

Possible self-assembly in linyphiid sheet webs

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Abstract

Most lines in the sheets of four linyphiid species bore numerous small droplets. Droplet-bearing lines of *Linyphia simplicata* (F. O. Pickard-Cambridge, 1902) and *Nerienne coosa* (Gertsch, 1951) adhered weakly to smooth, dry surfaces, contradicting previous statements that such lines in linyphiid webs are not sticky. Droplets at the intersections of lines tended to be larger than nearby droplets on the same lines, and were more widely separated from adjacent droplets than were other, nearby droplets on the same lines. A self-assembly hypothesis to explain these findings, that larger droplets accumulated at intersections as a result of lines in the sheet scraping against each other, was supported by confirming that larger intersection droplets were more widely separated from adjacent droplets than were smaller intersection droplets. These observations suggest a new, dynamic view of linyphiid sheet webs, in which the distribution of sticky material is adjusted advantageously immediately after lines are produced, due to the upward dabbing movements of the spider's abdomen that press the sheet lines against each other during sheet construction, and perhaps also to other movements of newly laid lines against each other. Larger droplets may be advantageous in binding lines together, and in adhering to prey.

Keywords: prey retention • sheet construction behaviour • sticky droplets

Introduction

Spider webs are often thought of as passive traps for prey, but web-building spiders are an ancient evolutionary

success story (Vollrath & Selden 2007), and one result of their long history has been the evolution of substantial diversity in how their webs function (Eberhard 2020). Some spiders have evolved behaviours with which they manipulate their finished webs (Kaston 1964; Gray 1983), while others adjust web construction behaviour to environmental variables such as wind (Wu *et al.* 2013). In some species, the materials in webs also adjust their own properties during and after web construction. For instance, the adhesiveness of the sticky spiral of some orb webs is adjusted by taking up water from the air (Opell & Hendricks 2007; Opell, Karinshak & Sigler 2011, 2013; Townley & Tillinghast 2013); and the sticky spiral connections to radii in some araneid webs break partially when stressed, allowing the spiral line to pass through the attachments without detaching from the radius and thus increasing the amount of stress that the line can absorb from the prey (Eberhard 1976; Craig 2003). The silk molecules themselves also self-assemble while moving through the ducts of silk glands (Malay *et al.* 2020).

Dynamic adjustments of this sort have not been described in the prey capture webs of the large family Linyphiidae (4674 described species in 621 genera: World Spider Catalog 2021). Most linyphiid webs include a densely meshed, more or less horizontal sheet (Kaston 1964; Shear 1986), and these sheet webs show a wide variety of designs (Eberhard 2020; G. Hormiga & W. Eberhard in prep.). Historically, there has been uncertainty concerning even such basic properties of linyphiid sheets as the presence or absence of sticky lines and their functions (Peters & Kooor 1991; Schütt 1995; Benjamin, Duggelin & Zschokke 2002). Early statements that linyphiid webs are in general composed of “dry silk” (Main 1976: 183), and that in the webs of *Linyphia triangularis* (Clerck, 1758) “none of the threads are sticky” (Bristowe 1958: 261) were contradicted by photographs of lines bearing apparently liquid droplets in *L. triangularis* as well as in linyphiid species belonging to five additional genera (Wiehle 1956; Millidge 1988; Peters & Kooor 1991; Benjamin, Duggelin

& Zschokke 2002). Kullmann (1971) found that the sheets of *Obscuriphantes obscurus* (Blackwall, 1841) were in fact composed nearly exclusively of droplet-bearing lines.

Even more widespread occurrence of droplet-bearing lines in linyphiid webs is suggested by spinneret morphology. The triads of spigots on the posterior lateral spinneret, consisting of one flagelliform gland spigot and two nearby aggregate gland spigots that add liquid glue from the aggregate gland to the flagelliform line as it emerges (Townley & Tillinghast 2013) occur in *L. triangularis* (Peters & Kooor 1991; Schütt 1995) and in numerous other linyphiid genera, including *Bolyphantes* (Hormiga 1994), *Ceratinops* (Hormiga 2000), *Diplocentria* (Hormiga 2000), *Diplocephalus* (Hormiga 2000), *Diplothyron* (Moreira & Hormiga in prep.), *Drepanotylus* (Hormiga 2000), *Erigone* (Hormiga 1994), *Frontinella* (Coddington 1989), *Gonatium* (Hormiga 2000), *Haplinis* (Hormiga 1994, 2000), *Helophora* (Schütt 1995), *Hilaira* (Hormiga 2000), *Laminacauda* (Hormiga 2000), *Lepthyphantes* (Hormiga 1994), *Linyphia* (Hormiga 1994; Schütt 1995), *Neriere* (Hopfmann 1935, Schütt 1995), *Novafroneta* (Hormiga 1994), *Oedothorax* (Hormiga 2000), *Orsonwelles* (Hormiga 2002), *Ostearius* (Hormiga 2000), *Pelecopsis* (Hormiga 2000), *Savignia* (Hormiga 2000), *Sciastes* (Hormiga 2000), *Stemonyphantes* (Hormiga 1994), *Tmeticus* (Hormiga 2000), and *Walckenaeria* (Hormiga 1994, 2000). There are a few exceptional linyphiids such as *Drapestica socialis* (Sundervall 1832), in which web lines lack droplets (Kullmann 1971; Schütt 1995), and triads are absent (the flagelliform spigot persists but the aggregate gland spigots are lacking) in *D. socialis* and *Neriere peltata* (Wider, 1834) (Schütt 1995).

An alternative possibility, that linyphiid triads produce adhesive lines for wrapping prey (as in theridiids) rather than for webs, is unlikely because linyphiids do not perform immobilization wrapping and apply only a few wrapping lines after the prey has been immobilized by biting (Bristowe 1940; Eberhard 1967; Peters & Kooor 1991; W. Eberhard, unpublished observations of *Linyphia simplicata* and *Neriere coosa*) (a revision in preparation by T. Moreira and G. Hormiga has found that *L. simplicata* should be placed in the currently monotypic genus *Diplothyron*) (G. Hormiga, pers. comm.). In summary, current evidence supports the conclusion of Millidge (1988) that linyphiid webs generally include lines bearing droplets of liquid. But the function of such droplet-bearing lines and their glandular origins remains controversial.

