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Web construction of *Linothele macrothelifera* (Araneae: Dipluridae)

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Abstract. Direct behavioral observations, plus deductions made from studying the lines in recently built webs, showed that *Linothele macrothelifera* Strand 1908 lays swaths of lines in relatively stereotypic ways that differ during sheet web and tube construction. Sheet construction occurs in brief bursts interspersed with returns to the retreat. The legs are not used to manipulate lines; the spinnerets attach lines to the substrate and are probably used as sense organs. Asymmetrical use of the spinnerets during sheet construction results in an increase in the variety of orientations of lines in the sheet.

Keywords: Mygalomorph, sheet web construction behavior

Spiders in the family Dipluridae build some of the most elaborate prey capture webs among mygalomorph spiders (Coyle 1986). In the subfamilies Ischnothelinae and Euagrinae, several species build complex arrays of numerous short tunnels that connect multiple small sheets and that mostly capture ambulatory prey (Coyle 1986, 1988, 1995; Coyle & Ketner 1990). Some species in the subfamily Diplurinae, including species in the genera *Linothele, Trechona* and *Diplura,* construct a single large horizontal sheet with a tubular retreat. Some of these sheets are suspended in the air many cm above the ground, and have tangles that extend up to a meter or more above the sheet, while others are built on the surface of the leaf litter or some other substrate (Coyle 1986; Paz 1988; Viera et al. 2007). It appears that other than the brief mention by Paz (1988) of the behavior of *L. megatheloides* Paz & Raven 1990, nothing is known regarding the behavior patterns used by diplurids to build their webs.

This note reports observations of the building behavior of *Linothele macrothelifer* Strand 1908, which builds sheet webs on the surface of forest leaf litter. This species, as is typical of non-orb weaving spiders in general, adds lines to its webs on successive nights. Our observations make use of the technique of damaging webs in the field and then observing newly constructed replacement webs, whose more sparse lines facilitate determination of patterns in the spider's building behavior (e.g., Eberhard 1987; Benjamin & Zschokke 2003; Lopardo & Ramirez 2007).

METHODS

We made field observations on 1–4 December, 2011, near the end of the rainy season, at the Reserva Forestal de Yotoco (03°51′50″N, 76°26′17″W), a 550 ha patch of subtropical wet forest (Florez 1996), between 1300 and 1700m AMSL in the Western Cordillera of the Andes near Buga, Colombia. Sheet web construction behavior of one adult female was recorded using a SONY DCR-TRV50 video camera equipped with +7 close up lenses and infrared illumination. Individual lines emerging from her spinnerets were visible in some frames due to occasionally favorable angles of illumination. We collected portions of webs on small cardboard frames coated with double-sided adhesive tape, taking care to avoid including lines of other webs (e.g., of ochyroceratids) that were often built near the diplurid webs. Photographs of new webs were obtained by destroying sheets (leaving the tunnel mouth intact) in the afternoon and then coating webs with talcum powder the following morning. We include multiple web photographs because webs varied substantially in some respects (e.g., Figs. 1 & 2). Not all spiders whose webs were observed in the field were collected; we judged them to be mature females on the basis of the sizes of the spiders and their tunnels.

