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## An organic coating keeps orb-weaving spiders (Araneae, Araneoidea, Araneidae) from sticking to their own capture threads

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### Abstract

More than 95% of orb-weaving spider species ensure prey capture success by producing viscous threads equipped with gluey droplets. However, this trap may bear serious risks for the web-inhabiting spider as well. The obvious question, how a spider avoids getting stuck in its own capture spiral, has gained little scientific attention up till now. In 1905, the French naturalist Jean-Henry Fabre concluded from anecdotal observation that orb-weaving spiders protect themselves by a fatty surface coating. Here, we test this hypothesis by indirectly measuring the force necessary to detach an autotomized spider's leg from the capture spiral of its own web (here called 'index of adhesion', IOA). Three groups of legs, each of the species *Araneus diadematus* Clerck, 1757 and *Larinioides sclopetarius* (Clerck, 1757), were tested. One was left untreated, one was washed with distilled water (H<sub>2</sub>O), and one was washed with the organic solvent carbon disulphide (CS<sub>2</sub>). In both species, we found a weak IOA between the spider leg and the gluey capture spiral in untreated and water-washed legs without significant differences between the two. The IOA approximately doubled, when spider legs had been washed with carbon disulphide prior to measurement, that is, the CS<sub>2</sub>-washed legs stuck significantly more strongly than the untreated and water-washed legs. These results provide indirect evidence for a protective anti-adhesive organic coating on the spider's body surface and so support Fabre's hypothesis.

**Key words:** Araneae – Araneoidea – Araneidae – capture threads – sticky threads – glue – evolution – adhesion – anti-adhesive coating

### Introduction

Modern orb-weaving spiders (Araneoidea) are a diverse group of spiders (e.g. Coddington and Levi 1991; Griswold et al. 1998; Jocqué and Dippenaar-Schoeman 2007) comprising roughly 11650 species worldwide (Platnick 2011). Limits and interrelationships of Araneoidea are still under discussion (Schütt 2000, 2003; Griswold et al. 2005; Blackledge et al. 2009). One key innovation in the evolution of araneoids occurred at the latest in the early Cretaceous, and probably even earlier in the Jurassic (Eskov 1984; Selden 1989; Zschokke 2003; Peñalver et al. 2006; Penney and Ortuño 2006; Selden and Penney 2010): the replacement of cribellate capture threads coated with puffs of dry adhesive fibrils in the orb-webs of araneoid ancestors (and in recent Deinopoidea, the sister group of araneoids) by viscous capture threads equipped with elaborate aqueous glue droplets in the orb-webs and their derivatives of modern araneoids (e.g. Peters 1983, 1984, 1987, 1992; Coddington 1986 with references therein; Bond and Opell 1998; Opell 1999; Opell and Bond 2001).

These gluey capture threads (especially their axial fibres) are significantly stretchier than those of cribellate spirals (Köhler and Vollrath 1995; Opell and Bond 2000, 2001; Blackledge and Hayashi 2006; Opell and Hendricks 2007) in this way increasing the overall stickiness of the araneoid capture thread. Furthermore, the stickiness per web area has been shown to be considerably higher in araneoids than in cribellate orb-weavers, and a unique suspension bridge mechanism that recruits multiple glue droplets to simultaneously resist detachment by dynamic interactions between the stretchy axial fibres and the viscoelastic glue droplets increases the efficiency of the araneoid orb-web as well (Opell 1999; Opell and Hendricks 2007, 2009;

Opell et al. 2008; Agnarsson and Blackledge 2009; Opell and Schwend 2009; Sahni et al. 2010). Energetic costs of web building (especially metabolic costs) may be higher in cribellate orb-weavers (Lubin 1986) although material costs of cribellate thread stickiness are lower (Opell and Schwend 2009). Recently, it was suggested that one decisive advantage of Araneoidea is their ability to build sticky webs from the second instar on, while cribellates are not able to do so before the third instar (Szlep 1961; Yu and Coddington 1990; Opell et al. 2011a). Taken together, these and other facts may well elucidate the much higher diversity of araneoid as compared to cribellate orb-weavers: today, over 95% of all orb-weavers belong to the Araneoidea (Coddington and Levi 1991; Bond and Opell 1998).