Peters & Kooor (1991) argued that earlier studies, which employed the light microscope rather than the SEM and relied only on the presence of droplets to identify capture threads, were inadequate. These authors apparently identified the glandular origins of lines largely on the basis of the numbers and diameters of axial fibres, details that usually cannot be resolved in the light microscope but are often visible in the SEM (though sometimes one line is hidden by another, and the diameters of the lines of a given type can vary) (Peters & Kooor 1991). They confirmed that many lines in the sheet of *L. triangularis* bore small droplets

and that others did not (Peters & Kooor 1991). They found some lines in the SEM that lacked droplets but that nevertheless appeared to adhere to each other: a thin sheet of an apparent liquid was visible at points where pairs of such lines separated from each other; the two fibres pulled each other out of line, demonstrating that they adhered to each other (Peters & Kooor 1991; Benjamin, Duggelin & Zschokke 2002). Peters & Kooor (1991) suggested that these adhesions were due to thin coatings on the lines derived from minor ampullate gland products. Contrary to other authors, they stated that the lines in the sheet were mainly ampullate gland lines "... ampullate gland fibers [lacking droplets] form a very dense irregular network" (Peters & Kooor 1991: 11), and proposed that these lines in the sheet were largely bound to each other by this coating: "Differently directed fibres joining together in the sheet are bound ... by secretions of the minor ampullate glands" (Peters & Kooor 1991: 15). They explained the abundance of droplet-bearing lines in the sheets by their finding that capture threads from the triads "often fuse with ampullate gland fibres" (Peters & Kooor 1991: 13). They noted, however, that "there was some suspicion" of occasional single triad threads (Peters & Kooor 1991: 13), a detail subsequently confirmed in the SEM photos of Benjamin, Duggelin & Zschokke (2002).

The usual assumption in studies of spider webs has been that droplets on lines are adhesive and function to retain prey in the web, as is the case, for instance, in the sticky spiral lines of araneid orb webs and the gumfoot lines of theridiids (Eberhard 2020). Although Millidge (1988) had demonstrated adhesion of droplet-bearing lines in the sheet of *Linyphia* (apparently *L. triangularis* and/or *L. montana* (Clerck, 1757)) to a dry, fine needle, some later authors maintained that "the assumption that the globules in linyphiid webs have the same viscid silk properties and function as in orb webs ... is unfounded" (Benjamin, Duggelin & Zschokke 2002: 58), and argued that linyphiid droplets serve instead to bind lines to each other in the sheet when the lines are laid and then dry up a short time after web construction (Benjamin, Duggelin & Zschokke 2002). Peters & Kooor (1991) also noted that the droplets may be adhesive in the short term, but not in the long term, and argued that they are not important in retaining prey: they "seem to play a minor functional role [in prey capture]". They thought that the droplet-bearing lines ("capture threads") of linyphiids were "simply attached to other threads by ... [the] sticky surface [of the lines themselves]" (Peters & Kooor 1991: 16). Schütt (1995: 553) also concluded, on the basis of spinneret morphology, that "gluey capture threads do not play an important role in the capture of prey in Linyphiidae".

The present study documents the presence of droplet-bearing lines in the sheets of four additional species in three additional genera of linyphiids, and shows that in at least two of these species the droplet-bearing lines are sticky. In addition, it tests the novel hypothesis that linyphiid droplets self-assemble dynamically in a process that may increase prey retention. Specifically, I hypothesize that droplet-bear-

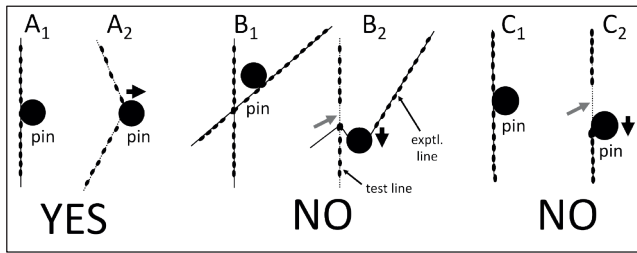


Fig. 1: Schematic representations (not to scale) of experiments to test for adhesions and movements of droplets on lines in sheets. In experiment **A**, a pin touched a droplet-bearing line and then moved away from it (black arrow in A_2). I checked to see whether the line moved when the pin was moved away (A_2); the result was as in the drawing (YES). In experiment **B**, the pin pulled one of the two lines at an intersection (experimental line) in a direction that was approximately parallel to that of the other line (test line) (black arrow); I checked to see whether the junction slid along the line, leaving a space lacking droplets (red arrow in B_2). Movements of this sort never or nearly never occurred (NO). In experiment **C**, the pin touched and was then moved so as to slide along a droplet-bearing line (black arrow); I checked to see whether the point of contact slid along the line, leaving a segment lacking droplets (red arrow in C_2). This movement also did not occur (NO).

ing lines in the sheet move relative to each other during sheet construction and perhaps afterward, and that when they do so their glue droplets are scraped along the lines and fuse with each other. I confirm three predictions of this hypothesis: that droplets at intersections of droplet-bearing lines are larger than other, nearby droplets; that intersection droplets are surrounded by larger spaces than those between other nearby droplets; and that larger intersection droplets are surrounded by larger spaces than are smaller intersection droplets. I discuss possible implications of this self-assembly hypothesis for details of how construction behaviour produces an interconnected sheet, and for how linyphiid webs function.

Material and methods

I collected adult females of *Neriene coosa*, *Frontinella pyramitela* (Walckenaer, 1841), and *Florinda coccinea* (Hentz, 1850) in October 2018 near Baton Rouge, LA, USA (30°25'13"N 91°11'21"W, 12 m), and adult and penultimate females of *Linyphia simplicata* between November 2018 and January 2020 near San Antonio de Escazu, San José Province, Costa Rica (9°53'51.41"N 84°08'15.99"W, 1320 m). Spiders wove webs in captivity on rectangular frames made of copper wire and wooden dowels; the frames for *L. simplicata* were 9 × 9 × 9 cm cubes, while those for the other, larger species were 21 × 15 × 7 cm (or 21 × 15 × 15 cm for *F. pyramitela*). The frames were placed in closed, transparent containers, generally in a shallow pool of water to discourage the spider from attaching lines to other supports.

Lines in unmanipulated webs built the previous night by mature females in captivity were tested for adhesion under a 40× Zeiss dissecting microscope. The possible stickiness of a line was tested by touching the side of a clean new, fine (#1) stainless steel insect pin (about 0.39 mm in diameter) to the middle of a segment that was on the order of 1 mm

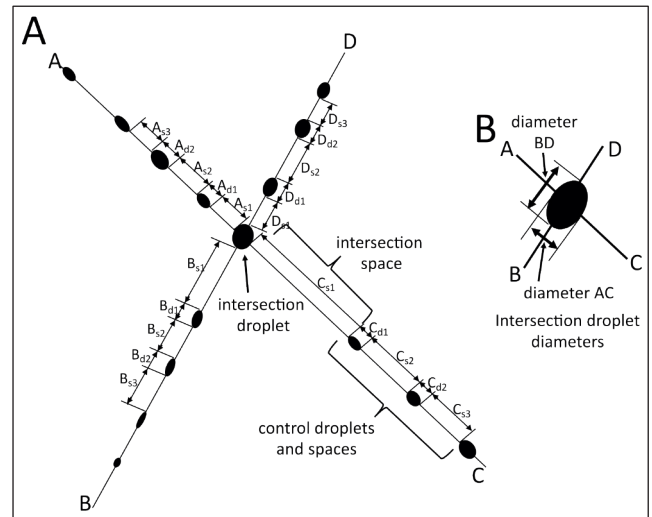


Fig. 2: Variables included in the analyses of droplet diameters and spaces between droplets (the intersection droplet in **A** is magnified in **B**). The intersection droplet diameters along the lines were AC and BD; the control values for AC were A_{d1} , A_{d2} , C_{d1} , and C_{d2} , while the control values for BD were B_{d1} , B_{d2} , D_{d1} and D_{d2} . The spaces for the intersection droplet on line AC were A_{s1} and C_{s1} , and the control values for these spaces were A_{s2} , A_{s3} , C_{s2} and C_{s3} . On line BD the intersection spaces were B_{s1} and D_{s1} , and the control values for these spaces were B_{s2} , B_{s3} , D_{s2} and D_{s3} .

long (between intersections with other lines), and then slowly withdrawing the pin in a direction approximately perpendicular to the line; I watched to see whether the line was displaced (Fig. 1A₂). I performed these tests near the edge of the sheet, where lines were more widely spaced and access was less hindered by lines above the sheet.

