

Frame line repair by the orb-weaver *Micrathena duodecimspinosa* (Araneae: Araneidae): possibly ancient behavior

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Abstract. Spider webs in general and orb webs in particular are delicate, ephemeral structures that are frequently damaged in nature. Some orb weavers respond to damage by quickly “shoring up” their webs with non-sticky dragline silk. This study of how *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) shores up damaged frame lines shows that repairs were largely based on a single, repeated pattern of attachments. These movements are shared with the distantly related family Pholcidae, suggesting a possibly ancient origin. Spiders tended to initiate repairs at the lower edge of a damaged sector, probably to reduce the damage produced when the spider’s own weight caused sticky lines in slack portions of the web to sag into and adhere to each other. Repairs of lateral frames recuperated capture area more successfully than did those of upper frames, probably because damage caused by the spider’s own weight during repair was reduced.

Keywords: Orb web, flexible construction behavior, behavioral evolution, damage from sagging

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Classic early studies established spider orb web construction behavior as an archetypical example of complex, inflexible innate behavior by small animals with limited brainpower. Pioneer observers believed that orb weavers were incapable of repairing their orbs, and cited this limitation as evidence that spiders do not “understand” the functions of their own construction behavior (Fabre 1912; Hingston 1920): “Introduce difficulties in its circuit ..., build up obstructions to impede the blind routine, and the spider can do nothing to overcome them; it can only struggle in its course. It can appreciate none of these difficulties; it can understand none of these obstacles; all it can do is but circle on.” (Hingston 1920, p. 134). While subsequent studies have confirmed the negligible role of learning in orb construction (summary in Eberhard 2020), the supposition that orb weaver behavior is inflexible has given way to the realization that orb construction, including orb repair behavior, is adjusted to many different stimuli (summaries in Herberstein & Tso 2011; Eberhard 2020). The ability to repair an orb does not necessarily imply, of course, that a spider understands its own behavior, because pre-programmed, innate behavior patterns could be used to perform web repairs. But regardless of what spiders understand, repairing a damaged web requires behavioral flexibility, because the spider must adjust its behavior appropriately to a large variety of conditions, depending on the location, size, and shape of the damaged sector.

Many animals build structures (Hansell 2005) that can become damaged and need repairs. Damage is especially common in the fragile orb webs of spiders, which generally last only a single day or less (Eberhard 2020), but the behavioral details of orb web repair are little-studied. Orb web repairs can be conveniently divided into two types: small-scale “shoring up” repairs, that are made soon after an orb is damaged and involve only placement of non-sticky lines; and “replacement” repairs, that include adding sticky as well as non-sticky lines that cover a substantial fraction of the web’s surface, and that are typically made many hours after damage occurs (Eberhard

1972). Replacement repairs are known in numerous taxa (summaries in Shinkai 1998; Eberhard 2020). Direct observations of the behavior of the uloborids *Uloborus diversus* Marx, 1898 (Eberhard 1972), *Zosis geniculata* (Olivier, 1789) (Eberhard 2020) and the araneid *Cyclosa confusa* Bösenberg & Strand, 1906 (Shinkai 1998) showed that replacement repairs employed some of the same behavior patterns that are used when building an entire orb from scratch; in some cases spiders first modified the form of the damaged sector in ways that simplified and standardized the repair tasks.

The shoring up repairs (hereafter “repairs”) that are performed soon after damage occurs (when, for example, a large insect, falling detritus, or a gust of wind causes damage) are less-studied. The functions of shoring up repairs are probably to recover load-bearing abilities and thus increase the web’s mechanical stability, and to re-extend collapsed portions of the web to improve prey interception. A few earlier studies have illustrated particular incidents of shoring up radii and frames in the araneids *Zygiella x-notata* (= *Zilla litterata*) (Clerck, 1757) (Wiehle 1927) and *Araneus diadematus* Clerck, 1757 (Peters 1933), but did not attempt to present general patterns other than to comment that spiders consistently responded to major web damage, and that repair lines were typically attached at the web periphery (Peters 1933). Tew et al. (2015) broke this tradition by observing repairs by *A. diadematus* after experimentally cutting an anchor line below the hub, thus collapsing a sector of the orb. Repair behavior was judged to be induced by tension changes, because spiders failed to make repairs after the sticky spiral lines in a similarly large sector of the orb were broken, a treatment that did not result in large tension reductions on other web lines. Spiders initiated repairs more quickly when the damage resulted in a greater loss of web area. Under windy conditions spiders repaired web damage more promptly, but their repairs resulted in less complete recovery of web area.

The present study searches for patterns in the order and pattern of lines laid by the araneid *Micrathena duodecimspi-*

