

The Common House Spider Alters the Material and Mechanical Properties of Cobweb Silk in Response to Different Prey

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ABSTRACT Many spiders depend upon webs to capture prey. Web function results from architecture and mechanical performance of the silk. We hypothesized that the common house spider, *Achaearanea tepidariorum*, would alter the mechanical performance of its cobweb in response to different prey by varying the structural and material properties of its silk. We fed spiders either large, high kinetic energy crickets or small, low kinetic energy pillbugs for 1 week and then examined their freshly spun silk. We separated mechanical performance into structural and material effects. We measured both types of properties for silk threads collected directly from cobwebs to test for “tuning” of silk performance to different aspects of prey capture. We compared silk from two different functional regions of the cobweb—sticky gumfooted threads that adhere directly to prey and supporting threads that maintain web integrity. Supporting threads from cricket-fed spiders were stiffer and tougher than supporting threads from pillbug-fed spiders. Both types of silk from cricket-fed spiders broke at higher loads than silk from pillbug-fed spiders. We explain this variation using a simple model of forces exerted by prey and spiders on single threads and propose potential mechanisms for this change in material properties. Two alternative, nonexclusive, hypotheses are suggested by our data. Spiders may tune silk to different types of prey by spinning threads that are able to hold prey without deforming permanently. Alternatively, as spider’s body mass differed dramatically between the two feeding regimes, spiders may tune silk to their own body mass. *J. Exp. Zool.* 309A:542–552, 2008. © 2008 Wiley-Liss, Inc.

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For many spiders, efficient web function has major consequences for prey capture. Web function is determined both by overall architecture and by the mechanical performance of individual silk threads. Mechanical performance of silk threads results from the inherent material properties of the silk and the thread’s overall structure. Material properties, such as ultimate strength and extensibility, are in turn determined by the molecular organization of silk proteins. In contrast, structural properties describe the overall shape of threads and include variation in the number or diameter of the individual strands that compose a discrete thread. Thus, spiders could potentially alter web function through several different mechanisms. For instance, a spider could spin webs that support more weight by attaching

more threads together, by producing silk with superior ultimate strength and stiffness, or simply by spinning thicker threads.

Web architecture is a plastic trait that responds to prey type and availability (ap Rhisiart and Vollrath, ’94; Sandoval, ’94; Schneider and Vollrath, ’98). However, the functional implications of this variation are poorly understood, and these studies largely focus on only a single type of web,

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the orb web. Most spiders spin other web architectures but little is known about functional variation in them (e.g. Blackledge and Zevenbergen, 2007; Zevenbergen et al., 2008). The mechanical performance of spider silk also plays an important role in web function (Denny, '76; Gosline et al., '86; Craig, '87). However, the degree to which spiders control the structural or material properties of silk in webs is even less understood than architectural plasticity. Silk material properties can vary among individual spiders within a species (Köhler and Vollrath, '95; Madsen et al., '99) and within single spiders (Madsen et al., '99; Garrido et al., 2002a). Although some of this variation may appear random, several consistent effects of environmental conditions on silk properties have been identified. Garrido et al. (2002b) showed that the orb weaving spider *Argiope trifasciata* produced silk that resisted higher loads when climbing compared with silk spun while walking on a horizontal surface. Pan et al. (2004) showed that the orb weaving spider *Araneus ventricosus* spun stronger dragline silk, with a higher ultimate strength, when housed in taller cages. The authors hypothesized that the spider assessed the risk of a fall from a higher height and spun stronger silk in response. Tso et al. (2007) studied the effect of prey type on the material properties of dragline silk of another orb-weaver, *Nephila pilipes*. They observed that spiders fed flies spun stiffer dragline silk compared with those fed crickets. These different studies indicate that spiders can control the mechanical performance and material properties of their silk. However, they primarily involve either silk forcibly drawn from restrained spiders or silk spun by walking spiders. Whether spiders can tune the material properties of silk used for prey capture in webs is largely unknown.

In this study, we tested whether the cobweb weaving common house spider *Achaearanea tepidariorum* (Araneae: Theridiidae) responds to different prey by altering the structural or material properties of silk in its web. Spiders were fed either large, fast prey (late instar crickets) or small, slow prey (pillbugs). The two prey differed in kinetic energy as well as nutritionally, either of which could affect silk production.