The glue droplets on the araneoid capture spiral are produced by the so-called aggregate glands and are composed of various organic and inorganic compounds. The droplets are complex in structure: glycoprotein nodules within each droplet make the capture thread sticky while a hydrophilic cover attracts moisture from the atmosphere and so maintains the thread's water content (Tillinghast and Townley 1987; Townley 1990; Vollrath et al. 1990; Townley et al. 1991; Vollrath and Tillinghast 1991; Edmonds and Vollrath 1992; Vollrath 1992; Tillinghast et al. 1993; Peters 1995).

The araneoid capture thread with its gluey droplets appears as a highly complex and dynamic multifunctional system (Opell and Hendricks 2010). The adhesion of gluey threads is always less than the tensile strength of their supporting axial fibres (Agnarsson and Blackledge 2009). So, if a capture thread is loaded too heavily, droplets get pulled off without breaking or splitting, then reform and can adhere again; in this way, web damage is efficiently prevented (Sahni et al. 2010; Opell et al. 2011b). In addition, glue droplets contain a central granule probably anchoring the glycoprotein glue to the axial fibre of the capture thread, in this way preventing slipping of the droplet on the axial fibre, especially when the capture thread gets stretched (Opell and Hendricks 2010). Glue droplets even contain different

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types of toxins, especially neurotoxic substances, directly involved in prey paralysis and killing without need for venom injection by the spider (Marques et al. 2005; Salles et al. 2006).

However, such an elaborate trap may bear serious risks for the web-inhabiting spider as well. Spiders do not only touch the capture threads with their leg tarsi, but also with practically all parts of their body, e.g., while struggling with a large prey (Vollrath and Tillinghast 1991; Christian Kropf, personal observations). The obvious question, how a spider avoids getting stuck in its own capture spiral, has gained astonishingly limited scientific attention up till now. In fact, hitherto mere anecdote-based ideas prevail that have found entrance even into popular literature (e.g. Dawkins 1996).

One of these ideas dates back to the year 1905, when the French naturalist Jean-Henry Fabre concluded from anecdotal observation that orb-weaving spiders protect themselves from getting stuck in their own capture threads by a fatty surface coating. Fabre tested the adhesiveness of webs of *Argiope bruennichi* (Scopoli, 1772) and/or of *Larinioides sclopetarius* (Clerck, 1757) by visual inspection and by applying an untreated versus a lubricated straw and a carbon disulphide-washed versus an untreated spider leg; he found that the former stuck, while the latter did not (Fabre 1905 sub *Epeira fasciata* and *E. sericata*, respectively).

Fabre's (1905) hypothesis has never been thoroughly tested. Here, we present experimental evidence in favour of his hypothesis by indirectly measuring the forces necessary to detach automatized araneoid spider legs that were experimentally treated in three different ways, from the capture spiral.

## Material and Methods

### Experimental design

Our experimental spider species *Araneus diadematus* Clerck, 1757 and *Larinioides sclopetarius* (Clerck, 1757) were collected in the city and surroundings of Bern, Switzerland. Adult and subadult females were allowed to spin orb-webs in the laboratory in boxes with open front sides with dimensions of 36 × 28 × 14 cm. Until the web building process was finished, the front side of each box was covered with cling film to keep the spider from escaping. Then, the spider was removed from the web, and both front legs as well as the second leg on the left side of the body of each spider (*A. diadematus*:  $n = 11$ ; *L. sclopetarius*:  $n = 20$ ) were collected by slightly squeezing the femur of the respective leg with a forceps, causing the spider to autotomize its leg.

