

## REVIEW

### Biomechanical costs and benefits of sit-and-wait foraging traps

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**Abstract** Traps are rarely used by animals, despite the plausible benefits of broadening the number and diversity of prey that sit-and-wait foragers might be able to capture. The most well-known trap building sit-and-wait foragers are among the invertebrates, i.e. antlions, wormlions, glow worms, caddisflies, and spiders. A plausible hypothesis for the paucity of trap building by other animals is that biomechanical limitations render them inefficient or ineffective at catching sufficient prey. Here I examined the literature to make a valued judgement about the validity of this hypothesis. It appears that antlion and wormlion pit traps cannot catch and retain the largest prey they might expect to encounter. *Arachnacampa* glowworm traps are functionally efficient, facilitated by the animal's bioluminescence. Nevertheless they only function in very moist or humid conditions. Caddisfly traps rely on flowing water to be able to capture their prey. Spiders are exceptional in developing a wide range of prey trapping strategies, from webs with dry adhesives, to sticky orb webs, to modified orb webs, e.g. elongated "ladder" webs, to webs with additional structures, and web aggregations. Some spiders have even redesigned their webs to minimize the high prey escape rates associated with web two dimensionality. These webs nevertheless are constructed and used at specific costs. While hard data across all of the invertebrate predators is lacking, there seems to be credence in the hypothesis that the biomechanical limitations placed on trap functionality can explain their limited use among animals.

**Keywords** antlion/worm lion traps; *Arachnacampa* glowworms; caddisfly nets; silk; sit-and-wait foragers; spider webs

#### Introduction

Animal foraging modes may be classified as sit-and-wait or active. The primary cost of the sit-and-wait mode compared to the active mode is a greater uncertainty of prey encounter (Nishimura, 1994; Fronhofer et al., 2011; Overgaard and Wang, 2012). Considering the energy saving and predator avoidance advantages of sit-and-wait foraging, any means by which a sit-and-wait forager might increase its chances of encountering and consuming more prey might be strongly selected for (Hansell, 2005). Building a trap might represent a way that a sit-and-wait predator might significantly increase its chances of capturing more prey and/or a wider range of prey. Nevertheless, trap building is exceptionally rare in animals; being restricted to a few trap building arthropods, e.g. antlions, wormlions, glow worms, caddisflies, spiders (Hansell, 2005; Meyer-Rochow, 2007; Ruxton and Hansell, 2009), and vermetid gastropods, whose mucus net functions as a trap to capture planktonic organisms (Kappner et al., 2000).

We do not know whether trap building has repeatedly appeared and become lost among different animals throughout evolutionary history or only ever appeared in

the aforementioned groups. Since traits that provide tangible fitness benefits, e.g. camouflage, chemical defences, sexual displays, tend to evolve repeatedly and/or are retained in groups within which they evolve (Gheiselin, 1974), it appears that trap building as a foraging strategy comes at substantial opportunity costs despite demonstrable benefits.

Plausible reasons for the apparent paucity of trap building among sit-and-wait foraging animals might be the extra energy expended finding and secreting the materials used to build the trap (Lucas 1985; Venner et al., 2003; Hansell and Ruxton, 2013), the energetic or nutritional cost of trap building (Blamires et al., 2015), the time taken away from foraging or mating (Stoltz et al., 2010), or the exposure to predators or extreme environments that the animal might suffer while building the trap (Tseng et al., 2011, Tew and Hesselberg, 2017). Such opportunity costs, nonetheless, seem to pale in comparison to those encountered when active foraging wherein considerable energy is spent each day moving around and chasing down prey (Brown and Nagy, 2007; Biro and Stamps, 2010). A plausible hypothesis is that the biomechanics of many traps render them

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somewhat inefficient and/or not universally effective at catching the majority of the forager's prey (Ruxton and Hansell, 2009; Scharf et al., 2011). To assess this hypothesis herein I reviewed the literature on the functional biomechanics of animal traps, focussing explicitly on the opportunity costs and benefits of trap building by antlions/wormlions, glow worms, caddisflies, and spiders.