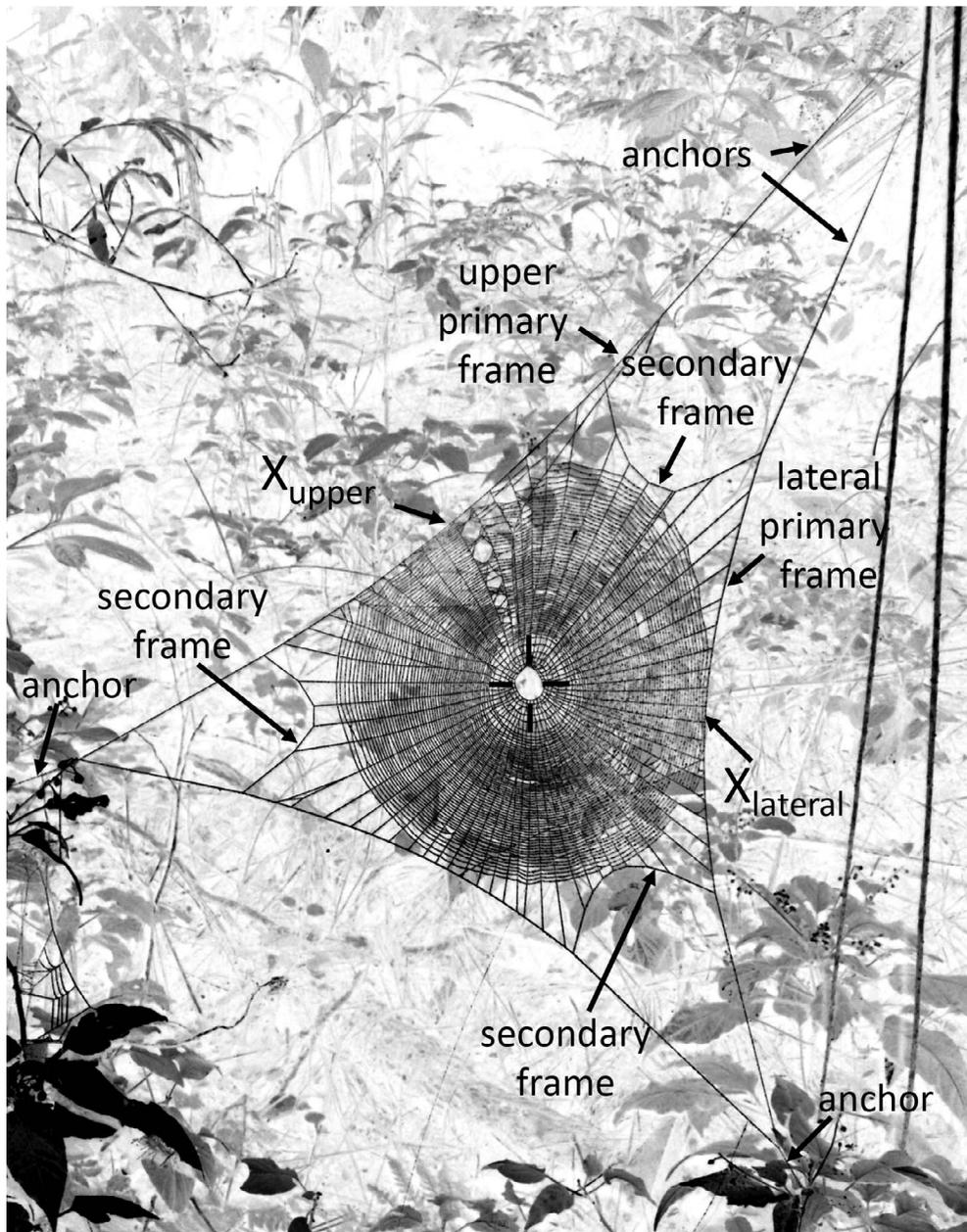


Figure 1.—An orb web of *Micrathena duodecimspinosa* that has typically long anchor lines, with the upper and the most nearly vertical lateral primary frame lines labeled. The sites where upper and lateral frame cuts would be made are labeled “X_{upper}” and “X_{lateral}”. The heavy lines near the center mark the width of the free zone in different directions. This web was atypical in that there were two anchor lines at the upper right corner.

nosa (O. Pickard-Cambridge, 1890) (Araneidae) to repair broken frame lines. This species builds steeply slanting orbs (mean angle with horizontal = $74.3 \pm 8.7^\circ$, $n = 70$) (Eberhard 2020) that are nearly invariably anchored to supporting objects at only three widely separated points. The orbs thus nearly always have three primary frame lines (Fig. 1), though their locations with respect to rest of the orb (above, below, to the sides) vary. Many other background details of orb construction behavior by *M. duodecimspinosa* are described elsewhere (Eberhard 2020). This study examines the possible adjustments to distortions of the web that are caused by the

spider’s own weight during the process of repairing a damaged orb. When damage causes the web to go slack, the sticky spiral lines adhere to each other and to the radii when they make contact, opening holes in the regular array of sticky lines. In a vertical web, the spider’s weight can cause the web lines to sag. If a spider is at the bottom of a slack vertical orb, the sagging produced by its weight pulls the web lines apart; but if it is farther up in the web, its weight causes lines below it to sag into each other and to adhere to each other. I tested the hypothesis that details of frame repair behavior would be appropriate to reduce sagging into areas that contained lax

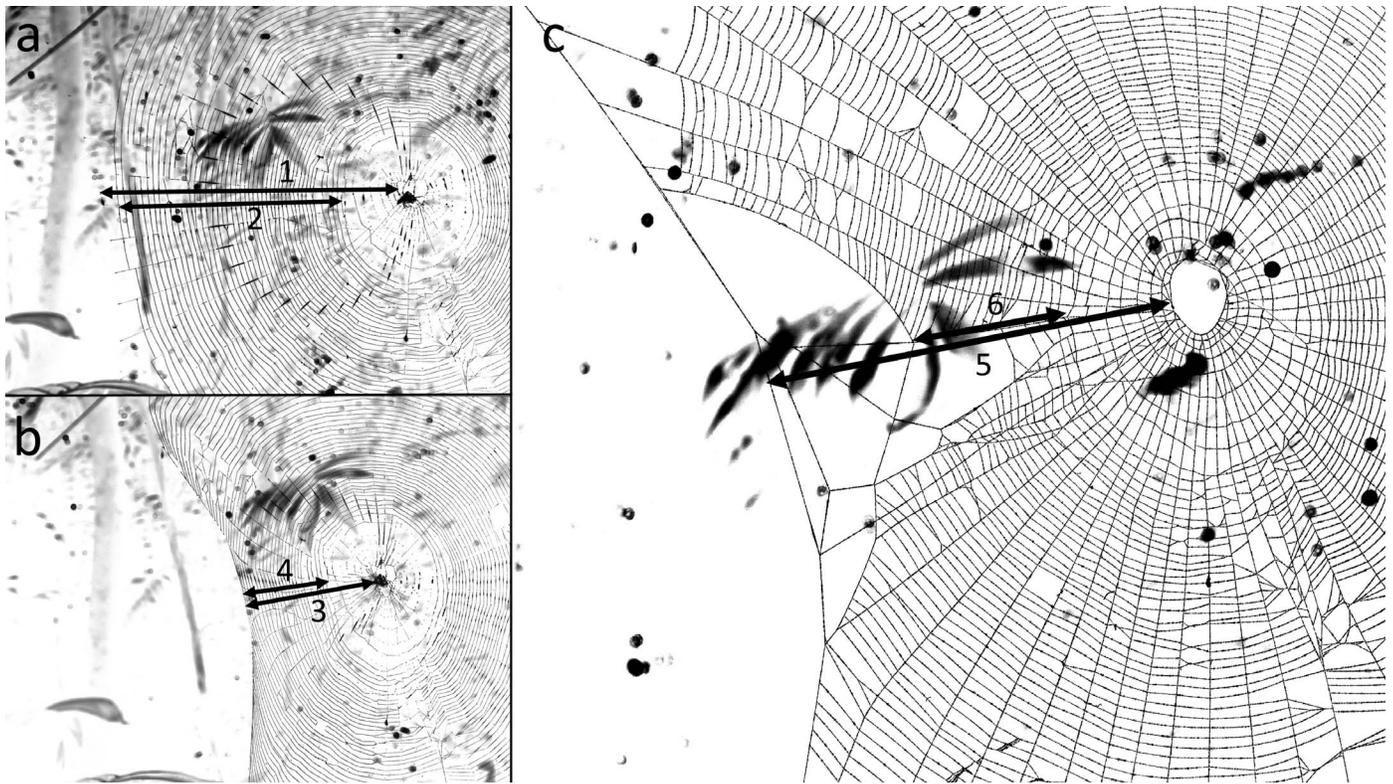


Figure 2.—The double-headed arrows show the two distances measured in intact (a), broken (b) and repaired webs (c): the minimum distance of the outermost line from the edge of the hub hole (1, 3, 5); and the distance between the inner and outer loops of sticky spiral (the width of the capture zone) (2, 4, 6).

sticky lines, and that repairs would be more effective when such sagging was reduced.

