2019. Journal of Arachnology 47:57–62

Radius construction by *Micrathena duodecimspinosa* (Araneae: Araneidae): a puzzle within a puzzle

William Eberhard: Smithsonian Tropical Research Institute and Universidad de Costa Rica (Emeritus); Louisiana State University (Research Associate); Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica; E-mail: william.eberhard@gmail.com

Abstract. Araneid orb weavers systematically weaken the radii in their orbs by partially or completely removing the provisional radial lines laid during radius construction. Removal of provisional radii by *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) tended to be less complete for those radii that were attached later during the radius construction stage to the same frame line; this pattern differed from previous observations of provisional radius removal in two other araneids. Patterns of removal in *M. duodecimspinosa* were not in accord with a previous hypothesis that provisional radius removal functions to adjust radial tensions. In addition, *M. duodecimspinosa* moved in complex, jerky paths during radius construction that did not occur in previous or subsequent stages of construction. These movements resulted from the spider vibrating the entire web as she moved; their functional significance is unclear.

Keywords: Orb construction behavior, weaken orb, double radii

The mechanical properties of the radii of an orb largely determine its ability to stop prey by absorbing their kinetic energy without breaking (Sensenig et al. 2012). It is thus puzzling that during radius construction, most araneoid orb weavers break and remove the dragline that is laid on the way out from the hub to the frame (the “provisional” radius of Zschokke 2000), and then replace it (instead of doubling it) with a new dragline laid while returning to the hub (the “definitive” radius) (Eberhard 1982; trait F_1). This removal behavior must substantially reduce the ability of the non-doubled portion of a radius to stop prey; the stresses of prey impact tend to break the lines near the point of impact, and a non-doubled portion of radius would be able to absorb less kinetic energy before breaking (Cranford et al. 2012; Eberhard, in press 2020).

Zschokke (2000) argued that leaving a greater portion of the provisional radius intact is associated with higher radial tension. In accord with this hypothesis, he found that the araneid *Zilla diodia* (Walckenaer, 1802) left approximately the outer half of each provisional radius intact, and left somewhat larger portions intact in the upper than the lower sector of the orb; the outer portion of each radius is generally under higher tension (due to tensions on the sticky spiral lines), as are the radii above the hub (Denny 1976; Eberhard 1981; Wirth & Barth 1992). Also, in accord with this hypothesis, there were larger numbers of sticky spiral loops in *Z. diodia* orbs (mean of 62 above and below the hub in Figure 4 of Zschokke 2000) than in those of *Araneus diadematus* Clerck, 1757, which broke each provisional radius near the frame, and whose orbs typically had only about 25–35 sticky spiral loops above the hub (Breed et al. 1964; Witt et al. 1968; Vollrath 1992). Less complete and more qualitative observations (Eberhard 1981) suggested that the site where the provisional radius is broken varies in other species: it was characterized as being near the frame in the araneids *Micrathena schreibersi* (Perty, 1833), *M. gracilis* (Walckenaer, 1805), *Eriophora* sp., *Argiope argentata* (Fabricius, 1775) and the tetragnthid *Leucauge mariana* (Taczanowski, 1881), but farther inward, nearer the hub in others such as the araneids *M. sexspinosa* (Hahn, 1882), *Neoscona* sp. and *Cyclosa caroli* (Hentz, 1850) and the tetragnathids *Tetragnatha* sp. and *Tylorida striata* (Thorell, 1877). In *C. caroli*, the break site varied from near the frame to about half the distance to the hub.

One puzzling detail in *Z. diodia* was that the spider did not use a piriform attachment to attach her dragline (the definitive radius) to the provisional radius when the she broke it while returning to the hub (Zschokke 2000). Instead, she left the broken end of the provisional radius free, and the two lines appeared to adhere to each other along their lengths (Figure 2 in Zschokke 2000). No additional silk was seen that might fasten one line to the other, and the mechanism by which they stayed together “remained unclear”. The lack of a strong attachment between the two lines would be expected to weaken their combined mechanical resistance to prey impacts.

