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# Gumfooted lines in black widow cobwebs and the mechanical properties of spider capture silk

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## Abstract

Orb-weaving spiders produce webs using two types of silk that have radically different mechanical properties. The dragline silk used to construct the supporting frame and radii of the web is stiff and as strong as steel, while the capture spiral is much weaker but more than ten times as extensible. This remarkable divergence in mechanical properties has been attributed to the aqueous glue that coats the capture spiral, which is thought to decrease capture spiral stiffness and increase its extensibility. However, discerning the effect of the aqueous glue on fiber performance is complicated because dragline silk and the capture spiral are assembled from different proteins, which may also affect mechanical performance. Here, we use the sticky gumfooted lines of black widow cobwebs to test the effect of the addition of aqueous glue on the mechanical properties of dragline silk. We also surveyed orb-webs spun by a broad range of species for bundles of looped silk. Such bundles, termed windlasses, have been thought to increase capture spiral extensibility by "paying out" additional lengths of silk. Our results suggest that neither plasticization of silk by aqueous glue nor excess silk in windlasses can by themselves account for the remarkable extensibility of orb-weaver capture silk compared to other spider silks. This argues that the unique amino acid motifs of the flagelliform fibroins that constitute the core of the capture spiral play an essential role in capture silk's extreme extensibility.


***Keywords:*** Major ampullate silk; Flagelliform fibroin; Orb-web; *Latrodectus hesperus*; Dragline silk; Capture spiral silk

## Introduction

Orb-weaving spiders in the taxon Araneoidea produce webs using two types of fibrous silks that have radically different material properties (Fig. 1). Dragline silk is spun from major ampullate glands and is used to construct the frame and supporting radii of webs. Dragline silk is renowned for its unique combination of high tensile strength, stiffness, and extensibility that makes dragline silk exceptionally tough. This allows dragline silk to absorb far more kinetic energy without breaking than do manmade high-performance fibers such as Kevlar (Gosline et al., 1986). In contrast, the sticky capture spiral of the orb-web is composed of silk fibers produced by the flagelliform glands and coated with aqueous glue from the aggregate silk glands. Capture spiral threads are over ten times more extensible than dragline silk, but are neither as stiff nor as strong (Denny, 1976). The low stiffness of capture

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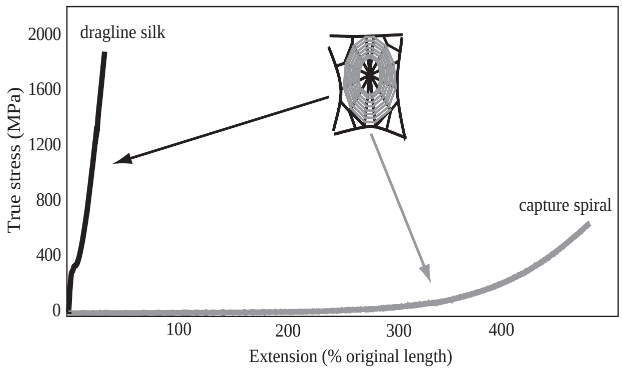


**Fig. 1.** Representative stress–strain curves for dragline silk (black) and capture spiral (gray) from the orb-weaver *A. argentata*. Major ampullate dragline silk provides a strong and stiff framework that supports the highly extensible, energy absorbing capture spiral. Note the one order of magnitude greater extensibility and the three orders of magnitude reduction in stiffness that characterize capture spiral relative to dragline silk.

spiral silk means that very little force is required to extend the silk 200–300% of its original length until the fiber gradually stiffens under the increasing strain. This results in a distinctive ''j'' shaped stress–strain curve, in contrast to dragline silk which is characterized by a stress–strain curve that is similar to the behavior of typical viscoelastic fibers in that it is initially a very stiff material and that it has a distinct yield region around 2–3% strain (Fig. 1).

The low stiffness and amazing extensibility of capture spiral relative to dragline silk is likely due to their different molecular structures. Though dragline and capture spiral silks are composed primarily of proteins from a single gene family, the genes coding for their silk fibroins are very divergent from one another (Gatesy et al., 2001). Therefore, the amino acid sequence of the flagelliform silk protein within the core of the capture spiral could result in a functionally unique molecular structure that increases extensibility. In particular, lengthy tandem arrays of $GPGGX_n$ amino acid subrepeats within flagelliform silk fibroins are hypothesized to form $\beta$-spirals that act as highly extensible molecular ''nanosprings'' (Hayashi and Lewis, 1998; Becker et al., 2003).

While the capture spiral and dragline silk do differ in protein sequence, it is possible that factors besides amino acid sequence may also explain the dramatic differences in mechanical properties between the two types of silk. At least two other hypotheses have been proposed to account for the unusual properties of capture spiral silk: (1) loosely coiled bundles of silk within glue droplets of the capture spiral, termed ''windlasses'', that unravel when fibers are stressed; and (2) hydration of the capture silk fibroins. These three explanations act at very different levels of organization and are not necessarily mutually exclusive.

The windlass hypothesis originated from a study by Vollrath and Edmonds (1989), where they coined the term ''windlass'' to describe the coiling of slackened flagelliform fibers within glue droplets that they observed when capture spirals of *Araneus diadematus* were relaxed to approximately 50% or less of their original length. While Vollrath and Edmonds originally proposed windlasses as a mechanism that maintained tension during *relaxation* of capture threads, windlasses have since been interpreted in the literature as structures that facilitate the extensibility of capture silks (e.g. arguments of Schneider, 1995 vs. Vollrath and Edmonds, 1995; see also Becker et al., 2003). Under this hypothesis, it is the paying out of excess silk from these windlasses that makes capture spiral threads so extensible. We test the windlass hypothesis by examining the webs of a phylogenetically diverse sampling of araneoid orb-weavers for the presence of windlasses in capture spiral. If windlasses are not present in capture spiral at native tension then they cannot function to enhance capture spiral extensibility.

The hydration hypothesis suggests that the difference in properties between capture spiral and dragline silks is caused by the hydration of the flagelliform core fibers of the capture spiral by water from the surrounding glue. Hydration is thought to alter the molecular bonding of silk fibroins to one another, causing the silk to behave as a rubber with a particularly low modulus of elasticity (Gosline et al., 1984). Thus, the aqueous coating of glue that makes capture spiral sticky may also plasticize the silk, thereby increasing capture spiral extensibility (Vollrath and Edmonds, 1989). This hypothesis is best tested by directly comparing the mechanical performance of the two types of silk with and without aggregate glue added to the fibers. Unfortunately, this test is difficult because normally an aqueous aggregate secretion coats the flagelliform core fiber of the capture spiral and never coats dragline silk. Thus, it is difficult to separate the effects of hydration by this gluey coating from the material properties of the flagelliform fibers themselves. However, the sticky gumfooted lines of cobwebs provide a unique opportunity to test the hypothesis that the extreme extensibility of araneoid orb-weaver capture silk is due to plasticization of the silk by aqueous glue. Black widows, *Latrodectus* spp. (Theridiidae), evolved from orb-weaving spiders, but now construct cobwebs rather than orbs (Griswold et al., 1998). Instead of capture spirals, gumfooted lines extend downward to the substrate from the supporting scaffolding of the cobweb, and only the bottom 5–15 mm are coated with aqueous glue (Fig. 2A; Benjamin and Zschokke, 2002, 2003). The aggregate glands that produce the sticky droplets of the gluey ''foot'' region are homologous to the aggregate glands