METHODS

All observations were of adult female *M. duodecimspinosa* in the field on freshly built, finished orbs (06:00–09:30) during July–Oct. 2020 in early second growth (an abandoned coffee field) near San Antonio de Escazu, Costa Rica (el. 1325 m, 9°53′ 51.41″ N, 84°08′ 15.99″ W). Spiders were not marked, but observations sites were rotated so that repeated observations of the same female were unlikely. Damage was produced experimentally while the spider was at the hub by cutting a frame line and the adjacent outer quarter (approximate) of the sticky spiral loops, using a sharp iridectomy scissors. I made two types of damage. For “lateral” frame repairs, I cut the central portion of the primary frame line (X_{lateral} in Fig. 1) that was most nearly vertical. “Upper” frame repairs were elicited by making a similar cut directly above the hub in the primary frame line that was above the hub and that was most nearly horizontal (X_{upper} in Fig. 1). I included all of the spiders that responded to damage within 10 min as well as some of the others that took longer.

I photographed webs before lines were cut, immediately after they were cut, and then once again after the repair was finished and they had been coated with talcum powder. In addition to web photos, I made written notes and drawings as the spider made the repair, video recordings of behavior, or sequences of still photos that were taken while or just after the

spider made each apparent attachment of her dragline. Video recordings and photos were made using Olympus TR-4 and Sony AX 53 cameras.

Two distances were measured in the three photos of the damaged sector of each web (Fig. 2) using ImageJ software: from the edge of the hub hole to the middle of the outermost line (the frame or the outer edge of the web); and from the innermost to the outermost loop of sticky spiral. Non-parametric statistics were used to make comparisons because variables did not have normal distributions. The terms “inner” and “outer” in the descriptions that follow refer to positions relative to the hub: inner is closer to and outer is farther from the hub; “lateral” movements were approximately perpendicular to radial directions. I use the phrase “normal orb” as a shorthand to refer to the construction of a complete orb web starting from scratch when comparing it with repair behavior, with no implication that repair behavior is “abnormal”. Because verbal descriptions of the networks of repair lines are inevitably imprecise, figures are emphasized in the accounts below.

Specimens collected earlier from this site where they are common were identified by H. W. Levi, and are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, MA.

RESULTS

Repairs of 17 lateral and 21 upper frame lines were observed, though the records were not complete in all respects

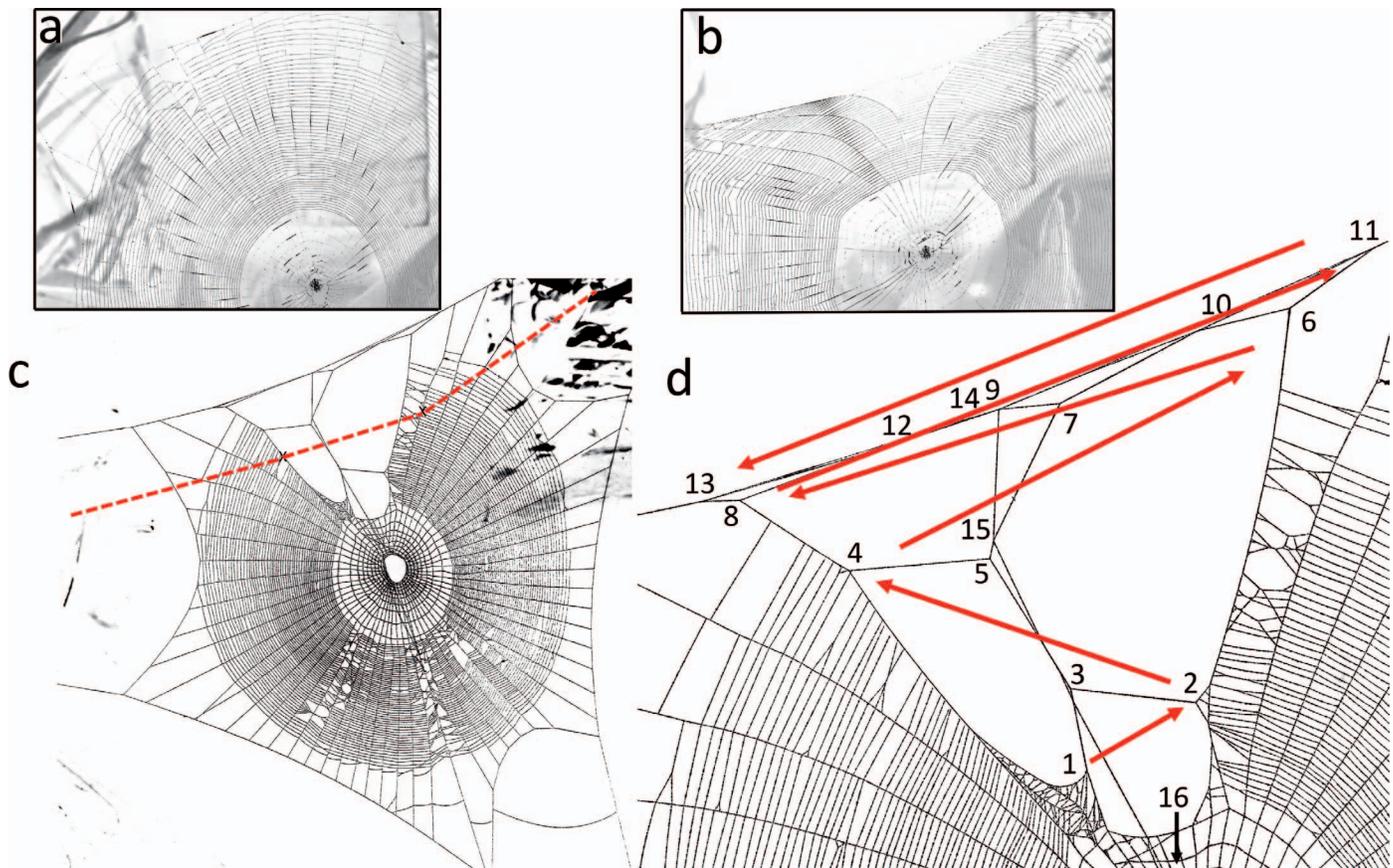


Figure 3.—This web illustrates an unusually extensive upper frame repair. The insets show the upper portion of the undamaged web (*a*) and the damaged web immediately after the upper frame was cut (*b*). The repaired web is shown in *c*, where the dashed line indicates the approximate position of the upper edge of the damaged web; in a closeup of the repair (*d*), the numbers show the order of attachments of repair lines. The spider made an unusually large number of passes (arrows) back and forth across the damaged sector (1 to 2, 2 to 4, 4 to 6, 6 to 8, 8 to 11, and 11 to 13) before returning to the hub (14 to 16).

for all of them. Delays between damage and initiation of repair varied from <30 to >900 s. Repair began when the spider turned to face the damaged sector; she often spent several seconds grasping different radii in the hub and the free zone with her legs I and II before she moved outward. Usually she eventually put her weight on the upper of the two radii bordering the broken sector (see below) and moved outward; her weight pulled this radius slightly below the plane of the web. Probably in all cases, the dragline that she laid as she moved was attached to the inner portion of the hub (attaching a dragline at this site is part of the behavior involved in removing the center of the hub following sticky spiral construction) (Eberhard 2020) but this detail was not verified in all cases.