In another test, I attempted to slide the droplets along a line (as can be done with droplets on the sticky spiral lines in araneid orb webs (Eberhard 1976)) by stressing intersections between droplet-bearing lines (like that in Fig. 2), using a finer pin (*minuten Nadel*, about 0.13 mm in diameter). I pulled one of the lines (the experimental line in Fig. 1B₂) in a direction that was approximately parallel to the direction of the other line (the test line) and slightly upward, and checked to see whether this caused the point of intersection to move (Fig. 1B₂). I also attempted to slide the pin along droplet-bearing lines, checking to see whether or not the point of contact with the pin slid along the line and left a space free of droplets behind (Fig. 1C₂). Only in those experiments in which I had exercised enough force to cause the test line to go slack and curl perceptibly did I count the experiment as having failed to move the droplet. The distance I could move the pin in these experiments was variable, due to restrictions imposed by the other lines in the sheet. In no case did my pull with the pin break either the experimental or the test lines.

I collected samples of sheets built in captivity to examine under a compound microscope onto glass microscope slides that bore a raised, strongly adhesive 6 × 2 cm frame that was formed by thin strips (about 2 mm across) of an approximately 1 mm thick double-sided adhesive tape stuck to the slide. I attempted to minimize the disturbance to the sheet during collection by pressing the slide against a more or less planar, peripheral portion of the sheet from below, where

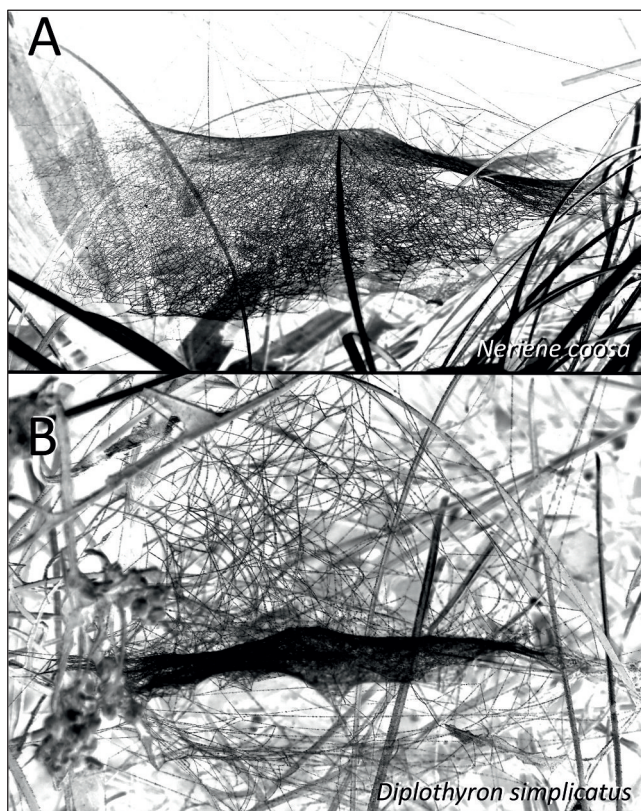


Fig. 3: Webs of mature female *N. coosa* (A) and *L. simplicata* (B) coated with talcum powder in the field. The sheet was weakly domed in both species; *L. simplicata* webs typically had more extensive tangles above the sheet.

there were fewer tangle lines. I freed the slide from rest of the sheet by pressing the sheet downward against the edges of the slide. Because webs in captivity (especially those of *N. coosa*, and to a lesser extent those of *L. simplicata*) often had reduced tangles, sheet samples were free or nearly free of tangle lines.

Web samples on slides were examined at ambient humidity under a Zeiss compound light microscope in an air conditioned room a week or more after they were built. The sizes and spacing of droplets at and near the intersections between lines that bore droplets of liquid were sampled by making transects across the width of the slide; I photographed each intersection between two lines (as opposed to intersections of three or more lines) that had at least 4 droplets without other intersections on all sides (Fig. 2). I used ImageJ (wsr.imagej.net) to measure the sizes of droplets and the spaces between them (Fig. 2) in the digital images after increasing the contrast. Most droplets were approximately ovoid, with the maximum dimension along the line. The sizes of droplets and the spaces between them varied widely and were not distributed normally, so I report medians rather than means, and tested for statistical significance with non-parametric Mann-Whitney U Tests using the program PAST (Hammer, Harper & Ryan 2001). The sizes of droplets and the spaces between them usually differed on the two intersecting lines, so I analysed the dimensions along each line separately (e.g. the droplet diameters and the spaces between droplets along line AC in Fig. 2 were analysed separately from those along line BD).

In the descriptions below I use the word line in the singular even though most lines in spider webs are composed of multiple fibres (Peters & Kooor 1991; Benjamin, Duggelin & Zschokke 2002). I use sticky to designate lines bearing multiple droplets of liquid, although a few of these lines had portions that lacked droplets and the adhesive nature of the droplets was tested in only a few. Lines that lacked droplets along their entire length in the sample are termed non-sticky lines, even though some of these lines may have been sticky when first laid (Peters & Kooor 1991). I use negative images of the webs in the illustrations to facilitate perception of patterns in the lines.

Gustavo Hormiga kindly identified *N. coosa*, and Thiago Moriera identified *L. simplicata*; *F. pyramitela* and *F. coccinea* were identified using Bradley (2013). Voucher specimens have been deposited in the Museo de Zoología of the Escuela de Biología, Universidad de Costa Rica and in the National Natural History Museum of the Smithsonian Institution in Washington, DC, USA.

Results

Observations under a dissecting microscope

The dense sheets of both *L. simplicata* and *N. coosa* were approximately horizontal and weakly domed (Figs. 3, 4A–C, 5A). Spiders rested under the sheet near the uppermost portion of the domed area, holding sticky lines with their tarsi (Fig. 6A). Sheets of *L. simplicata* had a few small peaks in the domed area (Fig. 4D) that may be associated with increased tensions in this portion of the sheet (Suter 1984). Sticky lines could be easily distinguished from non-sticky lines in the sheets (Figs. 4–5): each sticky line shone brightly with a golden colour (from the microscope lamps) along its entire length regardless of the angle it made with the light; and it bore closely spaced droplets that were visible at 40× and 80× magnification. Non-sticky lines, in contrast, only glinted in places (usually where they were perpendicular to the direction of the light), had a paler colour, and lacked droplets. I did not make precise counts, but it was clear in these two species (Figs. 4–5), as well as in *F. pyramitela* and *F. coccinea*, that the large majority of the lines in the sheets bore droplets. Exceptions were frame lines that formed the edge of the sheet, which always lacked droplets. Some droplet-bearing lines had short sections that lacked droplets (Figs. 4F, 5E). The tangles above and below the sheets also included lines with and without droplets in all species.

