

Chapter 20

Spider Silk: Molecular Structure and Function in Webs

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20.1 Introduction

The evolutionary and ecological success of spiders is founded in part on numerous innovations in the chemistry, production, and utilization of their silk toolkits (Bond and Opell 1998; Blackledge et al. 2009). Opisthosomal silk glands in fossil *Attercopus* indicate that spider evolved silk at least 386 mya (Selden et al. 1991). The lack of spinnerets in *Attercopus* and other early “protospiders” suggests that the physical control over thread placement provided to spinning glands placed on muscled spinnerets played an important role in early silk and web evolution in Araneae (Selden et al. 1991). However, the diversification of the genes encoding spider silk proteins and the development of distinct silk gland morphologies were likely far more significant (Craig 2003; Garb et al. 2010). Silk production is largely uninvestigated outside of model species of orb-weaving spiders so that the tempo of evolution and the degree to which silk genes and spinning physiology might coevolve are unclear. Most work relating silk production and functions therefore focuses on orb-weaving spiders.

20.2 What Is Spider Silk?

Most spider silks consist of semicrystalline fibroins (fibrous proteins) where the amino acid chains are spatially constrained into rigid nanocrystal structures in some regions and amorphously free in other regions (Eisoldt et al. 2011). This gives silk a combination of high strength, due to the confinement, and high extensibility because the protein chains in the amorphous region are kinetically free and can

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move when threads are stretched. Spider silks therefore require the continuous application of large forces to stretch a great distance before breaking. Although spider silks are impressively strong and extensible compared to most natural and synthetic materials (Gosline et al. 1999), it is this work of extension, termed “toughness,” that is truly remarkable—some spider silks requiring five times more energy to break than an equivalent volume of Kevlar (Agnarsson et al. 2010).

The nano-structured, composite nature of spider silk is determined by an interaction between the amino acid sequence of the proteins and how fibers are assembled from liquid feedstocks. Both play important roles in controlling the material properties of spider silks. More important, amino acid sequence and spinning physiology provide potentially independent mechanisms that could be acted upon by natural selection in the evolution of the function of spider silks (Blackledge et al. 2011; Blackledge 2012). The end result is that most spiders spin “toolkits” of several diverse types of silks (Blackledge and Hayashi 2006), and individual silk types can vary significantly in their performance among species (Swanson et al. 2006, 2007; Sensenig et al. 2010).

20.3 Spider Silk Protein (Spidroin) Structure

A single spider silk protein is termed a spidroin, for “spider fibroin,” and is typically quite large, 200–350 kDa (Ayoub et al. 2007; Garb et al. 2010). Spidroins consist of three regions—an initial N-terminus of ~100–400 amino acids, a long internal region of highly repetitive amino acid sequences, and a final C-terminus (Fig. 20.1) (Ayoub et al. 2007). The N- and C-termini are remarkably conserved across different types of silks (Garb et al. 2010), even among silk genes that diverged >240 MYA. This pattern suggests that the terminal regions are critical for shared properties among silk types, such as how diverse spidroins are stored as liquid dopes and then subsequently transformed into solid fibers (Eisoldt et al. 2011). The internal regions, in contrast, are highly divergent among silk types—to the extent that they cannot be homologized (Gatesy et al. 2001). However, the amino acid sequences of the internal regions are remarkably similar for a single type of spidroin compared across species and have a strongly hierarchical organization. The internal region of a spidroin can be divided into repetitive modules that are each 40–200 amino acids long and are repeated 20–100 times in tandem (Ayoub et al. 2007; Garb et al. 2010). Each repetitive module is nearly identical in amino acid sequence to the others, likely due to homogenization from concerted evolution (Hayashi and Lewis 2000). A repetitive module consists mostly of short, highly stereotyped amino acid sequences called “functional motifs” that are approximately five to ten amino acids in length with spacer regions in between them.

