

# Spiders avoid sticking to their webs: clever leg movements, branched drip-tip setae, and anti-adhesive surfaces

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**Abstract** Orb-weaving spiders construct webs with adhesive silk but are not trapped by it. Previous studies have attributed this defense to an oily coating on their legs that protects against adhesion or, more recently, to behavioral avoidance of sticky lines. The old evidence is very weak, however, and the behavioral avoidance explanation is inadequate because orb-weavers push with their hind legs against sticky lines hundreds or thousands of times during construction of each orb and are not trapped. Video analyses of behavior and experimental observations of isolated legs pulling away from contact with sticky lines showed that the spider uses three anti-adhesion traits: dense arrays of branched setae on the legs that reduce the area of contact with adhesive material; careful engagement and withdrawal movements of its legs that minimize contact with the adhesive and that avoid pulling against the line itself; and a chemical coating or surface layer that reduces adhesion.

**Keywords** Spider webs · Anti-adhesives · Drip-tip setae · Behavior

Fragmentary observations of pioneering naturalists (Fabre 1912; Hingston 1920) suggested that araneoid orb-weaving spiders avoid adhering to their own webs by coating their legs with an anti-adhesive oil from glands associated with their mouthparts. Their observations, however, were only superficially described and apparently neither replicated nor quantified. More recently, it was argued that this old story is a myth, and that orb-weavers do not need an anti-adhesive because they generally avoid walking on the sticky lines in their webs and minimize contact with glue on sticky lines by “tip-toeing” on fine tarsal hairs (Vollrath and Tillinghast 1991). During sticky spiral construction, however, araneoid orb-weavers thrust legs IV against the sticky spiral line just before each attachment to a radius (Peters 1954; Eberhard 1982; Agnarsson and Blackledge 2009), and are not caught by their own lines. The present study shows how orb weavers avoid adhering to sticky lines despite these repeated forceful contacts, using some of the same traits as those used by water-walking arthropods to avoid entrapment by water (Bush et al. 2008).

## Methods

We observed details of leg behavior and morphology and experimental modifications of legs to document mechanisms that reduce adhesion to webs. Sticky spiral construction behavior of mature females of *Nephila clavipes* (Nephilidae; in captivity) and *Gasteracantha cancriformis* (Araneidae; in the field) was recorded near San Antonio de Escazú, Costa Rica in July 2011 using a Sony DCR TRV50 camera equipped with close-up lenses. Lab tests of adhesion employed a Sanyo color CCD NCC-3912 video camera coupled to a dissecting microscope, allowing resolution of individual droplets of adhesive. Segments of sticky spiral

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lines were collected from orbs built the same day by adult female *N. clavipes* by bringing the modified upper edge of a 0.9-cm inner-diameter plastic vial into contact with the web and then cutting the sticky line free. Sticky droplet diameters were measured the day of construction at room temperature and humidity with a compound microscope. Most experiments involved adult female *N. clavipes* (Nephilidae). Because these large spiders move quite slowly and may thus experience reduced adhesion (Agnarsson and Blackledge 2009), we also observed the moderate-sized *G. cancriformis*.

The strength of adhesion was determined for legs IV that were detached manually from *N. clavipes* killed by hypothermia and frozen. At room temperature, the isolated leg was moved downward manually with a micromanipulator fashioned from a microscope stage to press against the central portion of a horizontal sticky line, and was then raised until it came free from the line. The tip of the tarsus of the leg was directed approximately downward and the line snagged on the setae on its side as the leg moved downward. Each test lasted on the order of 1–4 s, but the rate of movement of the leg up and down varied ( $0.56 \pm 0.26$  mm/s,  $N=15$  legs). To test for the possible effects of polar and non-polar coating substances on leg adhesion, some other tarsi were soaked in either hexane ( $n=30$  legs; one leg/animal) or water ( $N=30$  legs; one leg/animal) for 60 min, allowed to dry, and then tested. Setae were removed by scraping from still other untreated tarsi ( $N=30$  legs; one leg/animal), to test for the effects of the setae. Adhesion to the basal portion of the metatarsus was tested as just described with a further set of 30 control legs, 30 hexane-washed legs, and 30 water-washed legs (different legs IV from the same spider were used for different treatments).