In tests of adhesion (Fig. 1A), the droplet-bearing lines of *L. simplicata* adhered to the pin in eight out of 10 trials: as the pin moved away, the line was pulled for a short distance (about 0.5–1 mm) before the adhesion broke and the line snapped elastically back to its original position, still under tension. In contrast, none of 10 lines lacking droplets were displaced even slightly as the pin was withdrawn. In similar tests with *N. coosa* webs, all of 20 droplet-bearing lines were displaced when the pin was moved away, while none of 20 lines lacking droplets adhered to the pin.

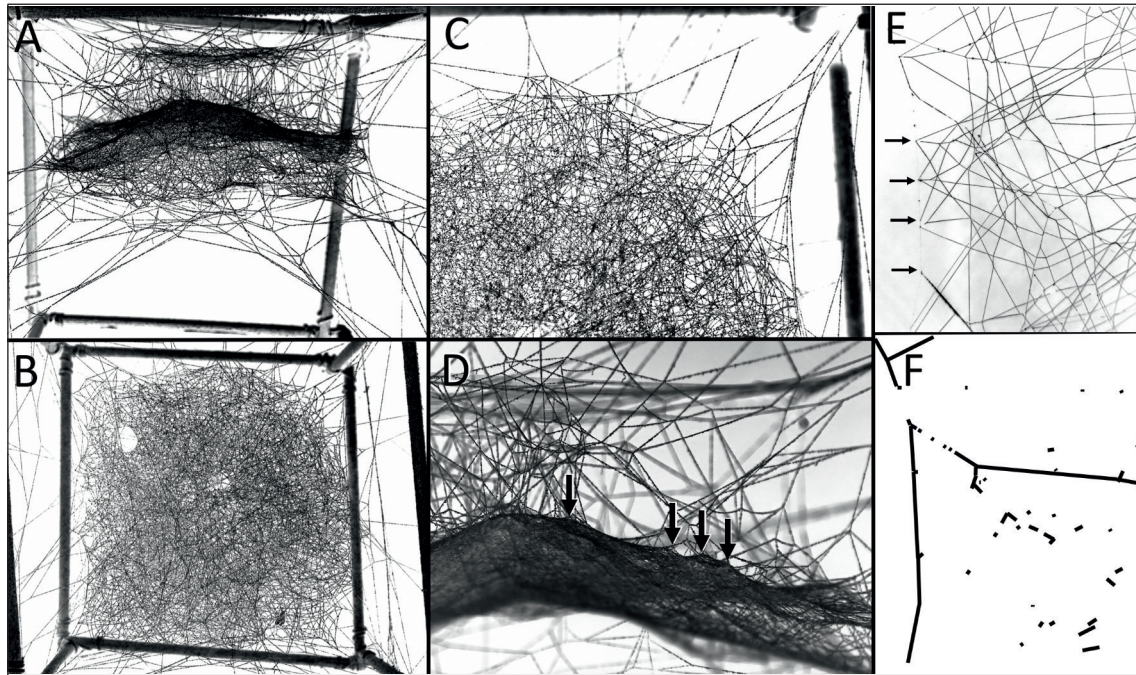


Fig. 4: Images of lines in webs of mature female *L. simplicata* that were built in captivity (A–D were coated with white powder to facilitate photography; E was an unpowdered web photographed under a dissecting microscope). The lateral view of newly built web (A) shows the tangles above and below the somewhat dome-shaped sheet. The view from below (B) and the closeup of this view (C) illustrate how the density of lines in the sheet decreased near the edges of the sheet. The lateral view of another web (D) shows small peaks in the sheet (indicated with arrows). The image in E, taken through a dissecting microscope at 40 \times , shows how sticky lines (dark lines) were much more common than the barely perceptible non-sticky lines, even near the edge of the sheet. Sites where attachments of sticky lines to the non-sticky line at the edge of the web and produced little or no deflection of the non-sticky line (thus indicating that the non-sticky line was under more tension) are indicated by arrows. The portions of lines in E that lacked droplets are shown in F.

I tested the mobility of sticky droplets at sites where two droplet-bearing lines crossed using intact, unaltered sheets that had been built the previous night by an adult female *L. simplicata*. I pushed one line (the experimental line in Fig. 1B₂) in a direction approximately parallel to the other line (test line in Fig. 1B₂) and slightly upward or downward with a fine pin. In 72 of 74 crossings tested, the lines adhered to each other: the test line moved when I moved the experimental line. In one of the two exceptional cases it was clear that one line was above the other and that they were not touching. In 24 of the 72 cases in which the lines adhered to each other, the force applied when I moved the pin caused the two lines to pop apart into different planes; they remained out of contact when I subsequently withdrew the pin. In 45 other cases, the lines remained attached at the same point, and the attachment did not slide along the test line (in the other three cases the experimental line became entangled with neighboring lines, and I was unable distinguish whether the point of contact had slid along the test line or whether the experimental and test lines had popped apart). In summary, lines that crossed in the sheet nearly always adhered to each other, even when, as was often the case, they proved to be in different planes when the attachment was broken. In no case was I able to confirm that the droplet at a point of adhesion moved along the line (as in Fig. 1B₂) when I applied stress.

Similar results occurred in less standardized manipulations of lines performed with unaltered sheets of *N. coosa* under a dissecting microscope. Most droplet-bearing lines

that crossed each other in the sheet adhered to each other: when I moved a droplet-bearing line experimentally with the tip of an insect pin, other lines in the vicinity also moved.

I tested the solubility of droplets by holding a small drop of water against droplet-bearing lines for a few seconds in the sheet of a *L. simplicata* web that had been built in captivity a week before and had been subsequently kept indoors. When I removed the water drop, the droplets on the lines were substantially reduced in size, but did not disappear entirely.

I did not measure the extensibility of droplet-bearing lines in either species. It was clear, however, that these lines were not nearly as extensible when I pulled on them as is typical of the sticky spiral lines of orb weavers (e.g. Eberhard 1976), nor did they contract nearly as extensively when they were relaxed.