### Antlion and wormlion traps

The larvae of antlions (Class Insecta, Order Neuroptera, Family Myrmeleontidae) and wormlions (Order Diptera, Family Vermileonidae) create conical shaped craters that entrap ants or other passing insect prey (Scharf et al., 2009, 2010, 2011; Beponis et al., 2014) (Fig. 1). The crater is dug by the antlion/wormlion by excavating sand with its mandibles while moving with a spiralling motion, thus creating a circular crater in the sand substrate (Fig. 1b). The antlion or wormlion then burrows downward to build a deep pit into which it hides (Tuculescu et al., 1987; Fig. 1b). The ultimate size, shape, and symmetry of the crater and pits depend largely on the animal's size, how hungry it is, its ability to excavate, and the sand texture, depth and grain size (Griffiths, 1980; Heinrich and Heinrich, 1984; Lucas, 1989, Scharf et al., 2009, 2011; Bar-Ziv et al. 2019). The construction of the trap is relatively energetically cheap

(Fertin and Casas, 2006), but the limits placed on trap geometry by soil characteristics and weather render it necessary to regularly move and rebuild these traps (Ruxton and Hansell, 2009), thus incurring undue additional costs.

These traps function by ants or other small insects moving toward the lip of the crater and then sliding into the crater as the loose sand at the lip gives way under the insect's weight. The ant or insect tumbles down toward the base of the pit, where the antlion or wormlion awaits to consume it, as soil gives way (Grzimek, 1979; Bar-Ziv et al., 2019). The length from the head of the crater to the base, the slope of the crater walls, and its conical symmetry, affect the capability of the traps to catch and retain prey (Lucas, 1989; Fertin and Casas, 2006). Indeed, the most efficient ant capturing craters are relatively shallow and perfectly symmetrical with a wall angle and sand coarseness sufficient to enable prey to slide into the pit while avoiding cave in (Fertin and Casas, 2006; Miler et al., 2018). The architecture of the pit directs the falling ants directly toward the awaiting antlion/wormlion and the steep walls lined with loose sand provides little opportunity for breaking the fall or escape (Fertin and Casas, 2006; Bar-Ziv et al., 2019). A drawback associated with this architecture, however, is that it is most effective at catching and retaining the smallest prey items the antlions/wormlions are willing to consume, since larger ones more easily climb out. Thus

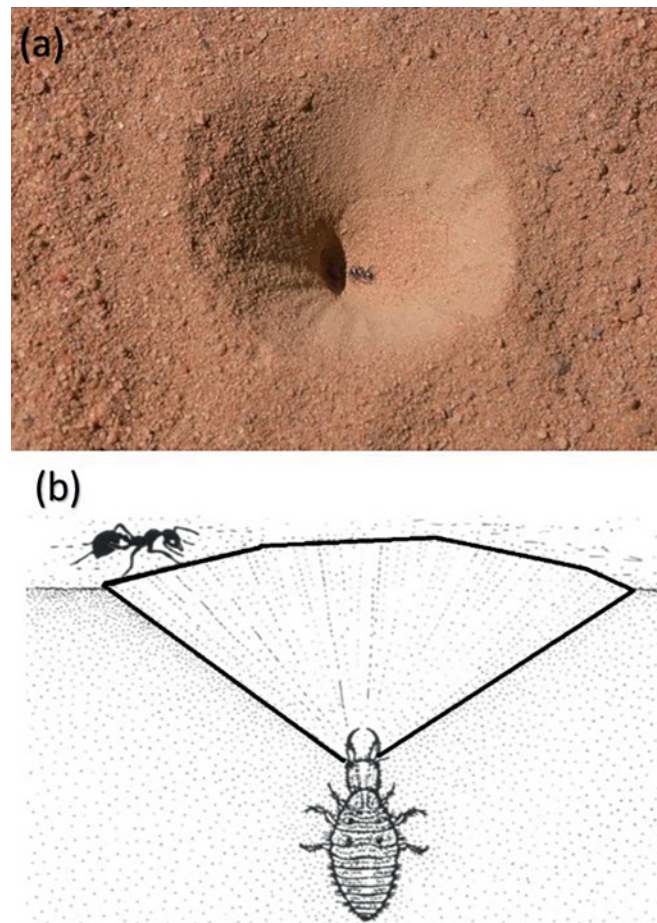


Figure 1. (a) Aerial view of the conical shaped crater an antlion uses to entrap passing insect prey. (b) A schematic of the inside of the crater showing the antlion hiding at the base of the crater waiting for an ant to fall in as the loose sand at the crater lip slides under it. The images were modified from <https://beetlesinthebush.com/>

rendering them committed to relatively prolonged foraging bouts (Ruxton and Hansell, 2009).