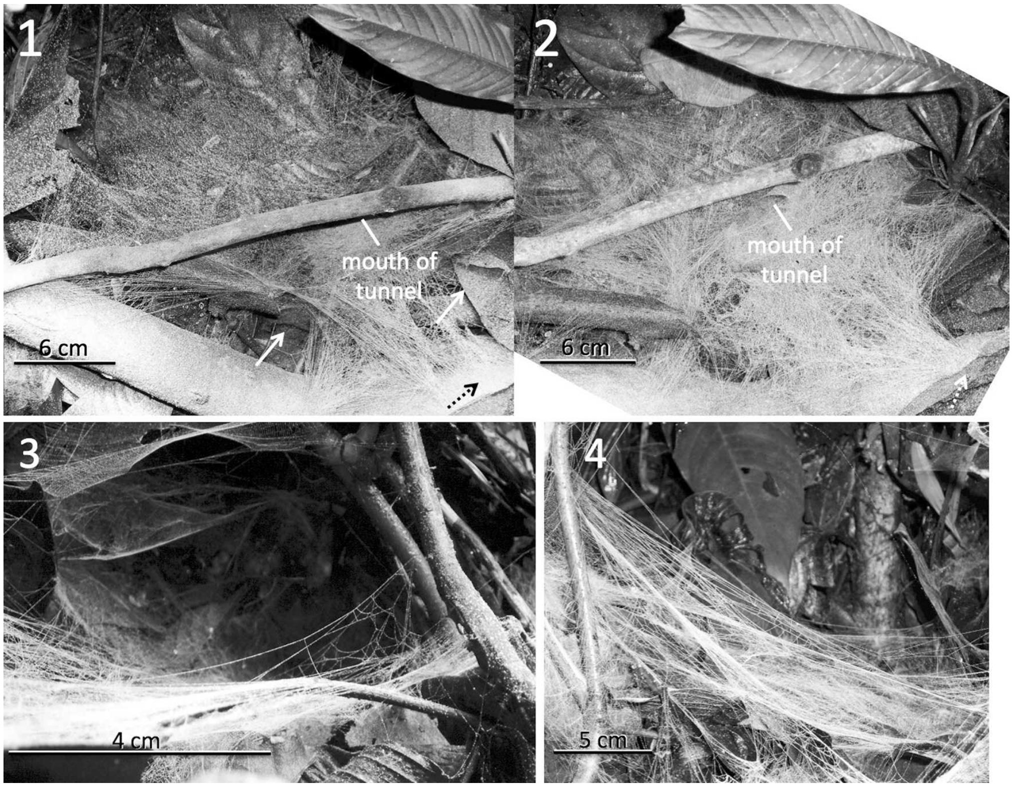
We made further observations of sheet web and tube construction in captivity by two other adult females by covering the bottom of each of two 30 × 20 cm terraria with moist earth and creating tubular retreat cavities by inserting one finger. Video recordings were made from above with a digital Canon PowerShot A800 camera.

Means are followed by ± 1 SD. Because of the small samples, they are meant only to provide general descriptions of magnitudes, rather than to characterize the behavior of this species.

RESULTS

We followed the webs of 12 individuals of *L. macrothelifera* over the course of 2–4 days. All consisted of a horizontal sheet extending from the edge of a tunnel, and were attached to the upper surfaces of leaves and twigs in the leaf litter (Figs. 1–4). The sheets were not perfectly flat, but followed the general contours of the objects in the litter. Usually nearly all lines formed a single sheet (Fig. 3), but some webs were somewhat multi-planar (Fig. 4). The individual lines in the sheets were relatively thin, and many were damaged or at least severely disorganized by the relatively moderate rains that fell daily (Fig. 5). In contrast, the walls of the tubular silk retreats were more dense and more protected, and persisted after rains. Thus the spiders largely rebuilt their sheets but not their tubes every evening following a rain. There were often large drops of water trapped in the complex, multilayered web near the mouth of the retreat, as also reported for *L. megatheloides* (Paz 1988).

Sheet construction behavior.—Spiders in the field were out of sight in their silk tunnels during the day, and came to the mouth of the tunnel about 18:00–18:30 to rest motionless, facing outward. Web construction in the field occurred in



Figures 1–4.—Webs of *L. macrothelifera*. 1 & 2. Dorsal views (from slightly different perspectives) of ''replacement'' webs built on two successive nights by the same spider at the same site after the web was removed the previous day. Solid white arrows in 1 mark empty areas that were covered by the sheet built on the second night (2); dashed arrows at the lower right mark areas with similar arrays of attachments to the substrate in both webs; 3. Lateral view of a replacement web that was nearly strictly planar, though sloping upward somewhat at the left rear (the web at the very top of the photo belonged to a different spider); 4. lateral view of a replacement web that was not strictly planar, with bands of silk in multiple dimensions.

