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Silk elasticity as a potential constraint on spider body size

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Abstract. Silk is known for its strength and extensibility and has played a key role in the radiation of spiders. Individual spiders use different glands to produce silk types with unique sets of proteins. Most research has studied the properties of major ampullate and capture spiral silks and their ecological implications, while little is known about minor ampullate silk, the type used by those spider species studied to date for bridging displacements. A biomechanical model parameterised with available data shows that the minimum radius of silk filaments required for efficient bridging grows with the square root of the spider's body mass, faster than the radius of minor ampullate silk filaments actually produced by spiders. Because the morphology of spiders adapted to walking along or under silk threads is ill suited for moving on a solid surface, for these species there is a negative relationship between body mass and displacement ability. As it stands, the model suggests that spiders that use silk for their displacements are prevented from attaining a large body size if they must track their resources in space. In particular, silk elasticity would favour sexual size dimorphism because males that must use bridging lines to search for females cannot grow large.

Key words: biomechanics, dispersal, minor ampullate silk, radiation, sexual size dimorphism (SSD)

Silk has played a key role in the radiation of spiders (Blackledge et al., 2009; Vollrath and Selden, 2007) following the colonisation of land by their ancestors in the early Devonian (Selden et al., 1991; Shear et al., 1989). The number of silk-producing glands and silk types that individual spiders produce has increased during the evolution of the group, and orb-weaving spiders spin seven different kinds of silk, including five fibrous silks that contain unique sets of proteins (Foelix, 1996). Regardless of the selective pressures leading to the initial production of silk by spiders, silk was quickly used to produce hunting devices, ranging from isolated threads to sophisticated webs (Vollrath and Selden, 2007) that have fostered the coevolutionary arms race between insects and spiders [e.g. (Blackledge et al., 2003)] – to the point that it has been suggested that the exponential diversification of insects may have resulted from selection favouring insects escaping from spider predation (Penney, 2004). It is possibly for this reason that most research on spider silk, be it on the mechanical properties of silk or their ecological implications, has focused on the major ampullate and spiral silks used in web building (Denny, 1976; Gosline et al., 1999; Kitagawa and Kitayama, 1997; Köhler and Vollrath, 1995) and very little is known about other silk types, such as the minor ampullate silk that those spider species that have been studied use for bridging displacements (Peters, 1990). In this paper we study the constraints that the physical properties of minor ampullate silk could set on the displacement ability of spiders.

The morphological traits allowing efficient locomotion in spiders that spend most of their life hanging upside-down from their webs are very different from those favoured in spiders that must support their weights on their legs while walking on solid surfaces (Moya-Laraño et al., 2008). As a result, spiders adapted to moving along silk fibres are clumsy when moving on hard surfaces. But these spiders have turned their weakness into strength, developing an efficient displacement mechanism: bridging. To use this displacement method, a spider releases a bridging line until it adheres to some substrate, spanning a gap in the vegetation. The spider then tightens the line (Moya-Laraño et al., 2008; Peters 1990) and crawls across the silk threads. Although bridging has received relatively little attention in the literature, in the only species that have been studied in detail

(*Linyphia triangularis* and *Araneus diadematus*) the bridging line is composed of two minor ampullate silk filaments (Peters, 1990). Bridging frees spiders at once from the need to support their own weight (Moya-Laraño et al., 2008) and the constraint to follow the complex, fractal-like three-dimensional structure of vegetation for their displacements. Bridging is widespread in the Orbicularia clade. It is such an efficient displacement mechanism that it has been secondarily adopted by vegetation-dwelling sit-and-wait predatory groups like the Thomisidae – a family belonging to the Dyonicha group which lost the web-building ability when it diverged within the RTA clade (Coddington and Levi, 1991).

Although bridging is made possible by the remarkable mechanical properties of silk, even the finest materials have their limits. Large spiders are seldom seen bridging in the field, and Morse and Fritz (1982) have suggested that the elasticity of silk fibres prevents large crab spiders from bridging. Bridging lines sag under the weight of crossing spiders, and bridging will only be successful if the sag is less than the clearance under the line – otherwise the bridging spider will be dragged into the soil or vegetation. To evaluate the possibility that the elasticity of minor ampullate silk makes bridging inefficient for large spiders, we develop a biomechanical model to calculate the relationship between the cross section of the fibre, its elastic properties, the mass of the spider, m , and the sag of the line, k (hereafter defined as the maximal vertical displacement of the bridging spider divided by the horizontal distance between the attachment points of the line), as the spider crosses it. For a given body mass, the relative sag of the line, k , depends on the stress, extensibility and cross section of the silk fibre. Because increasing the stress on the fibre eventually leads to its breaking, heavier spiders must release thicker silk filaments to prevent excessive sagging. Although in general the thickness of the silk fibre released by a spider depends on the number and type of silk glands engaged in the production of silk (Foelix, 1996), bridging lines are composed of two filaments, produced by the left and right minor ampullate glands (Peters, 1990), limiting the control that spiders have over the thickness of their bridging lines essentially to the ability of increasing the diameter of these two fibre silks. Thus, the radius of the minor ampullate silk