### Silk-based traps

Traps built by glow worm larvae (Diptera, Keroplatidae), caddisfly larvae (Trichoptera), and spiders (Arachnida, Araneae) differ from those of antlions and wormlions inasmuch as they are created from a substance secreted by the animal; silk. The unique material properties of silk make it popular as a fabric and desirable as a biomimetic for a range of purposes (Koh et al., 2015; Wolff et al., 2017), and render it extremely useful to use within traps. Of the aforementioned trap-building invertebrates, spiders have become silk virtuosos, with the most derived species spinning a toolkit of at five or more different silk types for specific uses in traps (Blackledge and Hayashi, 2006a; Blamires et al., 2017b).

Since silk used in traps is secreted mostly as a fibre, the standard tensile properties associated with fibres, such as strength, stiffness, modulus of elasticity, extensibility, toughness, and flexural and torsional properties are the most relevant to comprehend (Harmer et al., 2011; Blamires et al., 2017a). Some trap silks are secreted as solutions to form glues, cements, or films. In these silks viscosity, stickiness, compliance, and solubility may be more important properties (Van Nimmen et al., 2005; Swanson et al., 2007; Mortimer and Vollrath, 2015). Silk fibres used in traps can vary within species or individual (Boutry and Blamires, 2013) and variability in the constituent proteins across hierarchical levels has been attributed as driving this variation (Boutry and Blamires, 2013; Blamires et al., 2017a). I will thus overview the hierarchical structure of silk proteins, before focusing on specific silks.

Silks comprise of large (>150 kDa) proteins called fibroins (or spidroins in the case of spiders, which is a derivation of spider fibroins). Silk fibroins/spidroins have complex primary, secondary and tertiary structures (Crawford et al., 2016; Craig et al., 2019). Most silks contain repeated motifs, or domains, of a few amino acids, notably alanine ('ala' or 'A') and glycine ('gly' or G), which are highly conserved across species in many invertebrate silks (Sutherland et al., 2010; Sanggaard et al., 2014; Craig et al., 2019). Other common amino acids in the repetitive regions of the proteins include serine (ser or S), proline (pro or P), and tyrosine (tyr or Y) (Asakura et al., 1994).

Silk proteins conform into particular secondary structures such as  $\beta$ -sheets,  $\beta$ -coils,  $\beta$ -turns, random coils, and  $3_{10}$ -helices (Asakura et al., 1994; van Beek et al., 2000; Blamires et al., 2017a). The overall size, shape and conformation of the secondary structures give rise to various tertiary structures. In many silks  $\beta$ -sheet secondary structures crystalize into densely packed units while the  $\beta$ -coils,  $\beta$ -turns,  $\alpha$ -helices, and  $3_{10}$ -helices arrange into amorphous and lamellar matrices (Blamires et al., 2017a, 2018). The silk proteins thus contain a peculiar combination of crystalline, amorphous, lamellar, and other protein subunits (Sampath et al., 2012; Patil et al., 2014). Much evidence suggests that the primary, secondary and tertiary structures

of silk proteins and how they interact with each other has a profound influence over the silk's properties (Blamires et al., 2017b). In spider major ampullate (MA) silk, for instance, the primary, secondary and tertiary arrangements of its two proteins; major Ampullate Spidroin 1 (MaSp1, MW = ~250 kDa) and Major Ampullate Spidroin 2 (MaSp2, MW = ~310 kDa) are responsible for its strength, extensibility, and toughness (Blamires et al., 2017a).

### Glowworm traps

Glowworms in the context used here are the larvae of fungus gnat flies of the genus *Arachnocampa* from Australia and New Zealand. The most well studied species is *Arachnocampa luminosa* from New Zealand (Broadley and Stringer, 2001; Meyer-Rochow, 2007; von Byern et al., 2016, 2019). These live the majority of their six to twelve-month lifespan as larvae within ultra-moist environments, such as the mouth and ceilings of caves and within closed canopy wet rainforests (Meyer-Rochow, 2007; Plowman et al., 2013).