Three groups of legs were defined ('U', 'W' and 'CD', respectively) according to three different treatments: Group U was left untreated, group W was washed for two minutes in distilled water (H<sub>2</sub>O, control group), and group CD was washed for two minutes in an organic solvent, that is, carbon disulphide (CS<sub>2</sub>). Legs of groups W and CD were left to dry under a fume hood for ten minutes and then controlled for complete drying under a stereo microscope. Legs were assigned to one of the three groups in the following order: First specimen: right leg I was assigned to U, left leg I to W, left leg II to CD. Second specimen: right leg I to CD, left leg I to U, left leg II to W. Third specimen: right leg I to W, left leg I to CD, left leg II to U. Fourth specimen: as in first specimen, and so on.

Two legs (left legs I and II) of each species and of each experimental group were examined under a Low Vacuum SEM Hitachi S-3500 N without fixation or sputtering to check whether the different treatments cause any damages or differences in ultrastructure of cuticle or hairs.

### Measuring apparatus (developed by DB; Fig. 1)

The web in its box ('i' in Fig. 1) was placed horizontally (i.e. with the open front side of the box up) on a plastic platform (d in Fig. 1) (44 × 29.5 × 0.5 cm) equipped centrally on its bottom side with a rectangular styrofoam plate (e) (32.5 × 29.5 × 2.5 cm). The platform

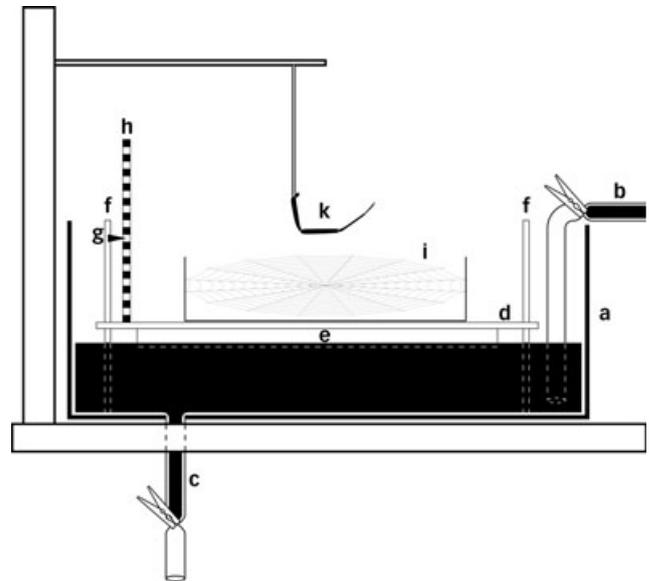


Fig. 1. Schematic illustration of the measuring apparatus used in this study. (a) basin filled with water (black); (b) water hose for adding water; (c) water hose for removing water; (d) plastic platform; (e) styrofoam plate; (f) vertical steel rod penetrating hole at the corner of plastic platform; (g): marking strip; (h): measuring block; (i): spider web in box; (k): fixed spider leg

was floating in a water-filled basin (a), and water could be added or removed by opening the relevant of two water hoses (b or c). Four fixed steel rods (f in Fig. 1; diameter 5 mm) protruded from the bottom of the basin and penetrated four holes (diameter 6 mm) in the plastic platform, one at each corner. One of these rods was equipped with a horizontal marking strip (g) that touched a vertical measuring block (h) (200 mm, accuracy 1 mm) fixed at the upper side of the plastic platform (d). When the water level in the basin was altered, the difference between two water levels could be measured by comparing the positions of the marking strip on the measure block before and after water level change.

One of the collected legs of a spider (k) was fixed above the platform in a way that the leg tibia was positioned horizontally above the web built by the same spider and at a right angle to one loop of the peripheral part of the capture spiral (where distances between two neighbouring loops of the spiral were wide enough to ensure contact of the leg tibia with a single loop only). The platform (d) with web (i) was moved upwards by elevating the water level until the middle part of the leg tibia touched the spiral. The position of the marking strip (g) on the measuring block (h) was recorded. Then, the water level was lowered by removing water from the basin at slow velocity (roughly 0.5 mm per second), and the platform moved downwards until the leg got released from the capture thread. The position of the marking strip was recorded again, and the difference between first and second position (i.e. the difference between water levels in mm) was used as an indirect measure for the force necessary to pull the leg off the capture thread (in the following termed 'index of adhesion', IOA).