Different functional motifs are predicted to form specific secondary structures. The identity and frequency of these secondary structures help explain variation in the material properties of spider silk. For instance, the crystalline regions in spider silk are formed from repeats of polyalanine and glycine-alanine. Both amino acids

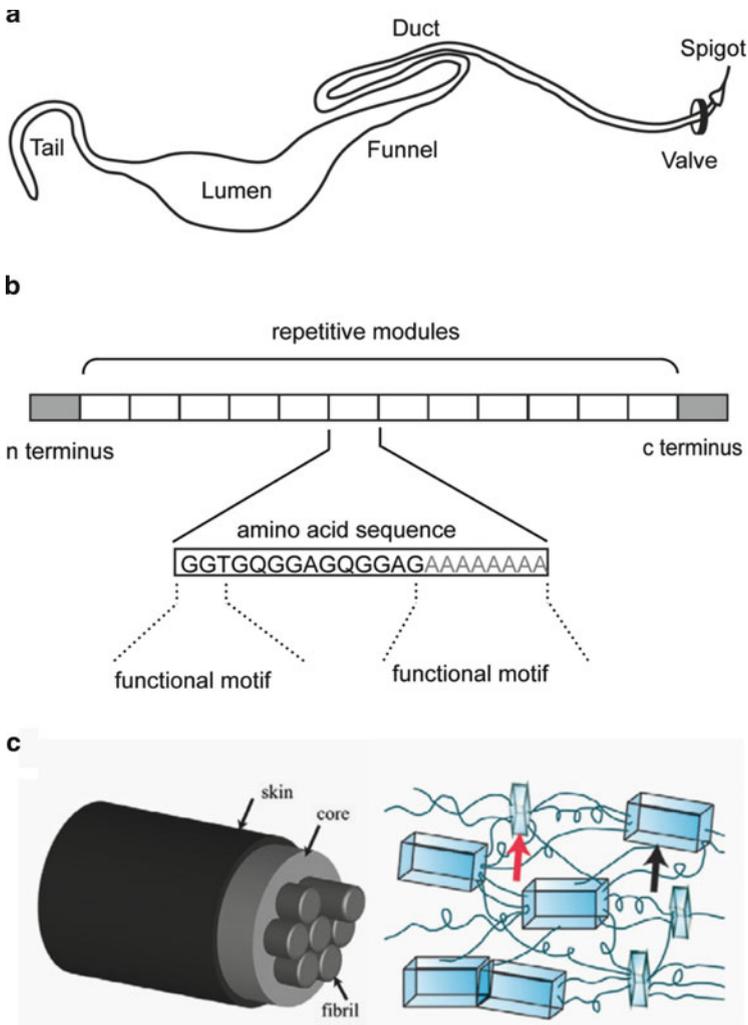


Fig. 20.1 Silk production and structure. (a) Spider silks are synthesized in the tail of the silk gland and are stored in the lumen as a liquid dope. As the dope passes through the spinning duct, a combination of shear forces, water uptake, and ion exchange produces a phase shift that causes nanocrystals to form and interlock the spider silks, thereby solidifying the fiber. The still wet silk fiber passes through a muscled valve that acts as a friction brake and controls the alignment of the spider silks along the fiber axis. (b) Spider silks consist of repeated modules of amino acids. Each module is composed largely of a few common functional motifs that form specific secondary structures. The N- and C-terminal regions are more heterogeneous, and their amino acid sequences are conserved among divergent silk types. (c) Hypothesized structure of major ampullate silk in an orb spider. A skin of lipids and glycoproteins surrounds a core of spider silks. The core likely consists of multiple fibrils. Individual spider silks are organized into highly crystalline domains embedded in an amorphous matrix. Two levels of crystalline domains are shown here. Adapted from Blackledge (2012) with panel C from Eisoldt et al. (2011)

contain small, hydrophobic side chains that fold peptides into β -sheets. Hydrogen bonding between adjacent peptide chains is particularly strong due to their nanoconfinement (Keten et al. 2010). These sheets stack together forming small nanocrystals that act as stiffeners and interlock multiple peptides. In contrast, the cyclic side chain of proline restrains the rotation of the carbon backbone of the amino acid forcing the peptide to coil, preventing β -sheet formation. Motifs of glycine-proline-glycine-X (where X denotes a limited subset of amino acids) instead fold into β -spirals that act like molecular nanosprings, increasing the extensibility of silk fibers (Hayashi and Lewis 1998; Jenkins et al. 2010). Other motifs exist, but their functions are more poorly understood. For instance, glycine-glycine-X is predicted to form a 3_{10} helix at the interface between the β -sheet crystals and the amorphous region of the spidroin.

