In situ three-dimensional spider web construction and mechanics

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Spiders are nature’s engineers that build lightweight and high-performance web architectures often several times their size and with very few supports; however, little is known about web mechanics and geometries throughout construction, especially for three-dimensional (3D) spider webs. In this work, we investigate the structure and mechanics for a Tidarren sisyphoides spider web at varying stages of construction. This is accomplished by imaging, modeling, and simulations throughout the web-building process to capture changes in the natural web geometry and the mechanical properties. We show that the foundation of the web geometry, strength, and functionality is created during the first 2 d of construction, after which the spider reinforces the existing network with limited expansion of the structure within the frame. A better understanding of the biological and mechanical performance of the 3D spider web under construction could inspire sustainable robust and resilient fiber networks, complex materials, structures, scaffolding, and self-assembly strategies for hierarchical structures and inspire additive manufacturing methods such as 3D printing as well as inspire artistic and architectural and engineering applications.

Spiders are among nature’s most efficient and prolific engineers: they design, build, use, and maintain high-performance and lightweight silk webs. They have inspired applications in the field of biomedicine (1), structural engineering (2), electronics (3), optics (4), art (5, 6), and music (7). Spiders produce silk fibers with outstanding mechanical and biological properties; they are strong and extensible while also being biodegradable and biocompatible. Their superior mechanical properties are rooted in their hierarchical organization that spans from protein amino acid chains to silk fibers to spider webs (8–10). They have survived and prospered through millions of years of evolution owing to their superb adaptation skills (11). Indeed, spiders can spin up to eight different types of silks with different properties and functions and create numerous web architectures that range from simple T webs and typical two-dimensional (2D) orb webs to complex three-dimensional (3D) webs such as funnel, cob, and tangle webs (12). Not only do they produce, build, and tune highly functional silks and large-scale web structures, they also monitor, repair, and recycle webs. Moreover, the complex structures seen in spider webs have been compared to other natural structures such as galaxies (13, 14).

Spiders use vibrational information to locate and identify potential mates, prey, predators, and defects on their webs (15–18). Webs avoid catastrophic failure because the interplay between the nonlinear behavior of dragline silk and complex spider web architecture localizes defects, making quick repairs possible (19). This makes the complex of spider, silk, and web a self-sufficient, self-monitored, and self-repairable system. This system can inspire sustainable and high-performance complex new materials, structural designs, and construction procedures (20). Spiders build web structures several times their size with very few external supports, using only silk fibers. Comparing them to traditional construction at the human scale, such a large structure would require bulky scaffolding, large construction equipment, and many workers. Understanding the construction stages of a spider web could lead to more efficient and sustainable construction.

Gaining such understanding can begin by analyzing the 2D orb web geometry and construction process by facing a camera to the plane of the web. Orb webs are composed of stiff dragline silk radial threads and extensible and sticky viscid silk spiral threads. Orb web construction starts with the spider building the frame of the web after exploring the site. Orb-weaver spiders build the hub with radial threads and then place the spiral threads using spiral scaffolding as a guide. Compared to 2D orb webs, 3D spider webs are more complicated to describe because of their complex fiber architecture and their nanoscale fibers. Su et al. (12) have reported a method to automatically quantify 3D spider web geometry by taking high-resolution images of slices of the web that are illuminated by a sliding sheet laser. Image-processing algorithms were then used to translate the sequence of 2D images into the fibers and nodes of the 3D web network (12). The scanned spider webs were built on top of a water container, necessary to deter the spider’s escape (21), and then brought to the experimental setup for scanning (12). The original manual scanning and spider web method was developed by Saraceno et al. (5, 22–26). Similarly, Yablonina (27) approximated 3D spider web architecture using infrared cameras and a sliding laser and investigated the importance of supporting threads, reinforcing threads, and joints between threads by recording spider movement during web construction. Arachnologists have studied 3D spider web construction through meticulous behavioral observations and video recordings. Jörger and Eberhard
characterized three stages of the construction of *Achaearanea tessellata* spider webs: exploration, construction of anchor lines and tangle web, and alternating construction of sheet and tangle webs. Other species follow a similar web construction process. For example, *Tidarren sisyphoides* spiders explore the surroundings, anchor the retreat, build the web scaffolding, and then construct the dome-shaped sheet, horizontal sheet, and upper tangle web (29). *Steatoda triangulosa* comb-footed spiders explore and then build a 3D supporting structure and gumfooted lines that connect the 3D structure and the substrate (30). Web construction observations have already inspired new automation methods (25) and algorithms (31) for fiber network construction. Other work (32) has recently investigated the mechanical behavior of *Cyrtophora citricola* 3D spider webs under uniaxial stretching and projectile impact. The interplay between the nonlinear behavior of dragline silk and the complex redundant architecture of the webs leads to robust and resilient webs under uniaxial stretching. The tangle web plays a crucial role in the functionality of the spider webs: it filters in prey and protects the spider from predators.