A. tepidariorum cobwebs consists of two regions (Fig. 1): an array of supporting threads and sticky gumfooted threads (Benjamin and Zschokke, 2003). The supporting threads are all dry dragline silk spun from the major ampullate silk gland. Sticky gumfooted threads are spun vertically from

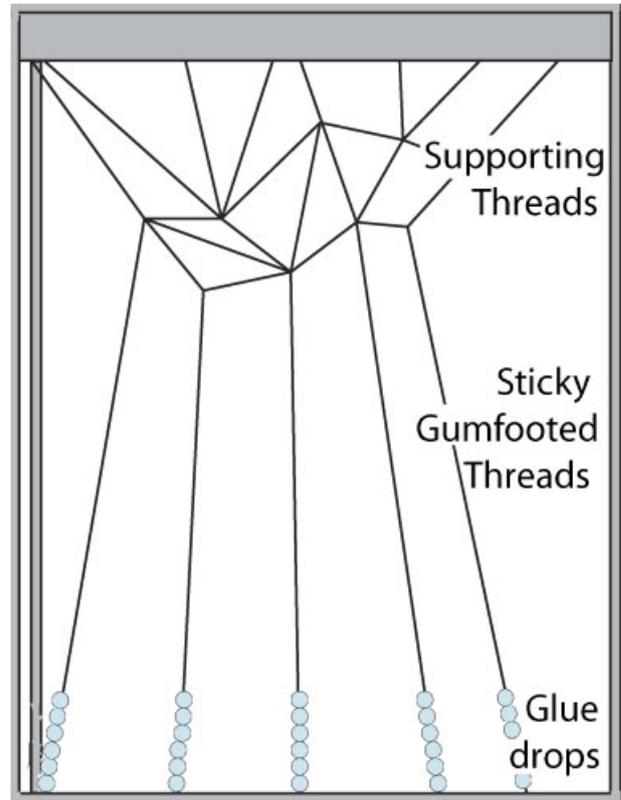


Fig. 1. *Achaearanea tepidariorum* cobweb. The supporting threads form a network in the upper region of the web. The supporting threads connect to near-vertical sticky gumfooted threads. These sticky gumfooted threads are gluey in their lower portion and adhere directly to prey during capture. (Note: the glue droplets are enlarged in the figure.)

the substrate to the supporting threads of the web and are also composed of major ampullate silk, sometimes with extra minor ampullate threads (Benjamin and Zschokke, 2002; Blackledge et al., 2005c). Most of the sticky gumfooted threads are dry, but their lower 1–2 cm are covered with glue secretions, produced from aggregate silk glands. These droplets adhere to insects during prey capture. Once a sticky gumfooted thread intercepts a prey, the thread detaches from the ground and tension in the web then pulls small insects off of the ground or restrains larger prey (Szlep, '65; Argintean et al., 2006). The spider then quickly attacks the prey and brings it to the retreat where it is consumed.

In our experiment, we investigated silk from both supporting threads and sticky gumfooted threads. Because these threads have different functions in the web, we expected them to potentially exhibit different material and structural properties that may relate to how spiders or prey interact with the web.

METHODS

Spiders

Adult *A. tepidariorum* were collected at the University of Akron's Bath Field Station (Bath, OH) and local homes in the surrounding area (Akron, OH). The animals were weighed to the nearest mg and their right femurs were measured to the nearest 0.1 mm. Body condition was then calculated as the residual of a regression of mass versus femur length (Jakob et al., '96). Spiders were ranked by condition and allocated to two different feeding regimes ($n = 14$ for cricket-fed spiders and $n = 13$ for pillbug-fed spiders) as follows: the spider in highest condition was allocated to the pillbug feeding regime, the second highest to the cricket feeding regime, the third highest to the pillbug feeding regime, etc. As a result, there was no difference between treatments in the initial condition or body mass of the spiders.

Spiders were housed in $40 \times 32 \times 24$ cm clear plastic cages (Kritter Keepers[®], San Marcos, CA), with cardboard frames to support webs (Fig. 1). The frames consisted of two 28×20 cm cardboard sheets, on top and bottom, which were joined by 34 cm high wooden sticks (two on back and one on front). This design allowed the spiders to spin webs between the top and bottom cardboard sheets, while assuring easy access to all regions of webs for silk collection. Borders, 2.5 cm wide, were added to the top and bottom to provide enclosed "corners" that encouraged spiders to build webs within the frames. Spiders were housed at a constant temperature of 24°C under a 15:9 hr light/dark cycle. The spiders were acclimated to the cages for 2 days before the feeding regimes started.

Feeding regime

The spiders were fed for one week on a diet of either crickets (purchased from Fluker's Farm, Port Allen, LA) or pillbugs (collected from University of Akron's Bath Field Station, Bath, OH and residences, Akron, OH). Crickets weighed (mean \pm SE) 230 ± 40 mg whereas the pillbugs weighed 49 ± 5 mg. Spiders received either one cricket every two days (three total over the week) or two pillbugs each day (14 total), so that the overall quantity of food was similar (98.6 mg per day of crickets versus 98 mg per day of pillbugs). However, ingested biomass differed between treatments, owing to spiders' inability to extract

as much material from pillbugs as from crickets (see below).

Silk collection

After one week of feeding, webs were destroyed and the spiders were given two days to build new webs. This ensured that all silk threads were spun only after spiders experienced the full feeding regime. Samples of silk were then collected for each web from the sticky gumfooted threads ($n = 3$) and from the uppermost supporting threads ($n = 3$). The silk was secured across 10.7 mm holes in cardboard mounts, fastened on either end of the gap with cyanoacrylate glue, and then cut free from the web with a hot soldering iron.

