The effect of spinning conditions on the mechanics of a spider's dragline silk

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We studied the mechanical properties of dragline threads of the edible golden silk spider *Nephila edulis* that are produced under spinning speeds ranging from 0.1 to 400 mm s^{-1} and temperatures ranging from 5 to 40 °C. These conditions affected the silk in all of the mechanical traits we tested (strain at breaking, breaking energy, initial Young's modulus and point of yielding). We argue that both trade-offs (between mechanical properties) and constraints (in the manufacturing process) have a large role in defining spider silk fibres.

Keywords: *Nephila edulis*; dragline threads; silk fibres; mechanical traits

1. INTRODUCTION

Spiders' webs are supreme examples of evolution in animal architecture and spiders' silks exemplify nature's ability for evolving materials that are considered supreme even by the most exacting human standards (Gosline *et al.* 1986). Silks and webs have evolved together hundreds of millions of years in a long iterative progression from weak filaments that cover eggs and line excavations to strong threads that are knitted into aerial nets (Schultz 1987; Selden 1989; Vollrath 2000*a*). The double fibre safety draglines of spiders have become the holy grail of modern polymer fibres and extensive research is being devoted to understanding and, eventually, to commercially 'copying' the dragline silk of advanced araneid spiders, such as golden silk spiders in the genus *Nephila* (Kaplan *et al.* 1994; Vollrath 2000*b*). Such silks can outperform the most energy absorbent (i.e. toughest) of man-made fibres, and as we are beginning to discover even tougher silks in other spider genera it is not unreasonable to assume that we might customize biomimetic silk polymers based on this and other silks (O'Brien *et al.* 1998). It is pertinent to ask how the silks' excellent strength and supreme toughness come about and to seek the mechanisms responsible for their outstanding mechanical behaviour. It is equally pertinent, and of basic importance for any understanding of this material, to examine the spider's spinning process and the constraints under which the spider produces such excellent fibres. The fibres are produced from protein feedstock that is prepared in the gland where it is stored (often for a considerable time), before being spun through a complex extrusion device with ample opportunity for affecting the material properties of the final thread (Vollrath *et al.* 1998; Vollrath & Knight 1999, 2001; Knight *et al.* 2000; Knight & Vollrath 2001). In the following, we present a study aimed at unravelling the interactive effects of speed and temperature at the time of spinning on the material properties of a major silk, which is used for lifelines and as supporting web components.

Biologists often propose that organisms and their character traits are optimized for their average living conditions (Ridley 1996). Any one feature (character trait) is an integral part of a set of dynamic state variables that are constantly modified by evolution, balancing conflicting selection pressures and design constraints. Constraints can be historical (phylogenetic), developmental (ontogenetic), economic (metabolic), mechanical (structural) and molecular (biochemical). Selection favours those individuals that find the best balance between these constraints and, thus, by accruing the most benefits while incurring the least costs, efficiently accumulate reserves, which can eventually be converted into more offspring than their compatriots. For spiders, silk is a crucial character trait and its economic and mechanical properties are clearly important for survival, growth and reproduction (Vollrath 1999). At present, we know little about the true cost of silk production, but with existing techniques we can at least probe the silk's mechanical properties. Our analysis of the changes in silk properties as a function of environmental variables provides the first insights into the interaction of options, constraints and trade-offs in the spider's manufacturing process. As we show, the mechanical properties of silk are affected by body temperature and spinning speed. We further show that the cross-over point between the conflicting effects on strength lies in the region of normal conditions, thereby suggesting adaptation towards a state that we might call 'optimized'. After all, for a spider it matters that the safety dragline thread that is always trailed behind it is just strong enough that it does not break when fully loaded under normal conditions. The same applies to a thread's action as a structural member in the web, where, in addition to breaking strength, other material properties are also important, such as its initial resistance to stretching and the extension at which it finally breaks.

Spiders are ectotherms, and the effect of ambient temperature on spider behaviour and life history is strong (Foelix 1996). Climate also affects the material properties of silk and, thus, the engineering of the whole web (Lin *et al.* 1995; Lin & Edmonds 1997; Vollrath *et al.* 1997). The question arises as to whether, when making its silk, a spider is constrained by temperature and, if so, to what extent. However, because in ectotherms the body's temperature typically affects their speed of movement (Heinrich & Esch 1997; Forsman 1999), there should also

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be an interaction between body temperature and their speed of spinning. After all, the speed of spinning in a spider is largely determined by its speed of moving. Thus, we first tested the hypothesis that the walking speed of a spider building a web is a function of ambient temperature. We did this for the garden cross spider *Araneus diadematus*, which builds webs in temperatures ranging from 5 to 25 °C in nature and which will consistently build in a range of 5–42 °C in the laboratory (Vollrath *et al.* 1997).

