Hz)	Maximum velocity (cm/s)	Weight (g)	Kinetic energy (Joules)
<i>Aedes aegypti</i>	Mosquito	0.35	360	360	0.00189	1.225×10^{-5}
<i>Drosophila funebris</i>	Fruit fly	0.40	170	170	0.006	8.67×10^{-6}
<i>Musca domestica</i>	House fly	0.55	190	261	0.012	4.08×10^{-5}
<i>Apis mellifica</i>	Honey bee	0.90	233	524	0.097	1.33×10^{-3}
<i>Bombus terrestris</i>	Bumble bee	1.6	130	520	0.388	5.25×10^{-3}
<i>Aeschna juncea</i>	Dragonfly	4.8	35	420	0.958	8.45×10^{-3}

strands, each $1.5 \mu\text{m}$ in diameter and 3 cm long will require the input of 5.08×10^{-5} Joules to break, equal to the energy of a mass of 0.025 g moving at a velocity of 2.01 m/s.

If, however, these spiral threads lie stretched as in the web between radial threads of frame silk the situation is changed. Assume that each radial thread is 15 cm long and consists of two strands $2 \mu\text{m}$ in diameter anchored at each end. When stretched just to their breaking extension the four spiral threads will exert a force of 1.44 mN on each of the radial threads. Assuming the radial threads to have a Young's modulus of 2.7 GN/m^2 each of the radial threads will be stretched to $\lambda = 1.17$ by the spiral threads. At this extension the radial threads will have absorbed a total of 5.62×10^{-5} Joules in addition to the 5.08×10^{-5} Joules absorbed by the spiral threads. A mass of 0.025 g must now be moving at a velocity of 2.93 m/s (in contrast to 2.01 m/s) in order to just barely break the structure on impact. Thus, by attaching the spiral threads to flexible rather than stationary structures the energy-absorbing capacity of the system is increased.

If this system were to more closely approximate the true behaviour of the orb-web the radial threads in turn would be attached to the flexible structures of the hub, the frame and other spiral threads. The frame would be attached to guys, and only then would stationary structures be encountered. Thus the catching structures of the web are buffered from stationary objects by several levels of flexible framework ensuring that the entire web will absorb the impact, the energy-absorbing capacity of the web thereby being enhanced. The estimate calculated above will therefore be somewhat low when compared to an entire web.

To test the accuracy of this estimation two webs of *A. sericatus* were turned horizontally and a small piece of wood weighing 0.025 g dropped from increasing heights on to the webs. At a height of 0.85 m, corresponding to a velocity on impact of about 4.00 m/s, the weight was caught about half the time when the contact involved four spiral threads of about 3 cm lengths and radii 15 cm long. Thus, when the factors mentioned above are taken into account, the calculated estimate of web strength proves to be a reasonable approximation.

It is of interest to note what sorts of insects would move with a kinetic energy such that they could be caught in *A. sericatus* web. Estimates of the kinetic energy of flying insects were made using a formula suggested by S. Vogel. The results appear in Table 9. Based on the experimental determination of web strength an *A. sericatus* web

is capable of trapping objects of kinetic energy up to about 2×10^{-4} Joules. From Table 9 it can be seen that *A. sericatus*, while capable of capturing house flies, can only capture honey bees if they fly at less than their predicted maximum velocity. Larger insects will in all probability not be captured by the web.

The spiders used in this study weighed 0.1–0.15 g. Thus the web is capable of capturing only those prey whose mass is equal to or less than that of the spider. Larger prey, that in a struggle could injure the spider, will fly straight through the web without being caught. Thus the web is capable of catching prey up to an optimal size, but no silk has been wasted in making the web strong enough to catch insects potentially harmful to the spider.

Once an insect has been stopped a web must hold the prey for the spider to make the final capture. Holding the prey would be difficult if the energy stored in the web were to be transferred back to the prey and the prey propelled back whence it came. The low initial resilience of both the viscid and frame silks ($R \approx 0.35$), coupled with the viscous behaviour of the frame silk, ensures that most of the energy taken up by the web in impact will be dissipated rather than being returned to the impacting object.

The aspects of web construction examined here provide evidence in support of the hypothesis that orb-webs are designed to be minimum volume structures capable of functioning as aerial filters. This minimization, allowed by the fact that the physical properties of frame and viscid silks and the mechanical configuration of web elements complement each other, may offer the orb-weaving spider a significant selective advantage. It is hoped that these considerations, when coupled with information concerning the neurological and anatomical capabilities of orb-weavers, will provide a fuller understanding of the overall design of orb-webs.

Without the inspiration, advice, and support of S. A. Wainwright this study would not have been possible. The forbearance and encouragement of M. Koehl, M. La-Barbera, G. Pearsall and B. Wygal was also invaluable in forming the ideas presented here.

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