bursts, at intervals on the order of 30–60 min when the spider made brief forays away from the tunnel mouth to lay lines. Multiple lines apparently emerged from all three spinneret segments of both posterior lateral (PL) spinnerets throughout

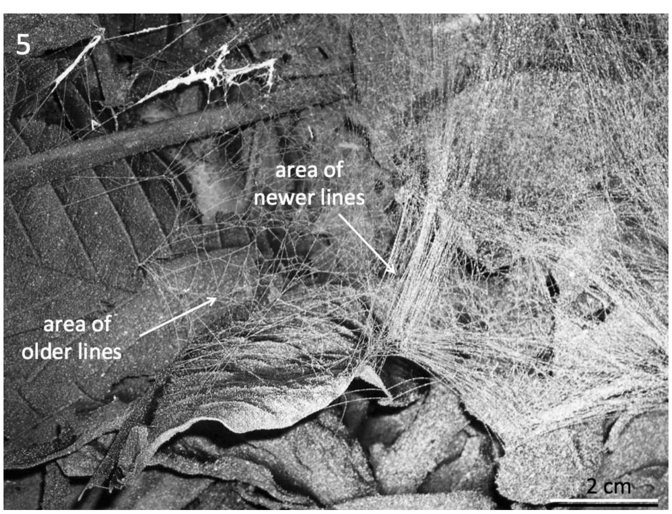


Figure 5.—Dorsal view of the edge of a web that had been rained on but destroyed the previous day. On left are sparse, disorganized, presumably older lines, and on the right are denser bands of parallel, presumably newer lines.

each foray. In some cases the angles of new lines captured in video recordings indicated that they were attached at the last site at which the spinnerets had tapped or swept across the substrate, so tapping and sweeping motions are assumed to have resulted in attachments in the descriptions below. The mean number of attachments/foray in the field by sweeping a PL spinneret against the substrate (below) was 10 ± 10 ($n = 7$). Our observations of other spiders that were visited repeatedly on two other nights and of the two spiders in captivity also showed that the spiders added to their webs only in short bursts, followed by periods of immobility at the tunnel mouth facing outward.

Sheet construction was relatively stereotypic in several respects. The spider we recorded in the field produced a swath of lines from both of her long PL spinnerets throughout each foray away from her retreat. Lines in this swath were probably initiated by attaching to the walls or mouth of the tube as the spider began a foray. After moving more or less directly from her retreat to the edge of the web (or what would be the edge), the spider swung her abdomen laterally and extended the PL spinneret laterally on the side toward which she had swung her abdomen (Fig. 6a; mean = $24 \pm 11°$; maximum 45° in 56 cases). At the apogee of the lateral movement of her abdomen, this spinneret swept across the substrate, apparently attaching the swath of silk lines it was producing. During a sweep, the spinneret was lowered and it appeared that all three segments