We then set out to test the thesis that dragline and radius silk is optimized for toughness under normal operating conditions. We did this for the edible golden silk spider *Nephila edulis*, which, being larger than *Araneus*, has become the 'benchmark' organism for silk studies. The silk of an adult female *Nephila* is thick and strong, and can thus be studied with acceptable measuring errors (Madsen *et al.* 1999). *N. edulis* is a semi-tropical Australian spider that is found in a wide range of habitats with corresponding ranges of temperature (York Main 1976). However, it occupies a climate that is warm (at least during the day) over most of its range. Thus, for our control we adopted an ambient temperature of 25 °C, at which web threads are laid down at *ca.* 2 cm s⁻¹. Clearly, temperatures in nature can be considerably colder (at night) or warmer (in the sun). Moreover, although a spider's average walking speed is supposed to be linked to temperature, a spider might independently choose to crawl slowly or rush quickly, for example when suspecting danger, escaping enemies or catching prey.

Our study shows that a spider's web-building speed is correlated with the ambient temperature. We further show that dragline silk is produced by balancing trade-offs between the different production conditions (i.e. spinning rate and temperature) under a natural range of spinning conditions. These conditions are likely to constitute physiological constraints, e.g. they would affect the rate of production of the silk feedstock (Knight & Vollrath 1999), flow in the lumen of the duct (Vollrath & Knight 1999) and epithelial pumping of the ion exchanger (Vollrath *et al.* 1998; Knight & Vollrath 2001). If these ambient conditions and physiological constraints were indeed balanced in trade-offs, then this would suggest that we could consider the finished fibre to be optimized for any given condition.

2. MATERIAL AND METHODS

For web building, we studied immature females of the garden cross spider *A. diadematus* (Araneidae) that were reared in-house and kept in square frames (30 cm × 30 cm × 5 cm) under controlled conditions at 50% relative humidity and 23.5 °C (both with a maximum deviation of 10%), and a 12 L : 12 D cycle. The spiders were fed a *Drosophila* fruitfly every day and had their webs sprayed with tap water for drinking; later the webs were cut down in order to encourage silk production. Under this regime, spiders build a new web every day with high regularity, even when the ambient conditions are modified considerably (Vollrath *et al.* 1998). We studied the webs of three individual spiders building webs under three different temperatures in ascending and descending sequence, with one day for each day in the sequence. The temperatures used were 10, 15 and 30 °C. The spiders also built webs at temperatures as low as 3 °C and up to 42 °C, but far less consistently (Vollrath *et al.* 1997). Spiders

building webs were filmed with a camera connected to a Macintosh computer via a Baker image analyser, and the spiders' movements were recorded and analysed, using our custom program MOVEWATCH (Zschokke & Vollrath 1995). Although we recorded the whole of the web-building activity, here we focus on the construction of the radii because radial silk is the same as dragline silk, which is the silk commonly investigated and best understood.

For the silk properties, we studied adult females of the edible silk spider *N. edulis* (Tetragnathidae) that were reared in-house and kept in square frames (50 cm × 50 cm × 10 cm) under the same controlled conditions as *Araneus*. The spiders were watered and fed *Musca domestica* flies every third day. Note that *Nephila* is not as suitable a subject as *Araneus* for web-building studies because it typically repairs a web for a few days rather than building a new one daily. Moreover, *Nephila* is less inclined to build consistently under laboratory conditions.

The experimental procedure and set-up of the silk sampling were as follows. First, the spider was lightly anaesthetized with CO_2 and fixed with tape to a metal block, facing centre upwards. We waited at least 30 min in order to minimize any residual effects of the anaesthesia (Madsen & Vollrath 2000). Antifreeze (95% ethanol) from a thermal bath was circulated through the metal block. Two thermocouples were positioned on the spider, with one on the dorsal side and one on the ventral side of the abdomen. With this set-up, it was possible to control and record the abdominal temperature of the spider (the average taken from readings from the two thermocouples) in the range 2–50 °C, with a temperature stability of 1 °C and a response time of 0.25 °C min⁻¹. A single monofilament of major ampullate silk was drawn under stereoscopic observation from one of the two anterior spinnerets onto a take-up spool that was driven by a micromotor positioned 10 cm above the spinnerets (Madsen *et al.* 1999). This spool was 9.0 cm in diameter with eight circumferential narrow rods giving thread sections of 3.5 cm. Two adjustable motors controlled the speed of reeling and advancing of the spool. Our equipment was capable of drawing silk from the spider with speeds in the range of 0.05–950 mm s⁻¹.