An individual glowworm larva spins a silken retreat from modified mouthparts, which it hangs sticky threads of up to 40 cm in length. The threads are comprised of a pair of silk axial fibres encased within a gluey, mucous-like silk (Plowman et al., 2013; von Byern et al., 2016, 2019; Piorkowski et al., 2018). This gluey mucous-like silk rapidly dries when outside its usual ultra-moist environments (Piorkowski et al., 2018). The larvae produce a phosphorescent glow, explaining the animal's common name, which is extremely alluring to a range of flying insects including mayflies, mosquitoes, caddisflies, midges, and moths (Willis et al., 2011; Plowman et al., 2013). These insects fly toward the phosphorescence only to becoming entangled in the sticky silk threads. Soon after ensnarement the glow worm begins to consume the silk along with the entangled insect.

The mucous-like sticky silk forms droplets along the axial fibers which superficially resemble beads along a string (Fig. 2). Not only does the gluey silk dry out if humidity drops but the silk rapidly loses adhesion at anything under 90% relative humidity (Piorkowski et al., 2018; von Byern et al., 2019). The droplets are not anchored to the thread but are hydroscopically suspended owing to a mix of highly dilute solutes (von Byern et al., 2016). Ongoing work in my laboratory is revealing that the solute mix differs substantially across the different glow worm species (unpublished NMR and mass spectroscopy data) but as far as I know the functionality of the droplets is conserved across species.

Only two studies have ever been done to determine adhesive values for glowworm threads, one for the Tasmanian species *Arachnocampa tasmaniensis* (Piorkowski et al., 2018), and one for *A. luminosa* (von Byern et al., 2019). Both showed glowworm sticky threads to be highly adhesive, albeit with energy to break values for *A. luminosa* exceeding those for *A. tasmaniensis* by around 100-fold. The axial threads of *A. tasmaniensis* have a greater breaking strength and strains. Quite possibly rather different



Figure 2. An example of glowworm capture threads, showing that the glue droplets coating the axial fibres resembles beads on a string. The threads pictured are those of *Arachnacampa tasmaniensis* within Mystery Cave, Tasmania. The image is an original photograph taken by the author.

methodologies used by each of the studies explains these differences, so not a lot can be gleaned from such comparisons (von Byern et al., 2019). It nevertheless appears that, at least for *A. tasmaniensis*, humidity driven extensibility of the axial thread plays an important role in the prey capture capabilities of glowworm threads (Piorkowski et al., 2018). As long as the axial threads and glue droplets are sufficiently hydrated, the sticky threads are highly effective as a prey catching trap. The primary drawback in using this trap seems to lie in the need for the sticky threads to always be placed in extremely humid environments, limiting glowworm foraging entirely to caves and wet forest understorey.

### **Caddisfly traps**

Caddisflies live their entire larval period in freshwater and many species build a kind of trap. They produce a silk from modified mouthparts to stick stones and other materials together, although some species use this silk to build shelters or a trap or, more literally, a net (Fig. 3). The net is constructed by stretching silk over aquatic vegetation and/or over stones in a flowing stream to form a barrier to flow and entrap small invertebrates and vegetation, which the caddisfly larvae then consume (Wallace and Malas, 1976).

Caddisfly are unique in using their silk entirely within water. Caddisfly silk is thus specialized for water use. It is unusually rich in serine, and about 60% of these serine residues are phosphorylated. The phosphorylated serine residues are predicted to give caddisfly silk proteins a partial negative charge (Addison et al., 2013). Calcium ions are present and are often exposed along the protein backbone of the silk. The resultant internal electrochemical charges enable the protein chains to interact with each other via ionic forces rather than hydrogen bonding, as is the case in most other silks (Addison et al., 2014). These forces induce the protein chains to rigidly align (Ashton et al., 2016). The charged proteins also seem to bring about molecular interactions between the proteins and water (Addison et al., 2013; Ashton et al., 2016; Ashton and Stewart, 2019).