filaments produced by a spider may determine its bridging ability.

The model

A spider of mass m bridges along a fibre composed of two silk filaments, each of them with radius r_0 and length L_0 when the fibre suffers no stress. The force exerted on the spider by the gravitational pull of the earth is directed downwards and has magnitude $m \cdot g$, where $g = 9.8 \text{ m}\cdot\text{s}^{-2}$ is the acceleration of gravity. We will neglect the gravitational pull acting directly on the silk fibre itself – the mass of the bridging fibre is a tiny fraction of the mass of the spider. Let φ_{\max} be the true breaking strain (log[stretched length/rest length of fibre] at the breaking point, (Roesler et al., 2007)) of the minor ampullate silk fibre used for bridging and τ_{\max} its true breaking stress (force/instantaneous cross section at the breaking point, (Roesler et al., 2007)). The breaking strain is an index of the extensibility of the fibre: larger values of the breaking strain indicate that fibres suffer greater elongation before breaking. The breaking stress, on the other hand, denotes how much force (per unit area) we must apply before the fibre breaks. The safety coefficient under which the fibre operates, β , is defined as the true breaking stress of the fibre divided by the maximum stress to which the fibre is actually exposed (Osaki, 1996; Osaki, 2003). Large safety coefficients indicate that the maximum stress (force per unit area) applied on the fibre is much lower than the stress required to break the fibre. The safety coefficient cannot be less than one: by definition, fibres break when the stress applied equals the breaking stress. Values only slightly larger than one indicate that the maximum stress applied on the fibre is close to the breaking stress.

To calculate the relationship between the radius at rest of the individual silk filaments, r_0 , the relative sag, k , and safety coefficient, β , we note that both the maximal vertical displacement of the spider and maximal stress on the fibre are achieved when the spider is at the midpoint of the fibre. By definition of relative sag, when the spider is midway through crossing its vertical displacement y satisfies the equation $|y| = k \cdot d$, and hence $\cos \alpha = 2k / \sqrt{4k^2 + 1}$, where d is the distance between the endpoints of the bridging

line (greater than L_0 if the spider has tightened the line) and α is the angle between the vertical

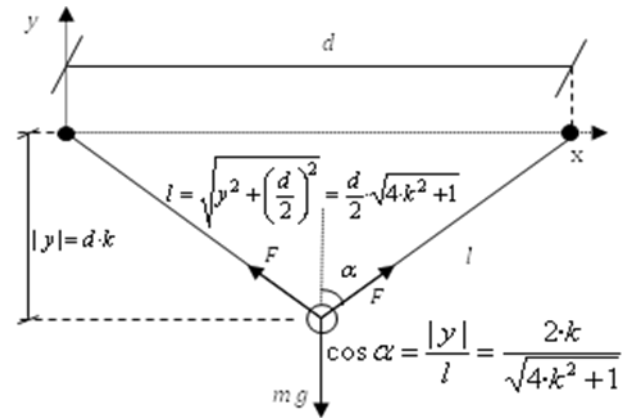


Figure 1. Force diagram. Schematic representation of the forces acting on the spider when it is midway between the starting and finishing points of the bridging line, when the vertical displacement ($|y|$) and forces along the silk lines (F) attain their maximum value. If d represents the distance between the starting and finishing points of the bridging line, the relative sag is $k = |y|/d$.

