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The scaling of safety factor in spider draglines

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SUMMARY

This study documents the effect of body mass on the size and strength of draglines produced by the orb-weaving spider *Araneus diadematus* and the jumping spider *Salticus scenicus*. Silk samples obtained from individuals spanning the range from first-instar juveniles to gravid adults were tested to determine both the properties of the silk material and the strength and static safety factor of the draglines produced by each individual spider. Analysis of material properties indicates that the tensile strength and extensibility of the silks employed by each species are identical over the entire size range of the species. Analysis of the breaking forces for individual draglines, however, indicates that the draglines scale allometrically with the spider's body mass. For *Araneus*, breaking force (N) scales with body mass (kg) as $F_{max}=11.2M^{0.786}$, and the static safety factor ($S_{BW}=F_{max}/Mg$) scales as $S_{BW}=1.14M^{-0.214}$. For *Salticus*, $F_{max}=0.363M^{0.66}$ and $S_{BW}=0.037M^{-0.34}$. Thus, static safety factors decrease as these spiders grow, with values falling to 4–6 for adult *Araneus* and to 1–2 for adult *Salticus*. Analysis of these results suggests that the safety lines produced by these two species are not able to absorb the impact energy of most falls with a fixed length of pre-existing silk, except in the smallest of the *Araneus* spiders. It is therefore likely that both spiders must draw new silk from their spinnerets during falls to keep the dynamic loads on their safety-lines below failure levels.

Key words: dragline, safefy factor, spider silk, *Araneus diadematus*, *Salticus scenicus*.

INTRODUCTION

The relationship between the material properties of a structure and its function are a common theme in engineering. The safe construction of bridges, buildings and vehicles, for example, depends on understanding how a material responds to both normal and peak forces imposed during the intended lifespan of the structure. Making strong structures, however, cannot be the only objective, since cost has to be considered as well. Hence, balancing these different constraints is an important part of design. A common measurement of the quality of design in a structure that is limited by tensile strength is the safety factor, or the non-dimensional ratio between the material's strength and maximum stress experienced in the use of the material in some functional structure. In an efficient design, the safety factor approaches 1.0 because the strength is exactly matched to the load. Due to variability in material properties and uncertainties in the loading regime, safety factors must exceed this theoretical optimum for the structure not to fail in normal use (Alexander, 1996). For example, under British Standards BS-449, a steel member under tension, with a yield stress of 2.5×10^{8} Pa, may not be loaded to more than 1.65×10^{8} Pa, an effective safety factor of 1.5 (Blockey, 1980).

Biological structures are similar in that design is shaped by a number of constraints. Even if the cost of failure is high, greater strength is offset by higher structural cost. The assumption that evolution would eventually lead to a decent compromise is not unreasonable. An optimal solution is, however, unlikely ever to be achieved in any biological system simply because parameters change with time. In fact, a 'sufficient' solution can be good enough unless additional selective forces act on the system.

Spider silk is interesting in this respect because it is a structural material that has been made by spiders for at least 380 million years (Selden et al., 1991) and has evolved into at least eight different types with different uses and properties. Dragline silk, in particular, is made by the vast majority of spiders, from first instars to adults, and is used for a wide variety of purposes including locomotion, safety-lines, web construction, signal threads and chemical communication (Foelix, 1996; Tietjen and Rovner, 1982). Spiders that make dragline, regardless of its other uses, will trail out this silk behind them as they walk around, attaching it to the substrate at intervals. The dragline can then act as a safety-line in the event of a fall (Brandwood, 1985).

When the spider descends or falls, a successful safety-line stops the falling spider without breaking the safety-line, and the spider can either climb back up or descend further. Safety factor can be used to evaluate the efficiency of dragline as a safety-line, and one method is to calculate the static safety factor (S_{BW}), where the subscript BW is used to indicate the safety factor in body weights, by dividing the silk thread's breaking force ($\mathbf{F}_{max}$) by the spider's body weight, $M\boldsymbol{g}$, where M is mass and $\boldsymbol{g}$ is the acceleration of gravity:

$$S_{BW} = \mathbf{F}_{max} / M\boldsymbol{g}\,. \quad (1)$$

Osaki calculated that adult *Nephila clavata* dragline has a static safety factor of $S_{BW}<6$ (Osaki, 1996), which seems to be higher than what would be expected for an efficient design. The static safety factor, however, does not take into account the true function of the safety-line, which is rarely used as a static support. It virtually always functions dynamically while absorbing the energy from a falling animal because it is loaded in impact. Thus, if the spider falls with a fixed length of attached silk as a safety-line, the impact force developed will be much greater than body weight. Therefore, the magnitude of the static safety factor required for a spider's dragline to survive the dynamic forces that arise in a fall onto a fixed length of silk will appear excessive, with a magnitude much greater than 1.

Spiders are frequently observed to lower themselves by spooling out new silk, and we recently reported that *Araneus diadematus* have an internal friction brake somewhere within the major ampullate gland complex that allows them to control the force required to pull new dragline silk from their spinnerets. When the animals are forcibly silked (i.e. silk is pulled from the spinneret by an external motor) the friction forces range from approximately 0.1 body weights to greater than 4 body weights (Ortlepp and Gosline, 2004). When freely walking *Araneus* fall, they typically apply frictional braking forces of up to approximately 2 body weights to bring their descent to a halt. Thus, by spooling out new silk, spiders have the ability to control the dynamic loads that develop when they fall, and they may, therefore, be able to lower the static safety factor of their safety-lines and still survive the dynamic loads of a fall. The issue we consider in the present study is whether spiders make their safety-lines strong enough to survive a fall on a fixed length of silk or whether they reduce the size of their safety lines to the point that they must rely on the production of new silk during a fall to reduce the dynamic force. In the following analysis we test the hypothesis that spiders can survive falls with a fixed length of silk.

To investigate the maximum dynamic force experienced, we chose to consider a spider that falls without reaching terminal velocity, with a fixed length of attached silk as a safety-line; that is, the spider produces no additional silk. If the safety-line is attached at the spider's initial height, the spider is initially in free-fall until the silk becomes taught and the dragline is then loaded in impact. This scenario is essentially a bungee jump (see Fig. 1A).

A safety-line absorbs the energy of a falling spider by being stretched, and the greater the stretch, the lower the impact force. This relationship arises from Newton's Second Law, $\mathbf{F}=Ma$, where $\mathbf{F}$ is force and a is acceleration, because greater stretch implies lower deceleration and, hence, lower impact force. Thus, the actual dynamic safety factor is determined by the stretchiness of the material and the strength of the fibre. In the analysis below we will model the dynamic loading of the safety-line in terms of the breaking force of the fibre, $\mathbf{F}_{max}$, and the breaking strain, ε_{max}, of the spider's silk.