### Statistical analysis

We tested the effect of the three treatments on the IOA on spider legs by applying Quade tests for both datasets. This test is suitable for non-parametric data (visual inspection indicated a potential deviation from a normal distribution) and takes into account that our data were paired (three different legs from the same spider in each treatment) (García et al. 2010). In the post hoc analysis, we tested the differences in IOA between the three possible pairs of treatments within species by applying a paired Wilcoxon Rank Sum test (Hollander and Wolfe 1973). The  $p$  values shown were adjusted by a step-down procedure (Holm 1979; García et al. 2010) to take multiple testing into account. Analyses were performed with the R software (R Development Core Team 2011).

## Results

In both species, the washing treatment had an influence on the IOA to spider legs in the gluey capture spiral (*Araneus diadematus*:  $F_Q = 8.98$ ;  $df_{(1,2)} = 2, 20$ ;  $p = 0.0016$ ; *Larinioides sclopetarius*:  $F_Q = 10.5148$ ;  $df_{(1,2)} = 2, 38$ ;  $p = 0.0002$ ; see also Fig. 2). Washing the legs with distilled water (W) or leaving them untreated (U) did not influence the estimated force needed to break the adhesion (Table 1 and Fig. 2); however, a weak adhesion between leg and capture spiral can be observed in both treatments and in both species (Fig. 2). When legs were washed with the organic solvent carbon disulphide (CD), adhesion approximately doubled compared to untreated (U) and water-washed (W) legs (Table 1 and Fig. 2) in both species. This shows that legs of *A. diadematus* and *L. sclopetarius* washed with carbon disulphide stick significantly more strongly to the capture spiral than untreated or water-washed legs. IOAs between left and right front legs and legs II, respectively, did not differ (data not shown).

Low Vacuum SEM control of spider legs of the three groups did not reveal any damages or differences in ultrastructure of cuticle or hairs, nor did we find any indication that the treatments were harsh enough to remove the setae on the spiders' legs.

## Discussion

### Organic protective surface coating in araneoid spiders

Our results show that carbon disulphide-washed legs of *A. diadematus* and *L. sclopetarius* adhere to the capture spiral roughly twice as strongly as untreated or water-washed legs, with no significant difference in IOA between the latter two. As carbon disulphide is a strong (and fat-dissolving) organic solvent, our results provide evidence for an organic anti-

Table 1. Pairwise comparisons of indexes of adhesion (IOA) of spider legs and capture spiral when treated in three different ways, namely untreated (U), washed with distilled water (W) or washed with carbon disulphide (CD). The factor of increase in the mean IOA of treatment 1 and treatment 2 is given for each pair. Test statistics are given for each comparison (for details see Material and Method section)

Treatment 1 versus Treatment 2	Factor of increase in IOA	Wilcoxon's T	Sample size $n$	Adjusted p-value
<i>Araneus diadematus</i>				
U versus W	1.03	21	11	0.905
U versus CD	2.01	5	11	0.029
W versus CD	1.95	1	11	0.024
<i>Larinioides sclopetarius</i>				
U versus W	0.99	87	20	0.64
U versus CD	2.31	26	20	0.007
W versus CD	2.34	17.5	20	0.003

adhesive surface coating protecting araneoid orb-weaving spiders from getting stuck in their gluey capture threads, in this way supporting Fabre's (1905) hypothesis. As spiders frequently touch their capture spiral with all possible body parts, this protective coating should not only occur on the legs, but on the total body surface. However, whether this protective surface coating truly consists of fatty or chemically related substances must be explored in the future.

Interestingly, the untreated and water-washed legs also adhered a little to the capture thread. This could mean that additional (e.g. physiological, morphological or behavioural) mechanisms exist, which enable araneoid spiders to prevent too close contact with the potentially hazardous gluey threads. Such mechanisms seem indeed to occur, at least in tropical orb-weavers (William Eberhard and Daniel Briceño, personal communications).