axis and the segment connecting the spider with an endpoint (Fig. 1). The vertical component of the forces exerted by the silk fibre on the spider (forces F in figure 1) must balance the gravitational pull. Therefore:

$$m \cdot g = 2 \cdot F \cdot \cos \alpha = \frac{4 \cdot F \cdot k}{\sqrt{4 \cdot k^2 + 1}} = \frac{8 \cdot \pi \cdot r^2 \cdot T \cdot k}{\sqrt{4 \cdot k^2 + 1}}, \quad (1)$$

where r is the instantaneous radius of the silk filaments and T the true stress to which they are subject. Note that, in going from forces to stress we have multiplied the numerator by the cross section of the two minor ampullate silk filaments that constitute the bridging fibre (i.e., $F = 2 \cdot \pi \cdot r^2 \cdot T$). From the definition of the safety coefficient, $\beta \cdot T = \tau_{\max}$. Substituting in equation 1 and rearranging,

$$r = \sqrt{m \cdot g \cdot \beta \cdot \frac{\sqrt{4 \cdot k^2 + 1}}{8 \cdot \pi \cdot k \cdot \tau_{\max}}}. \quad (2)$$

Assuming constant volume during extension (Vollrath et al., 2001),

$$r_0 = \sqrt{m \cdot g \cdot \beta \cdot \frac{\sqrt{4 \cdot k^2 + 1}}{8 \cdot \pi \cdot k \cdot \tau_{\max}} \cdot \frac{L}{L_0}}. \quad (3)$$

The stress-strain diagram gives us the relationship between elongation and stress, and

hence between L and β . For simplicity, we will assume a linear relationship between true stress and true strain, so that $\log(L/L_0) = \varphi_{\max} \cdot T/\tau_{\max}$. [Note that, due to the strain hardening of minor ampullate silk – i.e., its stress-strain curve is j-shaped (Blackledge and Hayashi, 2006), this assumption underestimates the value of r_0 : spiders will have to produce bridging lines slightly thicker than the model predicts – although the approximation is fairly good when $\beta \leq 2$.] With this final assumption, and noting that because L in equation 3 represents the maximum length of the fibre, so that $T/\tau_{\max} = 1/\beta$, we have

$$r_0 = \sqrt{m \cdot g \cdot \beta \cdot \frac{\sqrt{4k^2 + 1}}{8\pi \cdot k \cdot \tau_{\max}} \exp\left(\frac{1}{\beta} \varphi_{\max}\right)}. \quad (4)$$

Comparison of the value of r_0 computed from equation 4 with the radius of the minor ampullate silk filaments produced by a spider of mass m tells us whether the spider can bridge with the specified values of the safety coefficient and relative sag. We have only been able to obtain the radii of minor ampullate silk filaments produced by adult *Argiope trifasciata* (Hayashi et al., 2004) and *A. argentata* (Blackledge and Hayashi, 2006) females of unreported body mass. We know, however, that the average radius (in metres) of single major ampullate silk filaments produced by *Araneus diadematus*, ranging from 0.00036 g first-instar hatchlings to gravid 1.15 g females, increases with the mass of the spider, m (in Kg) according to $r \approx \sqrt{2.93 \cdot 10^{-9} \cdot m^{0.739}}/\pi$ (Ortlepp and Gosline, 2008). Assuming that this relationship is similar in magnitude within and among species, we can write the radius of minor ampullate silk filaments, r_{\min} , as

$$r_{\min} = \xi \cdot \sqrt{\frac{2.93 \cdot 10^{-9} \cdot m^{0.739}}{\pi}}, \quad (5)$$

where ξ is the ratio between the radii of minor and major ampullate silk filaments. Equating r_{\min} from equation 5 and r_0 from equation 4 we obtain the bridging threshold, or the maximum body size for which bridging is possible for a specified set of parameter values, m_{\max} :

$$m_{\max} = \left[\frac{2.34 \cdot 10^{-8} \cdot k \cdot \xi^2 \cdot \tau_{\max}}{g \cdot \beta \cdot \sqrt{4k^2 + 1}} \exp\left(-\frac{\varphi_{\max}}{\beta}\right) \right]^{1/0.261}. \quad (6)$$

Choice of parameter values

Although the mechanical properties of minor ampullate silk fibres have been little studied, the breaking stress τ_{\max} and breaking strain φ_{\max} of minor ampullate silk have been measured for a few species. For *Argiope trifasciata*, $\tau_{\max} = 752$ MPa and $\varphi_{\max} = 0.442$ (Hayashi et al., 2004), and for *A. argentata* $\tau_{\max} = 923$ MPa and $\varphi_{\max} = 0.330$ (Blackledge and Hayashi, 2006). These are the values we use for our calculations.