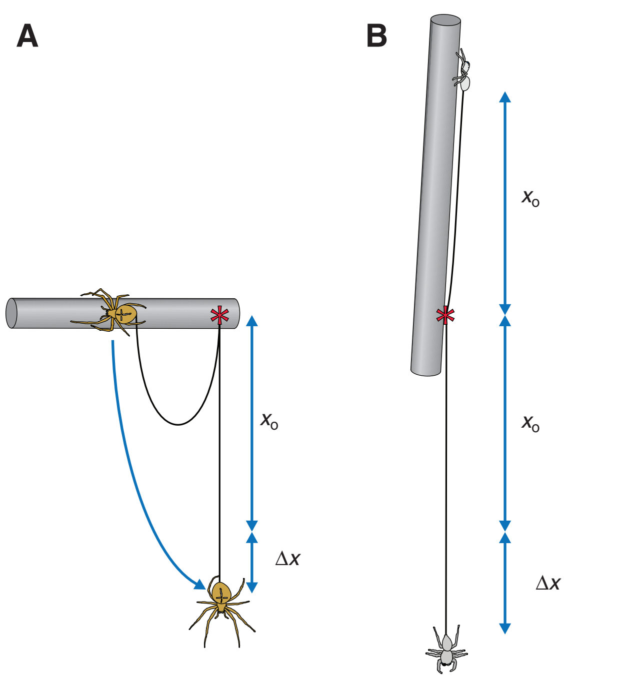

Fig. 1. Overview of bungee jumping spiders. (A) A spider bungee jumping with pre-made silk of length x_o. The silk attachment point is marked with a red star. When the silk starts to take the load of the spider, x_o below the attachment site, the silk is stretched Δx before the spider comes to a stop. (B) Worst-case scenario in which the spider falls $2x_o$ before silk is loaded.

We assume that the dragline functions as a linear spring, so that the maximum energy ($E_{s,max}$) absorbed when stretching any individual silk thread to its failing point is:

$$E_{s,max} = \tfrac{1}{2}\mathbf{F}_{max}\,\Delta x_{max}\,, \tag{2}$$

where Δx_{max} is the breaking extension of the thread.

Failure of the thread will occur when the gravitational potential energy released in the fall of the spider exceeds the capacity of the silk to absorb this energy. During free-fall, the gravitational energy released is $M\boldsymbol{g}x_o$, where x_o is the initial length of the silk thread. As the thread stretches, the additional gravitational energy released is $M\boldsymbol{g}\Delta x$. Thus, the total gravitational energy release at $E_{G,max}$ fibre failure is:

$$E_{G,max} = M\boldsymbol{g}x_o + M\boldsymbol{g}\Delta x_{max}\,. \tag{3}$$

When $E_{s,max}$ is equal to $E_{G,max}$:

$$M\boldsymbol{g}x_o + M\boldsymbol{g}\Delta x_{max} = \tfrac{1}{2}\mathbf{F}_{max}\,\Delta x_{,max}\,. \tag{4}$$

Under this condition, the safety-line can just support the impact load, yielding a dynamic safety factor of 1. By substituting Eqn 1 into Eqn 4 and rearranging, we can calculate S_{BW} required for a safety-line made from a material with a failure strain ($\varepsilon_{max}=\Delta x_{,max}/x_o$) to just survive a bungee-jump fall, as:

$$S_{BW} = (2 / \varepsilon_{max}) + 2\,. \tag{5}$$

If the spider climbs above the silk's attachment point, more gravitational energy must be absorbed by the silk. The worst-case scenario occurs when the spider falls from a distance x_o above the attachment point (see Fig. 1B), such that the total distance of the fall is $2x_o+\Delta x$. The static safety factor required to survive a worst-case fall is:

$$S_{BW} = (4 / \varepsilon_{max}) + 2\,. \tag{6}$$

Two examples illustrate how breaking strain and static safety factor interact. Kevlar is a man-made material with exceptional stiffness and strength but low breaking strain. The breaking strains for single filaments of two types, Kevlar 29 and Kevlar 49, range from 0.028 to 0.036, and the minimum S_{BW} required for a Kevlar safety-line would be 58–73 according to Eqn 5 (see Fig. 2). That is, for Kevlar 49, the safety line would require a breaking force that is 73× the weight of the object attached to it. Also shown in Fig. 2 is natural rubber, which is at the opposite end of the spectrum, with low strength and stiffness but with very high breaking strains. With maximum strains of 2.5–6, the static safety factor would only need to be in the order of 3 for a successful bungee jump. It is important to recognize that this analysis is based on the assumption of a linear force–extension curve to failure, which in the case of Kevlar is quite reasonable. Rubber, however, has a J-shaped force–extension curve, and this analysis overestimates the magnitude of the energy absorbed and hence under-estimates the static safety factor required for a successful bungee jump.

The comparison above shows that a safety-line made with a stretchier material will generally not need to be as strong to successfully absorb the impact of a bungee jump. Furthermore, the range of static safety factors associated with a range of strains becomes smaller as the material becomes more extensible because Eqn 5 is an inverse function with a slope that changes from vertical to near horizontal with increasing extensibility. Because there is

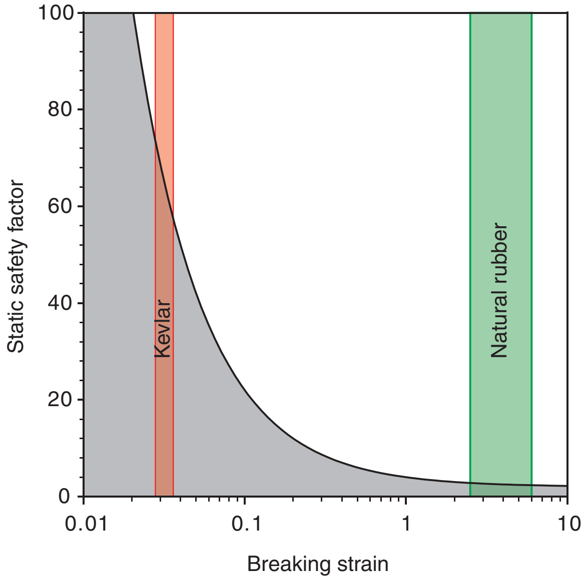

Fig. 2. The solid line shows the form of Eqn 5, which indicates the effect of breaking strain on the minimum static safety factor required for bungee jumping. The gray shaded area below the solid line represents strain–safety factor combinations that would fail during bungee jumping. For example, a strand of Kevlar would require a static safety factor of at least 58, while natural rubber would only need a static safety factor of approximately 3 to survive a bungee jump.

variation in the property of any material, the range of minimum static safety factors needed for a successful bungee jump decreases as the material becomes stretchier.