Spidroins are encoded by a single family of genes, whose evolutionary history consists of repeated bouts of gene duplication followed by diversification of the internal repetitive regions (Garb et al. 2010). A single spider in the Orbiculariae can produce up to seven or eight distinct types silks from discrete glands (Blackledge and Hayashi 2006), although spiders in other clades produce fewer types. Most silks are composed primarily of one or sometimes two types of spidroins. For instance, major ampullate (MA) silk in orb-weaving spiders contains both major ampullate spidroin 1 (MaSp1) and major ampullate spidroin 2 (MaSp2). MaSp2 is distinct in its prevalence of glycine-proline-glycine-X motifs, while MaSp1 contains more polyalanine and glycine-alanine motifs. Thus, the material properties of MA silk are determined in part by variation in the expression levels of these two proteins. Moreover, cDNA libraries reveal that diverse silk genes can be expressed, at least at low levels, in some silk glands (Garb et al. 2006).

20.4 Spider Silk Processing

Fibrous spider silks are spun from liquid “dopes” stored in the lumens of silk glands that solidify nearly instantaneously as the dopes are pulled through the ducts of the glands (Fig. 20.1) (Eisoldt et al. 2011). The continued lack of success in accurately reproducing the remarkable material properties of native spider silk in fibers spun from recombinant or reconstituted silk proteins suggests that how a spider “spins” silk may be as critical as the composition of the dope. The process of fiber assembly is well-characterized for the MA silk glands of orb-weaving spiders (Eisoldt et al. 2011). Spidroins are secreted in the tail of the gland and stored as micelles in the lumen. The spidroins reach a remarkably high concentration, up to 50 % wt/vol, as the relatively hydrophilic terminal regions isolate the hydrophobic repetitive regions in the interior of the micelle. Fibers begin to solidify as the dope passes into the “S”-shaped spinning duct. Initially shear forces align the spidroins, while ion uptake and a slight drop in pH cause the terminal regions of spidroins to dimerize, thereby cross-linking molecules. This process exposes the repetitive regions of the spidroins, leading to the rapid formation of β -sheet crystals.

The still wet fiber is then subjected to further shear force that continue to align the crystals with the fiber axis as the fiber passes through a muscled valve that is present in the MA spinning duct, prior to exiting the spigot.

Orb spiders exert significant control over the shear forces applied to silk threads such that they can influence the relative alignment of the amorphous fraction of the fibroins. More force results in greater pre-straining of the silk making it measurably stiffer and less extensible. In fact, the material properties of MA silk produced by a single spider can vary by as much as 50 % under different spinning conditions due at least in part to this final draw down phase (Guinea et al. 2005).

Nutrition also influences the amino acid content of silk, which may be a response to the costs of synthesizing different amino acids (Blamires et al. 2012). The chemical composition of viscid glues appears particularly plastic (Higgins et al. 2001). However, the response is not universal (Blamires et al. 2010). Spiders change the performance of their silk in response to diet simply by altering structural properties of silk. The theridiid *Parasteatoda tepidariorum* spins thicker threads after encountering larger prey (Boutry and Blackledge 2008), and the thickness of threads closely scales with changes in body mass for many spiders (Blackledge and Zevenbergen 2007). *Argiope trifasciata* (Araneidae) even alters the properties of its dragline silk when shifting from horizontal to vertical surfaces (Garrido et al. 2002).

The final functional properties of a silk thread result from an interaction between the protein composition of the silk and spinning conditions. Amino acid sequence, determined by gene expression, sets the boundaries for a range of potential performance properties, while the spinning conditions—acidification, ion exchange, water resorption, and drawdown of the wet fiber—determine precisely where in that “performance space” a particular silk thread occupies. It is also useful to distinguish between the material properties of silk threads versus actual mechanical performance (Fig. 20.2). The former measures the intrinsic performance of materials, regardless of dimensionality, while the mechanical performance of any object is determined as much by its size and shape as by the material from which it is built. Thus, a thin cotton thread and thick cotton rope have identical material properties but radically different mechanical performance (Fig. 20.2b).