Only the dry regions of sticky gumfooted threads were collected because the glue droplets alter mechanical performance of the silk (Blackledge et al., 2005b). Supporting threads were collected from the top 5 cm of the web. For both types of silk, most threads were double stranded, but we were occasionally unable to find enough double-stranded samples and therefore collected some three- or four-stranded samples. Spiders normally spin threads consisting of two strands because of their paired spinning organs, whereas four-stranded threads are actually two separate threads spun at different times. Therefore, we rationalized that the double-stranded threads are the best standardized material for testing because the two strands were produced simultaneously and thus were probably more similar to each other in tension and material flaws compared with four-stranded threads.

Diameter measurements

Polarized light microscopy was used to take two digital photographs of each sample at $1,000 \times$. The diameter of each strand in a sample was measured twice from each photograph using ImageJ (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, MD, <http://rsb.info.nih.gov/ij/>, 1997–2007) and the number of strands per thread was counted. The multiple measurements accounted for the slight shape anisotropy of silk so that cross-sectional area could be approximated by a single average diameter (Blackledge et al., 2005a). From these measurements, both the total cross-sectional area of the silk sample and the average diameter of single strands within the sample were computed.

Mechanical and material properties of the silk

The mechanical performance of silk threads was then tested on a Nano Bionix UTM (MTS Corp., Eden Prairie, MN) using established protocols (Blackledge et al., 2005b,c). All fibers were extended at 1% strain/sec and the resulting force values measured. We first considered raw failure load, which represents the force supported by the thread before breaking, without normalizing to thread diameter. Failure load is thus a direct determinant of how threads interact with prey and spiders. We also measured the material properties of threads, which describe the intrinsic quality of the silk spun by spiders. Material properties combine with the structural aspects of threads (size and number of strands) to determine how threads interact with prey. We recorded six material properties for each sample (Fig. 2): Young's modulus, yield stress, yield strain, extensibility (breaking strain), ultimate strength (breaking stress), and toughness (breaking energy). Young's modulus measures the initial stiffness of the material. The higher Young's modulus is the more the silk resists deformation under a given load. The yield point measures the transition of silk from elastic to plastic behavior. Before yield, silk is perfectly elastic, which means that when a force applied to the material is removed, the silk returns to its original shape and retains its original mechanical performance.

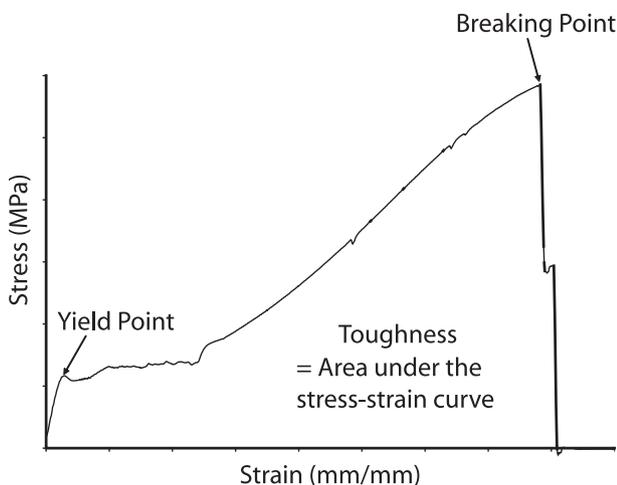


Fig. 2. Stress-strain curve for spider dragline silk. The yield point is indicated by the initial change in the slope of the curve. The breaking point appears as a second, final peak. The area under the stress-strain curve measures the toughness, or ability to absorb kinetic energy, of the silk.

After yield, silk permanently deforms, altering its future mechanical performance. In general, silk extends more easily after yielding. Yield stress and yield strain are, respectively, the true stress and true strain at yield. Similarly, ultimate strength and extensibility are the true stress and true strain at the breaking point.

We used true stress and true strain, rather than engineering stress and engineering strain, because these are more reliable for very elastic materials such as spider silk (Blackledge et al., 2005c). True stress (σ) measures the force supported per area of thread and is calculated as

$$\sigma = \frac{F}{A}$$

where F is the force exerted on the material, and A is the instantaneous cross-sectional area of the silk fiber at time t . The cross-sectional area at time t is computed by assuming a constant volume for the fiber (Vollrath et al., 2001). A is calculated as

$$A = \frac{V}{l} = \frac{A_0 l_0}{l}$$

where V is the volume of the fiber, A_0 is the original cross-sectional area, l is the length of the fiber at time t and l_0 is the original length of the fiber. True strain (ϵ) measures the relative extension of the fiber and is calculated as

$$\epsilon = \ln\left(\frac{l}{l_0}\right)$$

where l is the instantaneous length of the fiber at time t and l_0 is the original length of the fiber.

Toughness, or breaking energy, represents the total energy that can be absorbed per volume of silk before breaking. It is calculated as the area under the stress-strain curve.