Observations under a compound microscope

In sheets examined under the compound microscope, the droplet diameters (not counting droplets at intersections) in four webs of adult female *L. simplicata* ranged from 0.573 to 16.0 μm (17 to 474 pixels in the photos), and from 0.135 to 4.35 μm (4 to 129 pixels) in three webs of adult female *N. coosa*. The droplets at intersections between *L. simplicata* lines were on average 1.6 \times larger than other nearby droplets on the same lines (the control droplets in Fig. 2)

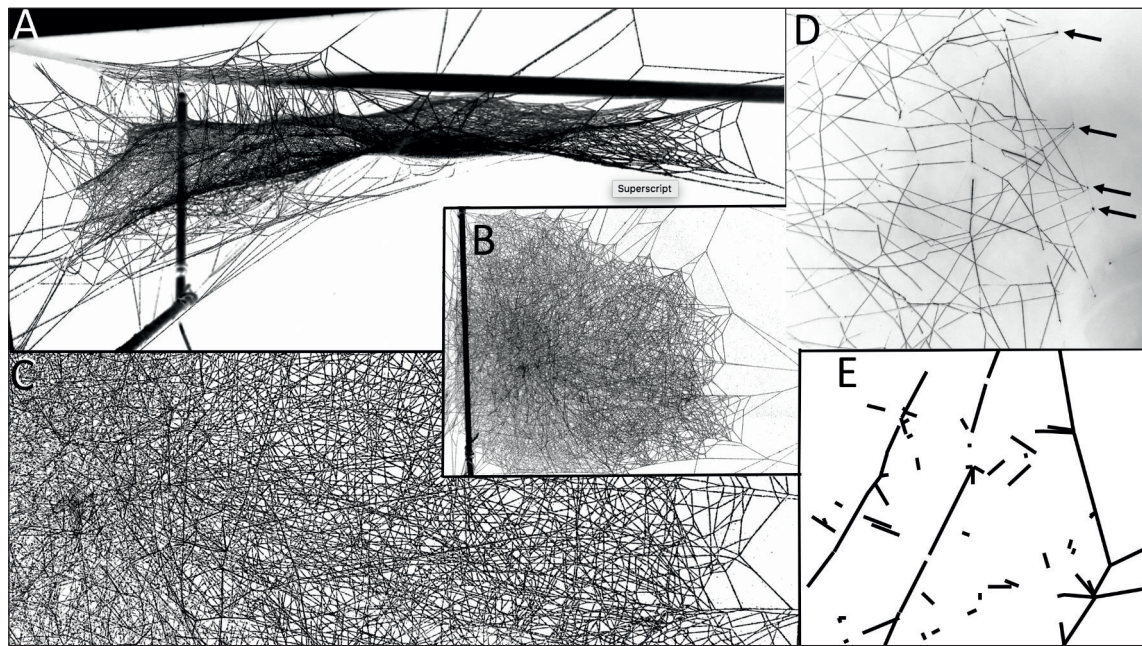


Fig. 5: Images of webs of *N. coosa* built in captivity (A–C were coated with white powder to facilitate photography). The lateral view (A) shows the relatively sparse tangle above the sheet and the even less extensive tangle below it, and the sheet’s only slightly domed outline. The ventral view in B shows the dense array of lines in the sheet; C shows a closeup of a portion of the web, showing the somewhat less dense weave near the edge. The image in D of the edge of an unpowdered sheet taken through a dissecting microscope at 40× shows how sticky lines (dark lines) were much more common than the barely perceptible non-sticky lines, even near the edge of the sheet. Sites where attachments of sticky lines to the non-sticky line at the edge of the web and produced little or no deflection of the non-sticky line (arrows), indicating that the non-sticky lines were under more tension than the droplet-bearing lines. The portions of lines in D that lacked droplets and were thus non-sticky are shown in E.

(Table 1) ($p \ll 0.0001$). In more direct intersection-by-intersection comparisons in *L. simplicata* web samples, the diameter at the intersection was larger than the median control diameter in 103 of 116 comparisons on line AC, and in 105 of 117 comparisons on line BD (ignoring cases when the medians were equal). Combining these counts, the difference in frequencies from the expected ratio of 1:1 was highly significant ($\chi^2 = 144$, $df = 1$, $p \ll 0.0001$).

Similar differences occurred in the *N. coosa* webs. The diameters of 92 intersection droplets along each of the two lines (Fig. 6B–D) were on average 1.4× larger than the median diameters of the two control droplets on either side

of the intersection on these same lines (Table 1) ($p \ll 0.0001$). In intersection-by-intersection comparisons, the diameter at the intersection was larger than the median value for control droplets on the line AC in 82 of 91 comparisons, and in 77 of 89 similar comparisons for droplets on the line BD (ignoring cases when the medians were equal). Combining the counts, intersection droplets were larger than adjacent control droplets much more often than the expected ratio of 1:1 ($\chi^2 = 112$, $df = 1$, $p \ll 0.0001$).

The median spaces between droplets at intersections were on average 1.8 times larger than spaces between nearby control droplets in the sheets of *L. simplicata* (Table

Species (no. webs)	N	Portion of intersect. (Fig. 2)	Droplet diameters		Statistical significance	Length of spaces between droplets		Statistical significance
			Intersect.	Control		Intersect.	Control	
<i>L. simplicata</i> (4)	125	AC	2.50	1.61	$z = 10.5$ $p \ll 0.0001$	4.17	2.43	$z = 7.76$ $p \ll 0.0001$
		BD	2.56	1.58	$z = 12.1$ $p \ll 0.0001$	4.96	2.71	$z = 8.58$ $p \ll 0.0001$
		Mean	2.53	1.59		4.56	2.50	
<i>N. coosa</i> (3)	92	AC	2.21	1.52	$z = 7.6$ $p \ll 0.0001$	2.81	1.77	$z = 7.3$ $p \ll 0.0001$
		BD	2.26	1.57	$z = 7.4$ $p \ll 0.0001$	2.30	1.67	$z = 5.0$ $p \ll 0.0001$
		Mean	2.23	1.54		2.56	1.72	

Table 1: Sizes of droplets and spaces (medians, in μm) in different webs built in captivity (N = number of intersections; letters designating portions of the intersection refer to labels in Fig. 2). In the statistical tests of differences in diameters, the diameter AC (of the intersection droplet) was compared with the median of the four control diameters (A1, A2, C1 and C2) on the same line; the diameter BD of the intersection droplet was compared with the median of B1, B2, D1 and D2. Similarly, differences in spaces between droplets involved spaces on the same line: the median of the spaces A and C was compared with the median of the spaces A1, A2, C1 and C2; and the median of the spaces B and D was compared with the median of the spaces B1, B2, D1 and D2.