20.5 Silk Diversity

Eight to nine types of silk occur in Orbiculariae (orb-weaving spiders; see also Appendix, this volume), differentiated by their glandular origins, with fewer types occurring in other clades. The material properties and chemical compositions of each type of silk are distinct (Blackledge and Hayashi 2006) as are their functions (Fig. 20.3). Up to six types of silk play an integral role in the function of most webs. Adhesive silks—viscid aggregate glue and dry cribellate fibrils—are covered in Townley and Tillinghast (2013) and Opell (2013). The other silks are briefly outlined below.

Major ampullate (MA) silk forms the backbones of most araneomorph prey capture webs and is used extensively in other structures such as draglines,

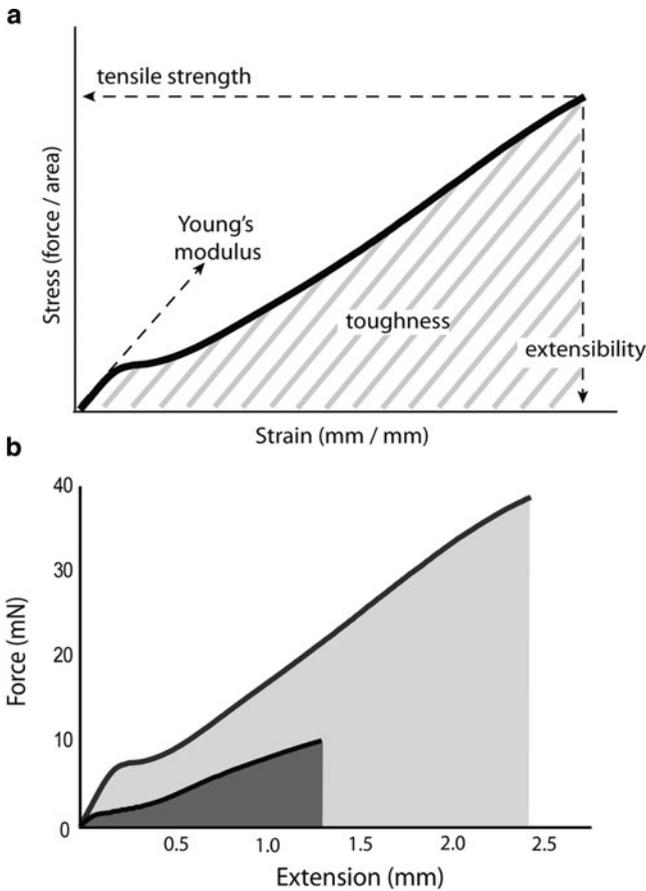


Fig. 20.2 Performance of silk threads. (a) Several material properties are typically quantified for silk threads. Young's modulus measures the stiffness in the initial "elastic region" where nearly all the energy of deformation is stored internally so that silk recovers completely when relaxed. Toughness measures the total energy per volume of silk necessary to extend a thread to failure. (b) Material properties are independent of the dimensions of the silk. Thus, two silk threads with identical material properties could perform very differently. Here, a longer thicker thread in *gray* requires more force to break at a greater extension compared to a shorter, thinner silk in *black*. The area under the force-extension curve represents the work that thread can perform—resisting moving prey, etc.

ballooning threads, and retreats. MA silk is also the best characterized silk, with material properties, chemical composition, and structural data for a small, but phylogenetically diverse set of species. MA silk is typically stronger compared to other silks and is also relatively stiff and less extensible. The tensile properties of MA silk also vary phylogenetically—orbicularian spiders produce measurably stronger and tougher MA silk threads compared to their sister RTA clade and basal taxa (Swanson et al. 2006). These differences correlate with the origin of MaSp2, which is currently known only from Orbiculariae.