While completed 3D web-construction patterns and topologies have been investigated, little is known about the structure and mechanics of 3D spider webs during construction. We provide insights into these heretofore unknown processes in this paper. In the current study, we will investigate the mechanical behavior of the different construction stages of a *T. sisyphoides* spider web and determine whether the web can carry out its biological functions during construction. We use image processing and computational simulation methods to quantify and validate what has been observed in nature.

Our paper is organized as follows. First, we present the different topological and mechanical properties of the web under construction. Second, we conclude with a summary and investigate future applications of web-inspired structures and construction processes. Finally, we describe the experimental and computational methods to obtain the topology of a 3D spider web during construction. We also describe the mechanical model and simulation setup of the 3D spider web during this time.

### Results

**3D Spider Web Construction.** We first investigate the different web architectures at different stages of construction. Under laser light and a restricted web-building environment, the spider built a tangle web, which is similar to *T. sisyphoides* spider webs found in nature (33, 34); however, some *T. sisyphoides* add aerial sheet elements to their webs, as described in refs. 29 and 35. Fig. 1 shows the scanning setup used for imaging the spider web under construction. Fig. 2 compares the web scans and models over time. The density increases from $0.07 \times 10^{-3}$ to $3.56 \times 10^{-5}$ kg/m$^2$ over 7 d of construction. The scans and models show that the spider builds the foundation of the web geometry during the first 2 d of construction, after which the spider reinforces the exiting network with limited expansion of the structure within the frame. The spider web construction progress is not linear, as the main structure of the web is built in the first 2 d. Indeed, the web density increases by 700% between day zero and day 1, 400% between day 1 and day 2, and only 9% between day 2 and day 3. This behavior is similar to what has been described in ref. 29; the *T. sisyphoides* spiders use one to four nights to build complete and functional webs and then add silk threads to the web the following nights.

**Movie S1** is a montage of the consecutive scans taken along the depth of the spider web, in which each video frame is a superposition of all the scans over 7 d of one slice of the web. The days are color coded from dark blue to yellow. The video shows the changes in the 3D web structures over time. We observe that the nodes connecting the same fibers shifted position over time; otherwise, all the video frames would have the color of the last day (yellow). By adding silk structures to the web, the spider tunes web tension and fiber connection locations.

The construction behavior of the *T. sisyphoides* spider can also be observed through the fiber length distribution of the different web construction stages (Fig. 3A). We observed that most fibers making the web are spun during the first 2 d of construction, after which, the number of fibers increases slowly over several days. From day zero to day 1, the fiber length median increases from 2 mm to 3 mm. From day 3 of the construction, the fiber length median is stable at 4 mm. This confirms, once again, that the main structure is built within the first 2 d, then, the structure is reinforced without expansion over the following days. The *T. sisyphoides* spider web here follows a similar skewed fiber length distribution to the *C. citricola* spider web described in ref. 12. Moreover, the average fiber length of the *C. citricola* web is of 3 mm (12), which is comparable to the web described in this study. Fig. 3B shows the node degree distribution of the different web construction stages.