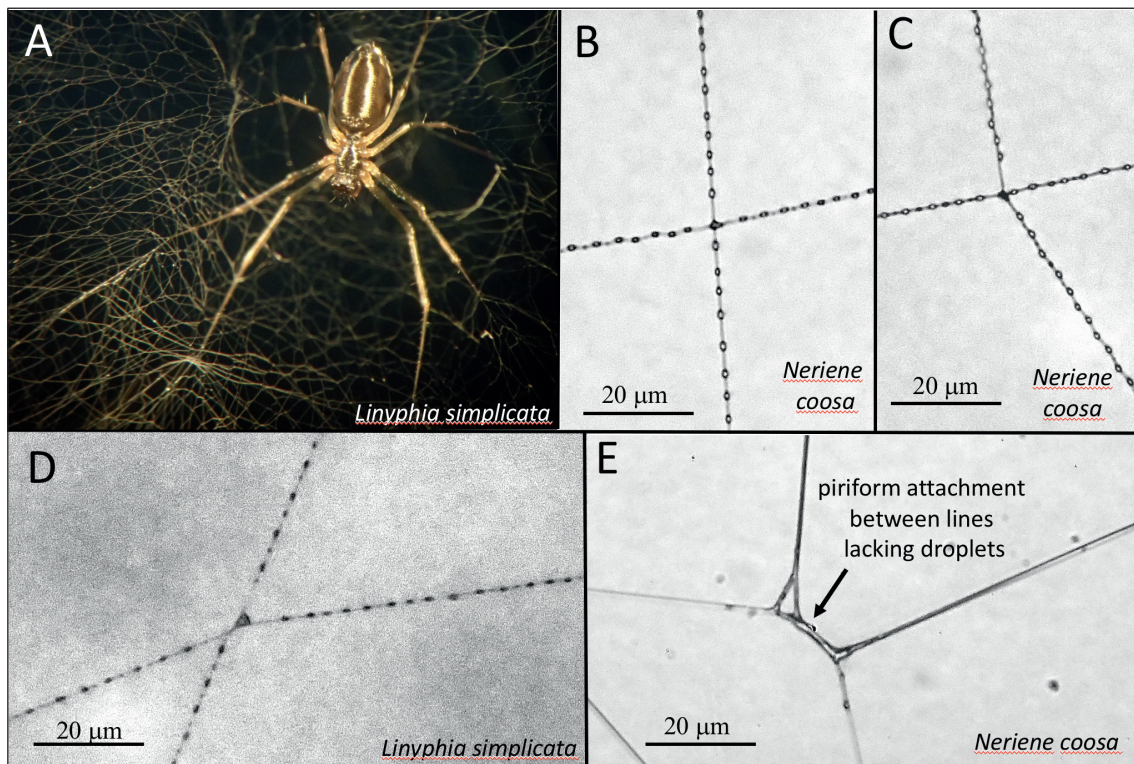


Fig. 6: A mature female *L. simplicata*, viewed from above while she rested under the dome of her sheet, displaced the multiple droplet-bearing lines that she held with her tarsi (A). Lines in the sheets of mature females of *N. coosa* (B, C, E) and *L. simplicata* (D) seen in a compound light microscope illustrate typical intersections between lines bearing droplets; the droplets are larger at the points where lines cross each other, and most of the spaces between droplets are larger at these intersections. Junctions between non-sticky lines with piriform attachments (E) were not common in the sheets of either species.

1; $p < 0.0001$). Intersection-by-intersection analyses also showed this pattern. The median of the spaces A and C adjacent to an intersection (intersection spaces in Fig. 1) was larger than the median of the four control spaces on line AC in 102 of 125 cases; the median of B and D was larger than control spaces on line BD in 105 of 125 cases. The combined counts deviated significantly from the expected ratio of 1:1 ($\chi^2 = 108$, $df = 1$, $p < 0.0001$).

Spaces between droplets in the webs of *N. coosa* showed the same pattern, with spaces between droplets at the intersection being on average 1.5× larger than those between nearby control droplets (Table 1; $p < 0.0001$). In intersection-by-intersection comparisons, the median of the two intersection spaces was larger than the median of the four control spaces on line AC in 74 of 92 cases, and in 70 of 92 on line BD, deviating significantly from the expected ratio of 1:1 ($\chi^2 = 58.8$, $df = 1$, $p < 0.0001$).

There was a positive correlation in both species between the relative sizes of the intersection droplet (diameter AC/ median diameter of control droplets on A and C; diameter BD/ median diameter of control droplets on B and D), and the relative sizes of the spaces adjacent to the intersection droplet (median of space A and space C/ median of control spaces on A and C; median space B and space D/ median of control spaces on B and D). Using the data from the lines AC and BD as separate observations, the coefficient of correlation was 0.34 (one-tailed $p < 0.0001$) in *L. simplicata*, and 0.104 (one-tailed $p = 0.024$) in *N. coosa*.

One additional type of data also implies that self-assembly occurred. Only 6 of 122 intersections in *L. simplicata* sheets between droplet-bearing lines lacked a droplet; the corresponding number for *N. coosa* was 0 of 92 intersections. The fraction of the lengths of the lines AC and BD in the vicinity of these intersections that corresponded to spaces between droplets was 68.5% in *L. simplicata* and 59.5% in *N. coosa*; thus, the likelihood of the lines crossing at a point where both lines lacked a droplet was $(0.685)^2$ or 46.9% in *L. simplicata*, and $(0.595)^2$ or 35.4% in *N. coosa*. This gives expected numbers of crossings that lacked droplets in the two species as 57.2 and 32.5, significantly higher than the observed 6 and 0 ($p < 0.0001$ in both with χ^2 tests). These higher than expected frequencies of droplets at intersections can be explained if droplets accumulated at sites where the lines scraped against each other.

Sheet construction behaviour

I observed short periods of apparent sheet construction by mature female *L. simplicata* in the field (in the morning following a light rain) and in captivity (in the early evening), and by *N. coosa* in captivity. The small sizes of the spiders, their thin lines, and inadequate illumination precluded seeing the line(s) that they were presumably laying, but I could follow their general movements. The spider did not hold the line she was producing with a leg IV in either species. This same detail was noted in *L. triangularis* and *L. hortensis* (Benjamin & Zschokke 2004), where it distin-

guished the production of droplet-bearing lines from that of other lines. My observations presumably involved sticky line production, because nearly all lines in the interior portions of finished sheets were sticky (as noted above), and because I never saw behaviour typically associated with the production of attachment discs (grasping lines with legs IV to hold them against the spinnerets) that were associated with non-sticky lines.

My observations also resembled those of Benjamin & Zschokke (2004) in that the spiders spent most of the time (an estimated 80–90%) walking across the sheet, crossing repeatedly from near one edge of the sheet to near the opposite edge (as in fig. 4 of Benjamin & Zschokke 2004). In no case did a spider drag her spinnerets across the sheet as she walked. Instead, she swung her abdomen rhythmically from side to side while walking, periodically dabbing her abdomen briefly upward toward the sheet as if attaching the line being laid to lines already in place in the sheet (but see below). During the upward movements, the spider's legs did not hold lines near the site where her spinnerets approached the sheet. Dabbing behaviour contrasts with the dragline attachment behaviour of orb weavers, in which the spider consistently holds the line on either side of an attachment with ipsilateral legs III and IV and presses the line against her spinnerets (Eberhard 1982, 2020; Wolff & Herberstein 2017). The small diameters of tarsi IV, the thin lines, and the spider's brisk movements precluded certainty on details regarding the positions of lines. It was clear, however, that any possible contact of the spider's spinnerets with the sheet would have occurred much less often than the frequency with which she crossed lines as she walked; she surely did not use attachment discs to attach the new line that she was laying to each of the many sheet lines that she crossed.