The properties of dragline silk are well known for a number of species (Gosline et al., 1999; Köhler and Vollrath, 1995; Stauffer et al., 1994), and these studies include values for breaking strain, which fall in the range of 0.2–0.35. For many of these species, the force–extension curves are quite linear, and thus the minimum static safety factors required for a successful bungee jump should be between 8 and 12. Thus, the static safety factor of 6 measured by Osaki (Osaki, 1996) for adult *Nephila clavata* dragline suggests that dragline cannot function as safety-lines in bungee-jump falls. This is surprising if one considers that 380 million years should be enough to match property and function for something as important as a safety-line. Brandwood showed that the silk from the spider *Meta segmentata* would break during a worst-case scenario where the animal falls from above its attachment point (Brandwood, 1985) but it remains to be seen if dragline is suitable for falling from its attachment point, i.e. bungee jumping.

In the current study we present data on the scaling of mechanical design in spider safety-lines in two species, the orb weaver *Araneus diadematus* (Clerck 1757) and the jumping spider *Salticus scenicus* (Clerck 1757). We show that the mechanical properties of dragline silk, such as tensile strength and extensibility, remain unchanged over the full range of size in *A. diadematus*, from 0.0004 g first-instar hatchlings to 1.2 g gravid females. By contrast, the silk cross-sectional area and breaking force scale strongly with body mass. The pattern of scaling produces static safety factors that decrease with increasing spider mass, such that only the smallest individuals can bungee jump safely, and even fewer individuals can fall from above the attachment point. Preliminary data for *S. scenicus* indicate a similar relationship, but static safety factors are below the threshold over the entire size range. These results suggest that both spiders must rely on the production of new silk to reduce the dynamic forces that develop during a fall.

MATERIALS AND METHODS

Spiders

Dragline was gathered and tested for *Araneus diadematus*, an orb weaver, and *Salticus scenicus*, a small jumping spider. Adult spiders were collected from July to November locally in Vancouver, Canada, and kept indoors with a 14 h:10 h day:night cycle at ambient temperatures. The orb weavers were placed in 60 cm×60 cm×10 cm wooden boxes with Plexiglas™ sides, while the jumping spiders were kept in 500 ml glass jars with a large twist of paper for increased surface area. Spiders were misted every few days and fed with a variety of insects once or twice per week.

To obtain silk from the entire weight range of *A. diadematus*, an egg case was hatched in the laboratory and dragline was taken from the spiders as they grew. Silk was obtained by taking the spider on a hand, waiting for it to attach the dragline to the hand and then gently brushing it off so that it dropped on its dragline. This dragline was wound up on a small cardboard frame while the spider hung on the silk. Immediately afterwards, the spider's mass was measured on a Mettler H31 (±0.1 mg) or Mettler H54 (±0.01 mg) microbalance (Fisher Scientific Company, Ottawa, Ontario, Canada).

Samples of jumping spider dragline could not be obtained in the same way, as more often than not they jumped off the hand without an attached dragline. These spiders do, however, spool out dragline as they move around, so silk was collected by putting a spider in a plastic container and picking up the silk behind it. In addition, silk was also obtained by having the spiders jump off glass rods and winding the dragline onto cardboard frames if any was present. Because two adult females laid eggs, two samples of silk were obtained from very young *S. scenicus* in addition to adult silk.

For adult spiders, silk diameters were measured using a Wild M21 microscope (Wild Heerbrugg Ltd, Heerbrugg, Switzerland) under polarizing light with a 100× oil immersion lens and 15× filar-micrometer eyepiece. The width of a double-stranded piece of silk was measured and the distance divided by two to determine the diameter for a single strand of silk. Silk from smaller spiders and selected adults was sputter-coated with gold and placed in a Cambridge 250T (Leica, Cambridge, UK) or a Hitachi S4700 scanning electron microscope (Hitachi High-Technologies Canada, Inc., Toronto, Ontario, Canada) for measurement. Photos were taken at magnifications ranging from 18,000× to 100,000×, and silk diameters were measured and converted using the scale bars on the photos. With one exception, all silk sampled was double-stranded, as is the norm. One adult *A. diadematus* spider, however, produced dragline with three strands of equal diameter. The dimensions of this unusual sample were determined by SEM and it is clear that its appearance was not due to contamination of a normal, double-stranded dragline (produced by the major ampullate glands) by a single strand from an accessory thread (produced by the minor ampullate glands). We therefore included this sample and calculated its cross-sectional area as 3× the area of a single strand. All figures and regressions presented in the current study are based on the full data set, and values for the three-strand sample were very close to the trend based on the full data set. Removal of this sample from the analysis did not significantly affect any of the quantitative conclusions presented in this study.

At least one piece of silk was tested for each spider. When multiple samples from a single piece of silk were tested, the results were averaged to avoid pseudo-replication. Starting from slightly slack silk, all silk was tested to failure, and tests in which silk broke within 2 mm of either attachment point were considered damaged by the gluing process and discarded. The silk length at which the first rise in force was observed was taken to be the initial length (x_o) and was used to calculate instantaneous strain (ε), as the change in length (Δx) divided by the initial length. To compensate for the 3000-fold range of spider weights, force was expressed in spider body weights by dividing the breaking force, **F** (in N), of a spider's silk by that spider's weight, Mg (in N), because the body weight is the relevant functional unit for a safety-line. Additionally, breaking force was converted to breaking stress, σ (Pa), by dividing by the total, initial cross-sectional area, A (m^2) of silk when known. The initial slope, or initial modulus, E_i (Pa), was calculated from the resulting stress–strain data by fitting a least-squares regression to the linear portion of the stress–strain curve before the yield point. The yield strain and yield stress were determined to be the point at which the dragline's stiffness decreased after an initial stiff region.

Quasi-static testing

Because of the large range of spider weights and corresponding silk breaking forces, two different methods were used to measure the failure force of the silk. Most spiders weighing more than 0.150 g were tested on an Instron model 1122 tensile testing machine (Instron Canada, Inc., Burlington, Ontario, Canada) with a custom-built stain gauge force transducer with 100 g full-scale sensitivity.

Silk samples were glued with Loctite Superbonder 409 cyanoacrylate superglue (McMaster Carr, Elmhurst, IL, USA), 5 Minute Epoxy (ITW Devcon, Danvers, MA, USA) or nail polish onto thin cardboard from which a 6 cm×6 cm window had been cut. This frame was mounted in the Instron and the cardboard carefully cut away to expose the silk. If necessary, crosshead distances were adjusted to make the silk slack. Crosshead speed was set to $3.3\times10^{-4}\,m\,s^{-1}$, giving strain rates ranging from 0.0056 to $0.0066\,s^{-1}$.