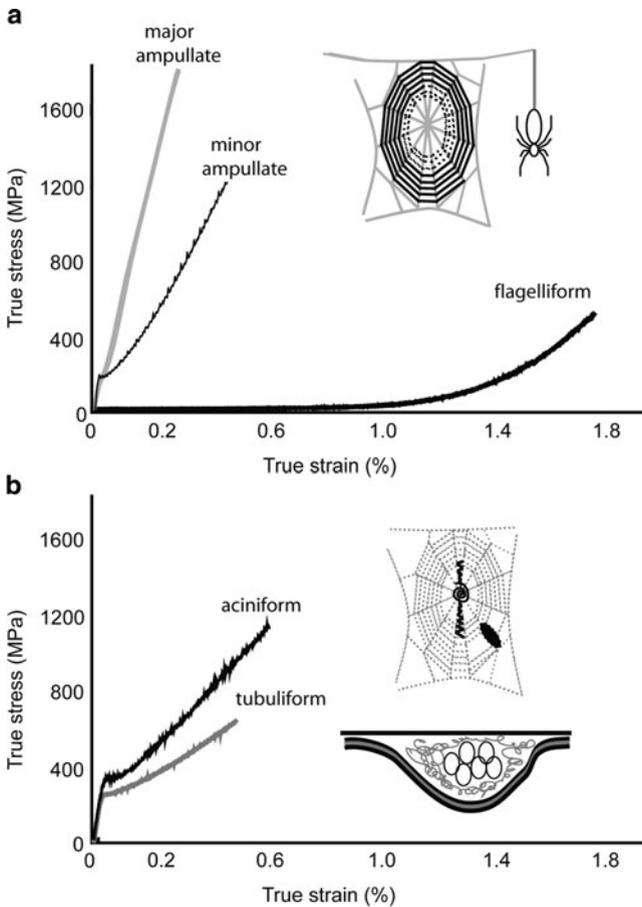


Fig. 20.3 The spider silk “toolkit.” Araneid spiders produce five distinct fibrous silks as well as piriform silk that form attachment disks and adhesive silks that coat capture threads (see Townley and Tillinghast 2013; Opell 2013). (a) Orb webs are composed primarily of major ampullate silk backbones and glue-coated flagelliform silk capture spirals. These two silks differ greatly in their ultimate strength, extensibility, and stiffness. Minor ampullate silk may be used to spin the temporary or auxiliary spiral, but evidence is unclear. (b) Aciniform fibers are sometimes added to webs to produce stabilimenta and are also used to wrap prey. Adult female spiders also possess tubuliform glands that are used, along with several other silk types, to construct egg sacs. From Blackledge et al. (2011)

Minor ampullate (MiA) silk is typically thinner than MA and also weaker but more extensible. Its composition is similar to MaSp1 and lacks the glycine-proline-glycine-X motif found in orb spider MA silk. MiA silk is used for aerial bridging and possibly the temporary spirals of orb webs. MiA threads also sometimes supplement draglines and web elements spun from MA.

Flagelliform (Fl) silk forms the axial fibers of capture threads in araneoid spiders (see Townley and Tillinghast 2013). It is notably more extensible and orders of magnitude more compliant than all other spider silks (Swanson et al. 2007). The

repetitive modules in Fl lack polyalanine repeats, thereby reducing cross-linking among the spidroins. Fl spidroins are instead dominated by glycine-proline-glycine-X motifs, where the proline residues fold into β -spirals that act as molecular “nanosprings” (Hayashi and Lewis 1998). Also, Fl silk is normally hydrated by water in the surrounding aqueous coating (see Townley and Tillinghast 2013), which increases molecular mobility also promoting extensibility (Vollrath and Edmonds 1989).

Piriform secretions join threads to one another and fix threads to the substrate. The secretions come from multiple spigots and consist of thin fibers embedded in a cement-like matrix (Blasingame et al. 2009). At least two unique proteins are expressed in piriform glands and may compose the fibers (Blasingame et al. 2009; Perry et al. 2010), but the chemical composition of the matrix is unknown. Piriform secretions produce mechanically diverse structures including permanent attachment disks and the quick-releasing attachments of gumfoot threads in cobwebs (Blasingame et al. 2009; Argintean et al. 2006). How the same set of glands can produce such divergent properties remains to be discovered.