In graph theory, the degree of a node is the number of edges connected to a vertex (36), which, in the case of the spider web, means the number of fibers that are connected to a node. The node degree ranges from 1 to 16, but only one or two nodes have a degree above 7. The high degree nodes could be artifacts from image processing on scans with higher laser light noise. Nodes of degree 1 and 2 are nodes that are attached to the frame, in which the spider spins the web. The fibers are considered straight, so there are no nodes of degree 2, unless they are attached to the boundary frame. Most nodes have a degree of 3, which means that most fibers are attached to two other fibers. The degree distribution is very similar to the *C. citricola* spider web, which also has most nodes with a degree of 3 (12). The number of nodes of degree 3 increases greatly in the first 2 d, which is consistent with what has been observed in the scans, models, and fiber length distribution.
The upgraded, remote, and automatic method for scanning and modeling spider webs can be used efficiently for tracking stages of construction of a spider web, and it can be used consistently for different types of spider species. However, there is a trade-off between web imaging frequency and quality. High-quality images of a spider web require the spider not to move excessively, as this can disturb the web structure and lead to blurry images over the duration of the whole web scan (34 min). A higher scanning speed lowers the chance of the spider moving but leads to lower resolution web images. *T. sisyphoides* spiders, belonging to the Theridiidae family, usually build their webs at night, as they are sensitive to light, which could disrupt web construction (29, 34). Increasing the web-scanning frequency would show more details of the construction over time; however, more laser scans would likely slow down or even stop web construction. As an opportunity for future work, the current experimental setup could be improved by adding infrared light and a camera that could record the position of the spider over time without the need for visible light. With an infrared component, we would be able to follow the position of the spider, which would help with deriving the fiber placement and reinforcement sequence.

**Spider Web under Stretching.** In nature, spider webs that are attached to moving supports, such as tree branches, sliding windows, and cupboard doors, are being constantly stretched. Under those natural stretching conditions, spiders are able to build strong and resilient webs that are functional and repairable. To understand whether the web can withstand stretching during construction even before being fully complete, we investigate the mechanical performance of 3D spider web construction stages over time under uniaxial stretching. The composite stress-strain curves of the spider web over 7 d of construction under uniaxial stretching along the *x*, *y*, and *z*-axes are shown in Fig. 4A. The stress–strain curves show that the spider webs first follow a linear elastic behavior and then a nonlinear stiffening until the failure of the first fiber, after which the web is subject to continuous fiber failures. The nonlinear behavior and failure of individual silk fibers can be found within the composite stress–strain curve of the web. Indeed, the spikes coincide with individual fibers breaking. After the fiber bearing the load reaches its failure stress and breaks, the load is transferred to its connecting fibers. Because of redundancy in the structure and the nonlinear behavior of dragline silk, the spider web does not fail catastrophically at any stage of construction. A similar behavior can be found for the tangle regions of a *C. citricola* spider web, which is more than 10 times denser, under uniaxial stretching (32). In addition, web strength increases with web density, which increases as the construction progresses. Denser webs have a higher strength because more fibers contribute to carrying the load generated by the uniaxial stretching of the web. In particular, web strength increases greatly in the first 2 d of construction, which is when the main web structure is built. After the second day of construction, the web strengthens slowly, as the spider reinforces its web without expansion.

Using nondestructive uniaxial stretching simulations of the different stages of web construction, we show that spiders first focus on building the main structure within only a few days, which is strong and resilient. Even at the early stages of construction, the web avoids catastrophic failure, as sequential fiber failure distributes the loads to the connected fibers via the combination between web redundancy and nonlinear dragline silk. This allows the spider to repair the existing web without needing to build a new one. From this strong web foundation, the spider adds silk to reinforce the web on subsequent days, increasing web density and consequently web strength. The spider’s construction method consists of prioritizing a fast build of the structure followed by slow structural reinforcement while using only silk as material and keeping the structure stable and functional throughout construction. This approach could inspire more sustainable fiber structure construction methods that are stable, functional, repairable, and always reinforceable.

