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B. D. Opell

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The ability of spider cribellar prey capture thread to hold insects with different surface features

B. D. OPELL

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA

Summary

1. Cribellar thread is the most primitive type of capture thread found in the aerial webs spun by spiders and is composed of thousands of dry, looped fibrils that are spun from the spigots of a spinning plate.
2. Comparison of the strength with which cribellar threads produced by two species of spiders in the family Uloboridae held five insect surfaces demonstrates that the size, type and density of insect setae influence a thread's stickiness.
3. Moth wings were held the least strongly, as their detachable scales easily pulled free of the wing and remained attached to the cribellar threads.
4. Two forces were responsible for holding the other insect surfaces: setal snagging caused the stout setae of a fly notum to catch on the fine fibrils of the cribellar thread, whereas an uncharacterized force held the smooth surface of a beetle elytra and the setose surfaces of a bug hemelytra and a fly wing.
5. The force with which non-snagging surfaces that have well-attached setae were held was directly proportional to the area of contact between the cribellar thread and the surface.
6. Together, these mechanisms create prey capture threads that effectively but differentially hold a range of insect prey.

Key-words: *Hyptiotes cavatus*, silk stickiness, spider webs, Uloboridae, *Uloborus glomosus*

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Introduction

The origin of aerial spider webs marked the appearance of a device that allowed spiders to capture flying insect prey. It also correlates with the evolution of spiders in the infraorder Araneomorphae. The araneomorph spiders comprise 86% of all spider families, 90% of all spider genera and 94% of all living spider species (Coddington & Levi 1991). If aerial webs are to be effective prey-capture devices, they must not only intercept prey, but retain it long enough for a spider to locate it, run to it and subdue it, either by envenomating the struggling prey or wrapping it with silk (Craig 1987). It often takes an orb-web spider as long as 10 s to reach a prey (Eberhard 1989). Therefore, the ability of a spider's web to retain insects after they have been intercepted is crucial to the spider's prey-capture success.

Associated with the origin of aerial webs in the Araneomorphae was the appearance of sticky prey-capture threads. When these capture threads are deposited on the web's non-sticky thread network, the web more effectively retains the insects that it intercepts. The first capture threads produced by spiders were dry, composite threads. These threads are still

produced by members of 22 araneomorph families and are formed from two or four supporting axial threads, each with a diameter of about 500 nm, that are surrounded by a cloud of thousands of very thin, looped fibrils each with a diameter of about 30 nm (Fig. 1a,b; Peters 1984). The axial lines are spun from spigots on a spider's posterior spinnerets. The fibrils are spun from spigots on an oval spinning field, the cribellum, located on the ventral surface of a spider's abdomen just anterior to its spinnerets. Using setal combs on its fourth legs, a spider draws fibrils from the cribellum and combines them with axial lines to form a fuzzy thread known as cribellar capture thread (Eberhard 1988).

Not all members of the infraorder Araneomorphae produce cribellar threads. Some, such as jumping spiders and wolf spiders, have abandoned web production in favour of other hunting tactics. In the more highly derived orb-weaving spiders, cribellar threads have been replaced by viscous capture threads. These threads derive their stickiness from small, regularly spaced droplets of viscous glue (Foelix 1982; Vollrath *et al.* 1990; Townley *et al.* 1991). However, spiders that produce cribellar threads are distributed

among most major lineages of the infraorder Araneomorphae (Coddington & Levi 1991), indicating that, along with aerial webs, cribellar threads contributed to the early success and diversification of this dominant group of spiders.

Although it is clear that cribellar threads play an important role in prey capture, the mechanism by which they hold prey is not fully understood. By catching on the setae and surface irregularities of prey, a thread's coiled fibrils might act like the soft part of a Velcro fastener as it catches on its counterpart (Kaestner 1968; Opell 1979). However, cribellar thread also sticks to such smooth surfaces as glass, steel and graphite (Eberhard 1980; Peters 1986). Scanning and transmission electron microscope studies (e.g. Opell 1979, 1989a, 1990; Kullmann & Stern 1981; Peters 1983, 1984, 1986, 1992) reveal no adhesive droplets on cribellar fibrils that might explain this ability. Therefore, a second force appears to contribute to the ability of cribellar thread to hold objects. Electrostatic charge has been suggested as a possible force (Peters 1984, 1986), although there are no data to support this hypothesis.