Aciniform (Ac) fibers are produced from numerous spigots on the posterior median and lateral spinnerets (Coddington 1989), forming sheets or bands of silk, which are likely used in functionally similar ways to early silks. Ac glands occur in all araneomorph spiders, and their similarity to the poorly studied glands in mygalomorphs suggests that Ac silk was one of the earliest silks to evolve. The amino acid sequence, inferred from the only known cDNA transcript, shows a remarkable homogeneity among the repetitive modules—each of the 14 known modules is nearly 100 % identical in their ~200 amino acid sequence (Hayashi et al. 2004). Ac silk lacks the highly iterated crystalline-forming motifs found in MA silk (Rousseau et al. 2009) and is significantly more extensible than other dry silks (Hayashi et al. 2004). AC fibers are used to wrap prey, to line the interior of egg sacs, and to construct stabilimentum web decorations.

20.6 Function of Silk in Prey Capture Webs

Prey capture webs range in complexity from simple, silk-lined burrows to irregular sheets of silk spread across a substrate to aerial webs suspended on discrete frameworks of MA silk (Blackledge et al. 2009). While some webs primarily extend a spider’s sensory environment, such as the trip lines extending from many liphistiid and mygalomorph burrows, most prey capture webs also interact mechanically with prey—slowing or even adhering to the prey. The function of prey capture webs is determined by an interaction between the material and structural properties of silk threads and how those threads are arranged in webs (i.e., architecture). Orb webs offer the best understood example (Blackledge et al. 2011; Harmer et al. 2011; Blackledge 2012). The capture of flying insects by orb-weaving spiders is determined by how effectively their orb webs first intercept insects, then stops their flight, and finally retains the insects long enough for capture. In addition, orb webs must quickly

transfer information about the location of trapped prey to the spider and resist perturbations in the environment such as wind.

Prey interception is influenced mostly by the location of a web and its architecture. Thus, it is largely independent of the material properties and structures of silk. Eberhard (1986) modeled the spacing between rows of the capture spiral to maximize the number of insects intercepted by orb webs and found the optimal solution was just larger than an insect's wingspan. For a given amount of silk, a narrower mesh reduced orb size too much and decreases the total prey contacting the web, while greater spacing allowed too many insects to fly through the plane of the web without contacting threads. Web visibility presents an important exception to the independence of prey interception from silk properties because thicker threads are structurally stronger but also more visible.

The importance of amino acid sequence for silk function is dramatically illustrated by how orb webs stop and retain prey. Orb webs consist largely of two fibrous silk types and multiple adhesive silks (see Townley and Tillinghast 2013; Opell 2013). MA silk comprises the supporting radii and frames of orbs, as well as the backbones of most other types of prey capture webs, while Fl silk forms the core of the capture spiral. Both types of silk are remarkably tough—requiring great energy to rupture. However, MA silk is approximately 1,000-fold stiffer than Fl, with a breaking strength of 1–2 GPa and extensibility of 30–60 %. Fl, in contrast, is weaker and breaks at an engineering stress of \sim 250 MPa after stretching three to seven times its original length (Fig. 20.3a). These differences in material properties are determined primarily by the preponderance of crystal-forming polyalanine and glycine-alanine amino acid motifs in MA versus glycine-proline-glycine motifs in Fl.