The most common, basic behavioral unit of subsequent repair behavior for both upper and lateral frame repairs is illustrated in Figs. 3 and 4 (see also Figs. 5, 6). The spider walked along one border attaching her dragline to it, then walked back in the opposite direction and attached her dragline to the opposite side, stringing a tense spanning line across the open sector (point 3 in Fig. 4*a*). She then turned back and moved along this line; she attached her dragline part way along it, and made a second spanning line by attaching her dragline to the first border at a point (point 5 in Fig. 4*b*).

In all cases, the second attachment to this border was beyond the first and the second spanning line was farther from the hub. By repeating these operations and laying successive spanning lines farther from the hub (e.g., Figs. 3, 4*c*), she pulled earlier spanning lines outward, and pulled the more distal portions of the borders laterally, closing the damaged sector (arrows at 5 and 7 in Fig. 4*d*).

Despite this overall similarity of repair movements, the patterns of the lines themselves in repairs varied substantially (Figs. 3, 5–9). The simplest sequence of lines consisted of three spanning lines (from 1 to 2, 2 to 4 and 4 to 6 in Fig. 5) and a return to the hub (6 to 7 in Fig. 5). In contrast, a particularly elaborate repair had 6 spanning lines (Fig. 3). The mean number of spanning lines was lower in lateral frame repairs (Fig. 7) (3.44 ± 1.79 , range 2–5, $n = 16$) than in upper frame repairs (Fig. 8) (4.29 ± 1.08 , range 2–6, $n = 21$) (Mann-Whitney $U = 93.5$, $z = 2.37$, $P = 0.02$).

Several additional patterns were clear. The spider nearly always walked along the outermost non-sticky line (radii, hub spiral or frame lines) when crossing the damaged sector, and attached her dragline to the outermost non-sticky line along the way when several lines were available (exceptions occurred when she was in the process of returning to the hub). She always gradually worked outward, rather than beginning

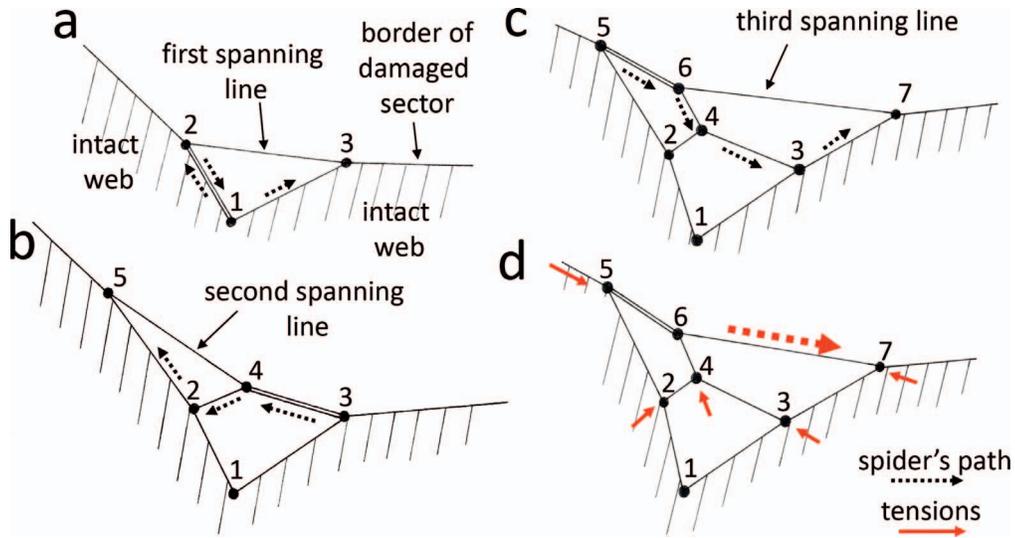


Figure 4.—Simplified, schematic drawings of the spider's movements (dotted arrows) and the sequence of attachments of repair lines in *a-c* illustrate the basic module of *Micrathena duodecimspinosa* frame repair behavior. The spider first builds the first spanning line across the empty sector, attaching it to its two borders points 2 and 3 in *a*. She then moves back along this line, attaching her dragline part way along it (at point 4 in *b*) and then farther out along the border, beyond the previous attachment, to attach the second spanning line (to point 5 in *b*). The tensions on these lines pull the borders of the damaged sector toward each other, and also pull the first spanning line away from the hub. When she repeats this sequence (attaching her drag line part way along the line just produced (at point 6 in *c*) and then to the opposite border (point 7 in *c*), she produces a third spanning line and pulls more distal portions of border toward the open space (at 5 and 7). The solid arrows in drawing *d* depict the approximate directions (but not the magnitudes) of forces exerted at different sites by the tension on the third spanning line (dotted arrow) when the spider attached it at point 7, pulling the sides of the damaged zone toward each other.