The source of this protective surface coating remains unknown. Promising epithelial glands distributed all over the body or at least in the legs are not known to us. Putative secretory setae especially around the tips of the tarsi (Nikolaj Scharff, personal communications) need to be explored in more detail in this respect. All spiders frequently pull their legs through the mouthparts during cleaning and then rub the legs on different body parts (Schlott 1932; Melchers 1963). So, a gland associated with the mouthparts such as the rostral gland (labral gland) in the labrum, which seems to be present in most spiders (Snodgrass 1948), might also be involved in producing the protective secretion in araneoids, as was also suggested by Hingston (1922). Finally, the protective substance could simply form the outer layer of the natural epicuticle of araneoid spiders.

Another old idea, how spiders avoid getting stuck in their capture threads, was brought back into discussion, e.g. by Vollrath and Tillinghast (1991). According to this idea, the spider should avoid contact with the capture thread by running on the dry threads of its web only (radial and frame threads, hub). However, this is not always true. In certain situations, especially while struggling with a larger prey, spiders easily get in touch with the capture thread many times with all parts of their body and never adhere to the thread or get trapped (Vollrath and Tillinghast 1991; Christian Kropf, personal observations). Thus, behavioural avoidance of sticky threads by the spider alone obviously cannot sufficiently explain why araneoid spiders never get trapped in their capture spiral.

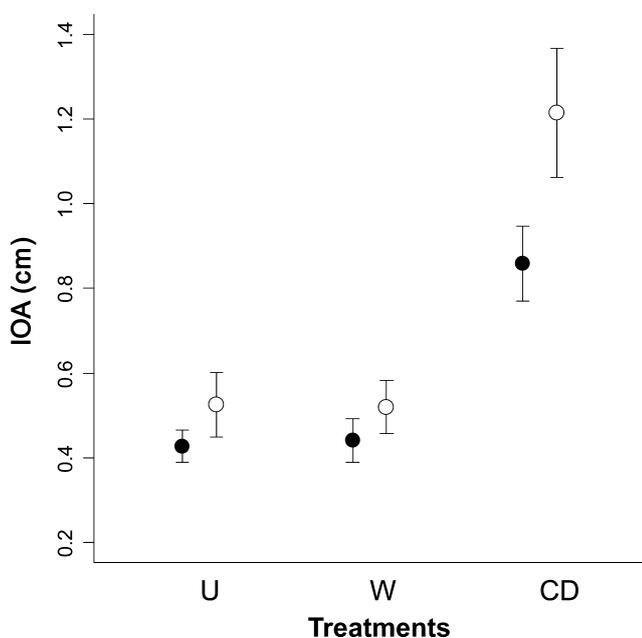


Fig. 2. Mean index of adhesion (IOA) to spider legs in gluey capture spiral in relation to three treatments. Legs of two spider species (solid circles: *Araneus diadematus*; open circles: *Larinioides sclopetarius*) were either left untreated (U), washed with distilled water (W) or with the organic solvent carbon disulphide (CD) prior to measurement. Bars indicate standard errors

### Evolutionary considerations

Recently, Opell et al. (2011a) gave experimental evidence for their new hypothesis that the transition between cribellate and araneoid orb-weavers could have occurred via composite cribellar–viscous capture threads to enable cribellate second instar spiderlings [who show no functional cribellum but rely on capture webs as well (Szlep 1961)] to build more efficient traps. If this plausible scenario has indeed taken place, one may speculate that the protective surface coating has evolved at the latest in parallel with the composite cribellar–viscous capture thread in the stem lineage of modern araneoids and so predates the appearance of the ‘pure’ gluey thread of modern orb-weavers. Nothing is known yet about (presumably much older) mechanisms protecting cribellate orb-weavers from getting stuck in their capture threads.

Another interesting case within Araneioidea is represented by the Linyphiidae. Robust phylogenetic trees (citations above) indicate that this large-derived spider family has replaced the ancestral araneoid orb by a sheet web. No typical adhesive glue droplets can be found in this sheet. Instead, linyphiid aggregate gland secretion dries out quickly and is used to cement different layers and threads of the sheet (Benjamin et al. 2002). Presuming that all araneoids using sticky glue to trap prey are equipped with the here supposed protective coating (Christian Kropf, preliminary data), the question arises whether linyphiid spiders and several other araneoid taxa with modified aggregate gland secretion (still) have it.