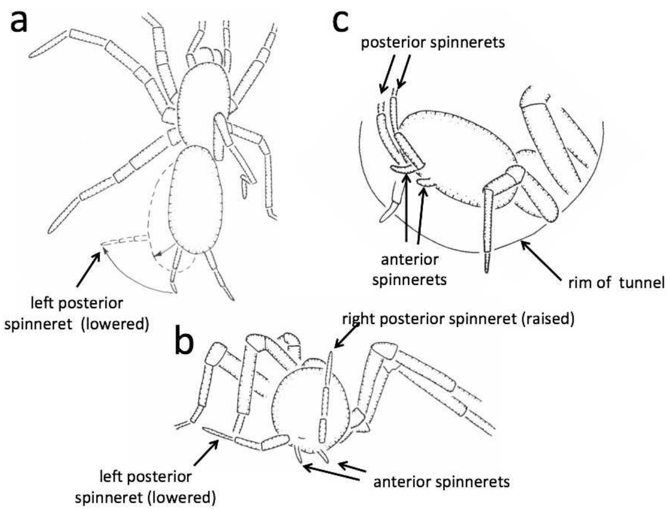


Figure 6a–c.—Drawings of construction behavior. a & b. Attachment behavior during sheet construction. a. In dorsal view, the left PL spinneret is directed laterally, while the abdomen is swung laterally and posteriorly to make an attachment; the right PL spinneret remains extended but does not touch the substrate (dotted lines follow solid lines by 1.70 s); b. in posterior view, the anterior spinnerets are lowered and are visible and the right PL spinneret is directed dorsally; c. in posterior-lateral view, the anterior spinnerets are lowered during tunnel construction to make simultaneous attachments by both PL spinnerets.

contacted the substrate (Fig. 6b). Attachments to objects in the leaf litter and to sheets of lines already in place were produced by similar swinging movements of the PL spinnerets and the abdomen.

Usually (46 of 56 cases), successive attachments during sheet construction were to the same side. In two cases with a favorable angle of view, the anterior lateral (AL) spinnerets were visible and were also lowered to the sheet (Fig. 6b). Often the spider turned her cephalothorax slightly to the side opposite that to which she swung her abdomen; for instance, the spider's cephalothorax turned to the right as she swung her abdomen to the left and extended her left PL spinneret laterally.

Meanwhile the other PL spinneret usually stayed out of contact with the substrate (74.1% of 54 cases in which this detail could be seen). Often (44.4% of these 54 cases) it was directed dorsally (Fig. 6b). The lines emerging from this spinneret were sometimes not attached until the spider later swung her abdomen to the opposite side and lowered this spinneret and extended it laterally, or until she returned to her tunnel. The spider made up to ten consecutive attachments with one spinneret before attaching with the other. The spider usually directed both posterior lateral spinnerets dorsally while walking between attachment points, thus elevating the swaths of lines she was laying above the sheet and above leaves and twigs in the litter. The lines from the two PL spinnerets were thus often attached at different sites, the swaths of lines from the two spinnerets were often laid in different directions, and the lines laid from the less active PL spinneret were sometimes slack.

In no case did any leg hold any line that was being produced or to which the spider was attaching. Nor did legs tap as if locating potential attachment sites. Attachments were usually made to sites that had not been contacted previously by any legs (88.2% of 51 cases in which this detail could be seen). Instead it appeared that the spider used her long PL spinnerets as sense organs, and that their sweeping movements informed her of the presence of nearby objects.

The spider always made several attachments to the substrate during a foray away from the tunnel, but eventually returned to it by a more or less direct path. On arriving at her retreat, she attached several times in quick succession with her spinnerets directed more or less posteriorly (simultaneously with both spinnerets in five of seven cases) (Fig. 6c), then went inside and turned around to face outward.

All of these details were similar in a recording of sheet building by a spider in captivity (except that it was not possible to see either the lines emerging from her spinnerets or the positions of her anterior spinnerets). The spider that was recorded building a sheet in the field paused and struck through the sheet at a site where one of her tarsi had just dislodged a lump of earth that rolled below the sheet, raising the possibility that the sheets may be used to capture prey walking below the sheet as well as on it.

Tunnel construction.—Tunnel construction was seen only in captivity ($n = 2$ spiders). The movements differed sharply from those used to build sheets. The two PL spinnerets were usually both extended more or less directly rearward, and both touched the substrate simultaneously and repeatedly in close succession along their basal segments and at least sometimes also more distally. In some cases it appeared that the AL spinnerets were also lowered and made repeated contact with the tunnel wall (Fig. 6c). Spinneret contact with the substrate resulted mostly from an anterior-posterior rocking movement of the entire body, combined with minor ventrally directed movements of the spinnerets themselves. The PL spinnerets moved slightly apart as the spider rocked posteriorly, and then moved slightly together as she rocked forward. Contacts with the wall of the tunnel in successive taps or thrusts with the spinnerets were frequently closely spaced. As in sheet construction, the spider never used her legs to manipulate either the lines being laid or the lines to which they were being attached.