This note compares several aspects of the behavior associated with provisional radius construction and removal in another araneid, *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) with these previous accounts, and evaluates hypotheses regarding their functional significance.

METHODS

Direct observations and video recordings of radius construction behavior and orb designs of mature female *M. duodecimspinosa* were made in the field in September and October, 2017 in early second growth near San Antonio de Escazu, San José Province, Costa Rica (el. 1325 m). Probably no female was observed more than once, because different websites were checked each day. The video recordings allowed more precise measurements of the positions of many break points on the radii, but were in some cases less clear regarding where breaking behavior occurred on those radii above the hub. Webs whose construction had been observed were later photographed after being coated with cornstarch. Other webs were collected just after radius construction ended by fastening them to a large rectangular styrofoam frame (30 × 48 cm inside dimensions) that was coated with double-sided sticky tape, so that intact lines could be examined under dissecting and compound microscopes.

I follow the terminology of Zschokke (2000): a “single” line or “dragline” refers to the pair of fibers (presumably a

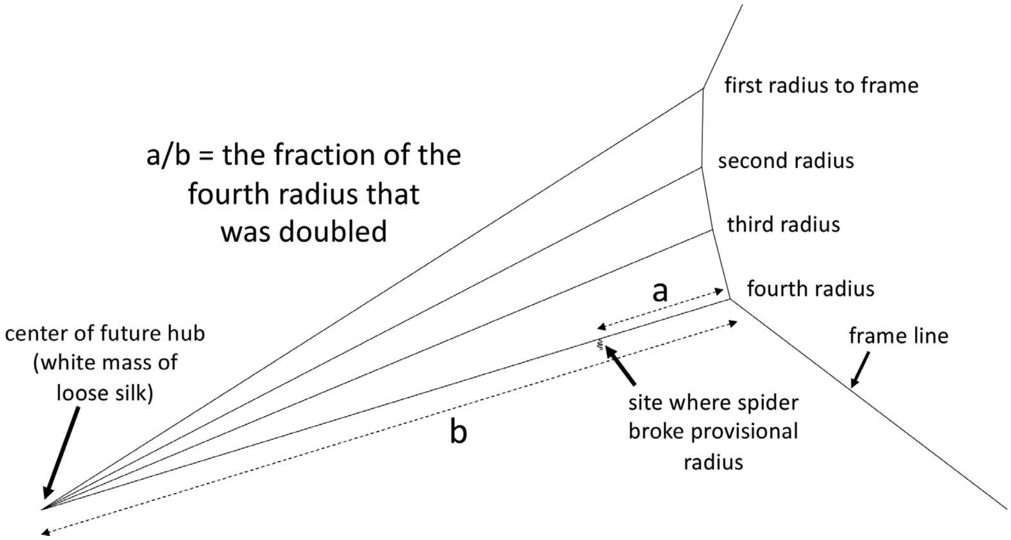

Figure 1.—Definitions of terms used in the text.