Silk from smaller spiders proved to be too weak to be measured accurately with the Instron, so an alternative set-up using glass rods was used, as described previously (Fudge et al., 2003). Briefly, a glass rod of known stiffness (E) and radius at tip (r_t) and base (r_b) is glued parallel to a glass slide. If silk is glued to the glass rod at distance l from the base, any deflection (d) of the rod at the attachment point can be used to calculate the force acting on the rod:

$$\mathbf{F} = (3\pi E r_t r_b^3 d) / 4l^3\,. \quad (7)$$

One end of a 3.4–5.7 cm piece of silk was glued with either Loctite Superbonder 409 cyanoacrylate or 5 Minute Epoxy to the glass rod and the other end to a hook pulled by a variable-speed DC motor set to $2.27\times10^{-4}\,m\,s^{-1}$, giving a strain rate of 0.0057 to $0.0093\,s^{-1}$.

To measure rod deflection, the glass rod was placed under a Wild M21 microscope with a 4× or 10× objective lens and projected onto a television. Deflection was measured with a video dimensional analyser (model 303, Instrument for Physiology and Medicine; San Diego, Ca, USA) by measuring the movement of the rod boundary at the attachment point relative to an arbitrary reference point. Voltage output proportional to rod deflection was collected by chart recorder and/or PC computer with LabTech Notebook 6.1.2 (Laboratory Technologies Corp., Wilmington, MA, USA) or LabView 5.0 (National Instruments, Austin, TX, USA). A calibration slide with 10 µm scale increments (Bausch and Lomb; Rochester, NY, USA) was used to determine the voltage per unit distance.

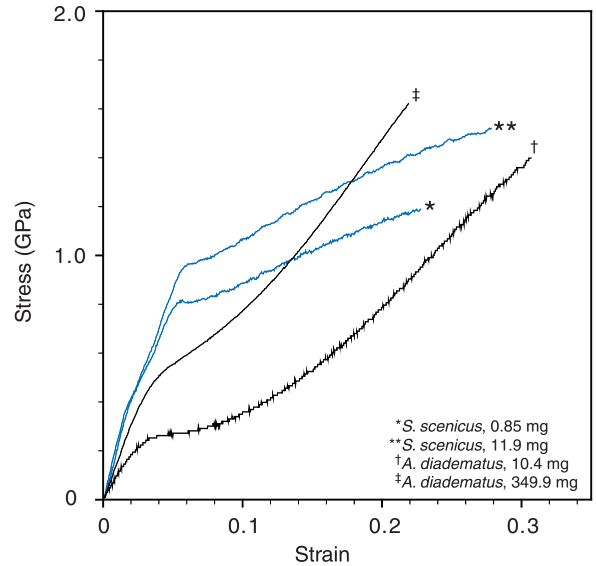

Fig. 3. Sample data from several silk tests to failure from juvenile and adult spiders. *Salticus scenicus* are shown in blue and *Araneus diadematus* in black. Note the difference in shape of the stress–strain curves for the two species.

RESULTS

Silk was collected from the entire size range of *A. diadematus* spiders, ranging from 0.00036 g first-instar hatchlings to gravid 1.15 g females, with silk tested from 35 individuals. Silk samples from *S. scenicus* were sampled from two adult, one juvenile and three first-instar spiders. Fig. 3 shows sample silk tests to failure from juvenile and adult spiders of both species. The tests were chosen to show the full range of stress–strain curves observed. All samples showed an initial region of high stiffness followed by a yield point where subsequent stiffness is dramatically reduced. In *S. scenicus*, the lower stiffness was maintained to the failure point, giving a 'two-slope' curve. In *A. diadematus* silk, the stiffness typically rose again before failure, resulting in a 'three-slope' curve. Table 1 summarizes the data that have been derived from these tests, namely breaking strain, yield stress, yield strain, breaking stress and initial modulus for both species. Note that *S. scenicus* dragline silk has a significantly higher initial modulus, yield stress and yield strain, but the tensile strength and extensibilities for the silks from both spiders are the same.

Analysis of the mass dependence of material properties revealed that there were no significant effects of body mass on breaking strain, initial modulus or the tensile strength of the dragline silks from the two spider species. Fig. 4 displays data for the scaling of breaking

Table 1. Summary of average dragline material properties

Property	*A. diadematus*	*S. scenicus*
Yield strain	0.033±0.002* (20)	0.049±0.009* (5)
Yield stress (GPa)	0.392±0.07** (12)	0.77±0.09** (4)
Breaking strain	0.249±0.010 (20)	0.252±0.026 (6)
Breaking stress (GPa)	1.11±0.08 (12)	1.19±0.25 (4)
Initial modulus (GPa)	10.6±1.0** (12)	15.7±0.2** (4)
Scaling exponent of breaking force	0.786±0.027 (33)	0.660±0.130 (6)

Two-tailed *t*-tests were used to identify significant differences between the two species (**P*=0.025, ***P*=0.04, ****P*=0.034). Values are means ± s.e.m. (*N*).

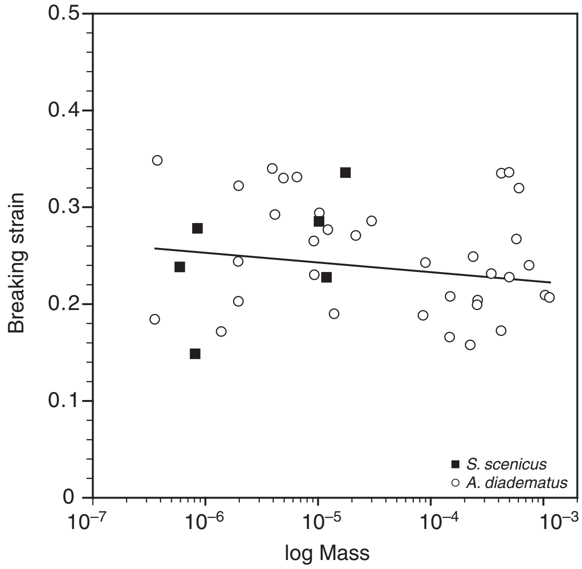

Fig. 4. Breaking strain is normally distributed (P=0.47), with a mean (±s.e.m.) 0.249±0.009, for combined data from both *A. diadematus* and *S. scenicus*. There is no statistically significant trend with log-transformed spider mass (M). The least-squares regression best-fit for the combined data was ε_{max}=0.237–0.008log$M$, r^2=0.02, P=0.35.