We present measurements on the silk sampled under two kinds of spinning condition. In one condition, the abdominal temperature of the spider was held constant at the ambient room temperature of 22 °C, and the speed at which the silk was drawn from the spider was varied. In the other condition, the reeling speed was held constant at 20 mm s⁻¹ (a speed comparable to the natural spinning rate) (see Shao *et al.* 1999), while we varied the abdominal temperature of the spider.

Each experimental silking session of an individual spider included a sequence of three to eight different spinning conditions (variations in either speed or temperature) together covering the full working range of our equipment. We randomized the order of testing in order to exclude carry-over effects. We took precautions in order to ensure that the spinning system of a spider was fully acclimatized for any new experimental condition. When varying the temperature, we waited 20 min for the spider to acclimatize before sampling the silk for 5 min. When varying the drawing speed, we adjusted the sampling time in order to ensure that a minimum of 1 m (for slow speeds) and a maximum of 20 m (for fast speeds) of silk thread was collected. Only the last 25 cm of a silk thread sampled for each spinning condition were used for any measurements. If a silk thread broke during sampling, then this silk was excluded from measurements and further silking abandoned.
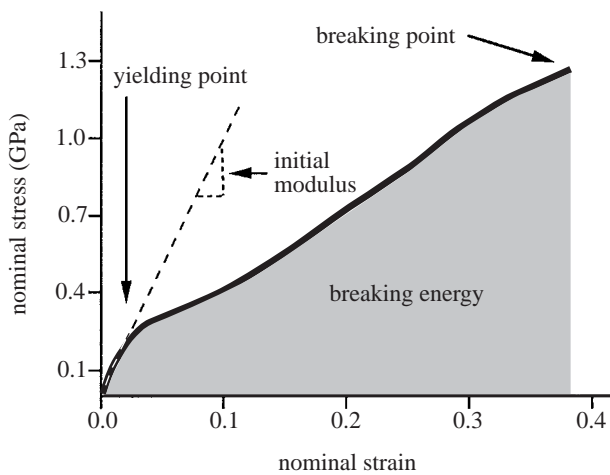
Figure 1. Typical stress–strain curve of a single major ampullate dragline thread from *Nephila edulis* showing the properties measured and calculated in this study. The curve starts to deviate significantly from the first linear part at the yielding point, thus showing yielding stress. The thread snaps at the breaking point allowing us to calculate the breaking stress and breaking strain. Further parameters calculated from the stress–strain curves were the initial modulus (the slope of the first linear part of the curve) and breaking energy (the area covered by the curve). We assumed a constant fibre density of $1.350 \, \mathrm{g \, cm^{-3}}$ (Zemlin 1968) for our calculations of the breaking energy.

Silk thread sections on the take-up spool were carefully transferred on a pair of dividers, using a micromanipulator, to either scanning electron microscope (SEM) stubs or to our custom-built micro-scale materials testing instrument. Threads on stubs were sputtered with gold for 5 min and were then examined at ×5000 magnification in a CamScan Maxim SEM (Cambridge, UK) at 5 kV. The diameter of each 10 mm length of silk was independently measured twice on A4 SEM micrographs with an accepted measuring error of 0.1 μm. The force transducer (FORT 10 force transducer, World Precision Instruments, Sarasota, FL, USA) on our mini-tester showed a linear response with a resolution of 24 μN, and the position resolution of the motor (Linear Pen Motor Assembly, Hewlett Packard Palo Alto, CA, USA) was 16 μm. The instrument was controlled and recorded using LABVIEW (v. 4.0; National Instruments, Austin, TX, USA) on a Macintosh Powerbook 5400, via a LABVIEW PCMCIA 1200 card. In order to measure the force–extension characteristics of a silk, a thread was fixed (using Loctite Super Glue, Watchmead, UK) between the two hooks of the instrument, which had a gauge length of 12 mm with a measured error of 0.1 mm. Before testing, the thread was brought to a zero tension position so that it neither sagged nor pulled the force transducer. Two different types of mechanical test were performed. In one, the thread was stretched until it broke, and in the other, the thread was subjected to one stretching–unstretching cycle with an amplitude of 1.8 mm (=15%). The strain rate was $0.1 \, \mathrm{mm \, s^{-1}}$ (=50% min⁻¹) for both types of test, and data for the extension and force were recorded at a sampling rate of 20 data points per second. The controlled environmental conditions in the measuring room were 22 °C and 50% relative humidity (both with 10% maximum deviation).