The average diameter of single major ampullate silk filaments was 3.24 and 3.5 μm for *A. trifasciata* and *A. argentata*, respectively, while the average diameter of single minor ampullate silk filaments was 0.69 and 1.1 μm for the same species (Blackledge and Hayashi, 2006; Hayashi et al., 2004). According to the relationship found by Ortlepp and Gosline (Ortlepp and Gosline, 2008) for *Araneus diadematus*, the major ampullate silk diameters would correspond to spiders of 350 and 450 mg, very reasonable for *A. trifasciata* and *A. argentata* adult females. In these two species, the ratio of minor over major ampullate silk filament diameter is $\xi = 0.69/3.24 = 0.21$ and $\xi = 1.1/3.5 = 0.31$. Inspection of scanning electron microscope photographs of bridging fibres produced by *A. diadematus* and *Linyphia triangularis* (Peters, 1990), however, suggests values closer to $\xi = 0.5$. It seems likely that the value of ξ changes with the size of spiders, and it is possible that the value of ξ differs between spiders producing silk fibres for bridging (Peters, 1990) and spiders from which silk is actively extracted by experimenters (Blackledge and Hayashi, 2006; Hayashi et al., 2004). To obtain a conservative estimate of the constraints that silk imposes on bridging spiders, we calculate the maximum body size for which bridging is possible (equation 6) for $\xi = 0.5$ and 0.667.

Osaki (1996; 2003) reports that the safety coefficient for dragline silk used as lifeline (silk used for hanging while dropping from relatively high places) is $\beta \geq 2$. Our calculations are based on $\beta \leq 2$. Note that by choosing relatively small values of β and relatively large values of ξ , as compared with those measured in the lab, we ensure that we have conservative results: if silk elasticity limits spider's bridging, the real constraints will most likely be stronger than those we find.

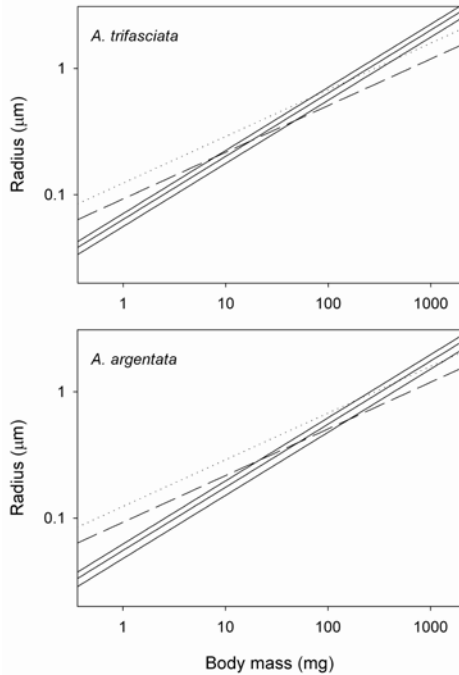


Figure 2. Minimal filament radius required for bridging. The solid lines represent the relationship between the mass of a spider, m , and the minimum radius of single minor ampullate silk filaments that spiders need for bridging, r_0 (equation 4), when the relative sag cannot exceed the value $k = 0.3$. The values of r_0 have been calculated using the mechanical properties of *A. trifasciata* (top panel) and *A. argentata* (bottom panel) minor ampullate silk. Each line represents a different safety coefficient (from top to bottom, $\beta = 1.0, 1.5$ and 2.0). The dotted and dashed lines represent the expected radii of single minor ampullate silk filaments, r_{\min} (equation 5), calculated with $\xi = 0.5$ (dashed lines) or $\xi = 0.67$ (dotted lines).

Results

Figure 2 shows the square-root relationship between the mass of a spider, m , and the minimum radius of single minor ampullate silk filaments, r_0 , that bridging *A. trifasciata* and *A. argentata* individuals require (eq. 4) for different values of the safety coefficient, $\beta = 1.0, 1.5$ and 2.0 , if the relative sag cannot exceed the value $k = 0.3$. In a log-log plot, the safety coefficient and elastic properties of silk affect the intercept, but not the slope, of r_0 . The intercept of r_0 increases with the safety coefficient and the breaking strain of the silk, and decreases with its breaking stress. For comparison, the dotted and dashed lines in figure 2 represent the expected radii of single minor ampullate silk filaments, r_{\min} (equation 5), calculated with $\xi = 0.5$ (dashed lines) or $\xi =$

0.67 (dotted lines). Because r_0 increases with m faster than r_{\min} , beyond a certain body mass the