Statistical analysis

We used t -tests to compare the average single-strand diameter between treatments because the data were normally distributed (Shapiro-Wilks normality tests, $P = 0.0560$ for pillbug-fed spiders' support threads, $P = 0.3838$ for pillbug-fed spiders' gumfooted threads, $P = 0.3763$ for cricket-fed spiders' support threads, and $P = 0.0981$ for cricket-fed spiders' gumfooted threads). However, spider mass was correlated with diameter (Griffiths and Salantri, '80; Vollrath and Köhler, '96; Osaki, 2003). Therefore, we removed the effect of spider mass by using an analysis of covariance (ANCOVA) with mass and treatment as covariates.

For sticky gumfooted threads, the failure loads were not normally distributed (Shapiro–Wilks normality test, $P = 0.6082$ for pillbug-fed spiders but $P < 0.0001$ for cricket-fed spiders), so we compared the failure load of silk from cricket-fed spiders and silk from pillbug-fed spiders using a *U* Mann–Whitney *U* test. For supporting threads, the data were normal ($P = 0.1254$ for pillbug-fed spiders and $P = 0.5563$ for cricket-fed spiders), so we instead used a *t*-test. To test for a potential influence of spider mass on failure load, we ran an ANCOVA with mass and treatment as covariates. As the data for sticky gumfooted threads were not normally distributed, we inverse transformed them (Shapiro–Wilks normality test after transformation, $P = 0.9100$ for pillbug-fed spiders and $P = 0.4231$ for cricket-fed spiders).

The effect of prey type on all six aspects of material properties was tested using a Hotelling T^2 (Johnson and Wichern, 2002). According to χ -plots, all samples were multivariate normal. We ran post hoc Tukey's HSD tests to determine which of the variables were affected by the treatment. To test for a potential effect of spider mass on material properties, we ran a multiple analysis of covariance (MANCOVA) with mass and treatment as covariates.

Forces exerted by spiders and prey on the web

To better understand web performance, we calculated the forces exerted by spiders and prey on webs and compared them with the mechanical performance of silk threads. A prey initially exerts a force on a sticky gumfooted thread that is proportional to the prey's kinetic energy. We computed the average kinetic energy (KE) of jumping crickets and crawling pillbugs as

$$KE = \frac{1}{2}mv^2$$

where m is the mass of the prey and v its speed. We measured the average mass of each prey type for 6 crickets and 13 pillbugs and calculated the average speed of each prey type by racing 4 crickets and 12 pillbugs on a 40-cm race track, twice for each individual.

We also calculated the energy E_f that can be absorbed by a single sticky gumfooted thread before failure as

$$E_f = TAh$$

where T is the toughness of the silk (as measured during the tensile test), A is the average cross-

sectional area of the thread and h is the average height of the thread (~ 8 cm in our experiment). We determined h by averaging the height of ten randomly chosen sticky gumfooted threads measured on pictures of five webs.

To better understand the effects of small prey on silk, we computed the energy absorbed by sticky gumfooted threads before yielding. The yield point measures when a viscoelastic material starts showing plastic behavior and deforms permanently. A silk thread that passed yield may not function optimally during subsequent prey capture events because of this permanent deformation. In contrast, silk threads that function exclusively within their elastic region, i.e. before yield, maintain the original performance of the web in terms of stopping power, structural tension, and transmission of vibrations. Thus, producing silk that does not yield in response to prey may be almost as important as producing silk that does not break. We computed the energy that can be absorbed by silk earlier to yielding by integrating stress to the yield point.

We also considered how the static loading of spiders or prey suspended in webs might interact with supporting threads. We computed the average static load generated by the weight w of spiders, pillbugs, and crickets, as

$$w = mg$$

where m is the average mass and g is the acceleration owing to gravity. However, supporting threads must maintain their functional integrity through repeated bouts of prey capture. Thus, it is important to consider whether spiders tune their silk to prevent yielding. If prey apply large loads to webs then a high yield stress may prevent supporting threads from permanently deforming during prey capture. We computed the load at yield (L_y) using the average yield stress (ε_y) and the average thread cross-sectional area (A) for supporting threads as

$$L_y = \varepsilon_y A.$$

RESULTS

Spider mass

Cricket-fed spiders were heavier than pillbug-fed spiders (*t*-test, $t = -4.68$, $df = 19$, $P = 0.0001$; mean \pm SE = 91.9 ± 8.8 mg and 49.8 ± 2.9 mg, respectively). Cricket-fed spiders were also in better

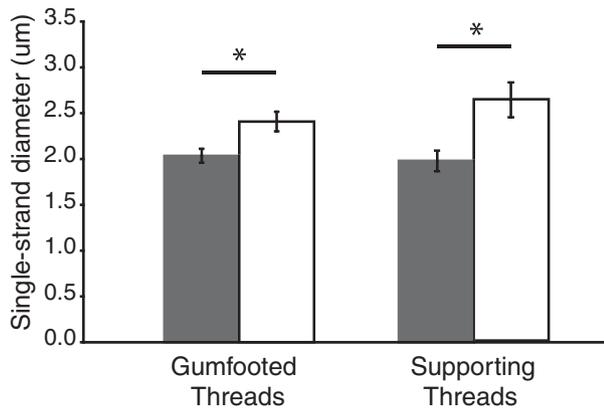


Fig. 3. Diameter of silk threads spun by spiders fed different prey (mean ± SE). Dark bars represent pillbug-fed spiders and open bars represent cricket-fed spiders. Asterisks indicate a significant difference.

body condition than pillbug-fed spiders (t -test, $t = -4.76$, $df = 21$, $P = 0.0001$).