Tunnel construction resulted in silk being spun across the tunnel entrance. At the end of a bout of spinning, the spider broke through this sheet at the mouth. She inserted her anteriorly extended legs I and II between lines there, then moved the legs laterally and stepped forward, thereby forcing her body through the sheet.

Web photographs.—Patterns of lines captured in web photographs confirmed and extended the direct observations of sheet construction behavior. Replacement sheets were mostly attached to the substrate near their edges. Some replacement sheets were attached at only a few points (as few as about 12), with multiple lines fanning out from each of the attachment sites (Figs. 1, 2, 5). Attachment sites with lines fanning out from them were generally at the edge of the sheet, and there were seldom any points with lines fanning out from them in the central area of a sheet. These patterns confirmed the behavioral observation that attachments were concentrated near the edges of the sheet. One attachment point at an especially sparse edge of a web had approximately 20 lines

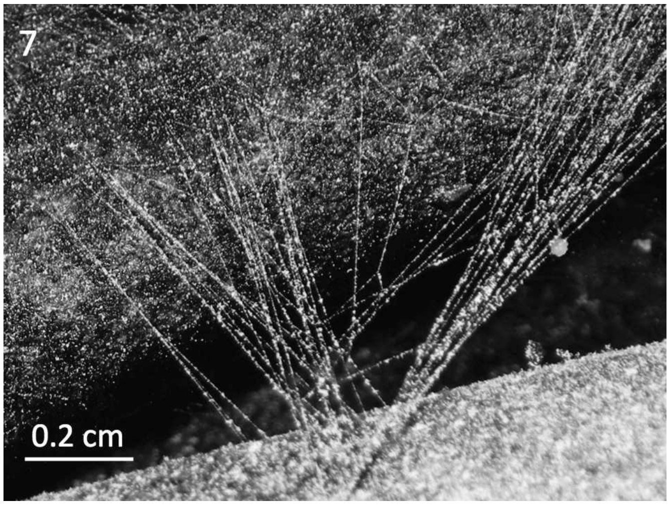


Figure 7.—Approximately dorsal view of a site to which the spider apparently made only one sweep with one spinneret, depositing approximately 20 lines.

running to it and an equal number away from it (Fig. 7); another swath of parallel lines in an especially sparse web also had approximately 20 lines (Fig. 8). Thus a single spinneret probably produced on the order of 20 lines. Some peripheral attachment points in replacement webs had many lines radiating from them (Figs. 1, 2, 5, 8), suggesting multiple visits and indicating that there were substantial variations in the directions from which the spider arrived at the point and in which she moved when leaving it. One ‘‘older’’ web (which had been destroyed the day before) had a highly reinforced band of lines running from the retreat and between four adjacent peripheral attachment sites, suggesting that the spider had repeatedly left the retreat and travelled from one to the next to the next of these sites (Fig. 5).

Two replacement webs that were built on successive nights by the same spider at the same site showed differences in the arrangements of the lines (Figs. 1 & 2). Thus, building movements were not highly stereotypic, even for webs at the same site.

Web samples under the microscope.—We examined samples of the sheets of four webs under the microscope. The lines clearly had multiple diameters (Figs. 9a & 9b). Most lines were relatively straight, and in only a few cases did lines appear to adhere to each other and exert tension (as indicated when one line pulled another line into an angle $< 180^{\circ}$; Fig. 9c); there was no sign of substantial thickenings such as attachment discs at such sites (Fig. 9c). There were some complex arrangements, however, such as cables of multiple lines, extensive lax lines, and apparent adhesions between loose lines (Fig. 9d).