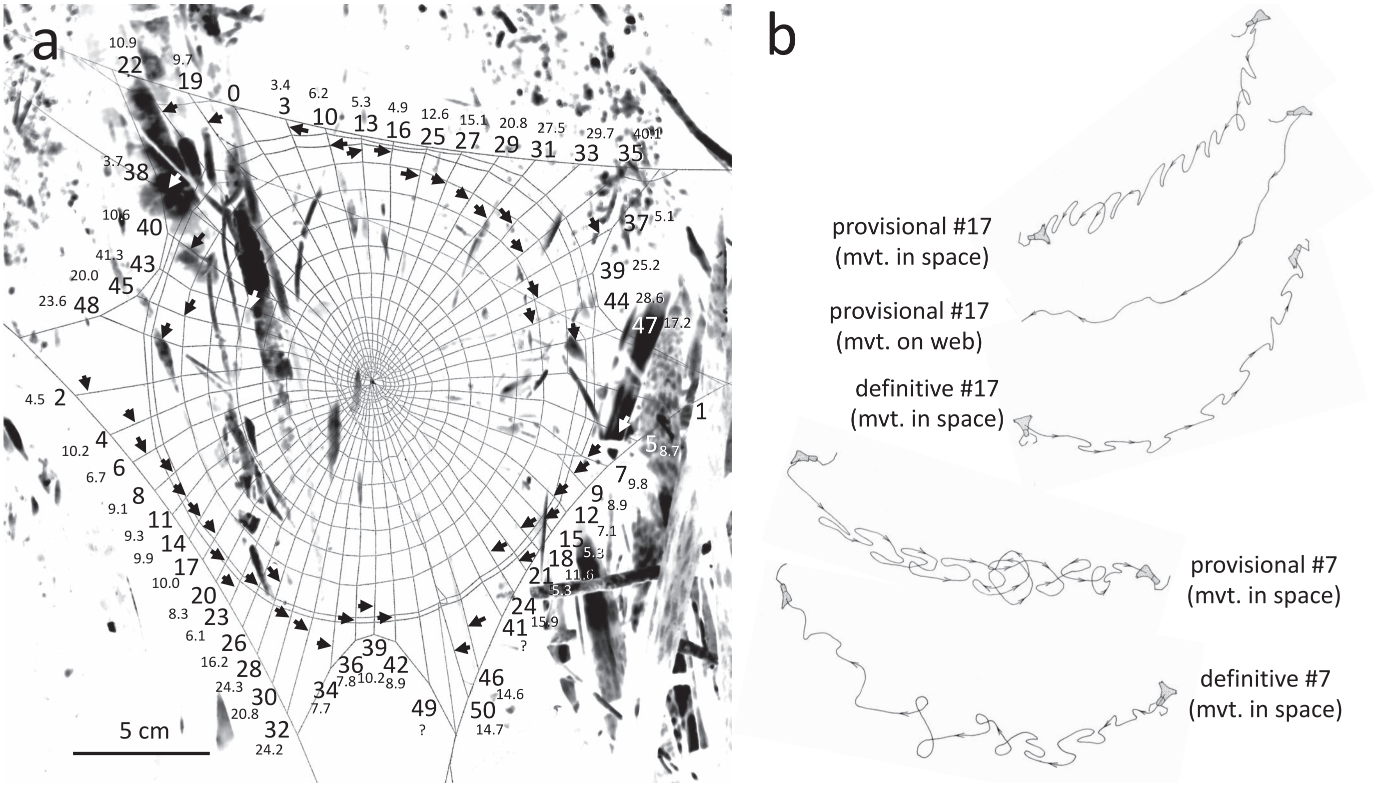

Figure 2.—(*a*) Web of a mature female *M. duodecimspinosa* that was interrupted after only two loops of sticky spiral had been built (the temporary spiral is still in place). The order in which radii were added to this web is indicated by the larger numbers (0 is the first radius, 1 the second, etc.); the estimated fraction of each radius that was doubled is indicated by the smaller numbers (the approximate sites are marked with the arrowheads. (*b*) These paths of the spider's body ("movements in space") when she moved away from the hub to the frame and then back again while building two radii (#17 and #7) were traced from video recordings. The arrowheads mark the positions of the center of her abdomen; a few of the lines connecting them are slightly more curved than the actual path of the spider to allow them to be distinguished. The path of the spider with respect to her web ("movement on web") was also determined for provisional radius #17 by superimposing the video recording on a photo of the completed web, and adjusting the position of the photo in each frame to the position of the web in that frame. The spider's path across the web was relatively smooth when the movements of the web itself were taken into account this way. The total durations of the spider's trips across the web was varied between 3 and 4 s. Some individuals moved in somewhat less jerky paths than did this one.