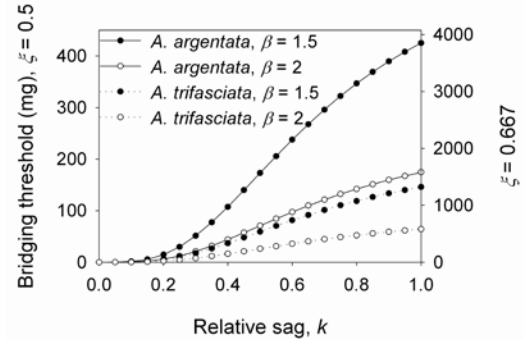


Figure 3. Bridging threshold for *A. argentata* and *A. trifasciata*. Relationship between bridging threshold, m_{\max} , and relative sag, k , when the silk fibre has the mechanical properties characteristic of *A. argentata* (solid lines) and *A. trifasciata* (dashed lines) minor ampullate silk and the safety coefficient is $\beta = 1.5$ (solid circles) or $\beta = 2$ (empty circles). Because ξ has a multiplicative effect, it changes the scale, but not the shape, of the relationship. As a consequence, the same graph can be used to plot the bridging threshold when the ratio between major and minor ampullate silk filament radii is $\xi = 0.5$ (left scale) or $\xi = 0.667$ (right scale).

silk filaments produced by spiders are thinner than the filaments they would need for bridging with the desired parameters ($r_{\min} < r_0$) and therefore bridging is not possible without increasing the relative sag or decreasing the safety coefficient. The body mass beyond which bridging is not feasible with the desired specifications is the bridging threshold, m_{\max} (equation 6).

The bridging threshold, m_{\max} , depends on the safety coefficient, β , the maximum relative sag allowed, k , and the physical properties of minor ampullate silk, τ_{\max} and ϕ_{\max} . Figure 3 plots the bridging threshold of *A. argentata* and *A. trifasciata* as a function of the relative sag, k , for $\beta = 1.5$ and 2 . Note (equation 6) that the coefficient ξ used to estimate the radii of the minor ampullate silk filaments produced by spiders (equation 5) has a multiplicative effect on the bridging threshold and therefore acts as a scale parameter.

Due to the uncertainty in the estimate of τ_{\max} , ϕ_{\max} and ξ , we have used equation 6 to calculate the relationship between the bridging threshold, m_{\max} , and these parameters when the safety coefficient is $\beta = 2$ and the maximum relative sag allowed is $k = 0.3$ (Fig. 4). If spiders produce minor ampullate silk filaments

substantially thinner than major ampullate silk filaments ($\xi \leq 0.6$), bridging should be inefficient for spiders over 200 mg for

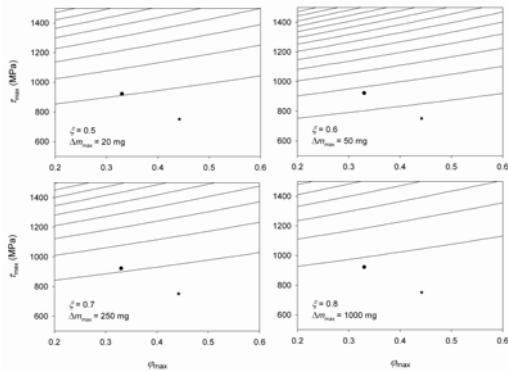


Figure 4. Contour plots of the bridging threshold. Panels represent, for different values of ξ , the relationship between the bridging threshold, m_{\max} , and the elastic properties of minor ampullate silk, τ_{\max} and ϕ_{\max} , in a wide region that probably includes the true values for most species. The properties of minor ampullate silk in *A. trifasciata* (star) and *A. argentata* (circle) are indicated for comparison. Within each panel, the bottom line represents the set of points where the bridging threshold is $m_{\max} = \Delta m_{\max}$. As we move upwards within each panel, lines represent the set of points where the bridging threshold is $m_{\max} = 2 \cdot \Delta m_{\max}$, $m_{\max} = 3 \cdot \Delta m_{\max}$, and so on. The values of ξ and Δm_{\max} are given in the lower-left corner of each panel. Bridging thresholds have been calculated from equation 6, with $\beta = 2$ and $k = 0.3$.

reasonable values of τ_{\max} and ϕ_{\max} . When $\xi = 0.7$, the bridging threshold should lie around 250 mg if the values of τ_{\max} and ϕ_{\max} measured for *A. trifasciata* and *A. argentata* are representative of the elastic properties of minor ampullate silk in other species, but the bridging threshold could increase substantially in species with stiffer (lower ϕ_{\max}) or stronger (higher τ_{\max}) minor ampullate silk. Finally, if minor ampullate silk filaments are about as thick as major ampullate silk filaments ($\xi \geq 0.8$), it seems unlikely that bridging is inefficient even for the larger spiders.