DISCUSSION

We made only fragmentary observations, and further studies are needed. Nevertheless, the combination of direct observations of behavior and deductions from web photos are sufficient to clarify some basic points. The standard pattern of movements used by *L. macrothelifera* to build a sheet web appears to be to lay a swath of lines while the spider walks, to use asymmetrical movements of the two long PL spinnerets to attach the lines at several points near the periphery of the web, and then to return more or less directly to the retreat, laying

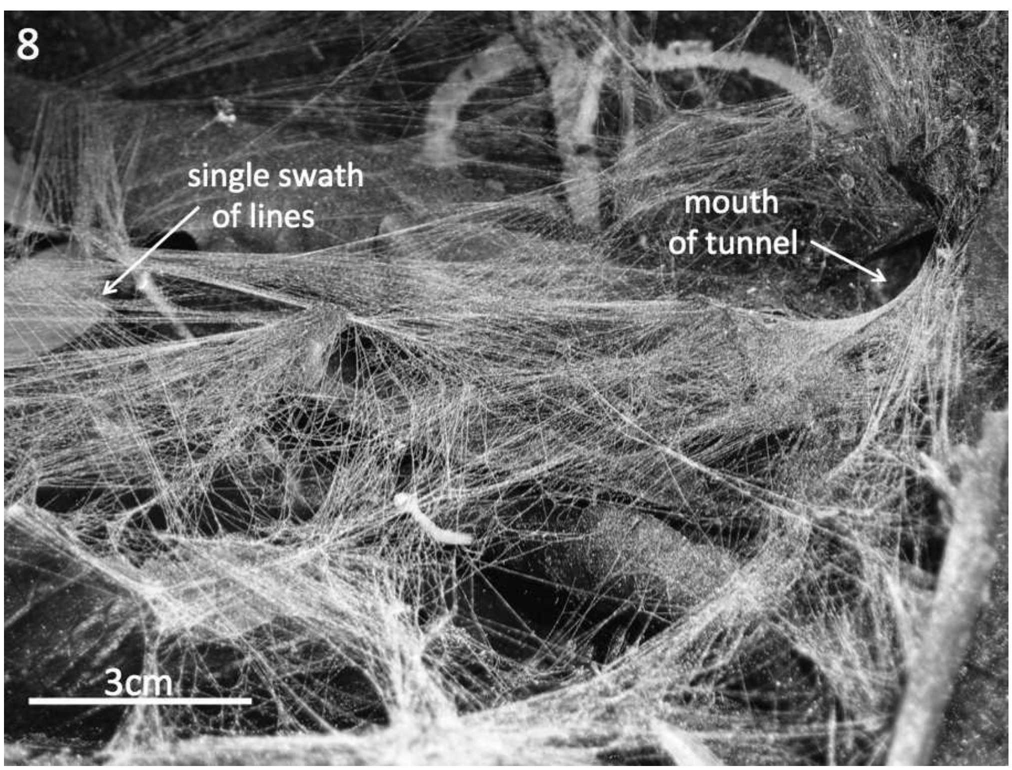


Figure 8.—Dorsolateral view of a relatively sparse replacement web, showing how bands of parallel lines were attached to upward projecting objects in the leaf litter. A single swath of about 18 parallel lines that was laid on top of other lines is visible at the left.

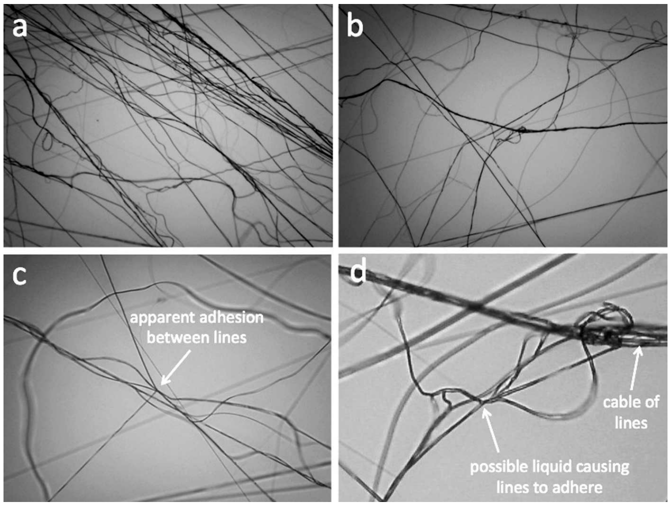


Figure 9.—Lines in a sheet seen under a compound microscope. a & b. Typical arrays of many more or less parallel lines of different diameters, with some lines loose and others tight; c. an unusual site where two lines apparently adhered to and deflected each other; d. a cable of multiple lines and a possible small accumulation of liquid at a site where lines apparently adhered to each other.