Web strength and toughness increase with density, which increases with construction time, as is summarized in Fig. 4B. The increase of web strength and toughness has also been described for a *C. citricola* spider web in ref. 32. Web strength and toughness variations with web density are fitted using the following equations:

\[
\sigma_x = d \times 2.929 \times 10^4 + 0.2096, \quad [1]
\]

\[
T_x = d \times 5.923 \times 10^4 + 0.09969, \quad [2]
\]

\[
\sigma_y = d \times 5.18 \times 10^4 + 0.07719, \quad [3]
\]

\[
T_y = d \times 5.445 \times 10^4 - 0.05103, \quad [4]
\]

\[
\sigma_z = d \times 2.491 \times 10^4 + 0.115, \quad [5]
\]

\[
T_z = d \times 4.109 \times 10^4 + 0.008784, \quad [6]
\]

with \(\sigma\) and \(T\), web strength and toughness along the *x*, *y*, and *z*-axes, and \(d\), density. The web strength increases more with...
density along the $y$-axis because more fibers are aligned in the $y$ direction. Web toughness increases with density because of the web redundancy; the uniaxial stretching load is transferred to one or a few fibers at a time, which is transferred to other fibers once they break.

Uniaxial stretching simulations are a nondestructive method to measure the strength and toughness of the *T. sisyphoides* spider web throughout construction. Through web visualization (Fig. 2) and an analysis of mechanical properties (Fig. 4), we show that most of the web’s structure and mechanical performance is realized between day 1 and day 2 of construction. Taking inspiration from the mechanics of webs during construction could lead to lightweight and high-performance network composites with stable architecture and tunable properties throughout construction.

Fig. 3. Fiber length and node degree distribution histograms over 7 d of web construction. (A) The fiber lengths follow a skewed distribution (bars in blue), as most fibers are shorter than 4 mm. As the construction progresses, the fiber length median increases within the first 2 d, then is stable after the third day of construction. The increase in the fiber length distribution between each day and its previous day (bars in green) shows that most of the long fibers (length $>10$ mm) were constructed during the first 2 d, and after that short fibers (length $<10$ mm) were mostly used to reinforce the network. (B) The node degree is the number of fibers that are connected together at a node. Nodes of degree 1 and 2 are fiber extremities that are attached to frame boundary. Most nodes are of degree 3, which is consistent with what has been derived for the *C. citricola* spider web (12).
Spider Web under Projectile Impact. Spider webs are naturally subject to projectile impact from prey, predators, and debris, which is why webs are rarely found intact in nature. Here, we investigate the prey-catching performance of the T. sisyphoides under different stages of construction to test the hypothesis that spider webs are functional throughout construction. Projectiles, representing a fly prey, are thrown at a velocity of 0.5 m/s into the different locations of the web. Each simulation consists of one projectile thrown into the web under construction at one location. Fig. 5 shows the projectile deceleration map, in which the ratio of speed after impact over the speed at impact is colored from red to dark blue for high deceleration to no deceleration, respectively. The maps are mostly blue, which means that the velocity ratio remains high for most impact locations. The spider web lets most of the flies through without slowing them down because of the very low density of this spider web. Most projectiles would hit one or a few fibers and slide through the web. While most prey escape the web, we can identify a few locations where the projectile will considerably slow down each day of the construction from day 1.

The locations where the projectiles greatly decelerate are the areas where prey has a higher chance to get caught by the spider. After one day of web construction, the spider is able to catch food if the prey enters the web at a specific location. At each stage of web construction, the location of high prey deceleration changes, demonstrating that the spider tunes its fiber architecture over time, although the foundation of the structure remains the same. SI Appendix, Fig. S1 shows that the increase in web density is inhomogeneous, as several localized regions have a much higher densification rate than the rest of the web. The locations of these regions are correlated with the locations of high prey deceleration. While the T. sisyphoides spider used in this study did not create aerial sheet elements, some spiders of this species add an aerial sheet to their webs (29, 35). This allows the spider to sense prey entering the tangle web as it drops onto the sheet, allowing the spider to then attack (29). Similarly, the tangle region of the C. citricola web would help filter and slow down the prey entry into the tent region, where the spider waits (32). Here, we have shown that the web can efficiently decelerate prey projectiles. Consequently, the web increases the probability of catching prey at very specific locations in the web and after only one day of construction.