The purpose of this study is to compare the strength with which cribellar thread holds insect surfaces that have different setal types and densities. This will provide the first measurements of how effectively these threads retain prey and an indication of their ability to hold prey selectively. Additionally, these data will test the hypothesis that a force other than setal snagging contributes to the adhesive properties of cribellar thread. If such a force exists, then the strength with which cribellar thread holds a non-snagging surface should be proportional to the area of contact between the thread and the surface. If the surface has setae that prevent the cribellar thread from contacting the cuticle beneath them, then the area of contact is determined by the density and diameters of these setae. Thus, a surface with sparse, non-snagging setae should be held less strongly than a smooth surface, a surface with dense setae, or a surface with setae that snag the fibrils of a cribellar thread.

The wings of moths and butterflies are covered with detachable scales. When one of these insects contacts an adhesive capture thread, its scales remain attached to the thread's adhesive droplets, but pull free of an insect's wing, allowing it to escape from the web (Eisner, Alsop & Ettershank 1964). The ability of this mechanism to allow an insect to escape from webs containing cribellar capture threads has never been documented and will also be addressed in this study.

Materials and methods

For this study, the cribellar threads used were produced by members of the family Uloboridae. This family contains the most primitive orb-weaving spiders

and the only orb-weavers that produce cribellar threads. These threads are well suited to this study because their fibrils are deposited around axial threads as a regular series of torus-shaped puffs (Fig. 1a). As the width of these puffs is determined by the width of the spider's cribellum, the threads produced by an individual have a uniform width (Opell 1989a; Opell, Roth & Cushing 1990). This makes it possible to determine how well the thread of one spider holds insect surfaces that have different properties.

The cribellar threads produced by adult females of two uloborid species from south-western Virginia were used in this study: the orb-web weaver *Uloborus glomosus* (Walckenaer) and the triangle-web weaver *Hyptiotes cavatus* (Hentz). These species are of similar size, but the latter constructs a reduced web (Lubin 1986; Opell 1982) whose cribellar threads hold surfaces more strongly than those spun by *U. glomosus* (B. Opell, unpublished data).

The stickiness of cribellar threads from the same web or from sequential webs produced by the same individual was measured using five insect surfaces: (1) the elytra of the lady beetle *Hippodamia convergens* Guerin-Meneville, representing a smooth surface with sparse fine setae (Fig. 1c); (2) the distal portion of the hemelytra of the milkweed bug, *Oncopeltus fasciatus* (Dallas), representing a surface with dense fine setae (Fig. 1d); (3) the wing of the fleshfly, *Sarcophaga bullata* Parker, representing a surface with well-spaced setae of intermediate length (Fig. 1e); (4) the notum of the blowfly, *S. bullata*, representing a surface with sparse long setae (Fig. 1f), and (5) the wing of the wax moth, *Galleria mellonella* (Linnaeus), representing a surface with detachable scales. All surfaces used in this study were removed from insects that were killed by freezing and that were stored in a freezer for several hours to about 30 days. The dorsal surface of each wing type was used to measure stickiness.

To compare more precisely the setal features of the elytra, hemelytra and fly wing, four lines were drawn on enlarged scanning electron micrographs of these surfaces (Fig. 1c–e). At the magnification of these photographs, these lines represented total distances of 1178 μm , 129 μm , and 1069 μm , respectively. Setae crossed by these lines were counted and their widths were measured. From these measurements the following values were calculated for the elytra, hemelytra and fly wing: setal frequency, 0.003, 0.500 and 0.067 setae per μm line length; setal width, 0.0048, 0.331 and 0.158 μm setal width per μm line length. Compared with the beetle elytra that provides nearly 100% contact with a cribellar thread, the hemelytra presents only 33% and the fly wing only 16% as much surface area to a cribellar thread.

All insect surface types were used to test the stickiness of cribellar threads produced by 20 *Hyptiotes cavatus*, but only surfaces 1, 3 and 4 were used with