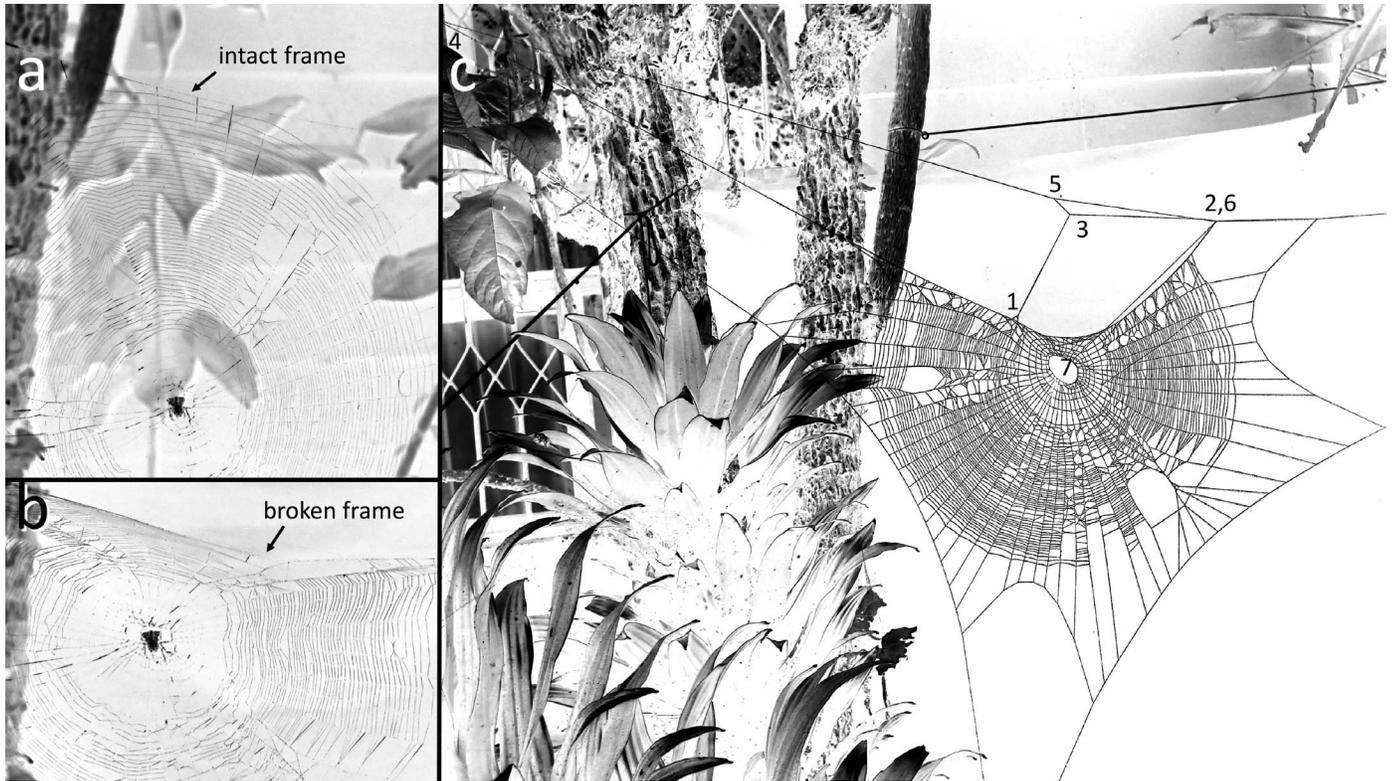


Figure 5.—The numbers indicate the order of attachments in this unusually simple and ineffective repair that consisted of only three spanning lines (1 to 2, 2 to 4, and 4-6) followed by a return to the hub (6 to 7); the capture zone was lost completely. This spider made an unusually long excursion (to point 4) on the left border.

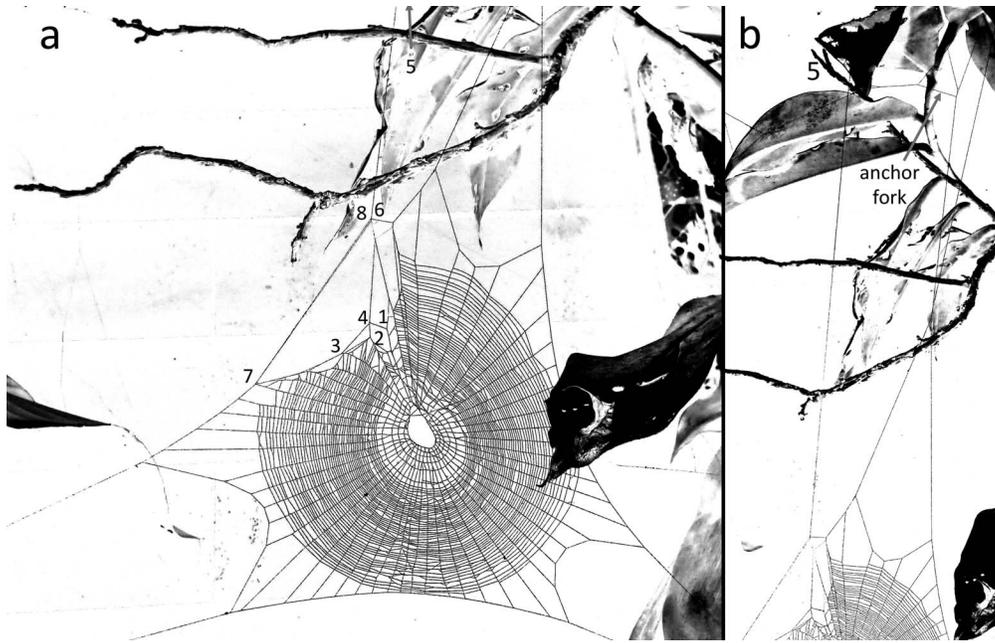


Figure 6.—This web illustrates an unusual attachment of a repair line directly to the substrate (at 5); this led to an unusually complete recovery of the web area enclosed within the outer repair line, but nevertheless only a moderate recovery of the capture zone.

repairs in an outer portion of a damaged zone and working inward. She usually attached her dragline part way across the damaged zone (points 4 and 6 in Figs. 4*b*, *c*) and then pulled the spanning line outward with the next attachment to a point

farther along the first border of the damaged sector. Generally (in 15 of 16 lateral frame repairs, and 14 of 17 upper frame repairs in which this detail was noted) the spider's first move along the damaged edge was toward the upper rather than

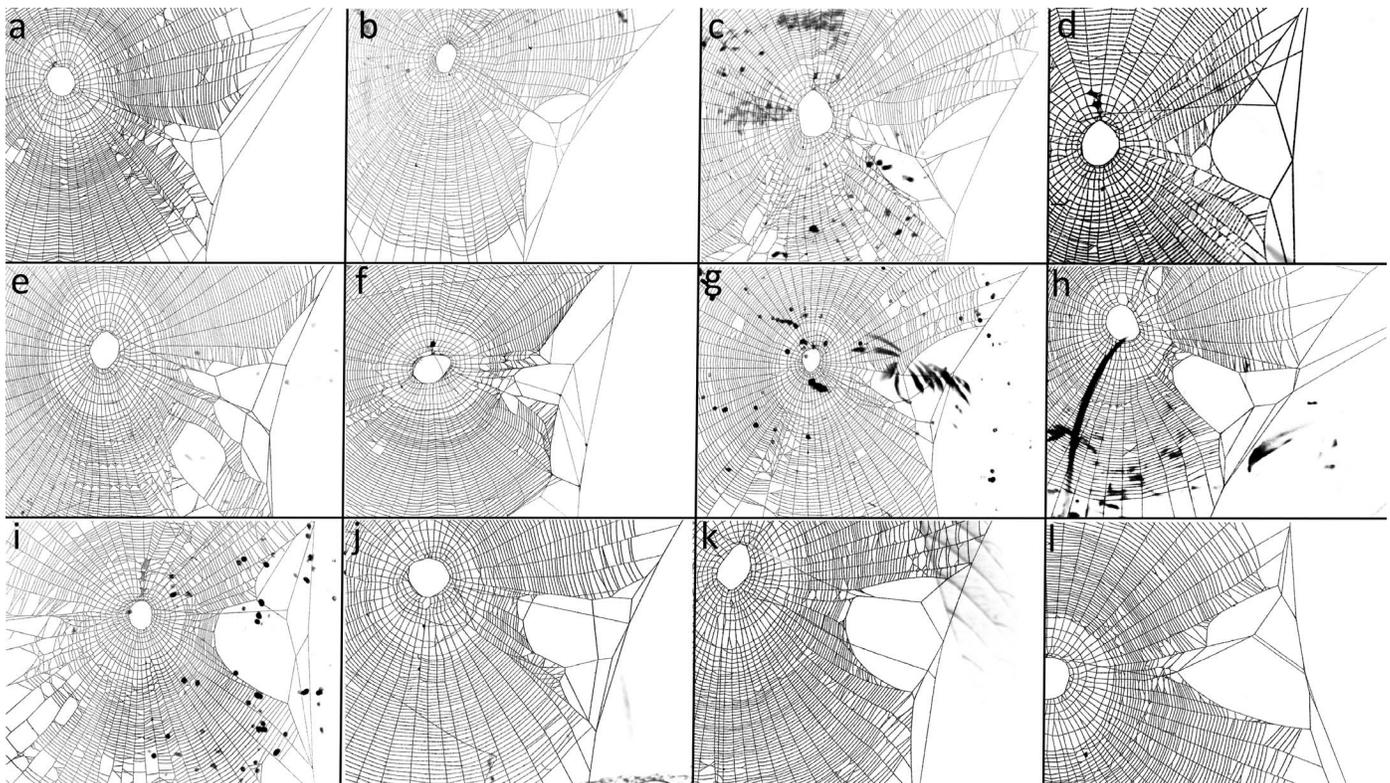


Figure 7.—Repairs of damage to the lateral frame line are arranged in approximate order from more complete to less complete recovery of capture zone area.