Orb webs must dissipate tremendous kinetic energy though the silk to stop prey in midflight. Energy is dissipated primarily by the high hysteresis (or damping capacity) of MA silk in the radii. As the MA silk extends, the kinetic energy is transferred to heat when spidroins in the amorphous fraction of the silk rearrange as threads extend under impact (Fig. 20.4a). This prevents insects from ricocheting out of the web. Silk threads are so thin that air interacts with them as a relatively viscous fluid, and some models of orb web function therefore suggest that aerial damping also dissipates substantial prey energy (Lin et al. 1995). However, recent empirical data show that aerial damping plays only a minor role, at least for medium to large orb webs (Fig. 20.4b) (Sensenig et al. 2012). While abundant, the Fl silk in the capture spiral is so compliant that it does very little work of stopping prey (Sensenig et al. 2012). Energy dissipation is concentrated in a remarkably small portion of the orb's surface— \sim 25–30 % of the orb's surface accounts for 90 % of all the work of stopping prey (Sensenig et al. 2012) due to the nonlinear tensile behavior of the MA silk (Cranford et al. 2012). Because MA silk becomes more compliant after it yields, stress is concentrated in the local area of deformation until the silk stiffens significantly when approaching failure. As a result, even a moderately damaged orb web retains the ability to effectively stop insects elsewhere on the web's surface (Sensenig et al. 2012; Cranford et al. 2012).

Capture thread adhesion is investigated extensively, and many of the details are covered by Townley and Tillinghast (2013) and Opell (2013). However, the role of

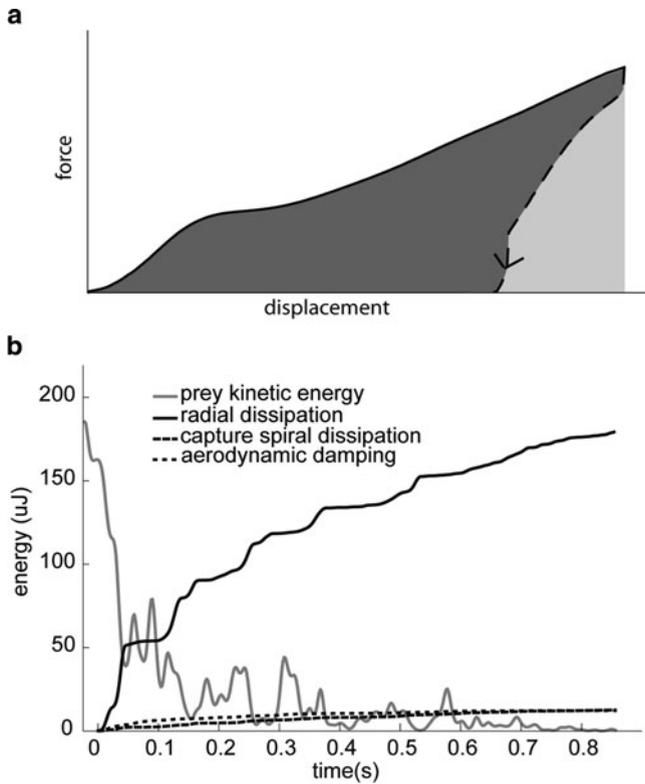


Fig. 20.4 Dissipation of prey energy. (a) Orb webs depend upon the high-energy damping of their major ampullate (MA) silk to stop prey. Approximately 60–70 % of the total work need to extend MA silk is transferred to heat. The 30–40 % that is stored (*light gray*) drives web oscillations. (b) The kinetic energy of prey can be dissipated through three routes—aerodynamic damping, damping in capture spiral silk, and damping in MA radial silk. At least for medium to large orb webs, most prey energy is dissipated through stretching of the radii in the local area of impact. Here, a 98 mg projectile strikes the web of *Araneus trifolium* (Araneidae) at time 0. Forward momentum is halted within the first 0.1 s, with energy stored in the silk being returned to the prey during each oscillation of the web (e.g., at 0.2 and 0.3 s). Although capture silk extends greatly during prey capture, the silk is so compliant that it does very little work. From Sensenig et al. (2012)

silk in prey retention at the whole web level is more poorly understood. Prey retention is particularly important for webs because many insects escape before spiders have adequate time to locate and subdue the prey. Simple architectural features of orb webs facilitate prey retention. Narrow spacing between rows of capture spiral increases the total number of threads adhering to any prey. The vertical orientation of most araneoid webs facilitates interception for vertical webs but, along with web asymmetry, also increases retention because insects that free themselves from one capture thread typically tumble down onto more adhesive threads (Opell et al. 2006). Townley and Tillinghast (2013) discuss how the mechanical performance of the axial Fl silk itself plays a critical role in promoting adhesion.