The models can also be used to inspire new materials designs, forming a route for bioinspired spider web architectures. Fig. 6 depicts physical models of the scanned webs. Fig. 6A shows a small section of the web on day 7, printed for close visual inspection at large scale. Fig. 6B depicts the entire web on day 1. The left shows the 3D model, and the right the printed specimen, in both cases, for direct visual comparison.

Discussion
This study presents insights into the mechanical and functional performance of a 3D spider web during construction and hence structural evolution during biologically relevant function. In particular, we focused on the tangle web of the T. sisyphoides spider. We advanced our existing web-scanning method, which previously could only be used for completed webs, into a fully automatic and remotely monitored scanning setup for spider webs under construction. Using image-processing algorithms, we transformed 2D images of slices of the web into a 3D fiber network. The scans and web models showed that the T. sisyphoides spider built most of the web structure in the first 2 d of construction, after which it used silk to reinforce and tune the structure without expansion. We used a
mesoscale bead-spring particle dynamic simulations of the web at different construction stages to investigate its mechanical behavior under uniaxial stretching and prey projectile impact. We found that web strength and toughness increased with web density, which increased over construction time.

Notably, throughout web construction, the *T. sisyphoides* spider web is robust and resilient; it avoids catastrophic failure because of its complex architecture and the nonlinear mechanical behavior of dragline silk. The spider can then repair defects to maintain web functionality, such as decelerating and catching prey. We then simulated prey projectiles being thrown at the spider web at hundreds of different locations per construction stages. Due to the web’s high porosity, most prey passed through the web. At very specific locations, starting from Day 1, the spider web could cause considerable deceleration of the prey, thus increasing the capture rate. Learning from and improving on the spider’s construction process could lead to an innovative assembly method for stable, functional, repairable, and reinforceable fiber structures.

In nature, *T. sisyphoides* spiders build tangle webs (33, 34), with some adding aerial sheet elements (29, 35). In the artificial environment created in this study, the *T. sisyphoides* spider did not add any aerial sheet components. This may be as a result of a number of environmental and biological factors such as diet, age, light sensitivity, and space constraints. Spiders adopt behavioral plasticity to change their silk-spinning and web-building behaviors in response to selective pressures (37). Indeed, web geometry could depend on the energy level of the spider; in one study, starved western black widow *Latrodectus hesperus* spiders designed their webs to catch prey more efficiently than fed spiders (37). Using the automated and nondestructive imaging, modeling, and simulation methods reported in this paper, we now have a way to study the effects of those parameters. For example, we can quantify the change of web construction behavior under external stimuli such as minimal substrate, expanding, vibrating, and long-span supports. Investigating how spiders adapt their web-building behavior to artificial environmental stimuli, may lead to flexible and adaptable 3D network structures and assembly methods in complex environmental conditions.

Moving forward, we can use these imaging methods and computational simulations to investigate the architectural and mechanical properties of webs built by different spider species in different artificial environments. Computational simulations are essential for studying the web over time without disturbing the

**Fig. 5.** Projectile impact deceleration map. The color map represents the ratio of the speed after web impact over speed at impact (0.5 m/s) (units in centimeters). Most prey projectiles fly through the web because of its high porosity. After the first day of construction, the web can decelerate prey projectiles at very specific locations and consequently increase its capture.