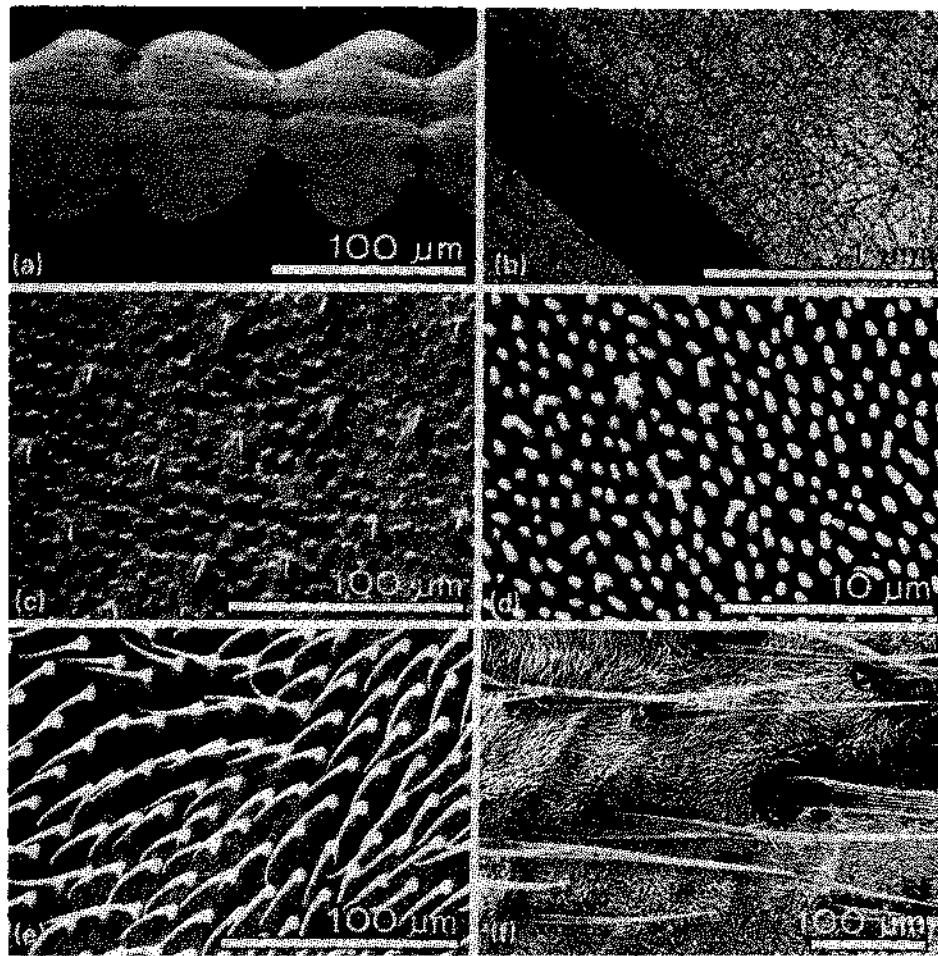


Fig. 1. (a) Cribellar thread of *Hyptiotes cavatus* showing regularly spaced puffs of cribellar fibrils. (b) Cribellar thread of *Hyptiotes cavatus*, showing larger axial threads and smaller cribellar fibrils. (c) Surface of the elytra of *Hippodamia convergens*. (d) Surface of the distal region of the hemelytra of *Oncopeltus fasciatus*. (e) Surface of the wing of *Sarcophaga bullata*. (f) Surface of the notum of *Sarcophaga bullata*.

threads of 20 *U. glomosus*. Each surface was frequently examined under a dissecting microscope to determine if cribellar fibrils had accumulated on it as a result of repeated use. This occurred only on the fly notum. Therefore, after the stickiness of each individual's thread was measured with the notum, these fibrils were removed from the notum with a fine needle. Because this procedure sometimes broke one or two setae, nota were replaced at the first sign of damage. This resulted in four nota being used to measure the threads of *U. glomosus* and two to measure the threads of *Hyptiotes cavatus*. As a caution, two moth wings were used to measure the threads of *Hyptiotes cavatus*, although the first wing did not show damage or register an increase in stickiness with repeated use.

Spiders used in this study were housed individually in plastic boxes that were kept in an environmental chamber. This prevented their webs from being contaminated by dust or pollen and increased the number of thread samples that could be obtained from a web. From each web, cribellar thread strands were collected on a microscope slide to which five raised, par-

allel, 4.8 mm wide, 2 cm long brass supports were glued at 4.8 mm intervals. Double-sided Scotch tape on top of each support securely anchored the threads across each of the sampler's four sectors and maintained their original tensions.

Cribellar thread stickiness was measured within 2–40 h of collecting thread samples. Before taking measurements, each thread sector was examined under a dissecting microscope and threads that were damaged, intersected by non-sticky radii, or too close to another thread to permit measurement of its stickiness were removed. The stickiness of each of four cribellar thread strands was measured with an insect surface and the mean value used as the stickiness of that spider's cribellar thread for that insect surface.