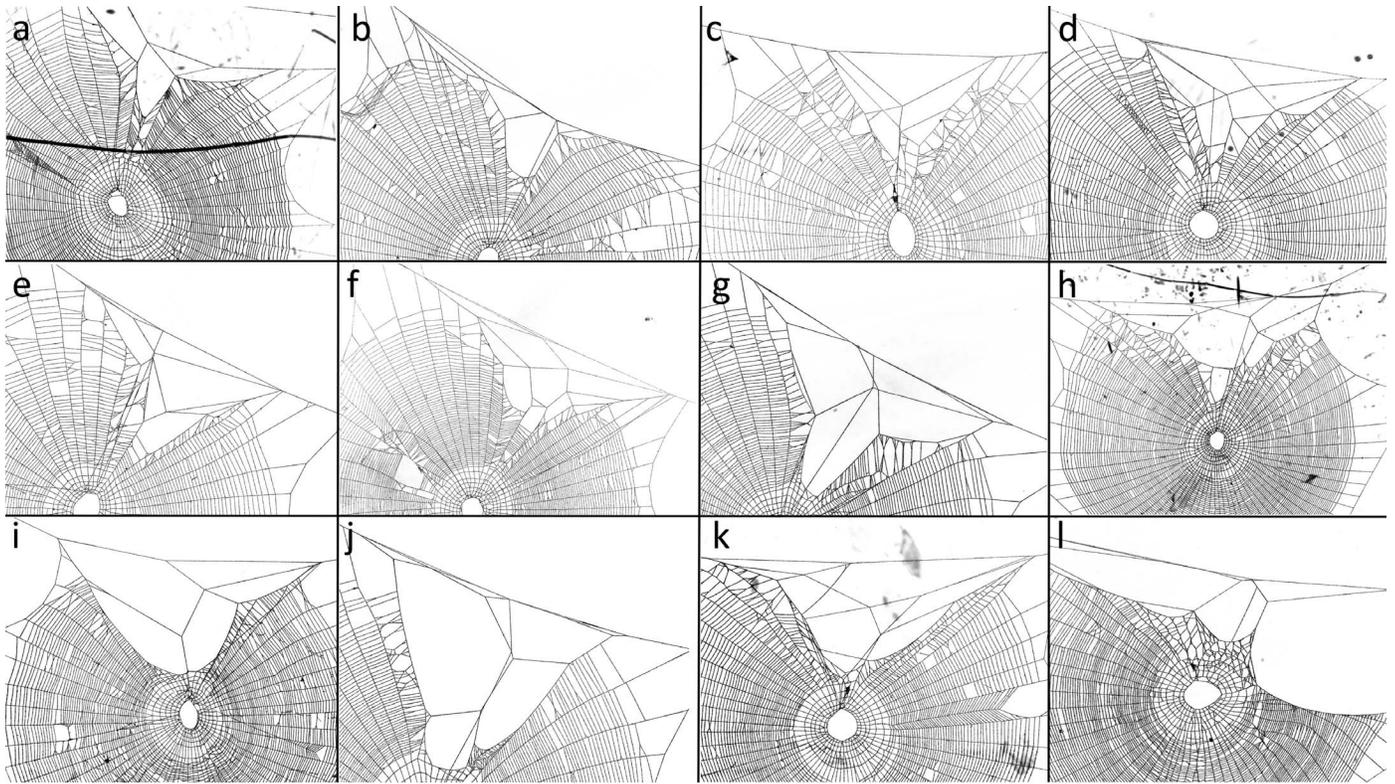


Figure 8.—Repairs of damage to the upper frame line are arranged in approximate order from more complete to less complete recovery of capture zone area.

toward the lower side of the damaged zone (e.g., upward toward point 2 in Fig. 4a). On making a repeat trip to a border to which she had previously attached a repair line, she usually placed the second attachment farther outward on the border (as in points 5 and 7 in Fig. 4c); this was true in 22 of 30 cases in lateral frame repairs, 35 of 44 in upper frame repairs (the second attachment was at nearly the same distance in 5 other cases in lateral frame repairs, and in 7 cases in upper frame repairs). The tension on each new spanning line thus usually pulled a more distal portion of the border toward the hole (Fig. 4d).

On completion of the repair, the spider usually returned to the hub by attaching her dragline at the outer margin of the central portion of the repair and then attaching it one or more times along the way to the hub (e.g., points 14 and 15 in Fig. 3). In no case was a spider seen to break and reel up a line that she had already laid. Break and reel behavior, in contrast, predominates in normal orb construction, during both exploration and radius construction (Eberhard 2020).

Minor variations in the basic behavioral unit depicted in Fig. 4 included the following: making an additional attachment to a border while walking outward along it; making an additional attachment to a spanning line while returning along it; making an additional attachment to the substrate (Fig. 6); making attachments to other nearby lines that she encountered while returning along a spanning line; and turning back after going only part way back toward the hub. In the most substantial deviation (Fig. 9), the spider began by walking across the intact web to the outer edge and then built only 2

spanning lines, each with multiple attachments along the outer edge of the repair.

Cutting the upper and lateral frames reduced the width of the capture zone to means of 37% and 33% of the capture zone widths in the intact web. Repairs resulted in little or no recovery; the means of the widths in repaired webs were 17% and 39% of intact values respectively (Table 1). The distance from the outer frame to the hub was also substantially reduced when upper and lateral frames were broken (means of 41% and 45% of intact values), but repaired webs largely recovered the original values in this respect (means of 85% and 96% of intact values respectively). Recovery of the web's original capture zone was greater in repairs of lateral frames than of upper frames. The median ratio of the width of the capture zone of the repaired web to that of the intact web was significantly higher in lateral frame repairs (0.39) than in upper frame repairs (0.09) (Mann-Whitney $U = 47$, $z = 3.05$, $n = 20$, 13 , $P = 0.0023$). All sticky lines were lost in 6 of 20 upper frame repairs (Figs. 8g–l) but in 0 of 13 lateral frame repairs ($\chi^2 = 4.77$, $P = 0.03$). In especially complete recoveries, a basal portion of the capture zone was preserved intact, and the two borders of the open area were pulled relatively close together (Figs. 7a, 8a–b, 9). In especially incomplete recoveries, on the other hand, the repair process resulted in even further reduction of the capture zone (Figs. 3, 5).