This interpretation that the spiders were not making attachment discs is in accord with the scarcity of attachment discs in the web samples observed under the compound microscope (as also reported by Peters & Kovoov 1991 for *L. triangularis*), where they were seen only joining the relatively scarce non-sticky lines (Fig. 6E). The paths of the spiders, laying lines from one edge to the other across the central portion, would result in the pattern of greater density of sticky lines in the central portion that was observed in finished webs of both *L. simplicata* and *N. coosa* (Figs. 4B–C, 5B–C).

Discussion

Sticky lines

Droplet-bearing lines in *L. simplicata* and *N. coosa* webs were adhesive. They comprised the large majority of the lines in the dense sheets of these species (Figs. 4–5), as well as in the sheets of *F. coccinea* and *F. communis*. Combined with previously published accounts of abundant droplet-bearing lines in the sheets of other species of *Erigone*, *Lept-hyphantes*, *Linyphia*, *Microlinyphia*, *Microneta*, *Mono-cephalus*, and *Ostearius* (Kullmann 1971; Millidge 1988; Benjamin, Duggelin & Zschokke 2002), these results con-

form to the pattern of abundant sticky lines in linyphiid sheets. Linyphiid droplets are liquid, at least when they are produced, as evidenced by their flowing partially onto other lines at intersections (Benjamin, Duggelin & Zschokke 2002 on *Microlinyphia* and *Linyphia*). The lines that bore droplets in *L. simplicata* and *N. coosa* sheets (presumably flagelliform lines—see below) differed from the flagelliform baselines of the sticky spirals of araneoid orb webs in not showing high elastic extensibility (Sensenig, Agnarsson & Blackledge 2010).

The force of adhesion of sticky lines of *L. simplicata* and *N. coosa* was relatively weak, as also found by Millidge (1988) in *Linyphia*, and the adhesion of a sticky line to a test object (Fig. 1A₂) always failed before the line broke. This modest stickiness may nevertheless have biological significance. Although any given line in the sheet is only weakly adhesive, even a prey that is relatively small compared with the spider's size is likely to contact many sticky lines in the dense sheet. In addition, these spiders attacked prey extremely rapidly; video recordings showed that mature female *N. coosa* often reached a *Drosophila* sp. fly within 0.1–0.3 sec after it fell onto the sheet. Attacks by *L. triangularis* and *Microlinyphia pusilla* (Sundevall, 1830) are also rapid (Benjamin, Duggelin & Zschokke 2002). Thus, even a short increase in retention time could result in increased prey capture. Adhesions between lines and between lines and the prey might also improve transmission of vibrations through the web, and thus increase the success of attacks on prey (Millidge 1988). The lines in the horizontal sheets of linyphiids may not be generally called upon to absorb large amounts of kinetic energy in order to stop fast-moving prey, but need only resist the impacts of prey that fall a short distance after being stopped by the tangle above the sheet (Benjamin & Zschokke 2004).

The abundance of sticky lines in linyphiid sheets raises the unsolved question of how these spiders avoid adhering to their own webs. Female *L. simplicata* and *N. coosa* observed under the dissecting microscope routinely held droplet-bearing lines with their tarsi while resting under their sheets (Fig. 6A). Of the recently documented behavioural, morphological, and chemical defences that orb weavers exhibit against adhesion (Kropf *et al.* 2012; Briceño & Eberhard 2012), only chemical defence seems feasible for these linyphiids. The means by which spiders avoided snagging lines with their curved tarsal claws as they ran across their sheets is unclear (in contrast, the tarsi of some prey insects snagged when they attempted to walk on the sheets of *L. triangularis* and *M. pusilla*: Benjamin, Duggelin & Zschokke 2002).

Non-sticky lines and attachment discs.

Just as in *L. triangularis* sheets (Peters & Kovoov 1991), attachment discs were relatively scarce in the sheets of *N. coosa* and *L. simplicata* webs, and were limited to the few lines that did not bear sticky droplets. Taking into account the density of lines in the sheet and the spider's sheet con-

struction behaviour, the lack of attachment discs joining sticky lines is not surprising. It would be impractical for a spider to stop and make an attachment to each line that she crosses while she is adding new lines to an already dense sheet. A few other adhesions between lines that lacked droplets in *N. coosa* and *L. simplicata* resembled those that Peters & Kovoov (1991) observed in *L. triangularis* webs. They support these authors' conclusion that such non-sticky lines are in fact somewhat adhesive, at least soon after they are laid.

Lines lacking droplets

Neither *L. simplicata* nor *N. coosa* webs adhered to test objects, however, and powder fell from these lines in a *N. coosa* web when they were jarred, so these lines were not perceptibly sticky later, after they were built.

The question of whether most of the abundant sticky lines in the sheets of *L. simplicata* and *N. coosa* were doubled by being laid onto non-sticky ampullate gland lines, as proposed by Peters & Kovoov (1991) for *L. triangularis*, cannot be resolved convincingly by the observations reported here. Nevertheless, I doubt that such doubling is common. I seldom saw sites in the light microscope preparations where droplet-bearing and droplet-lacking lines merged. The SEM images of droplet-bearing flagelliform lines in *L. triangularis* and *M. pusilla* (Benjamin, Duggelin & Zschokke 2002) show no signs of being associated with thicker ampullate gland fibres. The precise aim and alignment of the spider that would be required to lay sticky lines onto previously produced non-sticky lines would be very challenging, and would presumably require a slower rate of thread production than that observed. The apparent material wastefulness of laying the aggregate gland glue onto a flagelliform gland line (at the triad), and then laying this line onto still another line from the ampullate gland, gives further reason to doubt that such doubling was common.

Adhesions between sticky lines and how and where droplets form

Droplets of liquid on linyphiid lines presumably formed as do those in araneoid orbs: when the glue is applied as a cylindrical coat to the flagelliform baseline, it rounds up into droplets due to the glue surface tension and lower affinity for the baseline (Townley & Tillinghast 2013). The linyphiid droplets are relatively smaller and more widely separated compared with the araneid droplets, presumably due, at least in part, to the smaller amounts of glue. The humidity at the moment of construction might also influence the volume and viscosity of the glue and thus the sizes of the droplets, if linyphiid glue is hydrophilic like that of araneids.

The mechanism responsible for the droplets at intersections being larger and more widely spaced is less intuitively obvious. It is extremely unlikely that these differences resulted from the spider briefly altering the amount of glue

that she was adding to the baseline every time she crossed another web line during sheet construction. The spiders walked relatively rapidly and crossed many lines while spinning the sheet (*L. triangularis* walked approximately 8 m in the space of only 12 min of sheet construction: Benjamin & Zschokke 2004), and they did not make any perceptible adjustments when crossing individual lines. Indeed it seems unlikely that a spider could even sense the many individual lines that she crosses as she adds lines to a dense sheet. Capillary attraction might be involved in causing the sticky material to round up into droplets, but this would not explain why intersection droplets were larger than control droplets.