The strength of adhesion was estimated by measuring the angle of the sticky line in the last frame of the video before it pulled free from the tarsus, and comparing it with the angles made when one, two, and three small “S”-shaped hooks (1.24 mg) of copper wire that were hung from the line and from each other from the central portion of each of the same sticky lines for at least 30 s. A plot of the angles vs. the weights for all lines showed an approximately linear relation in the range of weights in this study (mean deflection angles for different tests ranged from  $20^\circ$  to  $45^\circ$ ), so linear interpolations were used to estimate the force ( $\text{mg} \times 9.807 \times 10^{-6}$  N) required to pull the tarsus free from the line. We used Mann–Whitney  $U$  tests to compare data for each treatment. Means are followed by  $\pm 1$  standard deviation.

## Results

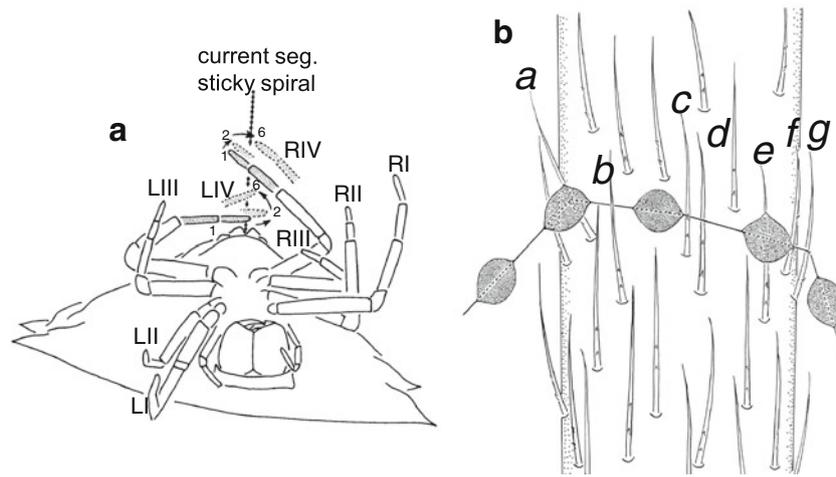
Although both species tended to move along non-sticky lines such as radii when moving on finished webs, just as

in other species (Hingston 1920), the tarsi IV of both species pulled sticky line from the spinnerets during sticky spiral construction with one (in *N. clavipes*) or up to eight (in *G. cancriformis*) ventral thrusting movements just before the sticky spiral was attached to each radius (Fig. 1a; Electronic supplementary materials (ESM) 1 and 2). Although these and most other spiders generally contact their webs with their tarsal claws and the tips of their tarsi (Foelix 1996), video recordings showed that in both species, contact with the sticky line during sticky spiral construction occurred on the dorsal and retro-lateral surfaces of tarsus IV (Fig. 1a; ESM 1 and 2) or occasionally the distal end of metatarsus IV. Contact with the sticky line during sticky spiral construction lasted on the order of 1–2 s during each thrust (*G. cancriformis*— $x=0.52 \pm 0.27$  s; range, 0.23–1.27 s; and  $N=37$ ; *N. clavipes*— $1.58 \pm 0.52$  s; range, 1.07–3.90s; and  $N=33$ ). The velocity of the thrusting movements was about 10–20 mm/s in *G. cancriformis* and about 30–40 mm/s in *N. clavipes*. The mean duration of the withdrawal movement, until contact with the sticky line was lost, was about 0.1 s in *G. cancriformis* (Fig. 1a) and 0.2 s in *N. clavipes*. The spider withdrew her leg from contact in a direction roughly aligned with the long axis of her tarsus, rather than by continuing the thrusting movement (Fig. 1a). The sticky line was generally displaced only slightly or not at all as the leg pulled away; it was not visibly deflected in 14 of 32 withdrawals by *G. cancriformis* and 18 of 34 by *N. clavipes*. Judging by finished webs, each leg IV pushed a sticky line on the order of 1,500 times during construction of a single *N. clavipes* orb, and  $>1,000$  times during that of a *G. cancriformis* orb.

The sticky spirals of both *G. cancriformis* and *N. clavipes* resembled those of other araneoids, which consist of a pair of non-adhesive, viscoelastic axial baselines that are coated with more or less regularly spaced droplets of a complex adhesive (Vollrath and Tillinghast 1991; Sahni et al. 2010; Craig 2003; Opell and Hendricks 2007; Opell and Hendricks 2010). In a *N. clavipes* web, the mean diameter of 37 droplets was  $0.058 \pm 0.011$  mm and the mean distance between droplets was  $0.057 \pm 0.036$  mm.