The rigid alignment of the silk's protein chains are thought to make it exceptionally strong, enabling the net to trap insects and particulate matter moving at exceptionally high velocities (Tsukada et al., 2010). Notwithstanding, net architecture is critically important for this trap's functionality. As such, there is immense variability in trap architectures within and between individual caddisfly larvae depending on species, and the likely water flow velocities and/or the type of particulate matter present (Plague and McArthur, 2003; Ashton and Stewart, 2019).

### **Spider traps**

#### **Cribellate orb webs**

Spider orb webs are characterised as having a two-dimensional circular-shaped capture area, containing a single capture thread spiralling outward from the hub and radial threads, which may be symmetrically or asymmetrically distributed, resembling 'spokes' of a wheel, that span from the hub to the web periphery (Blamires et al., 2017b; Blamires and Sellers, 2019). Orb-weaving spiders of the family Uloboridae within the Deinopoidea clade construct an orb capture webs that are horizontally aligned to the ground. The capture area consists of sticky capture spiral threads made from a dry adhesive silk secreted by a special gland called the cribellum, and is aptly labelled cribellate silk (Vollrath, 2006; Joel et al., 2015; Correa-Garhwal et al., 2018). Cribellate threads represent an ancient form of spider sticky threads, which predate the viscous sticky threads found in vertically aligned orb webs (Blackledge and Hayashi, 2006b). They are composites of a core of pseudoflagelliform silk fibers surrounded by a matrix of extremely thin cribellate nanofibrils. (Hawthorn and Opell, 2003; Blackledge and Hayashi, 2006b). The threads adhere to prey through a combination of van der Waals interactions, capillary forces, and physical entanglement (Vollrath, 1994; Hawthorn and Opell, 2003; Piorkowski and Blackledge, 2017) and in some instances by embedding into insect cuticles waxes (Bott et al., 2017). The nanofibrils at the outer edges of the thread are responsible for



Figure 3. An example of the silken net used by caddisfly larvae (Trichoptera) to capture passing prey. The image was modified from <http://lifeinfreshwater.net/>

the overall thread stickiness (Opell and Schwend, 2009). The pseudoflagelliform silk is relatively stiff, strong, and inextensible compared to the counterpart flagelliform axial fibres used in the viscous capture threads of the more derived orb weaving spiders (Kohler and Vollrath, 1995; Blackledge et al., 2012). Cribellate threads can, nevertheless, attain high extensibility if the cribellar nanofibril's contribution can extend after the axial fibers have ruptured (Blackledge and Hayashi, 2006b).

#### Ecribellate orb webs

The vertically aligned ecribellate orb webs of more derived spiders may contain seven or so silks secreted by specific glands, each with distinct mechanical properties (see Blamires et al., 2017b). Major ampullate (MA) silk is found in the radials or 'spokes' of the web and it absorbs and dissipates the exorbitant amount of kinetic energy imparted onto the web when insects are intercepted in full

flight by (Craig, 1987; Sensenig et al., 2012; Harmer et al., 2015). The spiralling capture thread comprises of a composite of two silks; (i) a highly extensible flagelliform silk threads, coated by (ii) an aqueous silk derived from the spider's aggregate glands which forms into droplets along the flagelliform silk to superficially resemble beads along a string (Wu et al., 2013; Amarpuri et al., 2017; Blamires et al., 2017b). The high extensibility of the flagelliform thread enables the kinetic energy of flying prey to be dissipated without breaking the web or releasing the insect (Blamires and Sellers, 2019). An aerodynamic damping effect enacted by the radial threads dissipates additional kinetic energy (Tarakanova and Buehler, 2012). Molecular springs and  $\beta$ -spiral sequences within the flagelliform silk proteins render the capture silk extremely elastic and compliant (Hayashi and Lewis, 1998; Becker et al., 2003).

The aqueous gluey silk of ecribellate orb webs serves to retain intercepted prey (Tarakanova and Buehler, 2012).