Discussion

Simple mechanical considerations allow us to calculate the minimal radius of the silk filaments that the spider must use for bridging once we know the mechanical properties of silk, the relative sag that the line can accept without hitting the ground and the safety coefficient under which the line can operate. This radius increases with the square root of the spider's

body mass and eventually becomes greater than the radius of the minor ampullate silk filament that spiders produce. When the model is parameterised with available data, it predicts that the elasticity of minor ampullate silk severely limits the bridging abilities of heavy spiders.

There is considerable across-species variability in the mechanical properties of major ampullate silk (Swanson et al., 2006) and it could be argued that heavy spiders are selected to produce minor ampullate silk stronger and stiffer than smaller spiders. Indeed, the minor ampullate silk of *A. argentata* is stronger and stiffer than the silk of *A. trifasciata* (Blackledge and Hayashi, 2006; Hayashi et al., 2004). Nevertheless, the model has been parameterised with data from relatively large spiders, *A. argentata* and *A. trifasciata*, and predicts that neither of these species is an efficient bridger: an *A. argentata* of 400 mg producing minor ampullate silk filaments with a radius of 0.82 μm (to be compared with the 0.55 μm measured by Blackledge and Hayashi (2006)) and operating under a safety coefficient of $\beta = 1.5$ would suffer a vertical displacement as large as the horizontal distance it tries to span through bridging ($k = 1$, figure 3) – the relative sag would be much larger for an adult *A. trifasciata* female – which would mean an overall travel distance 40% longer than in a normal bridging event. Therefore, even if heavier spiders produce stronger and stiffer minor ampullate silk than small spiders, they do not manage to compensate the effect of increasing body mass.

The relationship between spider size and the thickness of the minor ampullate filaments it produces, controlled by the parameter ξ of equation 5, plays an important role in determining bridging thresholds (equation 6, Figs. 2 and 4). If increasing ξ from 0.5 to 0.667 leads to a nine-fold increase in bridging threshold, reducing ξ from 0.5 to 0.4 (respectively 0.31) leads to a five-fold (respectively 39-fold) decrease in bridging threshold. The bridging thresholds we have calculated assume that minor ampullate silk filaments are at least half as thick as major ampullate silk filaments ($\xi = 0.5$ and 0.667), which is much thicker than the values actually measured ($\xi = 0.21$ and 0.31; Blackledge and Hayashi, 2006; Hayashi et al., 2004). We have chosen such conservative estimates because filament diameter has been measured forcibly silking spiders (Blackledge and Hayashi, 2006;

Hayashi et al., 2004), and it is therefore possible that the diameter of silk fibres produced in natural conditions is actually thicker.

Heavy spiders are less efficient bridgers than light ones. However, this does not mean that heavy spiders cannot bridge. Gravid giant orb-weaving females such as some species in the genera *Argiope*, *Araneus*, *Nephila* or *Caerostris*, for example, must use bridging during the initial stages of web building (Burnet, 1994; Levi, 1971). But they will only be able to do so when the clearance under their lines is large compared to the horizontal distance they must span (Fig. 3). Thus, according to the model, parameterised with conservative versions of available data, although spiders living in the canopy will be able to use bridging as a displacement mechanism, spiders moving through shrubs and annual plants, where horizontal distances can often be longer than the height of lines, will be unable to use bridging if their body mass exceeds 100 or 200 mg. The predictions of the model are supported by laboratory trials where 204 individual spiders of 13 species, in the families Araneidae, Tetragnathidae, Linyphiidae, Theridiidae and Thomisidae, were stimulated to bridge in order to escape from simulated high predation risk. There was a strong negative correlation between body mass and bridging propensity. No spider over 200 mg ($N = 46$) used bridging to emigrate from simulated risky patches, only one individual between 100 and 200 mg ($N = 7$) used bridging, while 81% of the individuals under 100 mg ($N = 151$) bridged away from risky patches – large individuals mainly dropped to the ground to leave the risky patch (Corcobado et al., unpublished manuscript).