Thread diameter

For both regions of the web, cricket-fed spiders spun thicker single strands of silk compared with pillbug-fed spiders (t -test, $t = -3.58$, $df = 22$, $P = 0.0016$ for sticky gumfooted threads and $t = -4.16$, $df = 18$, $P = 0.0006$ for supporting threads). Single-strand diameter for sticky gumfooted threads was (mean ± SE) $2.4 \pm 0.1 \mu\text{m}$ for cricket-fed spiders and $2.0 \pm 0.1 \mu\text{m}$ for pillbug-fed spiders. For supporting threads, single-strand diameter was (mean ± SE) $2.7 \pm 0.2 \mu\text{m}$ for cricket-fed spiders and $2.1 \pm 0.1 \mu\text{m}$ for pillbug-fed spiders (Fig. 3). For both types of threads, spider mass was positively correlated with single-strand diameter when included in an ANCOVA with prey type ($F = 13.05$, $P = 0.0049$ for sticky gumfooted threads and $F = 32.70$, $P < 0.0001$ for supporting threads). However, there was no effect of prey type on single-strand diameter for either sticky gumfooted threads ($F = 2.80$, $P = 0.0769$) or for supporting threads ($F = 1.79$, $P = 0.1828$) once spider mass was included. This suggested that the difference in diameter between the two feeding regimes revealed by the t -test was explained primarily by differences in spider mass rather than prey per se.

Mechanical properties

Silk from cricket-fed spiders broke at higher load, for both sticky gumfooted threads ($W = 13$,

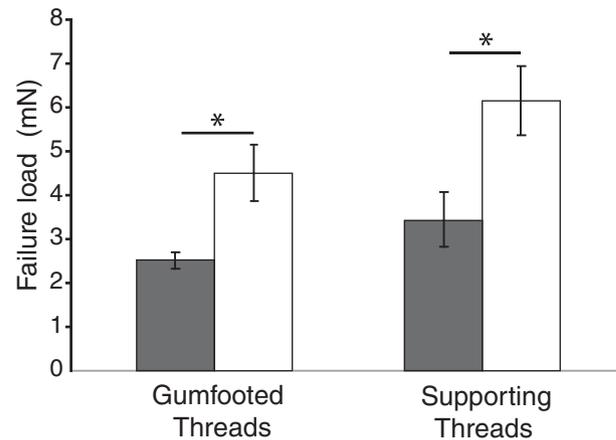


Fig. 4. Mechanical properties of silk spun by spiders fed different prey (mean ± SE). Dark bars represent pillbug-fed spiders and open bars represent cricket-fed spiders. Asterisks indicate a significant difference.

$P < 0.0001$) and supporting threads ($t = -3.47$, $df = 21$, $P = 0.0023$) (Fig. 4). Spider mass was positively correlated with failure load of both types of threads when included in an ANCOVA with prey type ($F = 14.15$, $P = 0.0008$ for sticky gumfooted threads (transformed data) and $F = 25.49$, $P < 0.0001$ for supporting threads). However, there was no effect of prey type on failure load for either sticky gumfooted threads ($F = 1.07$, $P = 0.0884$) or for supporting threads ($F = 0.59$, $P = 0.1897$) once spider mass was included. This suggested that the difference in failure load between the two feeding regimes revealed by the univariate tests was, like the difference in diameters, explained by differences in spider mass rather than prey per se.

Material properties

The type of prey captured by spiders affected the material properties of supporting thread silk (Hotelling T^2 , $P = 0.0073$), but not the material properties of sticky gumfooted thread silk (Hotelling T^2 , $P = 0.1514$) (Fig. 5). According to post hoc tests, cricket-fed spiders spun supporting threads made of silk with higher Young's modulus (Tukey's HSD, $F = 5.3918$, $df = 25$, $P = 0.0068$) and toughness (Tukey's HSD, $F = 2.830$, $df = 25$, $P = 0.0448$) than pillbug-fed spiders. For supporting threads, Young's modulus was significantly correlated with both prey type ($F = 6.68$, $P = 0.0163$) and spider mass ($F = 4.60$, $P = 0.0422$) in a MANCOVA. Toughness was correlated with prey type ($F = 4.36$, $P = 0.0476$) but not spider mass.