In addition to water, this silk contains a cocktail of dissolved proteins, glycoproteins and low molecular weight organic (e.g. GABamide) and inorganic salts (Townley and Tillinghast, 2013). The stickiness of these viscous threads is conferred by the glycoproteins (Opell and Hendricks, 2010). The salts facilitate water uptake from the environment into the droplets, keeping the droplets hydrated and plasticizing the glycoproteins (Sahni et al., 2011; Amarpuri et al., 2017). Since MA silk shrinks and becomes more elastic when exposed to water or high humidity, placing webs in humid environments has the additional effect of rendering the MA silks more compliant and much better able to absorb high prey impact energy (Boutry and Blackledge, 2013). The droplets dehydrate in dry and/or windy environments; which is a drawback of this type of adhesive (Wu et al., 2013; Diaz et al., 2018). Accordingly, the requirement for webs to be placed where relatively humid is high represents a limitation of these traps. Nonetheless, to some degree the mix of low molecular mass compounds within the aqueous capture material is selected to complement the humidity of a species habitat, so should hypothetically enable the droplets to resist drying out in the natural environment (Jain et al., 2018; Opell et al., 2018).

Unlike cribellate threads, the aqueous gluey silk of the capture threads contributes little to the tensile strength and elasticity of the web (Agnarsson and Blackledge, 2009). That falls squarely on the frame and radial threads (Sensenig et al., 2012; Blamires and Sellers, 2019). Rather they are principally involved in prey retention. This is

achieved when multiple glue droplets contact the cuticular surface of an intercepted insect and flexibly adhere to the surface by means of a so called a “suspension bridge” mechanism (Agnarsson and Blackledge, 2009; Opell and Hendricks, 2007, 2009; Guo et al., 2018) (Fig. 4).

The comparative costs of building and utilizing cribellate or ecribellate orb webs are subject to much conjecture. Some researchers point at the relatively short time it takes to construct an ecribellate web compared to a cribellate web as evidence that they are more cost effective traps (Lubin, 1986; Opell, 1998). Others suggest that the cocktail of compounds utilized by ecribellate orb webs must incur a substantial metabolic cost to the spider (Townley et al., 2006). Others speculate that by consuming the spirals daily these costs are recouped by spiders so need not be counted. Still others suppose that the requirement to recycle materials might represent a considerable construction cost for ecribellate webs as it means they need to be constantly disassembled and reassembled, whereas some cribellate webs may remain in place for weeks or months (Blackledge et al., 2011). The fact that the vast majority of modern orb web building spiders build ecribellate webs suggests that they are probably better performing and/or more cost effective, but confirmatory measurements are needed.

Elongated webs, three dimensional webs, and aggregated webs

Regardless of whether or not vertically aligned ecribellate orb webs are realized as more efficient web building strategies