### Methodological considerations

The accuracy of our measuring apparatus has proven to be very high: In a previous dataset on *A. diadematus* (excluded from and not shown in this study), IOAs on water-washed legs were intermediate between those of unwashed and carbon disulphide-washed legs. Searching for an explanation for this puzzling finding, we noticed that our water distiller was damaged and the water still contained small amounts of calcium carbonate that presumably had coated the spider leg with tiny crystals during drying and so caused slightly stronger adhesion as compared to untreated legs. Repeating the measurements with purified water brought the results presented here.

Our Low Vacuum SEM inspection of differentially treated spider legs (experimental groups U, W and CD, respectively) did not reveal any visible damages or changes in ultrastructure of cuticle and hairs. However, a more or less light damage of the delicate epicuticle, especially caused by the CS<sub>2</sub>-treatment, would possibly not be visible and, therefore, cannot be totally excluded.

As the measurements were performed under laboratory conditions, they cannot be directly compared with natural conditions. First, the contact area of the leg with the capture thread corresponded roughly to the diameter of the middle part of the tibia which will hardly occur in nature. In contrast, undisturbed spiders under natural conditions should touch the capture spiral at the most with the tips of their tarsi. However, tarsal tips proved to be hardly testable for a protective surface coating with our method, as the serrated claws and possibly also the numerous serrated hairs there may entangle in the capture thread, in this way distorting the measurements. Testing the tibia was more promising to us in this respect. Second, it has been shown recently that glue droplets on glass plates exhibited stronger adhesion when the pull-off velocity

was greater (Sahni et al. 2010). As sinking velocity of the water level was roughly 0.5 mm per second in our study, which presumably is much slower than natural withdrawal movements of spiders, our data may underestimate the adhesive forces of capture threads under natural conditions.

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### Zusammenfassung

*Ein organischer Oberflächenfilm schützt araneoide Radnetzspinnen (Araneae, Araneioidea, Araneidae) vor dem Festkleben am eigenen Fangfaden.*

Über 95% der Radnetz-bauenden Spinnen benutzen einen klebrigen Faden mit komplex aufgebauten Klebstoff-Tröpfchen zum Beutefang. Ein derartiger Fangfaden birgt aber auch für die Spinne Risiken. Die naheliegende Frage, wie es eine Spinne vermeidet, im eigenen Fangfaden kleben zu bleiben, wurde bisher kaum untersucht. Im Jahr 1905 schloss der französische Naturforscher Jean-Henry Fabre aus einzelnen Beobachtungen, dass sich Radnetzspinnen mittels eines fettigen Schutzfilms auf ihrem Körper vor dem Klebstoff schützen. Diese Hypothese wurde bisher nie überprüft. Wir maßen auf indirektem Wege die Kraft, die nötig ist, um ein autotomiertes Spinnenbein aus der Fangspirale des eigenen Netzes zu lösen. Je drei Gruppen von Beinen der Arten *Araneus diadematus* Clerck, 1757 und *Larinioides sclopetarius* (Clerck, 1757) wurden getestet. Eine Gruppe blieb unbehandelt, die zweite wurde mit destilliertem Wasser (H<sub>2</sub>O) gewaschen, die dritte mit dem organischen Lösungsmittel Schwefelkohlenstoff (CS<sub>2</sub>). Beine beider Arten hafteten schwach am Klebfaden, wenn sie unbehandelt geblieben oder mit Wasser gewaschen waren, ohne dass es einen signifikanten Unterschied zwischen den beiden Gruppen gab. Mit Schwefelkohlenstoff behandelte Beine hafteten etwa doppelt so stark wie die unbehandelten oder mit Wasser gewaschenen Beine am Fangfaden. Unsere Resultate liefern einen indirekten Beleg für einen organischen anti-adhäsiven Oberflächenschutzfilm bei araneoiden Spinnen und unterstützen daher Fabres Hypothese.

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