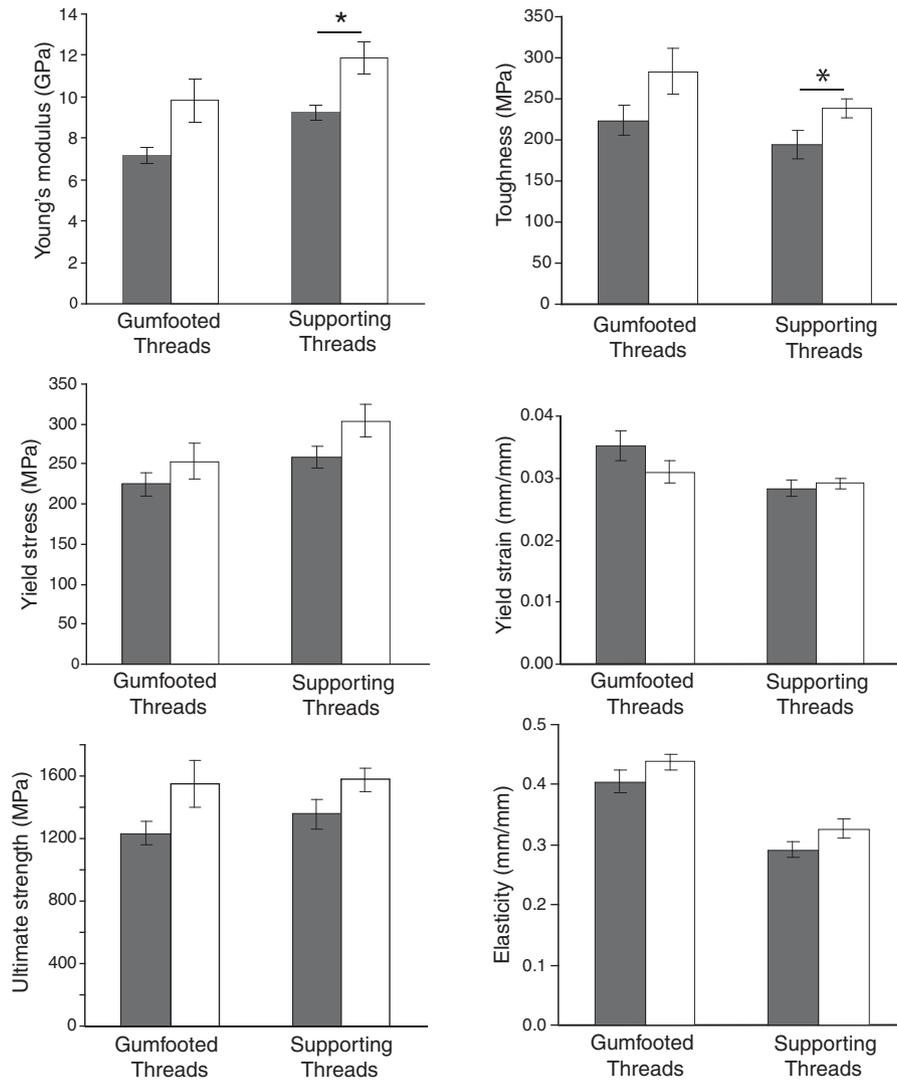


Fig. 5. Material properties of silk spun by spiders fed different prey (mean ± SE). Dark bars represent pillbug-fed spiders and open bars represent cricket-fed spiders. Asterisks indicate a significant difference.

Forces exerted by spiders and prey on the web

The average kinetic energy of a cricket was over 550 μJ whereas for a pillbug it was 2.6 μJ (Table 1). The energy absorbed before failure by sticky gumfooted threads was ~110 μJ for cricket-fed spiders but only ~50 μJ for pillbug-fed spiders. The energy absorbed before yielding was 1.8 μJ for cricket-fed spiders and 1.3 μJ for pillbug-fed spiders. The average weight of a cricket was 2.25 mN whereas the average weight of a cricket-fed spider was slightly under 1 mN (Table 2). Both pillbugs and pillbug-fed spiders weighed on average 0.5 mN. The load at yield of supporting threads was slightly under 2.2 mN for cricket-fed spiders and over 1 mN for pillbug-fed spiders.

TABLE 1. Kinetic energy of prey compared with energy absorbed by sticky gumfooted threads spun by spiders fed each type of prey

	Cricket	Pillbug
Prey kinetic energy (μJ)	579.72	2.61
Energy absorbed upon yield by the silk (μJ)	1.84	1.31
Energy absorbed upon failure by the silk (μJ)	112.74	50.78

Silk values were calculated for 8 cm long sticky gumfooted threads.

DISCUSSION

Silk threads spun by spiders fed faster, heavier prey (crickets) are thicker and absorb more force before breaking than threads spun by spiders fed

TABLE 2. Average mass of spiders and their prey compared with maximum sustainable load of individual supporting threads upon failure and upon yield

	Cricket-fed spiders	Pillbug-fed spiders
Spider weight (mN)	0.901	0.488
Prey weight (mN)	2.254	0.480
Load at yield of the silk (mN)	2.187	1.156
Load at failure of the silk (mN)	6.150	3.433

lighter, slower prey (pillbugs). Supporting thread silk is also stiffer and tougher for spiders fed faster, heavier prey. This suggests that spiders alter silk properties in response to different prey and that this response may tune silk to improve prey capture. However, alternative explanations involving intrinsic effects of spider condition or mass on silk production are important and are also discussed below.