The tarsi of all legs of both species are covered on all sides with distally directed setae (Figs. 1b and 2). Most setae on the dorso-retrolateral surfaces of tarsus IV had one or more distally projecting short branches or spurs on the “exterior” side of the seta, away from the tarsal surface near the base (Figs. 1b and 2a). Mean diameters of 30 setae at their bases and at approximately their midpoints on the retrolateral surface of one *N. clavipes* tarsus IV were  $0.0134 \pm 0.001$  and  $0.0075 \pm 0.001$  mm, respectively. The branches on the seta (Fig. 2) on a *N. clavipes* tarsus IV were nearly all in the basal half of the seta (137 of 143).

Observation of isolated legs under a dissecting microscope as they thrust against sticky lines showed that the line always snagged on the tarsal setae. The sticky droplets



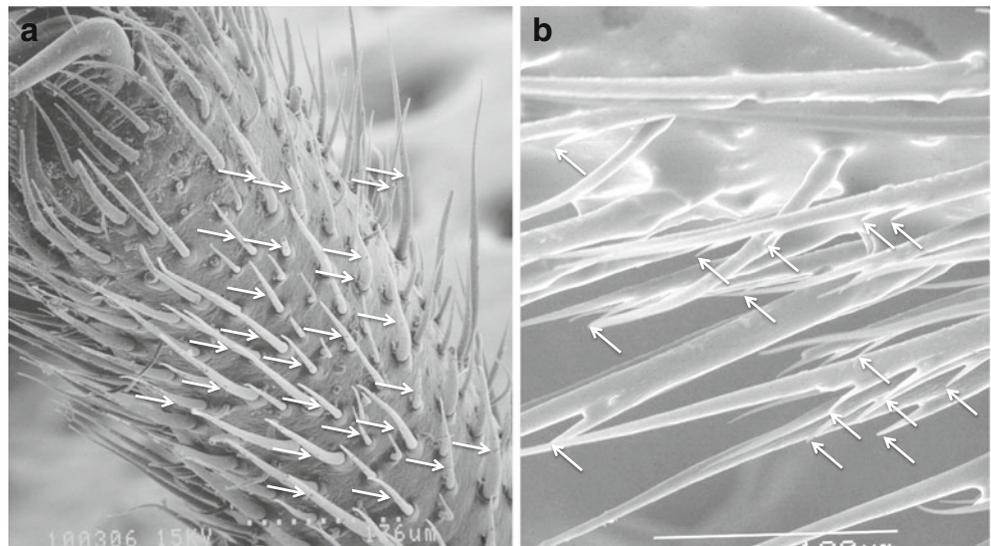
**Fig. 1** **a** Schematic drawing from a video recording (30 fps) of sticky spiral construction behavior of *G. cancrivormis* during alternate ventral thrusting movements of legs IV that pulled sticky line from the spinnerets (sticky line is represented by heavy lines with dots; most web lines are omitted for clarity). The numbers associated with positions indicated by dashed lines refer to the numbers of the frames following the position 1 (solid lines); arrows represent directions of leg movements. Leg LIV thrust to snag the line (1–2) and then pulled it from the spinnerets (2–6); at the same time, RIV ended a thrust (1–2) and pulled out of contact with the sticky line (2–6), scarcely deflecting the sticky line as it pulled free (6). In the following frames, RIV moved forward

to snag the line near the spinnerets and pull out an additional length of sticky silk. **b** An idealized drawing (with a reduced number of shortened setae to facilitate illustration) of different ways in which setae and sticky lines can interact. *a* Sticky droplet slides on the external surface of seta until line snags on a branch; *b* the line contacts the interior side of the seta, which may arrest the line’s basal movement; *c, g* the line snags on a setal branch but the sticky droplet does not contact seta; *d, f* the line fails to contact the exterior sides of setae; and *e* the line and sticky droplet slide basally on a seta but do not reach a branch. When the leg pulls away, the droplet on seta *e* can pull free before the droplet on seta *a*