We performed three to four mechanical tests on adjacent silk thread sections for each spinning condition and two threads were affixed to stubs for diameter measurements. Nominal
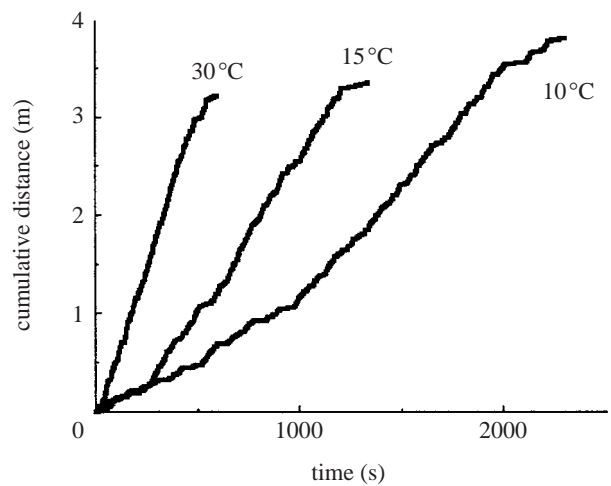
Figure 2. The effect of temperature on web-building speed. Walking speeds during radius construction (as cumulative distances) of one immature *Araneus diadematus* female, building a full web under three different temperature regimes on three consecutive days, are shown (temperature in °C).

(engineering) stress was plotted against nominal strain and the stress–strain data were analysed for a range of mechanical properties (figure 1). A single-classification ANOVA on the data for silk drawn under the control spinning conditions (at room temperature and drawing speed $20 \, \mathrm{mm \, s^{-1}}$) showed that there was a significant difference ($p < 0.0001$) between individual spiders for all the mechanical properties that we measured. In order to compare data between different spiders, we had to normalize the raw data. The measurements and calculations of each mechanical parameter for each spider are represented by X_{ij}, where i denotes the different spinning conditions and j denotes a single data point for each condition. The sample size under the different conditions is denoted by n_i. Given that $i = 0$ corresponds to the control condition, then the average (A) of the parameter under this condition equals $(X_{0j})/n_0$. In order to normalize the data of the parameter, each single reading is divided by A, i.e. X_{ij}/A for $i = 0, 1, \ldots, a$ and $j = 0, 1, \ldots, n$. Thus, all measured experimental data for each silking of a spider were divided by the average of the data from the control spinning conditions.

3. RESULTS

We filmed and analysed three *A. diadematus* spiders, with an average weight of $30 \pm 5 \, \mathrm{mg}$ (mean ± s.d.), building webs in two series of the three experimental temperatures of 10, 15 and 30 °C, going both up and down the sequence. The temperature was changed every day and one of the spiders built a new web every day at all points of the temperature scale. There were no discernible differences between the geometries (size, shape, number of radials and spacing of spirals) of the webs of any of the spiders built at the same temperature, whether in the ascending or descending sequence. However, there were very large differences in building speed between webs built at the different temperatures (figure 2). Not surprisingly, the highest temperature (30 °C) had the highest average radius construction speed at $6 \, \mathrm{mm \, s^{-1}}$ and the lowest temperature (10 °C) had the lowest average construction speed at $1.7 \, \mathrm{mm \, s^{-1}}$, whereas
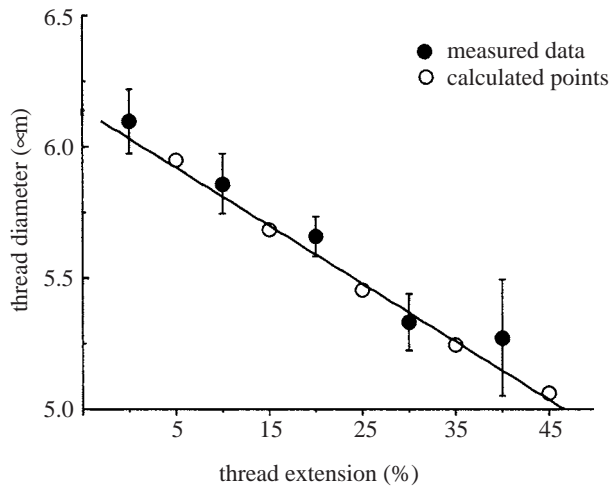
Figure 3. Thread extension affects diameter. Each experimental point (filled circles) is a mean (±s.d.) of four diameters measured on two thread sections at each extension. The theoretical points (open circles) were calculated assuming constancy of volume. Note that the measured Poisson ratio was well correlated overall ($p < 0.001$), but that the diameters were highly variable near the breaking elongation. The major ampullate dragline threads measured were drawn under control conditions for a large female *Nephila edulis* (2271 mg), producing thick threads in order to give small measuring errors during scanning electron microscopy.