pair of major ampullate gland fibers, one each from the two anterior lateral spinnerets) that were produced simultaneously as the spider moved; "doubled" lines refer to pairs of double-stranded lines (with a presumed total of four fibers each). Neither the numbers of fibers nor the glandular origins of any lines or attachments were confirmed directly in this study. I also follow Zschokke's use of slight pauses or reductions in the speed of the spider's movement toward the hub as indications of the sites where the spider broke a provisional radius. This supposition was supported by two types of observation. Under occasional optimum viewing conditions (when direct sunlight glinted off of lines seen against a dark background), I confirmed that there was a tiny white mass (an attachment of the dragline to the provisional radius) at each site where the spider had paused. In a few other cases videos showed that both the dragline and the provisional radius were visible behind the spider just before she made a pause, but that when she moved onward only a single line was visible behind her.

I analysed comparative measures of the sites at which spiders broke the provisional radius within each orb (the fraction of the distance from the frame to the future center of the hub; see Fig. 1), rather than absolute values; this helped reduce possible biases resulting from the effects of spider size and web size (which correlate several other design variables – Eberhard in press 2020). Similarly, I used relative rather than absolute positions in sequences (first, second, and third, second from last, first from last, and last) in the analyses, because the absolute numbers of radii attached to primary and secondary frames varied both within and between webs. The radii ending on the uppermost primary frame were analyzed separately, because the first radius to this frame was attached at variable sites in the middle portion of the frame, rather than at one end (e.g., radius 0 in Fig. 2), and subsequent radii were added sequentially on either side of this original radius. In contrast, the first radius laid to the lower, or more lateral frames was nearly always the uppermost radius attached to that frame, and subsequent radii were added in order below (e.g., radii 1 and 2 in Fig. 2) (Eberhard in press 2020). On the uppermost frame, I only analyzed the set of radii that were at the end farthest from the first radius (e.g., radii 3, 10, 13, 16, 25, 27, 29, 31, 33 and 35 in Fig. 2a).

As is typical for *M. duodecimspinosa* (Eberhard in press 2020), all of the 14 orbs observed had three primary frame lines, and three secondary frame lines, with one primary frame uppermost, and the other two more lateral (Fig. 2a). The secondary frames were added late in the sequence of radius construction, when most of the radii attached to the primary frames had already been built, as nearly invariably occurs in *M. duodecimspinosa* (Eberhard in press 2020). Therefore, the positions of break sites on radii that were attached to secondary frames were analyzed separately from those on radii that were attached to primary frame lines. Sample sizes varied due to occasional missed observations, doubts regarding break points in the videos, or reference points that were occasionally out of view in the videos. Means are given ± one standard deviation; Mann-Whitney U Tests were used in all statistical comparisons unless specified otherwise.

RESULTS

Site of breaking provisional radii.—The radii attached to secondary frames showed the clearest pattern (Table 1). The first two provisional radii attached to a secondary frame line tended to be broken nearer the frame (about a body length from it) than the last two provisional radii (up to approximately three quarters of the distance to the hub) (Fig. 2a, Table 1). The site where the first radius was broken was closer to the frame than was the site for the last radius to that same frame in 38 of 39 frame lines in 14 orbs ($\mathrm{Chi}^2 = 35.2$, $\mathrm{df} = 1$, $P < 0.0001$). The mean fraction of the distance to the hub at which the break occurred on the first radius was only about one third of that on the last radius (0.11 vs. 0.31) (Table 1; $z = -7.22$, $P < 0.0001$).

The same pattern for later radii to be broken farther from the frame was evident in the two more lateral primary frames. The mean fractions of the radius that were doubled on the last, next to last, and second from last radii attached to the frame were all significantly greater than the mean fractions on the first, second and third radii attached to that frame (Table 1). The fraction for the last radius was also significantly greater than the second from last ($z = -3.61$, $P = 0.0003$). With respect to the uppermost frame, the mean fractions doubled in the last, next to last, and second from last radii were all greater than those for the first, second and third radii (Table 1).