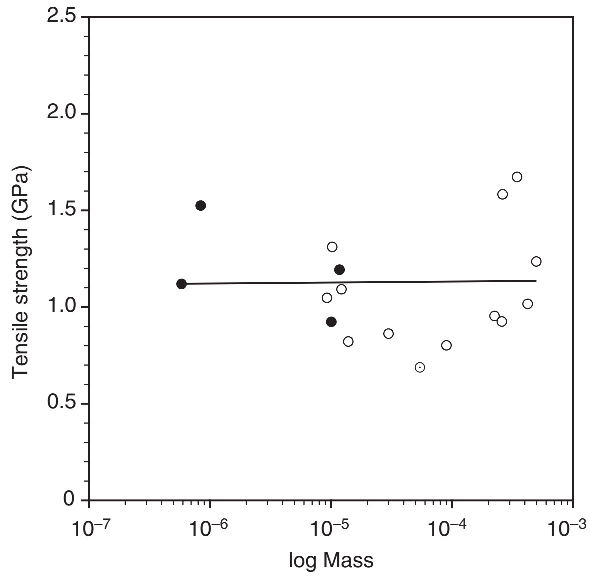

Fig. 5. Silk tensile strength (σ_{max}) plotted against spider mass (M). There is no statistically significant trend of tensile strength with log-transformed spider mass. The least-squares regression best-fit for the combined *A. diadematus* and *S. scenicus* data sets was σ_{max}=1.14×10^9+3.99×10^{-6}log$M$, r^2=0.0002, P=0.96.

strain observed for 35 samples from 24 *A. diadematus* individuals, and the least-squares regression slope is not statistically different from zero (P=0.19). Six samples from *S. scenicus* show similar values, but the small sample size makes it impossible to separate species and size-dependent differences. Similarly, Fig. 5 displays the data for the scaling of tensile strength observed for silk from 12 *A. diadematus* individuals and four *S. scenicus* individuals; and the least-squares regression of the combined data set indicates that slope of the relationship between tensile strength and log mass is not statistically different from zero (r^2=0.002; P=0.96). Again, the small sample size makes it impossible to separate species and size-dependent differences.

While both species have the same mean breaking stress, the relationship between cross-sectional area and spider mass is quite different (Fig. 6), with *S. scenicus* having much thinner silk than *A. diadematus* for spiders of the same weight. From this we would predict that there will be large differences in static safety factor, S_{BW}, between the two species. This is confirmed in the scaling of the dragline breaking force.

As Fig. 7 shows, the breaking force (N) of dragline silk scales with body mass (kg) for *A. diadematus* as:

$$\mathbf{F}_{max} = 11.2M^{0.786}\,, \tag{8}$$

and for *S. scenicus*:

$$\mathbf{F}_{max} = 0.363M^{0.66}\,. \tag{9}$$

Keeping in mind that Eqn 9 is based on only six data points, the exponents for silks of the two animals are not statistically different (Table 1). Analysis of the difference between the observed exponent for breaking force of *Araneus* dragline, 0.786, and the exponent for isometric scaling, 0.667, indicates that the observed exponent is significantly different (T=4.387; N=32; P<0.001). Thus, the breaking force of *Araneus* dragline scales allometrically with body mass. The scaling of the breaking force for *Salticus* dragline, however, is not different from isometry. Two silk samples had been tested from first-instar *A. diadematus* while the spiders were still gathered in a clump and not yet building webs, but because the breaking force for these spiders fell well below the best-fit for the other spiders, they were excluded from the calculation as outliers.

The consequence of this scaling relationship is that when the breaking force is expressed as a static safety factor (S_{BW}=$\mathbf{F}_{max}/M\mathbf{g}$), for *A. diadematus* it scales with body mass as:

$$S_{BW} = 1.14M^{-0.214}\,, \tag{10}$$

and for *S. scenicus*:

$$S_{BW} = 0.037M^{-0.340}\,. \tag{11}$$

The negative exponent of this relationship indicates that the static safety factor declines as spider mass increases.

In Fig. 8, the static safety factor data are plotted on a linear scale against log body mass in grams, and this clearly demonstrates that the relationship between safety factor and spider mass is not constant, or even linear. The best-fit power functions from Fig. 7 were added to the data and support the observation that adult *A. diadematus* spiders have silk capable of supporting 4–6 body weights, while the static safety factor for juvenile silk can be as high as 30. Again, first-instar silk breaking forces were well below the predicted values. The static safety factors for adult *S. scenicus* are very close to 1, although the small data set limits the precision of this observation.

Force and strain at failure provide an indication of how much energy a dragline can absorb before breaking, and when the failure force is expressed in body weights, it takes the load into account during a fall. Fig. 9 combines these data for all silk samples tested with the predictions for dynamic failure, as expressed in Eqn 5 (bungee-jump fall, solid line) and Eqn 6 (worst-case fall, broken line), to show which animal's dragline would have failed in a fall. Data points in the gray region represent failure. This graph suggests

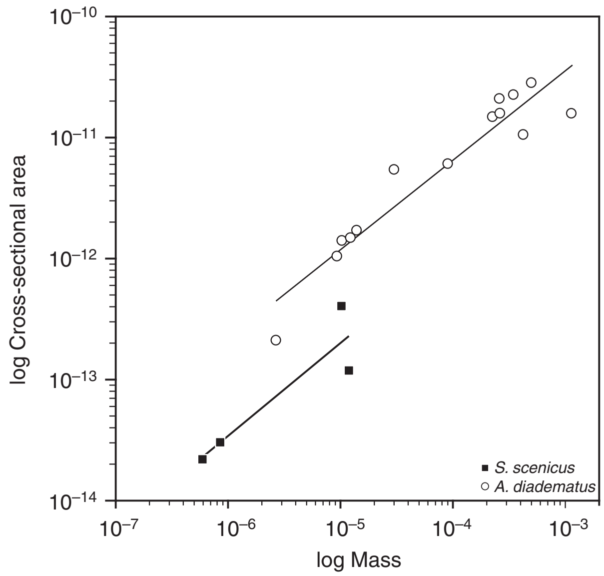

Fig. 6. Cross-sectional area (*A*) plotted against spider mass (*M*) with a least-squares regression applied to log–log transformed data from *A. diadematus* and *S. scenicus*. Area scales as $A=5.86\times10^{-9}M^{0.739}$, $r^2=0.90$ for *A. diadematus*, and $A=1.38\times10^{-9}M^{0.77}$, $r^2=0.83$ for *S. scenicus*.