Figure 4. The effect of drawing speed and abdominal temperature at the time of spinning on (*a*) the normalized silk diameter, and (*b*) the normalized energy required in order to break a thread. Reeling speeds (mm s^{-1}) are denoted by filled circles, and body temperatures (°C) are denoted by open circles. The temperature during the reeling trials was 25 °C, and the reeling speed during the temperature trials was 20 mm s^{-1}. The thread diameter (μm) and energy (GPa) were also calculated. The data points for each condition represent the average taken from several spiders (*n*), with four measurements (*n*) for each spider (temperature, $n = 7, 8, 10, 5$ and 5 and speed, $n = 4, 4, 5, 8, 11, 10$ and 5). The vertical bars give 95% confidence intervals.

there was an in-between speed of 2.8 mm s^{-1} at a temperature of 15 °C.

In order to study the effect of temperature and speed of spinning, we sampled silk from 21 individual females of *N. edulis* with an average weight of 527 ± 103 mg (mean ± s.d.). Under control spinning conditions (a drawing speed of 20 mm s^{-1} and a temperature of 25 °C), the average silk diameter was 3.35 ± 0.63 μm, the normalized average breaking strain was 0.39 ± 0.08, the breaking stress was 1.15 ± 0.20 GPa, the initial modulus was 7.87 ± 1.85 GPa, the yield stress was 0.153 ± 0.058 GPa and the breaking energy was 165 ± 28 kJ kg^{-1}. Note that the standard variations in this experiment typically ranged from 10 to 20% of the average values; given the inherent variability of the material (Madsen *et al.* 1999), this constitutes good data. Like most fibres, silk has a moderately positive Poisson ratio, i.e. the thread thins when stretched (figure 3). We measured a solid and linear relationship for the *Nephila* major ampullate dragline threads produced under control conditions over the whole range of extensions up to breaking at *ca.* 0.40 strain, i.e. at *ca.* 40% extension. This strain thinning was highly predictable until a point just before breaking at *ca.* 40% extension. Each 10% extension decreased a thread's diameter by only *ca.* 0.5%. We did not factor thinning further into the calculations of mechanical properties for three reasons. First, because it was within the typical variability for the properties of individual threads (Madsen *et al.* 1999); second, because for a typical thread of 3 μm diameter it would have been only marginally above our accepted measuring error of 0.1 μm for the magnifications used for data collection; and, third, because the ultimate reason for our study was to demonstrate that a spider's body temperature
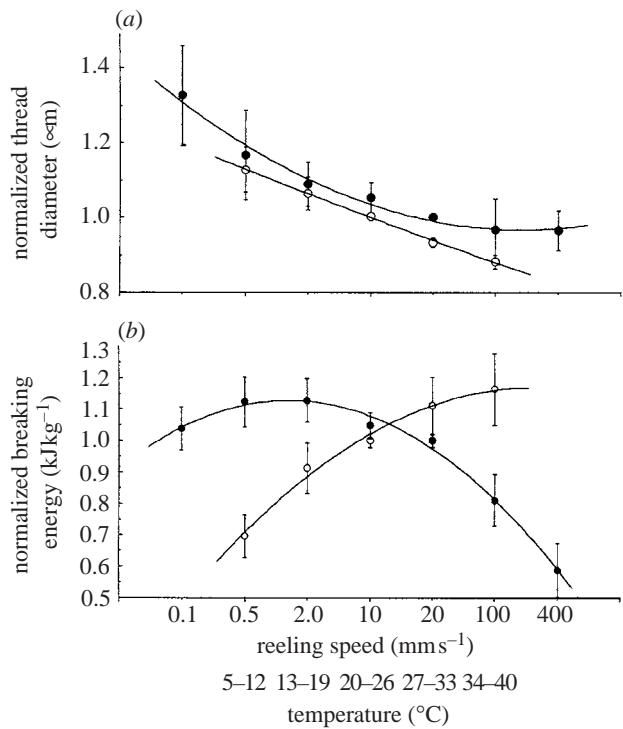
and running speed affect the absolute properties of a thread.