contacted the exterior surfaces of these setae, and slid along them toward their bases (Fig. 1b). The outline of each droplet indicated that it wetted the seta (Fig. 1b). When the leg was withdrawn approximately parallel to the long axis of the tarsus, each sticky droplet slid distally back along the seta (ESM 3). The rate at which a droplet slid along the seta was sometimes slower than the rate with which we withdrew the tarsus in our experiments; when withdrawal

was interrupted just before the leg pulled free, a droplet sometimes continued to slide toward the tip of the seta for about 0.1 s. When a droplet reached the end of a seta, it was in contact with only the thin tip of the seta. Thus the surface area contacting the leg was minimal at the moment when the droplet’s connection with the leg was about to be broken, just as in tropical plants, whose fine pointed leaf tips allow water drops to be shed easily (Dean and Smith 1978).

**Fig. 2** **a** Distal-lateral view of a control *N. clavipes* tarsus that had not pushed on sticky lines. **b** Lateral view of *N. clavipes* setae covered with an apparently viscous material on a hexane-washed tarsus IV that had pushed 400 times against a sticky line. Arrows indicate setal branches



Because tarsal setae were not in regular rows, the sticky droplets did not break free from different setae simultaneously but rather one by one. This prevented summation of the adhesive forces of multiple droplets, as occurs when a sticky line adheres to a flat surface (Opell and Hendricks 2007).

Tarsi washed in hexane or water adhered to sticky lines more strongly than control tarsi. The mean estimated force to break the adhesion after the first contact with control tarsi was less than half of those with hexane-washed and water-washed tarsi (control— $4.71 \pm 5.39 \times 10^{-6}$  N; hexane— $10.4 \pm 6.28 \times 10^{-6}$  N; and water— $11.6 \pm 9.02 \times 10^{-6}$  N;  $p < 0.0001$  for control vs. hexane-washed, 0.001 for control vs. water-washed). Averaging over the first five of 20 consecutive contacts for each of the 30 legs in each trial, the respective means were  $5.55 \pm 5.79 \times 10^{-6}$  N,  $12.1 \pm 6.47 \times 10^{-6}$  N, and  $13.1 \pm 5.79 \times 10^{-6}$  N ( $p < 0.00001$  comparing controls with both hexane-washed and with water-washed tarsi; hexane-washed vs. water-washed differences were not significant for either comparison). In unwashed legs from which setae had been removed, the strength of adhesion was about seven times that of controls ( $33.7 \pm 7.65 \times 10^{-6}$  N for first test), confirming the important role of setae.

Adhesion of lines to the basal portion of the unwashed metatarsus IV (which is similarly covered with setae but never contacts sticky lines during orb construction) was about twice as strong as that for control tarsi ( $11.7 \pm 4.81 \times 10^{-6}$  N;  $p < 0.0001$ ). Adhesion to the basal portion of the metatarsus also differed in that it was not significantly increased by washing in hexane ( $13.8 \pm 5.69 \times 10^{-6}$  N;  $p = 0.25$ ), and was more weakly increased by washing in water ( $16.7 \pm 6.86 \times 10^{-6}$  N;  $p = 0.003$ ).

The possibility that repeated contact would result in a gradual build up of adhesive material on the tarsal setae was tested by examining the tarsal setae of hexane-washed tarsi that had made 400 contacts with sticky lines; they had abundant liquid material on them (Fig. 2).

## Discussion

Both behavioral and morphological traits probably help reduce the strength of adhesion to tarsus IV during orb construction. Thrusting movements were oriented so as to bring the exterior surfaces of the setae on the dorso-retrolateral surfaces of the tarsus into contact with the sticky line, presumably causing the line to slide basally along each seta until it snagged on a branch on the exterior surface of the seta or on other setae. The orientation of the leg's withdrawal movement, approximately along the long axis of the tarsus, caused the sticky droplets to slide distally along the setae, and probably reduced the area of contact between the sticky droplets and the setae to the tips of the

setae at the moment leg IV pulled free. Finally, adhesion was reduced by a surface property (perhaps a coating) that could be altered by washing.