In low vegetation, therefore, species adapted to moving along silk lines may have little mobility once they cross the 100 mg body mass limit and may only be able to grow as large as they can continue growing without further displacements. Crab spiders over 200 mg, for instance, cannot move to patches some 10 m away once their patch has wilted (Morse, 2007). Since predator-prey body size ratios largely determine “who eats whom” in food webs (Brose et al., 2006; Woodward et al., 2005), this displacement constraint prevents crab spiders from reaching sizes sufficient to exploit resources that would, otherwise, be available to them, such as large carpenter bees and moths. Notice, however, that this constraint only applies to lifestyles that must track their resources in space. Strategies consisting in

finding as a juvenile a productive site where the individual remains through its life will be unaffected, and can continue growing as long as prey are abundant at their site.

The constraints imposed by minor ampullate silk elasticity on the displacement of large spiders are not limited to individuals looking for food: they apply to spiders searching for any other resources, such as mates. With few exceptions (Aisenberg et al., 2007), males are the searching sex in spiders. After their last moult, males abandon their web or nest and disperse looking for receptive females (Foelix, 1996). When females are too large for efficient bridging, males must be smaller than females or forego the possibility of using bridging for mate searching. Because, in many habitats, bridging could be a more efficient displacement mechanism than walking, the mechanical properties of silk may contribute to the evolution of sexual size dimorphism in spiders (Corcobado et al. unpublished manuscript).

Bridging plays an important role in the life of spiders adapted to moving along silk fibres (i.e. crab spiders within the RTA clade and Orbiculariae spiders). Because their morphology is unsuitable for walking along solid surfaces (Moya-Laraño et al., 2008), they are seldom seen walking on the ground and depend on bridging for their mid-range displacements. As we have seen, the elastic properties of minor ampullate silk may make bridging an inefficient displacement mechanism for large spiders. The extent to which large body size constraints bridging ability, however, will depend on the precise values of the silk elasticity parameters and on the diameter of the filaments produced by spiders of different sizes. While we have used published data to parameterise the model, and have chosen rather conservative parameter values rather than the published ones, the scarcity of data prevents us from reaching final conclusions. Nevertheless, we hope that the results of our model prompt groups studying the mechanical properties of silk to devote more effort to the analysis of minor ampullate silk. It is also important to confirm that all (or at least most) spider species rely on minor ampullate silk for their bridging lines, as this result has been obtained from only two species (Peters, 1990). It is important to understand how the physical properties of minor ampullate silk, including the thickness of the filaments produced, change with the size and ecology of species – and the extent to which aciniform silk filaments attached to minor silk

filaments, presumably to increase its drag (Peters, 1990), affect the mechanical properties of bridging lines. This knowledge is essential for a detailed understanding of the relationship between size and mobility in bridging spiders. Even more interesting, if confirmed, is the fact that spiders rely on minor ampullate silk fibres for bridging. Major ampullate silk fibres are thicker, stronger and stiffer: the breaking stress of major ampullate silk for *A. argentata* is 1495 MPa, and its breaking strain 0.205 (Blackledge and Hayashi, 2006). If *A. argentata* used two major ampullate silk filaments for bridging, an adult female could bridge with a relative sag of less than $k = 0.1$ and a safety coefficient of $\beta = 2$. Why, then, should spiders use minor ampullate silk filaments for bridging? Minor ampullate silk may form stronger attachments to the substrate, or it may be easier to initiate in the absence of any tension pulling the silk from the spider (Eberhard, 1987).

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Author's contributions

MAR-G, GC and JM-L conceived and designed the study. MAR-G developed the model and wrote the manuscript. GC compiled the information about the mechanical properties of spider silks used to parameterise the model. All authors read, made significant comments and approved the final manuscript.

Conflicts of interests

The authors declare that no conflict of interest may have affected their work.