An alternative, self-assembly hypothesis is that the accumulations of glue at junctions in *L. simplicata* and *N. coosa* sheets resulted from movements of the lines and the droplets themselves after they had emerged from the spider. I hypothesize the following: that the glue is still relatively liquid soon after it is laid, as indicated by the SEM images of intersecting lines in *L. triangularis* and *M. pusilla* sheets where the droplets on one line spread to cover part of the other line (Benjamin, Duggelin & Zschokke 2002) and as occurs in araneids (Townley & Tillinghast 2013); that the glue is able to slide along lines (as seen in araneids: Eberhard 1976); and that newly laid glue accumulates at intersections when lines in the sheet scrape against each other.

Newly produced droplets would be moved along lines when the lines in the sheet shifted relative to each other during the upward dabbing movement of the spider's abdomen (below), or when the spider moved across the web during subsequent construction (note the displacements of lines caused by the spider's weight in Fig. 6A). Other possible causes of line movements are wind, and movements of supporting structures. When one droplet-bearing line rubs across another droplet-bearing line, droplets will be scraped along the lines; and when one droplet slides into contact with another, the two will merge to form a larger droplet. Small movements of lines in the sheet could thus explain the formation of larger droplets of glue at intersections that were documented here. Presumably the glue, which (as shown above) is largely water soluble, later dries out enough that it does not slide easily along the line, but nevertheless remains sticky.

This self-assembly hypothesis explains the larger sizes of droplets at intersections, the larger spaces between droplets immediately adjacent to this larger droplet, and the correlation between relatively larger droplets at intersections and relatively larger spaces around the droplet.

Functions of the mysterious dabbing movements

The self-assembly hypothesis suggests new functions for the upward dabbing movements of the spider's abdomen during sheet construction. Benjamin & Zschokke (2004: 123) interpreted similar movements by *L. triangularis* and *L. hortensis* as "... making attachments of the line that the spider was producing to pre-existing lines with the spin-

nerets ... by moving its abdomen upward towards the structure"; indeed, similar upward movements of the abdomen are part of the process of making attachments in other web spiders (e.g. Eberhard 1972, 1992, 2020). But attachment discs were very rare in the finished sheets of *L. triangularis* (Benjamin, Düggelein & Zschokke 2002) as well as in those of *L. simplicata* and *N. coosa* (above), even though dabbling movements were common. In addition, the spider was unlikely to be able to sense the locations of lines already in place to which she could attach the line she was producing (above). Thus, I propose that the upward movements serve to push on lines in the sheet and to thereby promote their self-assembly, rather than to attach the new line with the spinnerets. The upward movement will press the new line that the spider is producing against previous lines in the sheet. This movement would result in the new line adhering at points where it intersects these lines in the sheet, due to the adhesion of its own droplets as well as those on the lines already present, rather than due to actions of the spider's spinnerets (the lack of common, closely spaced parallel droplet-bearing lines in sheets argues that the new line probably consists of a pair of fibres, one from each of the two flagelliform spigots). In addition, the lifting movement would cause the new line to slide against previous lines, thereby scraping the liquid droplets into larger accumulations where the lines slide past each other.

Dabbling movements could also bring previously laid lines in the sheet into the same plane. When adding lines to a sheet, any small deviation from a perfect plane that is greater than the diameter of the lines (on the order of 1.1μ in *L. triangularis*: Peters & Kovoov 1991) would be enough to keep these lines out of contact with each other; such precise alignment between many different lines that are only attached at relatively distant points in the sheet would seem difficult to achieve. By making dabbling movements, the spider could press both her abdomen and the new line she was producing against lines already in place. These contacts could both press the previous lines into contact with each other, and also cause them to slide against each other and to thus accumulate larger droplets of glue at intersections. The resulting adhesions would tend to bring both new and old lines into a single plane. This would explain both the nearly universal adhesion between lines that crossed each other in the sheets of *L. simplicata*, and the fact that when I broke these adhesions experimentally, the freed lines often rested in slightly different planes.

Were the larger droplets and spaces at intersections collection artifacts?

The process of mounting sheets on slides in order to view them under the compound microscope likely flattened the sheets, pressing the lines into the plane formed by the upper surfaces of the strips of sticky tape. The stresses applied to the sheet during mounting could have also caused some lines to scrape against each other. It might be thought that these possible artifacts of collection led to the observed pat-

terns in the sizes of droplets and the spaces between them at intersections. But the fact that I was not able to make droplets slide along lines in fresh webs (built the night before) indicates that droplets subsequently become less liquid following web construction (at least at indoor humidities), and that they would not have moved during collection of the web samples.

The biological realism of the self-assembly hypothesis might also be questioned, because the assumption that a linyphiid sheet is a planar array of intersecting lines might be misleading at a very fine scale. Some lines in sheets may not be perfectly co-planar and thus not make contact when they cross. Nevertheless, even though the spiders did not brush their spinnerets across sheets of lines that were already in place, the periodic upward dabbling movements of the abdomen were apparently sufficient to cause nearly all sticky lines in the sheet to adhere to each other; in only one out of 74 cases in which a pair of lines crossed in unmanipulated *L. simplicata* sheets was one line above and out of contact with the other.

In summary, collecting samples of sheets on sticky frames on glass slides may have caused some lines in the sheet to contact each other and perhaps moved lines in the sheets against each other; but most sticky lines in sheets were in direct contact with each other in unmanipulated webs, before the sheets were collected. In addition, my inability to cause droplets to slide along lines argues strongly against the possibility the larger droplets at intersections and the larger spaces adjacent to intersections were artifacts caused by movements that were produced while I mounted sheets on slides. It should be noted that the impact of a prey with a sheet would produce similar types of movements of lines and droplets; thus if artifacts in droplet size and spacing were generated during sheet collection, they would probably resemble the consequences of a prey striking an intact sheet.

A new perspective on linyphiid sheet webs and construction behaviour

The apparent dynamism of the sticky lines in linyphiid sheets documented here has potential biological importance. The increases in droplet size at intersections likely result in stronger adhesion between individual lines that is advantageous to the spider: greater adhesion would result in the stress produced by a prey's impact and struggles being distributed among more lines, increasing the sheet's ability to absorb stresses without breaking. Larger droplets at intersections might also produce stronger adhesion to the prey itself. Both stronger adhesions between lines and of lines to prey would likely result in increased retention times of prey in the web.

This dynamism brings the designs of linyphiid sheet webs into new focus. By making a sheet that contains many droplet-carrying lines, and by pressing each new line against others so that they adhere to and move against each other, the spider can redistribute the relatively small

amounts of sticky material that she disperses more or less uniformly throughout her sheet in ways that increase the mechanical coherence of the sheet. Even though she is unable to attach many of these lines to each other as she is laying them, the lines can be subsequently pressed against each other and the sticky material can aggregate at intersections to form larger droplets, thus improving the sheet's ability to stop and retain prey. The lower extensibility of the linyphiid flagelliform lines compared with that of the flagelliform lines of orb weavers (Sensenig, Agnarsson & Blackledge 2010) may represent an evolutionary adjustment in linyphiids to the mechanical challenges of forming part of a dense mat of lines in a sheet.

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