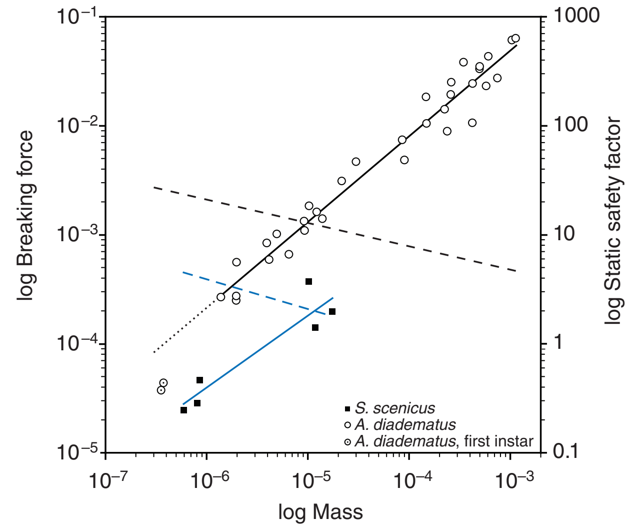

Fig. 7. Breaking force ($\mathbf{F}_{max}$) scales with mass, (*M*), as $\mathbf{F}_{max}=11.2M^{0.786}$, $r^2=0.96$, s.e.m. of the slope=0.027 for *A. diadematus*, and as $\mathbf{F}_{max}=0.363M^{0.66}$, $r^2=0.87$, s.e.m. of the slope=0.13 for *S. scenicus* (solid lines). The pre-web first-instar *A. diadematus* were excluded as outliers and fall well below the extended best-fit line (dotted line). The static safety factor (S_{BW}) determined from the force-mass scaling relationship, is shown as broken lines, where the black line indicates data for *A. diadematus* ($S_{BW}=1.14M^{-0.214}$) and the blue line indicates data for *S. scenicus* ($S_{BW}=0.037M^{-0.340}$).

that the draglines produced by *S. scenicus* of all sizes would fail in either kind of fall by a large margin. The situation is more complex for *Araneus*, with all draglines from animals weighing more than 0.1 g failing in a bungee-jump fall and with lighter spiders, having higher static safety factors, faring much better. Some of the draglines from the smallest individuals were capable of surviving even a worst-case fall. Thus overall, it appears that spiders have evolved a silk spinning system that may not be capable of producing a safety-line that can withstand the dynamic forces that occur in free-falls on a fixed length of preformed silk.

DISCUSSION

The present study attempts to establish if spiders produce draglines that are sufficiently strong to function as static safety-lines that can absorb the kinetic energy of a fall with a fixed length of pre-existing silk. If they cannot, then it is clear that the spooling of new silk, which may occur in a fall and would reduce the dynamic forces that develop (Ortlepp and Gosline, 2004), must be a key feature of the design of spider's safety-lines. The results presented in Figs 8 and 9 strongly suggest that orb weavers (*Araneus*) and jumping spiders (*Salticus*) produce dragline threads that are not sufficiently strong to withstand the dynamic loads that would occur with fixed lengths of pre-existing silk threads in either a bungee jump or a worst-case fall. The only exception to this is might be the very smallest *Araneus* instars, which produce draglines with static safety factors that can reach values of 20 or higher and are thus sufficiently strong to function as fixed safety-lines, even in the worst-case scenario.

It is interesting that both spiders produce their draglines from silks that have essentially identical extensibility and tensile strength (Table 1) and that these properties remain unchanged across the full range of the animal's size through development (Figs 4 and 5). There are, however, significant differences in the shape of the stress–strain curves for the dragline silks from the two spiders (Table 1; Fig. 3), and the spiders employ very different dragline silk dimensions, with *Araneus* using silk threads that have approximately five times greater cross-sectional areas than *Salticus* at the same body mass (Fig. 6). These differences suggest that the two spiders have very different patterns of use for their draglines and we therefore consider their dragline designs separately.

The scaling of *Araneus* draglines

Fig. 6 shows that the *Araneus* dragline cross-sectional area scales allometrically, as $A=5.86\times10^{-9}M^{0.739}$, and, because the tensile strength of its dragline silk remains unchanged through development, the force required to break the draglines of *Araneus* also scales allometrically as, $\mathbf{F}_{max}=11.2M^{0.786}$. This is interesting because Prange observed that the body dimensions of the wolf spider, *Lycosa lenta*, scale geometrically with body mass and therefore silk-spinning structures may also scale geometrically (Prange, 1977). Thus, one might predict that the cross-sectional area of the silk, and hence its strength, would scale as $M^{0.67}$. This is consistent with the observation that spider dragline silk diameters can change during an instar (Vollrath and Köhler, 1996; Witt et al., 1968) and can, therefore, be somewhat independent of exoskeletal size.

The consequence of the observed scaling of dragline breaking force is that the static safety factor ($S_{BW}=\mathbf{F}_{max}/M\mathbf{g}$) is not constant through growth but falls as body mass increases as, $S_{BW}=1.14M^{-0.214}$. Thus, juvenile spiders have draglines with higher safety factors, and their draglines are proportionally stronger than those of adult spiders. Fig. 9 predicts that spider draglines are too weak for bungee jumping for *Araneus* weighing more than 0.1 g, and only a few spiders weighing less than 0.1 g have draglines that would not break during a worst-case fall from above the silk attachment point. This is surprising, considering that a fall onto a flat surface from as little as 1 m can be fatal for large, gravid *A. diadematus* females (C.O. and J.M.G., personal observation). One expects that especially these spiders would have a safety-line sufficiently large to stop a fall, since eggs cannot be laid if the spider dies prematurely. Interestingly,

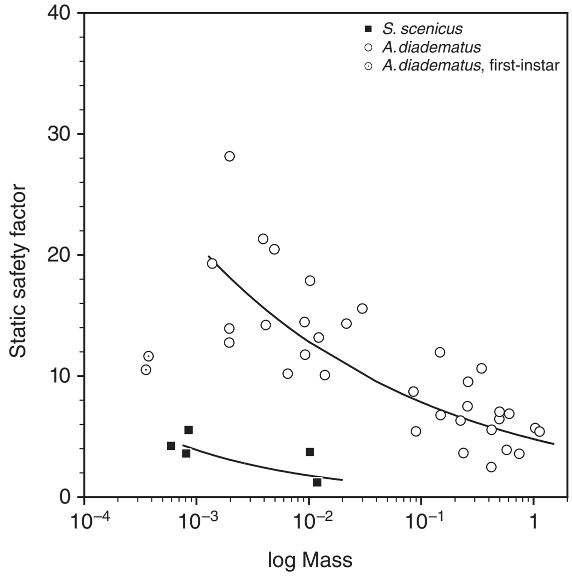

Fig. 8. Static safety factor (S_{BW}) plotted against spider mass for pre-web first-instar *A. diadematus*, adult *A. diadematus*, and *S. scenicus*. Adult *A. diadematus* have safety factors of 4–6 whereas small individuals can have safety factors as large as 30. Note that the first-instar spiders are well below the values predicted by the scaling relationship. Safety factors for *S. scenicus* approach 1 for adults.