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References

- Aisenberg, A., Viera, C., and Costa, F.G., 2007. Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae). *Behav. Ecol. Sociobiol.* 62, 29-35.
- Blackledge, T.A., and Hayashi, C.Y., 2006. Silken toolkits: biomechanics of silk fibers spun by the orb web spider *Argiope argentata* (Fabricius 1775). *J. Exp. Biol.* 209, 2452-2461.
- Blackledge, T.A., Coddington, J.A., and Gillespie, R.G., 2003. Are three-dimensional spider webs defensive adaptations? *Ecol. Lett.* 6, 13-18.
- Blackledge, T.A., Scharff, N., Coddington, J.A., Szuts, T., Wenzel, J.W., Hayashi, C.Y., and Agnarsson, I., 2009. Reconstructing web evolution and spider diversification in the molecular era. *Proc. Natl. Acad. Sci. USA* 106, 5229-5234.
- Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G., and Cohen, J.E., 2006. Consumer-resource body-size relationships in natural food webs. *Ecology* 87, 2411-2417.
- Burnet, B., 1994. *The Silken Web. A Natural History of Australian Spiders.* Reed New Holland Books, Sydney.
- Coddington, J.A., and Levi, H.W., 1991. Systematics and evolution of spiders (Araneae). *Ann. Rev. Ecol. System.* 22, 565-592.
- Denny, M., 1976. Physical properties of spiders silk and their role in design of orb-webs. *J. Exp. Biol.* 65, 483-506.
- Eberhard, W.G., 1987. How spiders initiate airborne lines. *J. Arach.* 15, 1-9.
- Foelix, R.F., 1996. *Biology of Spiders.* Oxford University Press, Oxford, UK.
- Gosline, J.M., Guerette, P.A., Ortlepp, C.S., and Savage, K.N., 1999. The mechanical design of

- spider silks: From fibroin sequence to mechanical function. *J. Exp. Biol.* 202, 3295-3303.
- Hayashi, C.Y., Blackledge, T.A., and Lewis, R.V., 2004. Molecular and mechanical characterization of aciniform silk: Uniformity of iterated sequence modules in a novel member of the spider silk fibroin gene family. *Mol. Biol. Evol.* 21, 1950-1959.
- Kitagawa, M., and Kitayama, T., 1997. Mechanical properties of dragline and capture thread for the spider *Nephila clavata*. *J. Mat. Sci.* 32, 2005-2012.
- Köhler, T., and Vollrath, F., 1995. Thread biomechanics in the 2 orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *J. Exp. Zool.* 271, 1-17.
- Levi, H.W., 1971. The Diadematus group of the orb-weaver genus *Araneus* north of Mexico (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 141, 131-179.
- Morse, D.H., 2007. Predator upon a flower. Life history and fitness in a crab spider. Harvard University Press, Cambridge, MA.
- Morse, D.H., and Fritz, R.S., 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena Vatia*. *Ecology* 63, 172-182.
- Moya-Laraño, J., Vinkovic, D., De Mas, E., Corcobado, G., and Moreno, E., 2008. Morphological evolution of spiders predicted by pendulum mechanics. *PLoS One* 3, e1841.
- Ortlepp, C., and Gosline, J.M., 2008. The scaling of safety factor in spider draglines. *J. Exp. Biol.* 211, 2832-2840.
- Osaki, S., 1996. Spider silk as mechanical lifeline. *Nature* 384, 419-419.
- Osaki, S., 2003. Safety coefficient of the mechanical lifeline of spiders. *Polymer J.* 35, 261-265.
- Penney, D., 2004. Does the fossil record of spiders track that of their principal prey, the insects? *Trans. R. Soc. Edinb.-Earth Sci.* 94, 275-281.
- Peters, H.M., 1990. On the structural and glandular origin of the bridging lines used by spiders for moving to distant places. *Acta Zool. Fen.* 190, 309-314.
- Roesler, J., Harders, H., and Backer, M., 2007. Mechanical behaviour of engineering materials. Springer, Berlin.
- Selden, P.A., Shear, W.A., and Bonamo, P.M., 1991. A spider and other arachnids from the Devonian of New-York, and reinterpretations of Devonian Araneae. *Palaeontology* 34, 241-281.
- Shear, W.A., Palmer, J.M., Coddington, J.A., and Bonamo, P.M., 1989. A Devonian spinneret - Early evidence of spiders and silk use. *Science* 246, 479-481.
- Swanson, B.O., Blackledge, T.A., Summers, A.P., and Hayashi, C.Y., 2006. Spider dragline silk: Correlated and mosaic evolution in high-performance biological materials. *Evolution* 60, 2539-2551.
- Vollrath, F., and Selden, P., 2007. The role of behavior in the evolution of spiders, silks, and webs. *Ann. Rev. Ecol. Evol. Syst.* 38, 819-846.
- Vollrath, F., Madsen, B., and Shao, Z.Z., 2001. The effect of spinning conditions on the mechanics of a spider's dragline silk. *Proc. R. Soc. Lond. .B-Biol. Sci.* 268, 2339-2346.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., and Warren, P.H., 2005. Body size in ecological networks. *Trends .Ecol. Evol.* 20, 402-409.