**Fig. 6.** Physical models of the scanned webs. A shows a small section of the web on day 7, printed for close visual inspection at large scale. B depicts the entire web on day 1. The left shows the 3D model and the right the printed specimen, in both cases, for direct visual comparison.
spider and destroying the web. The scanning, imaging, and simulations can be used in an automated and systematic way. Using this consistent method, we can investigate webs built by different species and generate more geometrical, construction, and mechanical web properties that can be used for deep learning to design spider- and web-inspired architectures, material assembly methods, and mechanical properties for specific functions. To obtain even more details on the fiber assembly sequence, we can add infrared lights and cameras to the experimental setup to minimize light disruption and follow spider movements during construction. This could lead to efficient spider-inspired fabrication sequences for complex fiber structures, tensile structures in architecture, and art. Expanding our knowledge of spiders’ web construction, silk recycling, web monitoring, and repair methods could inspire novel self-sufficient, self-reparable, and self-monitored smart structures. This knowledge can also inspire artistic, design, and architectural interventions—such as complex and large-scale tensile structures—via creative collaborations that both engage and inform materials and engineering sciences (5, 14, 38).

Materials and Methods

T. sisyphoides Spider. Spiders of the genus Tidarren build tangle webs with aerial Ellis (29). In this study, we focus on the webs of T. sisyphoides (Walckenaer, 1842) spiders (Fig. 1C). They can be found in a wide geographic range from the United States to Argentina (39). We purchased female T. sisyphoides spiders from Spider Pharm (https://spiderpharm.com/) and fed them crickets from Premium Crickets (https://www.premiumcrickets.com/). We chose to use female spiders for their web-building behavior and their larger size compared to male Tidarren spiders (40).

Spider Web Construction Scanning. We extended the experimental setup described in ref. 12 to scan the 3D spider web during construction. The setup for scanning the static 3D spider web consisted of a raised table, upon which the finished 3D spider web was placed, and a supporting stand of a moving rail machine, upon which the high-resolution camera and the sheet laser were placed at a fixed distance. The camera’s focus point was always aligned with the plane of the sheet laser; during scanning, the laser and the camera moved together along the depth of the spider web. The camera took high-resolution images of the slices of the web illuminated by the sheet laser (12). While the previous scanning method was automatic, it required intermediate manual interventions, such as placing the spider web on the raised table, starting the camera shutter timer together with the movement on the rail controlling the computer, and importing the images from the camera to a computer for processing. Moreover, this previous method would only work for a spider-less completed web (12). In order to follow web construction over time, we fixed a shallow water container on top of the raised table upon which an empty cubic $15.24 \times 15.24 \times 15.24$ cm fiber tube frame was placed. The frame was stabilized by four 3D-printed foot supports at the bottom corners of the frame, keeping the frame stable and above the water. When the spider was constructing the web, we placed a T. sisyphoides on the frame. The spider had to build its web inside the frame, as the water prevented it from escaping, and remained in the frame during scanning. Fig. 1A and B illustrates the upgraded scanning setup. This setup allows scanning of the web during web construction. To improve to a fully remote and automatic setup, we used the microcontroller board UNO (https://www.arduino.cc) to automate and synchronize the movement of the laser on the rail, the illumination of the web, and picture capture (Fig. 7A). All the images were saved directly to the computer from the camera using the software digiCamControl (http://www.digicamcontrol.com). Those images were instantaneously synced to the cloud through Dropbox (https://www.dropbox.com/). This allowed us to start and monitor the scanning process remotely, which minimized light in the laboratory to preserve image quality. Fig. 7B shows the scanning process sequence controlled by Arduino UNO. The laser stayed on for 20 min and was turned off for 1 min to minimize fire hazard. For each cycle, the laser and camera moved together 0.6 mm for 0.1 s, then, after 3 s of stabilization necessary to take a clear image, the camera took a picture with an exposure time of 2 s. To make sure that the picture had been saved to the computer, Arduino UNO ordered a laser hitting the metal frame, we superposed all the images from the eight web scans and identified the 2D coordinates of the corners of the frame. Then, for all the images, we converted all the pixels outside of the four corners previously selected into black pixels using MATLAB (https://www.mathworks.com/). After reducing image noise, we used the same image-processing and line-finding algorithms used in ref. 12. We changed a few parameters such as image dilation, pixel size, and gap size between slices. As the spider was present during web scanning, we measured the coordinates of the spider location in the web from the 2D color images.