DISCUSSION

Repair behavior by *M. duodecimspinosa* included the following suite of patterns: consistent directions moved and

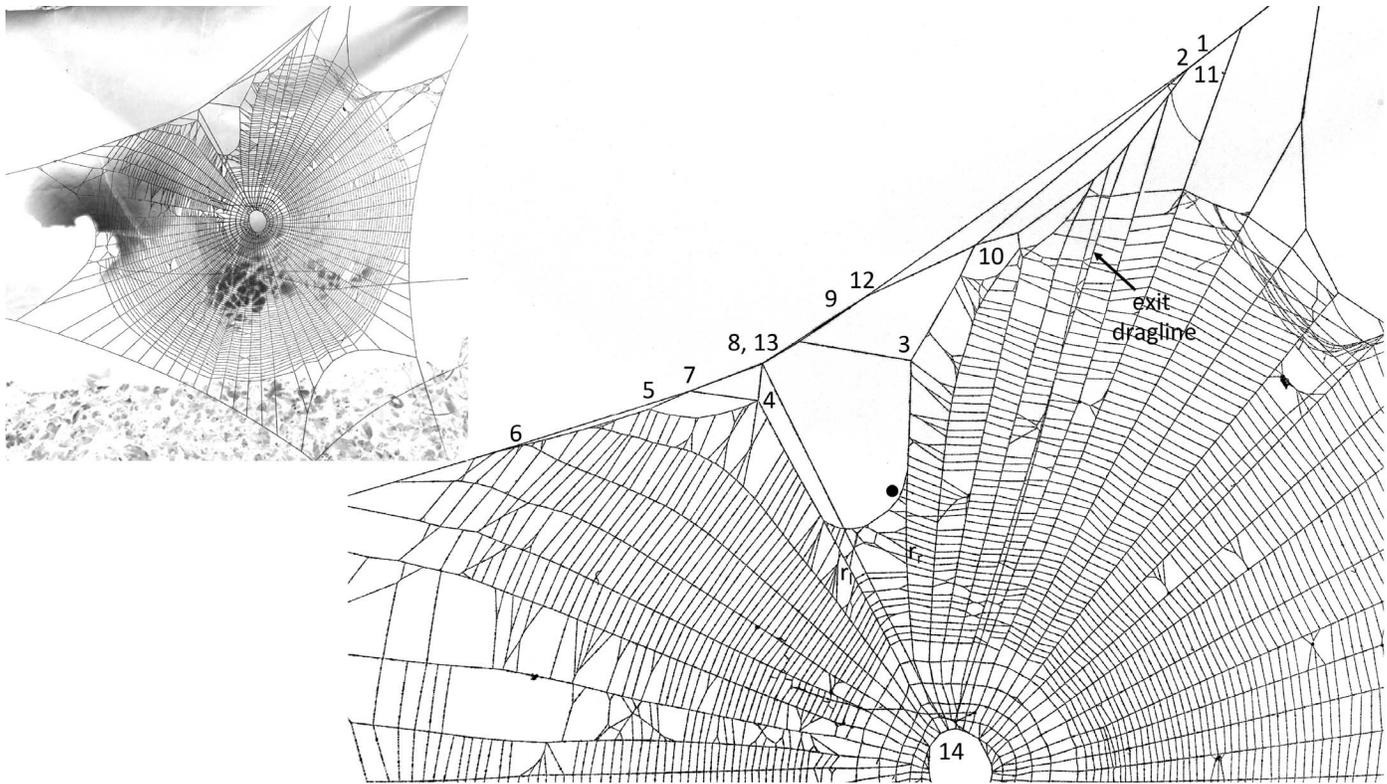


Figure 9.—An unusual pattern of attachments resulted in this relatively complete repair of a broken upper frame. The spider began by moving to the end of a radius (“exit dragline”) that was not a border of the damaged zone, rather than by walking along one border (e.g., Fig. 4). She attached her dragline to the intact frame (1) and turned back to walk across nearly the entire border of the damaged zone, making attachments 2 to 6 along the way (she reached across from the right to the left border at the site marked with a black dot). Turning and starting back, she reeled in but did not break the line 4-3, pulling the right border toward the left border while she held lines near point 4. She attached her dragline to this tensed line (at 7) and then walked along this line past point 3 and onward toward 2, attaching her dragline at 8, 9, 10 and 11, drawing the borders of the damaged zone together. She ended by returning to attach at 12 and 13 before moving to the hub (14).

choices of attachment points along the outer edge of the web (illustrated in Figs. 4a–c); tensions on new lines that pulled previous lines away from the hub (Fig. 4d); and lack of cutting lines and break-and-reel behavior (both are very common at other stages of orb construction) (Eberhard 2020). These patterns constitute an integrated set of operations that seems well-designed to extend and reinforce damaged webs. The tendency to add lines progressively farther from the hub may be based on memory of the location of the hub, like that demonstrated in other araneids (Peters 1932; Le Guelte 1969).

The back-and-forth pattern resembled the repairs of broken anchor lines by the araneid *A. diadematus* (Peters 1933; Tew et al. 2015); this species normally made only three passes across a damaged sector (Tew et al. 2015) and, at least in some cases, resembled *M. duodecimspinosa* in doubling lines rather than breaking and reeling them up (Peters 1933). Tew et al (2015) mentioned that *A. diadematus* used the same behavioral and motor patterns observed during early stages of normal orb construction, but did not cite specific patterns. In contrast, there was no clear similarity of the *M. duodecimspinosa* pattern

Table 1.—Dimensions of *M. duodecimspinosa* webs in which the upper frame ($n = 21$) or the most nearly vertical lateral frame ($n = 17$) was broken. The distances (in cm) are the following (see Fig. 2C): F-H = distance from frame to the nearest edge of the hub hole (1, 3 and 5 in Fig. 2); and CZ = width of the capture zone (2, 4 and 6 in Fig. 2). Means are followed by \pm one standard deviation.

Frame that was broken	Mean F-H	Median F-H	Ratio of F-H to intact (means, medians)	Mean CZ (cm)	Median CZ	Ratio of CZ to intact (means, medians)
Upper						
Intact web	8.62 \pm 2.13	8.80	-	6.66 \pm 1.56	6.66	-
Broken web	3.50 \pm 1.16	3.59	0.41, 0.41	2.47 \pm 0.99	2.42	0.37, 0.36
Repaired web	7.37 \pm 2.46	7.03	0.85, 0.80	1.13 \pm 1.14	0.61	0.17, 0.09
Lateral						
Intact web	7.22 \pm 2.14	7.72	-	6.20 \pm 1.27	6.35	-
Broken web	3.27 \pm 0.93	3.09	0.45, 0.40	2.02 \pm 0.87	1.70	0.33, 0.27
Repaired web	6.90 \pm 1.33	6.71	0.96, 0.87	2.39 \pm 0.62	2.49	0.39, 0.39