Assuming that the sticky line of *N. clavipes* contacts approximately the central half of the approximately 0.38 mm diameter tarsus (Figs. 1b and 2), there will be on average two to three sticky droplets on this portion of the line and 15–20 setae that they might contact (counting the spaces between droplets, there are about five setae/droplet). Those setae farther from the tarsal surface in the area of contact will be more likely to contact a droplet; the high density of setae makes it likely that one seta or another usually contacts each of the droplets. Both because the line contacts multiple setae and because the setae have branches, the chances are reduced that any sticky droplet will slide all the way to the base of a seta and reach the surface of the tarsus, where adhesion is much stronger.

Although setal branches are likely to have the effect of snagging sticky lines, this is apparently not their only function, because examination of legs with the SEM showed that branches also occur on other female tarsi that are not used to pull out sticky line (legs I and III), on the tarsi IV of mature male *N. clavipes* (which never build orbs), and on the tarsi IV of mature female *Cyrtophora citricola*, and araneid which build orbs that entirely lack sticky lines (Wiehle 1927; Lubin 1973). The greater adhesion to the basal metatarsus than to the tarsus suggests a localized tarsal defense against adhesion. The reduced effect of washing the metatarsus with hexane but not water suggests that part of this localized defense may be a hydrophobic chemical.

There are several reasons to suspect that our estimates of adhesive force may differ from forces experienced by spiders building orbs. A previous study using sticky droplets immobilized on small glass plates showed that adhesion correlated positively with the pull-off velocity (Sahni et al. 2010) (the highest pull-off rate in that study was approximately an order of magnitude slower than that of *G. cancriformis* leg withdrawal, however; thus the relation of their values to adhesion in nature is uncertain). The thrusting and withdrawal movements in our experiments were on the order of 0.6 mm/s, more than an order of magnitude slower than the movements of spiders during orb construction. In addition, the rate at which the adhesive material slid along a seta in our experiments was at least sometimes slower than the rate at which we moved the leg. This means that our slow thrusting movements may have allowed droplets to slide farther toward the bases of the setae, making for greater adhesion. On the other hand, our slower withdrawal movements may have allowed balls to slide farther toward the tips of the setae before pull-off, making for weaker adhesion. The relatively long duration of the spiders' thrusting movements (often 1–2 s), compared with the rapidity of their withdrawal movements (about 0.1–0.2 s) suggests that

on balance sticky droplets in our experiments may have tended to get closer to the tips of setae before being pulled off than they do during web construction, which would result in lower forces of adhesion in our experiments.

Our translations of angle measurements into force were also only approximate. We used linear interpolations between calibration values to estimate forces, while curvilinear relations are more likely. In addition, sticky lines of orb weavers show considerable “creep” over the space of 10–20 s when loaded, and this property changes somewhat with repeated loading (Denny 1976). Our pull-off experiments lasted only up to about 4 s while measurements of deflections produced by wire hooks lasted 30 s or more, so there was ample time for creeping to occur during calibration measurements. This could have caused us to underestimate the forces involved in pulling legs free during sticky spiral construction. Still another complication is that the angle of the leg with the long axis of the sticky line was more consistently near to perpendicular in our experiments than when intact spiders built orbs (Fig. 1a), perhaps causing sticky droplets to slide farther basally on setae.

Despite these considerations, however, our experiments are useful in understanding the effects of washing and seta removal, because our conclusions are based on comparisons, not on absolute values. None of the differences regarding the effects of washing, of seta removal, or contact with the tarsus vs. the metatarsus changed when we repeated the statistical tests using angle measurements rather than estimated forces. Our conclusion that legs have an anti-adhesive surface property is in accord with the unpublished results of another study that utilized a different technique with two other araneid species (Kropf et al. 2012).

Our washing experiments suggest that spider leg setae have either a chemical coating of anti-adhesive substance(s) or a structural surface layer that is altered by hexane and water, and that this coating or surface layer is limited to or more pronounced in the distal portions of the leg. Preliminary gas chromatography–mass spectrometry analyses of compounds washed from *N. clavipes* legs with *n*-hexane suggest the presence of several oily substances (*n*-dodecane, *n*-tridecane, and *n*-tetradecane) that might confer anti-adhesive properties (Gonzalez-Florez, personal communication). The source of possible anti-adhesive substances is unknown. Hingston (1922) concluded that the coating comes from the spider’s mouth. We confirmed that brief washing of tarsi in hexane induced *N. clavipes* to pass their tarsi through their mouthparts,

as observed by Hingston, but we did not test whether anti-adhesive material was applied.

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