Silk also needs to effectively transmit information about the location of trapped prey to spiders. The MA silk in the radii of orb webs is particularly efficient at propagating longitudinal, rather than lateral or transverse, vibrations so that information is efficiently funneled to the hub of the web (Masters 1984). The degree to which this selective vibration transmission might be influenced by the crystallinity of the silk, which is itself oriented longitudinally and which varies substantially depending upon the ratio of MaSp1 versus MaSp2, is unknown. However, the tensioning of the radii by the spider during web building does influence vibration transmission. The tightening of radii during hub construction by hungry *Octonoba* (Uloboridae) tunes orb webs so that they respond more strongly to the vibrations of smaller trapped insects, presumably facilitating an increase in diet breadth (Watanabe 2000).

20.7 Evolution of Silk in Orb Spiders

Body size shifts orders of magnitude among different araneoid clades, so it is not surprising that it is a critical factor in the evolution of orb web architecture and silk properties (Sensenig et al. 2012). The stopping potential of orb webs, estimated as the maximum absorbable energy per cm^2 of web surface, increases in lineages of large-bodied spiders due to concerted changes in web architecture and silk properties. Larger spiders spin orb webs with disproportionately tightly packed threads and produce silk that is tougher than smaller species (Craig 1987b; Sensenig et al. 2010). The adhesive strength of viscid threads also coevolves with their tensile strength (Townley and Tillinghast 2013).

On the other hand, significant trade-offs exist in how silk functions during the interception, stopping, and retention of prey by orb webs. For instance, spiders can allocate a given amount of silk to an orb with a larger capture area that samples a larger portion of the air column, thereby increasing the total number of prey intercepted. But, this necessitates producing thinner or more widely spaced threads, thereby reducing stopping potential compared to a more compact web of the same volume of silk. Evolutionary changes in material properties of silks may mitigate some of these trade-offs. Spiders can use stronger, tougher silk in larger, widely spaced orb webs to maintain stopping potential (Craig 1987a; Sensenig et al. 2010).

20.8 Looking Beyond Orb Webs

The technological limitations of measuring silk properties for the very thin fibers produced in small-bodied lineages of araneid spiders, such as the Symphytognathidae, mean that substantial gaps in our knowledge extend to whole clades. More important, orbs represent only a minority of the prey capture webs spun by spiders (Shear 1986; Eberhard 1990). The functional properties of silks outside of araneoid orb webs are largely unexplored, with the exception of investigations into

the adhesiveness of cribellate threads (see Opell 2013) and a few studies of the molecular structure (Dicko et al. 2008) and material properties of (Swanson et al. 2006; Boutry and Blackledge 2010) major ampullate silk.

The gumfoot trap threads of cobwebs are a notable exception that illustrates just how different the mechanics of prey capture can be from the orb web “model” because cobwebs capitalize on energy storage (Argentean et al. 2006). Gumfoot threads are held under tension by the cobweb and release from the ground when prey contact their gluey bases, pulling small prey into the air and resisting moment of larger prey (see also Townley and Tillinghast 2013). More discoveries clearly await intrepid investigators.

20.9 Conclusions

Integrating the molecular structure and properties of spider silk threads with the function and ecology of webs is a relatively new frontier (Harmer et al. 2011). Spiders inspire many biomimetic innovations such as sensors (Barth 2012), water-operated motors (Agnarsson et al. 2009), adhesives (Seidl and Vidoni 2013), and robotic legs (Spagna et al. 2007; Zentner 2013). Yet, these efforts pale in dimension next to the quest to synthesize spider silk in the laboratory for use by industry, the military, and medicine (Hinman et al. 2000; Altman et al. 2003; Scheibel 2004; Vollrath and Porter 2006). Web ecology and spider evolution bring new perspectives to this effort and yield discoveries such as using web-spinning behaviors to predict ultrahigh performance silks (Agnarsson et al. 2010) or new design principles for glues (Sahni et al. 2012). A holistic understanding of silk functions in webs is equally important, though, for understanding the evolution of spiders.

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