Both body temperature and drawing speed significantly affected silk diameters (figure 4*a*) (single-classification ANOVA, $p < 0.001$). Temperature was negatively correlated with silk diameter throughout the range, whereas the regression curve for reeling speed appeared to reach an asymptote at higher speeds. Comparison of the means for the reeling speed data demonstrated that speeds of 0.1, 0.5 and 2.0 mm s^{-1} were significantly different from speeds of 20 mm s^{-1} and above, but that there were no significant differences between speeds of 20, 100 and 400 mm s^{-1} (Tukey–Kramer method at a significance level of 5%). Thus, our data strongly indicate that silk diameters increase with decreasing speeds at reeling speeds below 20 mm s^{-1}, and stay more or less constant at speeds above this value. On one occasion, we attempted to draw silk at very high speeds of *ca.* 800 mm s^{-1}, but this resulted in thread breaking within a few seconds from the onset of reeling. The diameter of this silk was surprisingly large (approximately twice the diameter of silk drawn at 20 mm s^{-1}) and showed great variability along its length (a coefficient of variance (CV) ($= 100 \times$ s.d./mean) of 15.9% versus a CV of 8.1% in
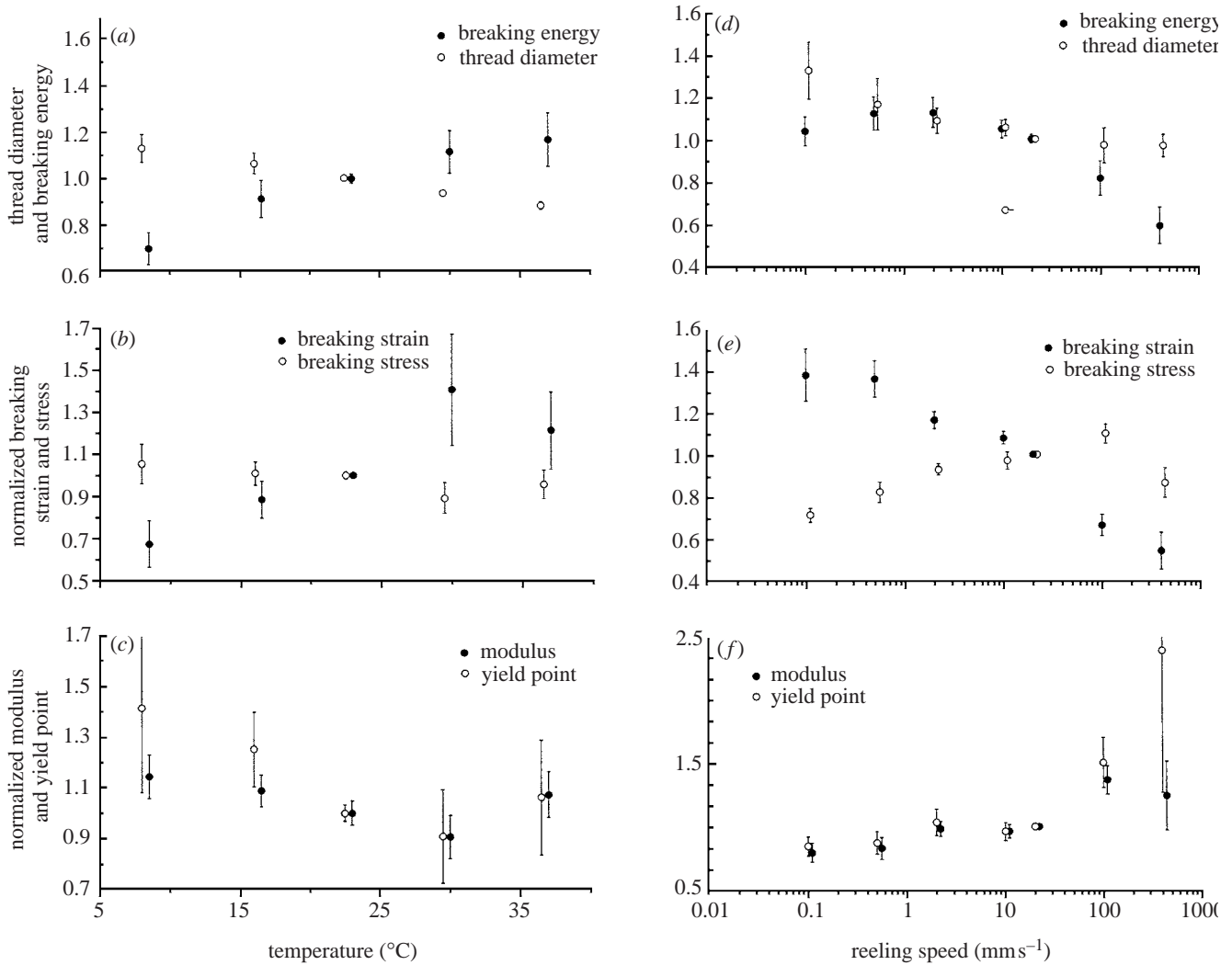
Figure 5. The effect of (*a*–*c*) abdominal temperature and (*d*–*f*) drawing speed on the normalized silk parameters. Shown here are the thread diameter and breaking energy (*a*,*d*), and stress and strain at breaking (*b*,*e*), as well as the initial Young's modulus and point of yielding (*c*,*d*). See figure 1 for a definition of the measured variables and see § 3 for the units of non-normalized data. Each point represents the average taken from several spiders, with three measurements for each animal. The vertical bars show 95% confidence intervals.

control silk). Comparison of the means for the effect of temperature at the time of spinning demonstrated that silk diameters varied significantly between the temperature intervals 5–12 and 19–26 °C, and between the temperature intervals 12–19 and 26–33 °C (Tukey–Kramer method at a significance level of 5%). Clearly, silk diameters decreased with increasing temperatures. Note that outside our experimental temperature range of 5–40 °C *Nephila* eventually stopped producing silk, with some individuals never recovering from these extreme exposures; hence, we did not analyse further any silks collected at these temperatures.