Nutritional effects on spider mass and condition

When confronted by long-term differences in prey, spiders may alter their silk either in response to how prey interact physically with webs or in response to differences in nutritional value of prey. Spiders fed heavier prey tended to be heavier themselves, even though we offered the same total amount of food to both groups. This difference was probably owing to the thick exoskeletons of pillbugs and their higher surface to volume ratios resulting in less ingestible material. We estimated the proportion of wet biomass extracted from crickets and pillbugs by weighing each prey just before it was released in the spider's cage and just after the spider finished feeding on it. Spiders extracted $69.1 \pm 6.1\%$ of crickets but only $53.5 \pm 6.4\%$ of pillbugs (mean \pm SE). The 16% less ingestible biomass available to pillbug-fed spiders likely explains why their body masses and body conditions were lower than those of cricket-fed spiders. Thus, the difference in the material and mechanical properties of the silk between treatments might be a response to different levels of starvation rather than a response to the physical challenges presented by different prey during capture. For instance, the strong, elastic silk spun by cricket-fed spiders may be metabolically expensive and

starved spiders simply might not have the energy to produce it.

Both thread diameter and failure load increased proportionally to spider mass. However, prey type did not influence either parameter. Some material properties (e.g. Young's modulus) were influenced by both spider mass and prey type. Other material properties (e.g. toughness) only depended on prey type. This demonstrates that spider body mass clearly plays an important role in determining variation in silk but that prey type was also important. This suggests that spiders alter different aspects of silk production in response to internal versus external stimuli. For instance, both structural and mechanical properties of silk varied in response to changes in spider body condition and mass but not in response to prey type. In contrast, the material properties of the silk were influenced by both spider body characteristics and the specific type of prey captured. However, further research is needed to fully explore this hypothesis.

Effects of prey interacting with webs

Nutritional quality of prey can affect silk by changing spider condition, but spiders may also alter their silk threads in response to how prey physically interact with webs. Prey present different physical challenges to different regions of the cobweb. Prey initially impact the sticky gumfooted threads with force proportional to their speed and body mass. Later, while hanging in webs, captured prey apply static loads to the supporting threads proportional to their mass. Spiders also exert static loads in the supporting thread region of webs proportional to their body mass. How do these physical challenges relate to silk performance?

The total energy that a moving prey exerts when stopped by a single sticky gumfooted thread is equal to its kinetic energy. This means that larger, faster prey transfer more energy to the sticky gumfooted threads of a web. Sticky gumfooted threads spun by pillbug-fed spiders can absorb 20 times the kinetic energy exerted by a pillbug before breaking (Table 1). In contrast, a single sticky gumfooted thread spun by a cricket-fed spider is unable to absorb the kinetic energy of a jumping cricket before breaking. Thus, their webs likely require crickets to contact multiple threads before the crickets are effectively stopped or require the supporting threads to absorb some of the prey energy transmitted through the sticky

gumfooted threads. This suggests that sticky gumfooted threads are overengineered for small prey such as pillbugs but underengineered for large, fast prey such as crickets.

Sticky gumfooted threads spun by pillbug-fed spiders can absorb only half of the kinetic energy of a pillbug before yielding. However, sticky gumfooted threads function only once because they detach from the substrate when contacted by prey. Thus, maintaining future performance by spinning sticky gumfooted threads that can absorb the energy of a prey without yielding may be irrelevant.

At rest, the spider stays within the supporting region of the web. This is also where it consumes prey. Therefore, a web spun in response to heavier prey may need supporting threads that resist higher loads and absorb more energy than threads spun by spiders capturing lighter prey. Heavier spiders also need stronger threads that will support their own weight. In our experiment, cricket-fed spiders gained more mass than pillbug-fed spiders. Thus, both supporting larger prey and spiders growing heavier when consuming larger prey should place increased demands on silk performance by cricket-fed spiders.

To investigate whether spider weight or prey weight affects silk strength, we computed the average static load generated by spiders, pillbugs, and crickets (Table 2). Both spiders and dead prey hanging in the supporting region of webs apply loads equal to their weight. The failure load for supporting threads spun by cricket-fed spiders is three times the average weight of a cricket and six times the average weight of the spider. For supporting threads spun by pillbug-fed spiders, the failure load is six times the average weight of both pillbugs and spiders. This large difference suggests that spiders do not tune threads in webs to prevent the threads from breaking under the static loads of prey or their own bodies.