Computational Model of Silk and Spider Web. For each web model representing a stage of web construction, we built a mesoscale bead-spring model for particle dynamic simulation using LAMMPS (Large-scale Atomic/Molecular Massively Parallel Simulator) (40) from the 3D spider web network data (list of node coordinates and list of pair of linked nodes). Similar to the method described in ref. 12, silk fibers were modeled as a chain of beads separated by springs that follow the nonlinear mechanical behavior of dragline silk. In particular, we used the dragline silk properties parameterized from refs. 19, 43, and 44. We assumed that the T. sisyphoides web is uniaxially composed of their webs as their webs are more permanent structures in nature (29, 34). The 3D spider webs tend to be more permanent structures, so they need silks that age well and can endure repetitive and prolonged stresses, such as dragline silk (45). Each bead described a dragline silk cylinder segment of length $l = 1$ mm and diameter $d = 3 \mu m$, which was within the range of silk fiber diameters measured for L. hesperus spiders belonging to the same family (Theridiidae) as the T. sisyphoides spiders (46). The modeled silk had density $\rho_{silk} = 1.3$ g/cm$^3$, which was the density of silk measured in ref. 47. This silk’s bending stiffness, damping effects, and breaking strain were described in ref. 12. In addition to parameterizing the silk and web models, we added a spherical bead that represented the spider at the location measured in the images. The bead had a diameter $d_{spider} = 6$ mm and weight $m_{spider} = 5.8 \times 10^{-2}$ g, which were the diameter and weight measured for T. sisyphoides females in ref. 40. Then, the fibers inside and passing through the spider bead were removed so that they were directly connected to the spider bead surface. We defined four types of beads: the boundary, free, spider-center, and spider-surface beads. Boundary beads represented the ends of the silk fibers attached to the metal frame: they were fixed during the simulation. Free beads were the beads belonging to the silk fibers: they followed the mechanical properties of silk and were free to move. The spider center was the bead representing the spider. Spider-surface beads were beads with silk properties that are attached to the surface of the spider bead. We used MATLAB to prepare the eight web models and simulation scripts. We used OVITO (Open Visualization Tool) (48) to render the visual representations of the model.

Spider Web Relaxation Simulations. The eight web models of the web stages over 7 d were equilibrated over 10 s. The simulation timestep is $1 \times 10^{-5}$ s.

Spider Web Stretching Simulations. We applied uniaxial stretching along the x-, y-, and z-axes at a rate of 0.1 m/s on the eight spider web models, resulting in 24 simulations. The simulations ended when the spider webs reached 900% strain. We output web stresses and web strain from the simulations.

Spider Web Projectile Simulations. Spider webs are subject to prey impacts, which are a source of food for the spider. Flies impacting the web, as commonly occurs in nature, were represented as sphere projectiles. The projectile had a
diameter of 7 mm and weight of 4.7 mg, which was calculated using the model in ref. 49. For each of the eight spider web construction stage models, sphere projectiles were thrown at the speed of 0.5 m/s, along the x, y, and z-axes following a 3D Cartesian 2 cm-spaced grid. The speed of 0.5 m/s was chosen from previous results from ref. 32; it is the threshold over which the fly will get caught in the tent region of a C. citricola spider web. For example, for one face of the spider web cube, the projectiles were thrown along the axis perpendicular to the face following a 2 cm-spaced grid. There were 36 different projectile impact locations for each face, which led to 1,728 different locations for eight web cubes. For each simulation, only one projectile was thrown. To save simulation time, we omitted impact locations where no fibers were in the way of the projectile’s trajectory, resulting in 1,504 projectile simulations. We output projectile position and velocity from the simulations. We used MATLAB to process and visualize the projectile impact results.

3D Printing of Spider Webs. Based on the computer models, we developed 3D printed models of the graph representations using Grasshopper (http://grasshopper3d.com) and Rhino 7 (https://www.rhino3d.com/) to build an STL model. The STL model is used for 3D printing and sliced into g-code using Cura (Version 4.9.1), then printed using PLA in a Fuse Deposition Molding Ultimaker S3 printer.

Data Availability. All study data are included in the article and/or supporting information.

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