The drawing speed and temperature at the time of spinning affected the energy required to break a silk filament (figure 4*b*), as well as all the other stress–strain characteristics that we measured or calculated. A single-classification ANOVA demonstrated that the drawing speed and temperature had significantly ($p < 0.012$) different effects on these five mechanical silk properties, with some being affected more strongly than others (figure 5). Note, for example, that with increasing

temperature, the breaking energy increases whereas the thread diameter decreases (figure 5*a*), yet with increasing reeling speed, both the breaking energy and diameter decrease together (figure 5*d*). The breaking strain (figure 5*b*,*e*) increased significantly with increasing temperature, whereas it decreased significantly with increasing reeling speeds (Tukey–Kramer, $p < 0.05$ for speeds of 0.5, 10 and 100 mm s^{-1} and the first four temperature intervals). Conversely, the breaking stress was not appreciably affected by temperature, although it was by spinning speed (figure 5*b*,*e*). This interaction between the breaking strain and breaking stress determines the magnitude of the energy required to break a thread and, because the breaking stress showed only a small temperature effect, it was therefore the breaking strain that determined the breaking energy (figure 5*a*,*b*). Spinning speed affected the breaking stress and strain in opposing directions, with a positive correlation for stress and a negative one for strain; accordingly, there was no significant difference in the breaking energy between the first five speeds, although it dropped significantly at higher speeds (figure 5*d*).

The effects of both spinning speed and temperature were more dramatic on the diameter, breaking energy, stress and strain of the silks than their effects on the initial modulus and yield. There was a tendency (but no clear and significant trend) of the initial modulus to increase with speed and decrease with temperature (figure 5*c*,*f*). This tendency was supported by a significant difference between the lowest and highest speeds, and between the temperature intervals 5–12 and 26–33 °C. The yield stress is determined by the magnitude of the initial modulus and, therefore, the pattern of this parameter (the point at which the stress–strain curve yielded strongly) resembled the behaviour of the initial modulus (figure 5*c*,*f*).

4. DISCUSSION

At higher temperatures, the spiders walked faster and, consequently, they also spun silk faster. As can be deduced from figure 2, at 10 °C, the spider walked $1 \, \mathrm{cm \, s^{-1}}$, at 15 °C, it walked twice as fast ($2 \, \mathrm{cm \, s^{-1}}$), and at 30 °C, it walked more than twice as fast again ($6 \, \mathrm{cm \, s^{-1}}$). Studies on spiders of different species also confirm a similarly strong correlation between ambient temperature and the speed of walking/running (F. Vollrath, unpublished data). Similar relationships have been shown for other ectothermal invertebrates, such as bees (Heinrich & Esch 1997) and grasshoppers (Forsman 1999). However, silk is crucial to spiders and clearly it is strongly affected by both ambient temperature and walking/reeling speed. This allows us to view the constraints and trade-offs in an animal production system and their effects on other traits (such as behaviour) of the organism. For example, the exceptionally large variability in the yield points, in particular at low temperatures and high reeling speeds, suggests that silk produced under those conditions is less uniform a material at low elongations and small extension forces.

Animals that were silked faster (which are equivalent to faster-moving spiders) produced threads that were not only of different diameter but also gave stress–stain curves that were, on the whole, rather different to those of 'slower moving' animals (figures 4 and 5). These differences were not just the effects of diameter, as they persisted in the engineering values (i.e. values that were calculated on thread cross-sections). Note that the effect of stretch thinning (5% thinning per 10% elongation) (figure 3) would not have significantly affected the mechanical data as it would have been nearly identical for all treatments. Our data clearly show that the silks produced at higher reeling speeds were less extensible (figure 5*e*); they were weaker and had a slightly higher yield point (figure 5*d*,*f*) than silks spun more slowly. Figure 5*e* shows that the breaking stress rises with reeling speeds up to $100 \, \mathrm{mm \, s^{-1}}$, with a rather steep drop at the highest reeling speed. This probably indicates a drastic change in the composition of the material at these unusual spinning speeds. The strong nonlinear component in the effects of spinning speed on a silk's mechanical properties indicates that the protein refolding and cross-linking is strongly affected by the spinning process.