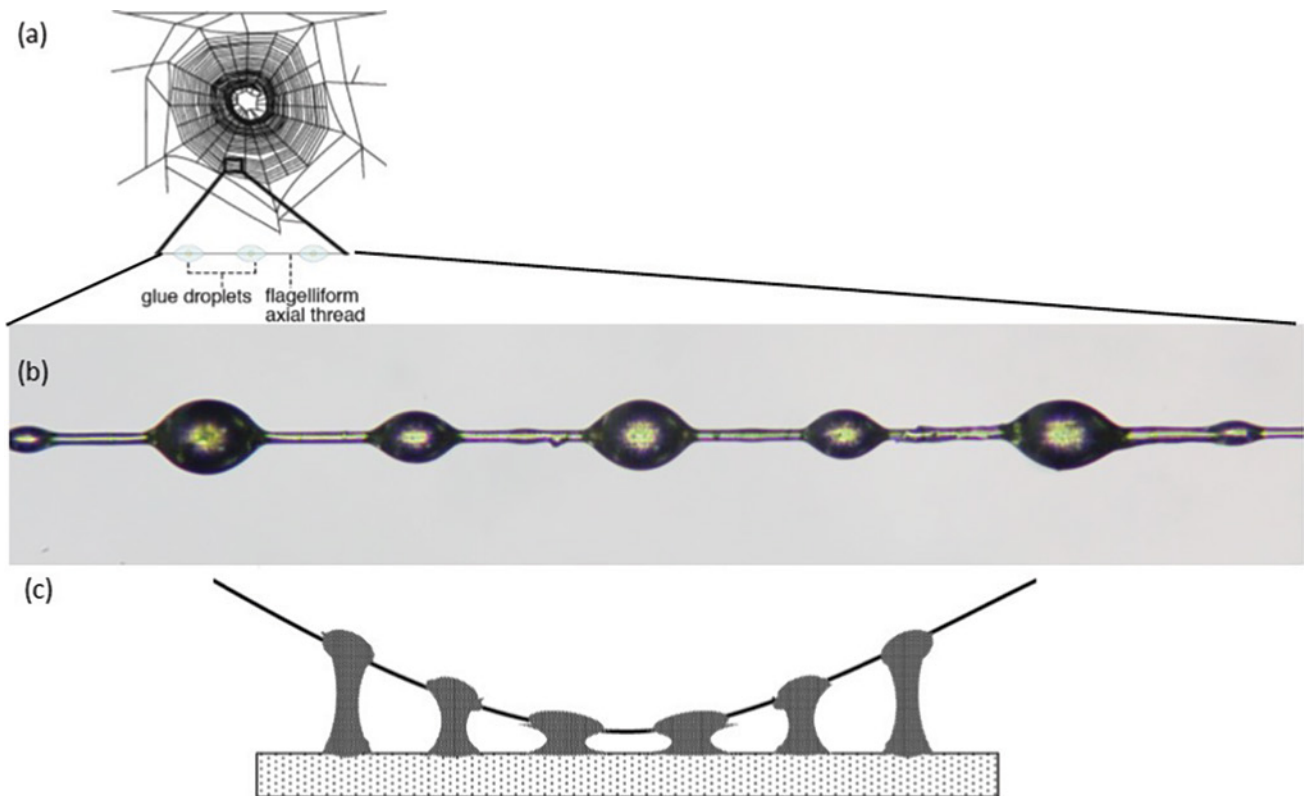


Figure 4. Structure and function of ecribellate spider webs and capture threads. Showing: (a) The spiral threads comprise of flagelliform axial silk threads coated by aqueous aggregate silk, which forms into droplets that superficially resemble beads along a string. (b) A 100x microscopic image of the spiral threads of the orb web spider *Nephila pilipes*, showing the beads along a string arrangement of the aggregate silk. (c) How multiple glue droplets promote adhesion to a surface by a “suspension bridge” mechanism. Image sources: Blamires et al. (2014) (a), Blamires et al. (2015) (b), Opell et al. (2018) (c).

than other strategies, they come with the substantive drawback of frequent prey escape. Large insects are able to tumble out under gravity (Nentwig, 1987), while other insects have adapted body surfaces to facilitate escape. Beetles and cockroaches have a waxy surface that the aqueous silk glycoproteins cannot adhere to (Nentwig, 1987). Moths and butterflies shed their wing scales to escape from the gluey threads (Diaz et al., 2018), while lacewings can physically detach themselves from the web by cutting away the sticky capture spiral (Masters and Eisner, 1990).

These costs are partly circumvented in many instances by some form of web modification. For instance, the vertical diameter in vertical orb-webs is typically longer than horizontal diameter, the area above the hub where the spider may sit, is often much smaller than that below, and the mesh is denser in the lowest part of the web. These modifications are thought to represent adaptations to capture intercepted prey that tumble down the web (Zschokke and Nakata, 2015). The Australian ladder web spider, *Telaprocera* spp. and South American *Scoloderus* spp. elongate their webs to eventually capture prey that tumble out under gravity (Blamires et al., 2017b). Moreover, unlike typical orb-webs, these webs need not be renewed daily. Other spiders add additional components to the web. These may include decorating the web with a particular silk, usually aciniform silk, prey carcasses, or eggsacs, and/or constructing barrier webs (Blamires et al., 2010). Web decorations are thought to attract prey, facilitated by the UV reflecting component of the aciniform silk or eggsacs, deter predators, or both, depending on the predators/prey in question, frequency of use, context of encounter, and size/shape/type of the decoration (e.g. discoid or cruciform in the case of *Argiope* spp.; Herberstein et al., 2000; Tan and Li, 2009; Cheng et al., 2010; Yeh et al., 2015). Barrier webs are effective at preventing access to the web by wasp and bird predators (Blackledge et al., 2003; Tseng et al., 2011), and can enhance prey capture efficiency by deflecting insects off their flight paths toward the web (Blamires et al., 2010).