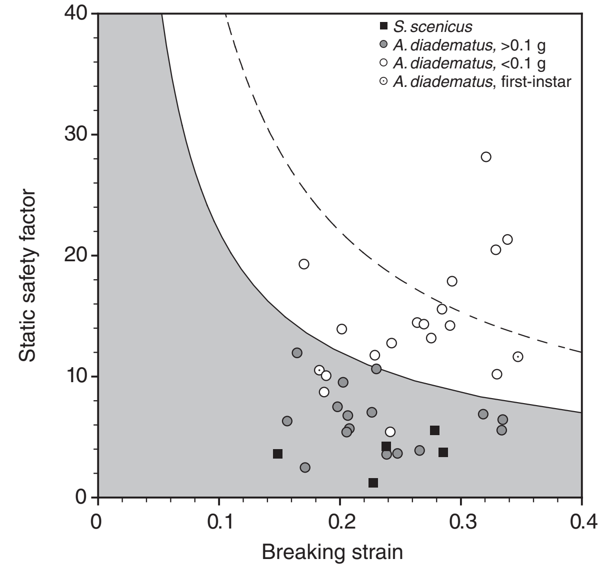

Fig. 9. Graph of static safety factor (S_{BW}) against breaking strain as in Fig. 1 but scaled for the silk data. Curves for bungee jumping (solid line) and a worst case (broken line) were included to predict whether silk of a known S_{BW} and strain at failure would support a spider successfully under these conditions. Silk with properties that place them in the gray area below the solid line would not survive a bungee jump, while only silk above both lines would survive a worst-case scenario.

Garrido et al. showed that the safety-lines produced by a large *Argiope trifasciata* (another orb weaver like *A. diadematus*), while climbing freely up a vertical surface have higher failure strains (~0.4) and larger cross-sectional areas than safety-lines formed while the animal walked on a horizontal surface (Garrido et al., 2002). Thus, it appears that spiders anticipate the need for a more robust safety-line when climbing upwards and they alter the properties of the silk material as well as the cross-sectional dimensions of the dragline itself. We now know that spiders can control the material properties of their dragline silk by adjusting the tension that they apply to the silk as it is drawn from the spinneret (Pérez-Rigueiro et al., 2005). The largest spider that produced a dragline while climbing vertically produced a safety-line with a static safety factor of 3 [fig. 4 in Garrido et al. (Garrido et al., 2002)]. Thus, even with the ability to control silk dimensions, this spider produced a safety-line with a static safety factor that is less than half that required by our model to survive in a bungee-jump fall.

At the other extreme, small spiders, which are not likely to be harmed by falling without a safety-line, have static safety factors well in excess of that required by our model to survive worst-case falls. The very smallest spiders have been observed floating away in the lightest breeze before they hit the ground and so would hardly need such a strong safety-line. In fact, Fabre (Crompton, 1951) found that a beam of sunlight onto a carpet in a closed room caused sufficient updraft for freshly hatched spiders to balloon to the ceiling. Why then are the static safety factors for the draglines of small spiders so high?

If there is a single value for static safety factor that would allow draglines to just survive a specific type of fall (e.g. a bungee-jump), then the most 'efficient' way to produce the safety-line would be to scale its cross-sectional area (and hence strength) as $A \propto M^1$ at a static safety factor that was just sufficient to prevent failure. But given that spiders appear to grow geometrically ($A \propto M^{0.67}$), it is possible that the developmental program that adjusts the dimensions of the silk production system during growth is not capable of accommodating such different scaling regimes over the very large range of body mass (~3000-fold) seen in *Araneus*. Perhaps the observed scaling of dragline cross-sectional area, $A \propto M^{0.74}$, is a compromise between these extremes that can actually be achieved during development.

An additional reason for the exceptionally high strength of draglines from small individuals might arise from the fact that the dragline is actually a multi-functional structure, and the formation of safety-lines is only one of its functions. The dragline silk is also employed in the frame, radii and guy-lines of the orb web, and its function in the web is likely to be of equal importance as in a safety-line. We believe that the action of wind-loading on orb webs may explain the unusually high strength of dragline silk in small spiders. This is because the guy-lines, frame and radii of webs function in a low Reynolds number flow regime, where the drag on the silk is largely independent of its cross-sectional area. The drag (D) on a piece of silk with radius r and length l in a wind velocity ($\mathbf{v}$) and dynamic viscosity (μ) can be calculated by the following equation for flow past cylinders at small Reynolds numbers (Vogel, 1994):

$$D = (4\pi l \mathbf{v} \mu) / [\ln (1/r) + 0.193]\,. \qquad (12)$$

Given that μ is $1.8\times10^{-5}\,\mathrm{kg\,m^{-1}\,s^{-1}}$, and assuming a wind velocity of $10\,\mathrm{m\,s^{-1}}$ acting on a 1 m length of silk from a 2 mg second-instar spider (thread radius, r<400 nm) with the silk oriented perpendicular to the flow, the drag acting on the thread is ~1.5×10^{-4} N, irrespective of the dragline doublet's orientation to the wind. This drag force is approximately 40% of the estimated tensile force required to break the dragline produced by spiders of that size (Fig. 7). The drag force, however, is oriented perpendicular to the dragline thread and, as a consequence, the tension force developed in the dragline will be amplified, particularly if the dragline does not stretch very much (Denny, 1976). For draglines that stretch by 20–35%, the amplified tensile force acting along the length of the thread would be roughly twice the drag force and, thus, dragline failure by wind loading is a distinct possibility for the smallest animals. In this particular scenario for a 2 mg spider, the dragline might just survive because the spider produces an exceptionally strong dragline with a static safety factor of <20. The largest diameter of silk measured from an adult spider, 3.7 μm, will experience a drag force that is only approximately 20% larger (1.7×10^{-4} N) from the same wind, and this is only approximately 0.2% of the breaking force for this spider's dragline. Therefore, the minimum strength of the silk for juvenile spiders is probably not determined by body weight or by the size of the intended prey but by the action of the wind or of wind-borne objects on dragline silk that functions in the spider's orb web. That is, the dragline silk for juveniles appears to be scaled for web construction, not for its function as a safety-line. For larger spiders, the forces generated by the spider's weight or by larger prey would greatly exceed the effect of wind and would, therefore, have more effect on defining dragline strength. Furthermore, making silk with larger cross-sectional area costs more protein and so gravid females may be sacrificing silk strength in favour of egg production. Thus, the observed scaling of the *Araneus* dragline breaking force may reflect a compromise to allow the silk to handle wind loading and falling across the full range of the animal's size.