Contrary to sticky gumfooted threads, supporting threads in the upper regions of cobwebs need to function during multiple prey capture events such that preventing yield could be an important constraint on their performance. Load at yield for supporting threads spun by cricket-fed spiders is twice the weight of a spider, but only slightly less than the average weight of a cricket (Table 2). Thus, a single supporting thread could not hold a large prey, such as a cricket, without deforming permanently. The load at yield for supporting threads spun by pillbug-fed spiders is twice the weight of either spiders or pillbugs, so that a single

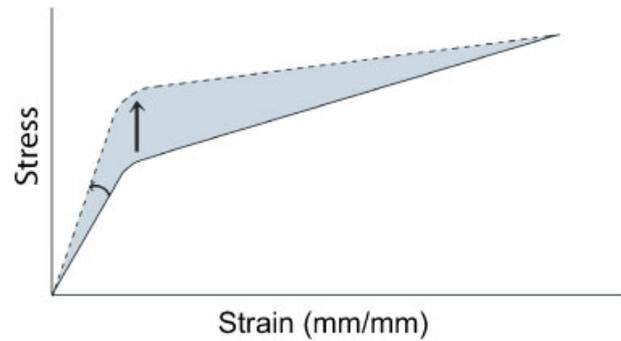


Fig. 6. Effect of increase in fiber yield stress on material properties. The dotted line indicates a material with a higher yield stress compared with a second material of equivalent breaking point (solid line). This increase makes the material both stiffer (by increasing pre-yield slope as indicated by the curved arrow) and tougher (corresponding to the extra gray area).

thread could easily support them. In conclusion, though single threads in webs usually function below yield, large prey generates enough load to permanently deform individual threads, impairing their future performance. Moreover, the importance of preventing fiber yield may also explain the observed increase in stiffness and toughness of cricket-fed spider silk because any increase in fiber yield would be accompanied by increases in both of these performance parameters (Fig. 6).

Potential mechanisms for control of silk material properties

Regardless of why spiders respond to different prey by altering the material properties of silk, the physiological mechanisms by which those changes occur are poorly understood. We examine three potential hypotheses.

Modification of the amino acid composition of silk

Variation in amino acid sequence confers different properties to spider silk by affecting the structural conformation of silk proteins (Hayashi and Lewis, '98; Hinman et al., 2000). In particular, proline gives more elasticity to the silk whereas alanine provides strength and stiffness (Hayashi et al., '99; Hayashi and Lewis, 2001). Spiders could assemble the same silk from different proportions of amino acids when consuming varied prey, thereby affecting silk performance. Indeed, differences in spider's diet are reflected in changes in the amino acid composition of the silk (Craig et al., 2000; Tso et al., 2005) and this can be

accompanied by differences in silk material properties (Tso et al., 2007). Thus, variation of silk material properties in *Acheaeranea* could potentially be a response to amino acid differences between crickets and pillbugs, but this remains to be tested.

Modification of the ratio of different proteins in silk

Orbicularian dragline silk is a blend of two proteins named spidroin 1 and spidroin 2 (Xu and Lewis, '90; Hinman and Lewis, '92; Lewis, '92; Gatesy et al., 2001; Ayoub et al., 2007). These proteins likely confer different material properties to dragline silk (Rising et al., 2005). Spidroin 1 is rich in alanine that is hypothesized to confer strength and stiffness to silk (Xu and Lewis, '90). Spidroin 2 is rich in proline that is hypothesized to confer elasticity to silk (Hinman and Lewis, '92). Therefore, spiders could alter the material properties of their silk by changing the ratio of these two proteins. In our experiment, cricket-fed spiders may have produced silk richer in spidroin 1 thereby making it stiffer than pillbug-fed spiders' silk. This could result directly from more amino acids that are used in the synthesis of spidroin 1 being available when consuming crickets. Alternatively, it could result from cricket-fed spiders incorporating relatively more spidroin 1 in their supporting threads silk in response to their heavier cricket prey.

Modification of spinning effects

Spider silk is stored inside the silk glands as a liquid dope. As the dope passes through the spider's spinning duct, it increases in crystal orientation and solidifies under the influence of several physico-chemical processes, including the application of shear forces that align the protein molecules along the axis of the fiber (Knight and Vollrath, '99; Ortlepp and Gosline, 2004). If spiders are able to control this process, they could manipulate the physical properties of their silk. In particular, spiders use a sphincter muscle to apply force to the silk as it is extruded, altering its material properties by affecting its molecular orientation (Ortlepp and Gosline, 2004). This provides a potential mechanism for cricket-fed spiders to spin stiffer silk in our experiment without necessitating a change in amino acid composition or protein expression.

CONCLUSION

We found that spiders modified silk in response to different prey and to changes in their internal condition. Spider body mass and condition affected mechanical and structural properties of whole threads whereas body mass and prey type induced changes in the silk material itself. Spiders fed large, fast prey spun thicker silk able to resist higher forces. The silk from their supporting threads was also stiffer and tougher. These modifications could function to allow webs to support the weight of heavy prey or spiders without deforming permanently or to stop prey with higher kinetic energy. However, because of a confounding effect of spider condition, this variation may also result from potential metabolic costs of spinning stiffer and tougher silk. We currently cannot separate these two hypotheses, but future experiments could better manipulate the physical interaction of different prey with webs while maintaining spider condition or nutritional status. Thus, this system provides an opportunity to explore why and how spiders tailor the performance of silk to different ecological conditions. Understanding the mechanisms of variation of silk material properties will also help develop processes that replicate the extraordinary performance of spider silk in synthetic fibers.

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