Sometimes hundreds of webs might aggregate together, such as occasionally seen with *Nephila* spp., *Metepeira* spp., and *Cyclosa mulmienensis* webs (Blamires et al., 2010, 2017b). Web aggregations mitigate the cost of prey escaping from two-dimensional vertically aligned orb webs. This strategy works because prey that escape from any one web will soon encounter another web, then another, until eventually becoming caught, a phenomenon called a ‘ricochet effect’ (Uetz, 1992). Ricochet effects can significantly increase prey capture efficiency and enhance the diversity of the prey captured (Blamires et al., 2010). Furthermore, when prey carcass or eggsac decorations are added to aggregated webs the efficiency of ricochet effects is enhanced up to threefold (Blamires et al., 2010).

#### Cobwebs

Other solutions utilized by different spiders includes completely redesigning the web. Theridiid spiders such as *Latrodectus* spp., *Steodota* spp. and *Theridion* spp. construct three dimensional cobwebs containing four components:

(i) a tangled retreat, a small “pocket” consisting of supporting tangle threads and a non-sticky sheet where the spider hides. (ii) Supporting threads, which form a large inaccessible tangle. (iii) Gumfooted threads that vertically descend from the tangled retreat to the substrate, and interact with prey crawling below the web, and (iv) gumfoot gluey silk droplets at the base of the ascending threads (Benjamin and Zschokke, 2002; Blamires et al., 2014, 2017b; see figures therein). The gumfoot gluey silk adheres directly to the body of a crawling insect. As the insect struggles to escape the gumfooted thread detaches from the substrate and the insect is lifted far enough of the substrate so that it is suspended and unable to use contact with the substrate to pull free of the thread. This allows the spider to run down to the prey and begin wrapping it. The MA silk within the tangled retreat and gumfooted threads are of similar strength and extensibility (Blackledge et al., 2005). Nevertheless, because the insects are not captured in flight the energy required to capture and subdue prey in cobwebs is lower (Becker et al., 2003; Blackledge et al., 2005). Accordingly, cobwebs might represent a more energy efficient trap than orb webs. Nevertheless, the range and size of prey that cobwebs are capable of capturing is much more limited that of orb webs (Craig, 1992; Blamires et al., 2017b).

A recent paper (Coddington et al., 2019) found that the use of silks as traps is plesiomorphic for spiders, with multiple instances of web loss, but not of gain. This study raises the question: if the use of traps by spiders is such an effective strategy, what are some of the factors that are likely to have tipped the balance in favor of active predation and simple sit-and-wait predation in these cases? It would be useful for future studies to consider this question in devising experiments aiming to understand the evolutionary significance of different web or trap types.

#### Conclusions

Uncertainty of prey encounter is a significant cost associated with sit-and-wait foraging. It might be speculated that strategies such as building traps might counter this cost. However, trap building among sit-and-wait foraging animals is rare. By examining the functional biomechanics of traps of antlions, wormlions, glow worms, caddisflies, spiders I have deduced that the various opportunity costs that trap building represents might be too great for the majority of sit-and-wait foragers to invest in traps. Such costs include expending the energy building the trap and the threat of exposure to predators. In most instances, this has not been estimated but is likely to be significantly lower than that spent when actively foraging. I contend nonetheless that the most substantial costs probably centre around the functional biomechanical limitations associated with the various traps. For instance, antlion and worm lion pits traps rely on ants and other prey sliding down the unstable crater walls and not crawling out once inside. It appears that this strategy is most effective for the smallest prey that the predators encounter so limits the daily biomass that the predator can consume. Silk traps, such as glowworm

sticky threads and caddisfly nets have specific habitat requirements, such as humid caves or flowing streams, so only capture only specific prey at specific locations. Spider webs on the other hand, use capture threads with specific requirements and are active within certain performance limitations. For instance, cribellate silks only functions within limited extensibility limits, while ecribellate silks operate best in more humid environments. Moreover many prey, due to features such as the shedding of wing scales, can easily escape spider webs. Some spiders might circumvent this cost by elongating the web, adding components to the web, aggregating, or changing web architecture altogether. Nevertheless, these come with the complication of using additional silk, thus utilizing proteins that might have otherwise been directed to growth or reproduction.

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