The instrument used to measure stickiness was a modification of that described by Opell (1989b). It incorporated a microscope slide holder that could be rotated and moved along X and Y axes, permitting orientation of the thread sampler. A motorized screw advancement moved the sampler towards a contact plate at a speed of 13.5 mm min⁻¹ and away from it at

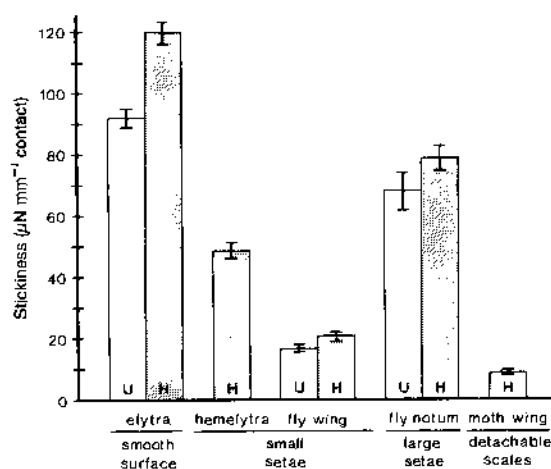


Fig. 2. Comparison of the mean ± 1 SE stickiness of cribellar threads produced by *Uloborus glomosus* (U) and *Hyptiotes cavatus* (H), as measured with different insect surfaces. Sample size in all cases is 20.

14.0 mm min⁻¹. A glass needle strain gauge mounted in a horizontal plexiglass frame was positioned so that the contact plate on the needle's protruding tip contacted a cribellar thread. Using 5 mg weights, the arbitrary scale over which the needle's free end passed was calibrated. By multiplying these scale values by the accelerating force of gravity, the force in Newtons required to deflect the needle was determined.

Two millimetre wide rectangles of insect wing or cuticle were glued onto the needle's tip to serve as contact plates. The widths of these plates were measured to the nearest 20 μm under a dissecting microscope and the force required to pull a thread free of the plate is expressed in $\mu\text{N mm}^{-1}$ width of contact plate. The sensitivity of this technique depends on the glass needle used and ranged from 1.77 to 3.24 $\mu\text{N mm}^{-1}$ contact, averaging 2.32 $\mu\text{N mm}^{-1}$ contact. For *Hyptiotes cavatus* thread, this sensitivity was equivalent to 2% of the mean stickiness registered for the beetle elytra (the surface held most strongly) and 19% of that registered for the moth wing (the surface held least strongly). The mean sensitivity of all needles used in this study was 7% of the stickiness of the surface on which they were used.

Before measuring the stickiness of a cribellar thread, the thread was orientated so that its length was perpendicular to that of the contact plate. The web sampler was then advanced until the thread was pressed against the plate with a force of 19.61 μN and then immediately the direction of the sampler's travel was reversed. The position of the strain gauge needle was observed as the cribellar thread was pulled away from it and the value registered at the instant the thread pulled free of the contact plate was recorded. After determining a sample's stickiness, the relative humidity (r.h.) at which its four replicate measurements were taken was recorded.

Kruskal-Wallis tests (K-W) tests were used for multiple comparisons and Wilcoxon two-sample tests (W) for pairwise comparisons. Values were considered to be significantly different if $P < 0.05$.

Results

The stickiness values recorded for insect surfaces are given in Fig. 2. The temperature at which these surfaces were measured ranged from 23 to 25 °C and the mean r.h. at which a surface was measured ranged from 56 to 57% with a standard deviation of 0.4–1.3%. For both species and all wing surfaces, the standard error of stickiness was greater when the mean of the four measurements taken from a spider's cribellar thread was used than when each of the four measurements was used. The former standard error exceeded the latter by a factor of 1.30–1.68 ($\bar{x} = 1.45$). Thus, using an individual's mean stickiness value provided a more conservative test of the hypotheses.

Of the five insect surfaces used in this study only the fly notum accumulated cribellar fibrils on its surface. These fibrils were so strongly caught that when a cribellar thread finally pulled free, broken fibrils remained attached to the notum. This is the only surface for which there is clear and direct evidence that setal snagging is responsible for the thread's stickiness. In the other three surfaces that had firmly attached setae, the cribellar thread pulled free without leaving fibrils behind.