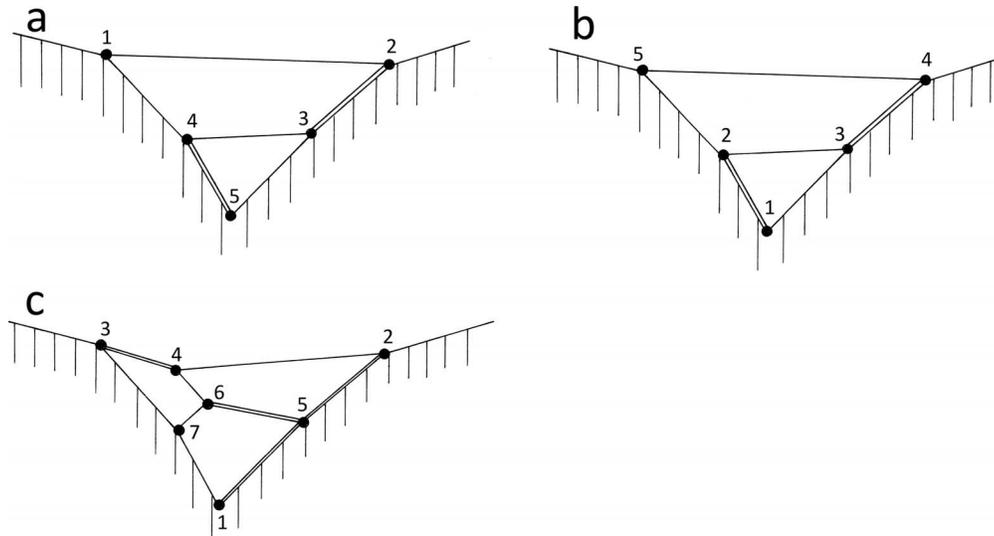


Figure 10.—Structurally and behaviorally feasible alternative strategies of frame repair that were never observed include first moving along one edge of the damaged sector to the web margin and then working inward (a), moving outward along the edge after building each spanning line (b), and working inward from the outer edge of the repair (c). Still another alternative that was rare, in which the spider began by moving to the outer edge across an intact portion of the web, is illustrated in Fig. 9.

in Fig. 4 with exploration or early radius and frame construction in this species (Eberhard 2020); the repair of this species thus seems more appropriately considered a trait specialized for this particular context.

One difference with the observations of *A. diadematus*, probably imposed by differences in experimental damage (Tew et al. 2015), was that *M. duodecimspinosa* attached the repair lines to lines at the edge of the damaged sector (presumably to radii or sticky spiral lines), rather than to the intact frame line. A second difference in *A. diadematus*, seen by Peters (1933) but not by Tew et al. (2015), was that the spider sometimes finished a repair by adding a loop of hub spiral just beyond the outer loop of the previous hub spiral; this behavior was never seen in *M. duodecimspinosa*. Still another difference was that *A. diadematus* often moved to the other side of the orb via the free zone when beginning a repair (Tew et al. 2015); this behavior was also never seen in *M. duodecimspinosa*.

One final, striking difference was that *M. duodecimspinosa* repair lines were generally not attached as far out on their orbs as those of *A. diadematus*. Only 2 of 38 *M. duodecimspinosa* webs had a repair line attached to the substrate (Fig. 6); in addition, the outermost repair attachment was usually to the side of the damaged capture zone (Figs. 2, 3, 9) rather than to an anchor line. In contrast, 9 of 16 repairs of *A. diadematus* webs built in rectangular plexiglass frames in captivity included a new anchor line that was attached to the substrate, and repair lines were attached to anchor lines in the other 7 (Tew et al. 2015). This difference may be related to the fact that *M. duodecimspinosa* orbs are normally anchored to the substrate at only three widely separated points (Fig. 1). The two exceptional *M. duodecimspinosa* repairs in which the spider attached a repair line to the substrate occurred in webs that were also unusual in having additional anchor points. Possibly the *A. diadematus* spiders ascertained (presumably during the often very extensive exploration stage – see Zschokke 1996) that the general shapes of their cages in

captivity provided additional, easily reached anchor points. Further observations to determine whether or not spiders remember details of this sort and exploit them while making repairs could be of great interest in understanding the poorly understood exploration stage.

A pholcid, *Modisimus guatuso* Huber, 1998, also used a back-and-forth pattern progressively farther from its resting area similar to the frame repairs of *M. duodecimspinosa* when extending the sheet of its web, moving back and forth along the outer edge and attaching the dragline part way along previous spanning lines and then to the substrate at sites progressively farther from the resting area (Eberhard 1992); this family is only distantly related to orb weavers (Wheeler et al. 2017; Kallal et al. 2020). The similarity is striking because many alternative patterns of orb web repair, such as starting at the outer edge and working inward (as occurs, for instance, in normal sticky spiral construction) are feasible (Fig. 10) but were not observed. Other patterns for extending webs have also been described in theridiids and linyphiids (Benjamin & Zschokke 2003, 2004). This orb weaver - pholcid similarity is thus not a constructional constraint that is geometrically or mechanically inevitable (Coddington 1986). The resemblance hints at an ancient origin for this pattern of adding lines, but this hypothesis is only speculative. Very little is known regarding web repair behavior in non-orb weavers, other than it does sometimes occur; for instance the zoropsid *Tengella radiata* (Kulczyński, 1909) repaired a hole in its sheet (Eberhard 2020), and the psechrid *Fecenia cylindrata* Thorell, 1895 made a more extensive replacement repair of the central area of its pseudo-orb (Bayer 2011; Eberhard 2020). Many non-orb weavers, including *Modisimus guatuso*, apparently remember the location of the retreat or resting area, as they return there repeatedly during construction (Eberhard 2020).

Two patterns in the frame repair behavior of *M. duodecimspinosa* supported the hypothesis mentioned in the introduction that repair activities would be more effective when

carried out while hanging from the lower edge of a damaged portion, instead of while sagging into the upper portion of a damaged area. Spiders consistently chose to initiate repairs by moving along the lower edge of the upper border of the damaged area, where their weight caused them to hang below the damaged area of the web. By keeping the first spanning line tense as she laid it (e.g., moving from point 2 to point 3 in Fig. 4), the spider largely supported her own weight and avoided causing the border to subsequently sag under her weight into lines below. In addition, the repairs of lateral frame lines, where the spider could more easily hang below the damaged area when she moved, were more effective in preserving areas covered by sticky lines than were the repairs of upper frames, despite the fact that spiders laid more spanning lines when they repaired upper frames.

The spider's reduced abilities to repair damage above the hub has implications for discussions of the effects of vertical asymmetries in orb webs on prey capture (e.g., Eberhard 1986, 2020; Nakata & Zschokke 2010; Zschokke & Nakata 2015). If orb weavers in general are less able to repair damage above the hub, then the expected payoffs from the portions of orbs above the hub may need to be reduced. The magnitude of this adjustment would depend on the frequencies of web damage in the field, and the effectiveness of repairs in recovering prey interception, stopping, and retention capabilities, and is uncertain. In addition, lower numbers and greater lengths of anchor lines would increase the web's susceptibility to damage when a large object such as a falling leaf breaks a frame line. In sum, the degree to which the spider can repair different web designs may need to be taken into account in evaluating the expected payoffs in prey capture from these designs.

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