further lines that are attached there. Even early excursions from the retreat reached the edge of the web (i.e., the web was not gradually extended outward away from the retreat). We saw no sign of the irregular forward, backward, and sideways movements mentioned by Paz (1988) for *L. megatheloides* (whose sheet is aerial, and not in contact with the leaf litter).

In contrast, tube construction by *L. macrothelifera* involved more synchronous and symmetrical movements of the PL spinnerets to produce more frequent, closely spaced attachments. The atypid *Sphodros rufipes* (Latreille 1829) also builds its tube using frequent, closely spaced attachments with her actively moving spinnerets (W.G. Eberhard unpubl. observ.).

A similar retreat-centered organization of web construction behavior also occurs in some sheet web spider such as the agelenid *Melpomene* sp. (Rojas 2011) and the theridiid *Parasteatoda tesselata* (Keyserling 1884) (Jörger & Eberhard 2006). Some other sheet web builders, in contrast, do not organize their sheet extension behavior around a central point; these include the pholcid *Modissimus guatuso* (Eberhard 1992), and the linyphiids *Linyphia hortensis* Sundevall 1830 and *L. triangularis* (Clerck 1757) (Benjamin & Zschokke 2004) (and also possibly an unidentified ochyroceratid – M. Ramirez pers. comm.). In all of these other sheet-web groups, the spider first produces a skeleton web for the sheet and later fills in this skeleton. We saw no sign of this possibly derived pattern in *L. macrothelifera*.

One apparent inconsistency between the direct behavioral observations and the deductions from web photographs was that the spiders showed no behavioral indications of testing for or sensing the presence of lines and attachments of lines; nevertheless, the photographs clearly showed repeated attachments to particular supports (e.g., Figs. 5, 8, 9). Perhaps these sites were more elevated, or distinguishable in some other way that did not require any overt searching behavior other than waving the spinnerets.

Paz (1988) reported that the anterior spinnerets of *L. megatheloides* produced glue that fastened lines together, but gave no evidence to support this claim; we saw no discreet masses of material that attached lines to each other in *L. macrothelifera* webs. In some places very small amounts of liquid appeared to join lines (Fig. 9d). Mygalomorphs are thought to lack piriform glands or spigots that could glue lines together (Blackledge et al. 2009). It seems likely that the lines of *L. macrothelifera* were slightly wet when they emerged (as in the aciniform lines of labidognaths – see Eberhard 2011), and that this explains their adhesion to the substrate and to each other.

The legs of *L. macrothelifera* played little if any role in either locating attachment sites or manipulating silk lines during any stage of web construction. Instead the spider's long PL spinnerets seem to be used as sense organs to locate attachment sites. Perhaps the flexibility that is presumably provided by the widespread pseudosegmentation of the long terminal PL article in diplurids (Coyle 1995) enhances this function. The frequent asymmetry in the use of the PL spinnerets during sheet construction, with one kept raised while the other was lowered and swept across the substrate to make an attachment, resembles prey wrapping behavior by the theraphosid *Psalmopeus reduncus* (Karsch 1880) and several araneomorph species (Barrantes & Eberhard 2007). Presumably its function in diplurid sheet construction, as perhaps also in these other contexts, is to generate lines running in a greater number of different directions. Paz (1988) noted that the spinnerets of *L. megatheloides* moved with respect to each other and the long axis of the spider's body, but did not describe the patterns we report here. The atypid *S. rufipes* also laid lines with bobbing movements of the abdomen and no direct involvement of the legs (W. Eberhard unpubl.).

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