The stickiness of each species' cribellar threads differed significantly among wing surfaces (K-W, $P < 0.0001$). Among surfaces without detachable scales (all those except the moth wing), surface texture affected the stickiness of both *Hyptiotes cavatus* and *U. glomosus* threads (K-W, $\chi^2 = 69.8$, $P < 0.0001$ and K-W, $\chi^2 = 39.6$, $P < 0.0001$, respectively). Surfaces that were extremely smooth and those that had stout setae were held most strongly, whereas those with intermediate setal density were held less strongly. The threads of *Hyptiotes cavatus* registered more stickiness for the beetle elytra than for the fly notum (W, $Z = 4.99$, $P < 0.0001$), more stickiness for the notum than the hemelytra (W, $Z = 4.45$, $P < 0.0001$), and more for the hemelytra than the fly wing (W, $Z = 5.16$, $P < 0.0001$). The threads of *U. glomosus* registered more stickiness for the elytra than the fly notum (W, $Z = 2.83$, $P < 0.005$), and more for the notum than the fly wing (W, $Z = 4.80$, $P < 0.0001$).

When the mean stickiness values measured for elytra, hemelytra, the fly wings with *Hyptiotes cavatus* threads are regressed against the area presented by these surfaces (0.99, 0.331 and 0.158 μm^2 of cuticle or setal contact μm^{-1} length, respectively) this relationship is significant ($t = 12.28$, $P = 0.049$, $R^2 = 0.99$). Thus, for non-snagging surfaces, stickiness appears to be directly proportional to the area of contact between the surface and cribellar thread.

Of the four insect surfaces without detachable

scales, fly wings were held least strongly by the cribellar threads of *Hyptiotes cavatus*. However, moth wings were held only half as strongly as these ($W, Z=5.35, P<0.0001$). After a cribellar thread was used to measure the stickiness of a moth's wing, a few scales remained attached to the thread, indicating that the thread did not pull free of the wing but that the scales it held detached from the wing.

Discussion

A number of factors, such as web architecture, insect flying speed and insect behaviour determine how easily insects are intercepted and retained by spider webs (Craig 1987). Here it is demonstrated that an insect's surface features also affect how strongly it will be held in a web. As surface features differ among the parts of an insect's body and as several parts of the body are likely to contact the capture threads of a web, this study does not actually measure how strongly a spider's web holds different types of insects. However, the extended wings of flying insects present such a large surface area that they are very likely to contact the capture threads of a web. Therefore, differences in the ability of cribellar threads to hold insect wings having different surface features strongly suggest that webs containing these threads selectively retain different types of insects. For example, the fact that a beetle elytra registered 5.7 greater stickiness than did a fly wing indicates that beetles are more effectively held in the cribellar threads of a web than are flies.

Just as the detachable scales on a moth's wing allow it to escape from adhesive capture threads, detachable scales also permit insects to escape more easily from cribellar threads than insects that have smooth surfaces or well-attached setae. Eisner *et al.* (1964) suggest that selection for this escape mechanism contributed to the evolution of detachable scales in the insect orders Tricoptera and Lepidoptera. If this is correct, then this study suggests that selection for this method of escape could have operated prior to the evolution of viscous capture threads present in more highly evolved orb-webs.

These results support the hypothesis that two forces are responsible for the operation of cribellar thread: setal snagging and an unexplained mechanism that holds non-snagging surfaces. The dual nature of a cribellar thread's stickiness permits it to hold insects that have a variety of surface features. As most orb-webs appear to intercept insects that belong to a number of taxa (Eberhard 1990), this may adapt orb-weavers that produce cribellar threads to the role of generalist predators.

Differences in the surface features of an insect determine which force is most important in retaining an insect and how strongly it is held. It is not surprising to find that surfaces like the fly notum used in this study are held strongly because their large setae snag

on the fibrils of a cribellar thread. However, it is surprising to find that smooth surfaces like the beetle elytra are held even more strongly by an unexplained force that does not rely on setal snagging. In fact, of the four surfaces with firmly attached setae, only the fly notum appears to have been held by setal snagging.

Thus, this unexplained force appears to be a principal rather than auxiliary force responsible for the operation of cribellar thread. It is responsible for holding both smooth surfaces and surfaces with non-snagging setae. The strength with which this force holds a surface is directly proportional to the area of contact between the thread and the surface. The area of contact is governed by differences in the density and diameter of the setae that cover the surface. Just as selection favouring escape from aerial webs appears to have contributed to the origin of detachable scales in moths and butterflies, this study suggests that it may also have affected the setal characters of other flying insects.

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