That the pre-web first-instar *Araneus* spiderlings fell below the calculated trend is not surprising. After the spiders emerge from their cocoon, they spend several days sitting in a clump before dispersing to build individual webs (C.O. and J.M.G., personal observation). Until they catch something, they will not have eaten and must rely largely on their egg yolk provisions. In fact, even once they build their webs, prey items small enough to catch safely are few and far between, and the spiders mostly survive on the pollen carried onto the sticky viscid silk by the wind (Smith and Mommsen, 1984). Therefore, it is not surprising that these very food-limited spiders would produce exceptionally thin silk as a method of saving energy until webs are built for prey capture.

Finally, we consider the assumptions that underlie our model for the static safety factor required for a dragline that will survive a fall with a fixed-length safety-line. The first assumption is that the silk material in the safety-line has a linear stress–strain curve and, hence, that the energy capacity is determined by the area under the secant of the breaking force. The three-slope curve that is characteristic of the dragline silks of orb weaving spiders (Fig. 3) rises above the secant slope at small extensions, due to the high initial stiffness leading up to the yield-point. Following the yield, the stress–strain curve becomes somewhat J-shaped and it falls below the level of the secant slope. Thus, the total energy to break is quite similar to that determined from the area under the secant slope. In the case of the draglines tested for the current study, the observed energy to break for *Araneus* dragline is approximately 10% greater than that predicted from the failure stress and strain. Thus, a modified version of Eqn 5 for the static safety factor required to survive a bungee-jump fall that takes account of this 10% increase in energy to break would be:

$$S_{BW} = (1.81/\varepsilon_{max}) + 1.81\,. \qquad (13)$$

This new equation shifts the lines in Fig. 9 down by 10% at all extensions for predictions based on the *Araneus* stress–strain curve, and this modest shift is not likely to have a large effect on the predictions illustrated in Fig. 9, which is that most large *Araneus* safety-lines would fail in a bungee-jump fall.

The other important assumption is that the silk properties measured at low strain rates in the current study, and in most other studies of spider silks, accurately reflect the properties of dragline silk loaded at the high strain rates that must occur when a spider falls. Silk from *A. diadematus* shows strain-rate-dependent properties, becoming stiffer, stronger and more extensible as it is stretched faster (Denny, 1976; Gosline et al., 1999), and therefore the energy absorbed by the safety-line during impact loading may be considerably larger than that estimated from quasi-static properties. This shift in mechanical properties would move the individual data points for *Araneus* in Fig. 9 closer to the lines indicating the safety factors required to survive bungee-jump and worst-case falls. Thus, significant increases in tensile strength and extensibility increase the probability of a large *Araneus* surviving a bungee-jump fall, but even a twofold increase in the dynamic breaking stress would likely not be sufficient for a large *Araneus* to survive a worst-case fall. Thus, *Araneus* must certainly take advantage of their ability to produce new silk during a fall and then use their friction brake to halt their descent.

The scaling of *Salticus* draglines

The situation for the jumping spider, *Salticus*, is quite different. Perhaps of primary importance, jumping spiders do not make a web to capture prey. They are wandering spiders that actively hunt their prey and they continually trail a dragline thread as they hunt. The dragline does, however, play an important role in prey capture. For example, when catching large prey, a jumping spider may attack the prey and then jump to dangle by its dragline in mid-air while holding onto the prey (Robinson and Valerio, 1977). This has the advantage of making it difficult for struggling prey to get a foothold and wrench loose. It is also a useful mechanism to avoid aggressive ants summoned by the attack on a member of the colony (Robinson and Valerio, 1977).

The fact that *Salticus* produces draglines with approximately one-fifth the cross-sectional area of a dragline from an *Araneus* of the same size suggests that *Salticus* may be carefully limiting the amount of material it leaves behind in its dragline. If we apply the wind-loading scenario described above to a 1 m long piece of dragline from a juvenile *Salticus* (body mass 0.6 mg), the drag force on the the 80 nm radius silk is approximately 1.3×10^{-4} N. With force amplification from perpendicular loading, this creates a tension force in the dragline that is roughly 10 times greater than the breaking force of this dragline. That is, a 1 m long dragline made by a juvenile *Salticus* should fail at a wind velocity of ~1 m s^{-1}. Thus, it is not surprising that our model predicts that *Salticus* cannot survive a bungee-jump fall from a fixed-length safety-line. We do not know at this point how jumping spiders spool out new silk as they fall and how they use their internal friction brake to halt their descent; however, jumping spiders are well known to lower themselves on their draglines by slowly spooling out new silk. Given the low static safety factors indicated for *Salticus* in Fig. 9, it is almost certain that they use this system to halt their descent in a fall.

There are additional indications that jumping spiders have evolved mechanisms to minimize the amount of material that they invest in their draglines. Specifically, their mechanical properties, as illustrated in Fig. 3 and Table 1, are quite different from those of *Araneus*. The stress–strain behaviour of *Salticus* dragline silk is a two-slope or r-shaped curve, which arises from the fact that the silk has a higher initial modulus, yield stress and yield strain than seen in *Araneus* dragline silk (Table 1), all of which place the stress–strain curve for *Salticus* dragline well above the secant of its breaking stress. This has the effect that for a given stress and strain at failure, the *Salticus* dragline absorbs considerably more energy than a dragline produced by *Araneus*. Based on the limited number of samples tested in this study, we estimate that the energy required to break a dragline produced by *Salticus* is approximately 45% greater than that predicted from the secant of the breaking stress.

Therefore, the static safety factors required for *Salticus* to survive bungee-jump and worst-case falls will decrease by 45% from the lines indicated in Fig. 9; however, this alone probably does not allow *Salticus* to survive bungee-jump falls and, certainly not, worst-case falls. If their dragline silk's properties are strongly strain-rate dependent, then the situation may change. We predict, however, that the r-shaped stress–strain curve for *Salticus* arises from a higher degree of crystallinity in its silk and, therefore, that there are longer blocks of crystal-forming poly-alanine or poly-glycine-alanine sequences to encode larger β-sheet crystals than are found in the dragline silks of orb weavers such as *Araneus* (Gosline et al., 1999). If this is correct, then the increased crystallinity likely limits or eliminates the strain-rate-dependent increases in stiffness and strength that are seen for *Araneus* dragline silk. We believe, therefore, that when *Salticus* falls, they must spool out new silk and employ a friction brake in a manner similar to that observed in *Araneus* (Ortlepp and Gosline, 2004) and, thus, when they fall they descend like a rappelling climber, rather than a bungee jumper.

In summary, the draglines of both *Araneus* and *Salticus* appear not to be designed for bungee jumping or for worst-case falls, where no additional silk is produced. Behavioral adaptations such as silk spooling make a 'perfect' structural design unnecessary. What remains to be determined is just how well the spiders can control the silk spooling forces and what the dynamic safety factors are in a rappelling fall. We will report these data in a future study.

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