Animals that were silked under conditions of rising temperature (which are comparable to sun-exposed

spiders) showed no difference to cooler spiders in silk strength (figure 5*b*), but produced significantly more extensible and, hence, tougher silk (figure 5*a*,*b*). Clearly, temperature at the time of spinning can have a drastic influence, probably by affecting the rheology of the feedstock. The effect of temperature on the viscosity η of a material is described by the equation

$$\eta = \eta_{\mathrm{o}} \exp(E_{\eta}/RT), \qquad (4.1)$$

with η_{o} and E_{η} depending on the atomic/molecular structure of the polymer (Askeland 1984). The activation energy E_{η} depends on the ease with which molecules slide past each other. Thus, the viscosity decreases as the temperature increases and this obviously facilitates viscous flow. We note that this effect is exponential.

Both the speed of drawing and the temperature at the time of spinning affect the silk with strong nonlinear components. The interpolation curves of the measured and normalized stress–strain values typically cross (at the two control conditions used for normalization). We could imagine points midway between the speed and temperature effects for each treatment set, which, in most cases, could be connected by lines that were almost linear. This would indicate that the spinning speed and temperature would cancel each other out in their effect on silk properties if, in nature, spiders always experienced a positive correlation between walking speed and ambient temperature. We showed that warmer spiders walk considerably faster than colder spiders. Thus, under natural conditions, the effects of temperature and reeling speed would tend to lead to the two spinning conditions of speed and temperature, which are likely to be constraints in the silk production apparatus, to be traded off against each other, thereby producing silk with, on average, similar mechanical properties. The fact that the interaction of temperature and spinning speed in spiders is a production constraint can be deduced from industrial manufacturing of polymer filaments, for which we observe a similar effect of spinning conditions on the mechanical properties of fibres (Askeland 1984). We conclude that, in spiders, the metabolic constraints resulting from the typical invertebrate impact of temperature on metabolism and walking speed lead to a surprisingly balanced end product.

The ambient conditions during testing, such as humidity (Lin & Edmonds 1997) and temperature (Madsen *et al*. 1999), affect the mechanical behaviour of a silk thread. This influence of climate on silk might require a spider to adapt its silk, as it is spun in response to the climate experienced by the animal. Spiders modify their web architecture in response to the climatic conditions found during construction (Vollrath *et al*. 1997). Humidity, temperature and wind loading affect the geometry of a web by somehow influencing a spider as it makes its building decisions. The data presented here lead us to propose that at least some of these macroscopic changes in web architecture are the result of environmentally induced changes in the animal's web-building material, which feed back on its web-building algorithm. Thus it is not unlikely that differences in silk properties might be sufficient for explaining some of the differences found between the webs of different orb-weaving species (Craig 1987). To generalize further, the pronounced differences

in the mechanical properties of silks taken from different genera (Madsen *et al.* 1999) are likely to represent different trade-offs and adaptations to different ecologies as much as (if not more than) phylogenetic constraints.

We have described the mechanical properties of a fibre and the specific effects induced by specific ambient conditions. At present, we know neither the mechanisms by which the drawing rate and temperature affect the spinning process, nor how the spinning conditions affect the molecular composition of the fibres. If we did, we would have solved a crucial part of the spider's secret of making its supreme threads. However, we can speculate that the rate of drawing silk affects the time given to the silk molecules for aligning in the different sections of the spinning duct; at the same time, it might increase the shear and the forces of elongational flow. We can further speculate that the spinning temperature affects not only the viscosity of the silk feedstock, but also the rate of the different metabolic processes (e.g. acidification and drawdown) (Vollrath *et al*. 1998; Knight & Vollrath 2001) as they occur in the duct. Remember that the feedstock is spun as required after having been prepared in advance and stored in the gland (Vollrath & Knight 2001). The observed changes in silk diameter as a function of both reeling speed and temperature suggest that changes in the elongational flow and viscosity might be important in moulding the silk. Increased drawing rates lead to decreased silk toughness, whereas increased temperatures lead to increased toughness. If toughness was a measure of molecular optimization, then we should be able to gain novel insights into the design of spider silk by investigating the molecular sizes and orientations of silks spun under different spinning speeds and temperatures. Indeed, the first results are emerging from such experiments. Thermal analysis of the glass transition of fibre bundles suggests differences in the molecular alignments in silks produced at two different speeds (Guess & Viney 1998); single-fibre Raman spectroscopy suggests some differences in molecular composition in fibres produced under a wide range of different speeds and temperatures (Sirichaisit *et al.* 1999) and, most clearly, X-ray diffraction of single fibres as they are spun demonstrates that large differences in spinning speed significantly affect molecular orientation (Riekel *et al*. 2000; Riekel & Vollrath 2001). We are positive that future studies in this direction will one day allow us to tightly correlate the mechanical and molecular properties and this will be a long way towards copying the spider's superb biopolymer to good effect.

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