When all radii were combined, there were no consistent trends for the values that were associated with the uppermost primary frame to be larger than those associated the lateral frames (Table 1; $Z = -1.27$, $P = 0.203$). Similarly, when radii laid in different positions (first, second, etc. radius attached to a frame) were compared between uppermost primary frame and the lateral frames, none of the differences were significant (Table 1).

The importance of the order of radius construction for a given frame line, as opposed to the absolute order of radius construction was emphasized by the fact that the value for the last radius to a primary frame, which often immediately preceded secondary frame construction, was just over three times greater than that for the first radius to a secondary frame ($z = -7.08$, $P < 0.00001$).

Attachment of the dragline to the provisional radius.—As noted above, a small white spot was sometimes visible on the definitive radius in the field at the moment when the spider slowed down briefly as she returned to the hub. Each of five radii observed under a compound microscope had a small mass not far from its attachment to the frame (Fig. 3a) that appeared to be a piriform attachment disc composed of many fine, tightly folded or tangled lines with a short, lax line (presumably the broken end of the provisional radius) (Figs. 3b, c).

Jerky movements during radius construction.—Soon after the upper frame had been built and the hub had been initiated (when the first radius to this frame was lengthened, thus lowering the hub to its definitive site) (Zschokke & Vollrath 1995; Eberhard in press 2020) and throughout the rest of radius construction, the spider ceased walking "smoothly" from one site to another. Instead she moved jerkily (Fig. 2), in a pattern that did not occur in any other phase of web construction. The jerky path of the spider's

Table 1.—The relative sites at which provisional radii were broken (a/b in Fig. 1) during radius construction are compared with respect to the order in which radii were attached to a given frame, and for the different types of frame lines to which they were attached. Values in the same row that share the same letter and number differed significantly between early and late radii with Mann-Whitney U Tests (a = $P < 0.05$, b = $P < 0.01$, c = $P < 0.001$, d = $P < 0.0001$) (numbers of radii are given in parentheses).

	Early radii			Late radii			
	First to that frame	Second to that frame	Third to that frame	Second from last to that frame	Next to last to that frame	Last to that frame	All of the attachments to that type of frame
Secondary frames	0.11±.05 d_1,d_2 (41)	0.17±.07 a_1,d_3 (38)	-	-	0.22±.12 a_1,d_2 (36)	0.31±.11 d_1,d_3 (41)	0.20±.11 (202)
Lower two primary frames	0.10±.04 d_4,d_5,d_6 (25)	0.13±.05 d_8,d_9,d_{11} (25)	0.14±.06 c_1,d_7,d_{10} (25)	0.21±.08 d_6,c_1,d_{11} (25)	0.27±.10 d_5,d_7,d_8 (21)	0.35±.13 d_4,d_9,d_{10} (25)	0.18±.10 (247)
Uppermost primary frame	0.13±.07 b_1,b_4,d_{12} (10)	0.13±.05 b_2,b_5,d_{13} (10)	0.12±.05 b_3,b_6,d_{14} (10)	0.20±.06 b_1,b_2,b_3 (10)	0.28±.11 b_4,b_5,b_6 (10)	0.38±.12 d_{12},d_{13},d_{14} (10)	0.20±.13 (113)

body resulted from the web itself moving rapidly back and forth (presumably due to jerking or swaying movements of the spider), rather than to jerky movements of the spider with respect to the web. The spider's path on the web itself was relatively smooth ("movement on web" for radius #17 in Fig. 2), and the major oscillations of her body were due to movements of the web itself ("movement in space" in Fig. 2).

DISCUSSION

The pattern of provisional radius replacement has now been studied in detail for three araneid species. It is different in each: *A. diadematus* broke all provisional radii near the frame; *M. duodecimspinosa* also broke most provisional radii near the frame, but tended to break the last few radii that were attached to each frame nearer the hub; and *Z. diodia* broke

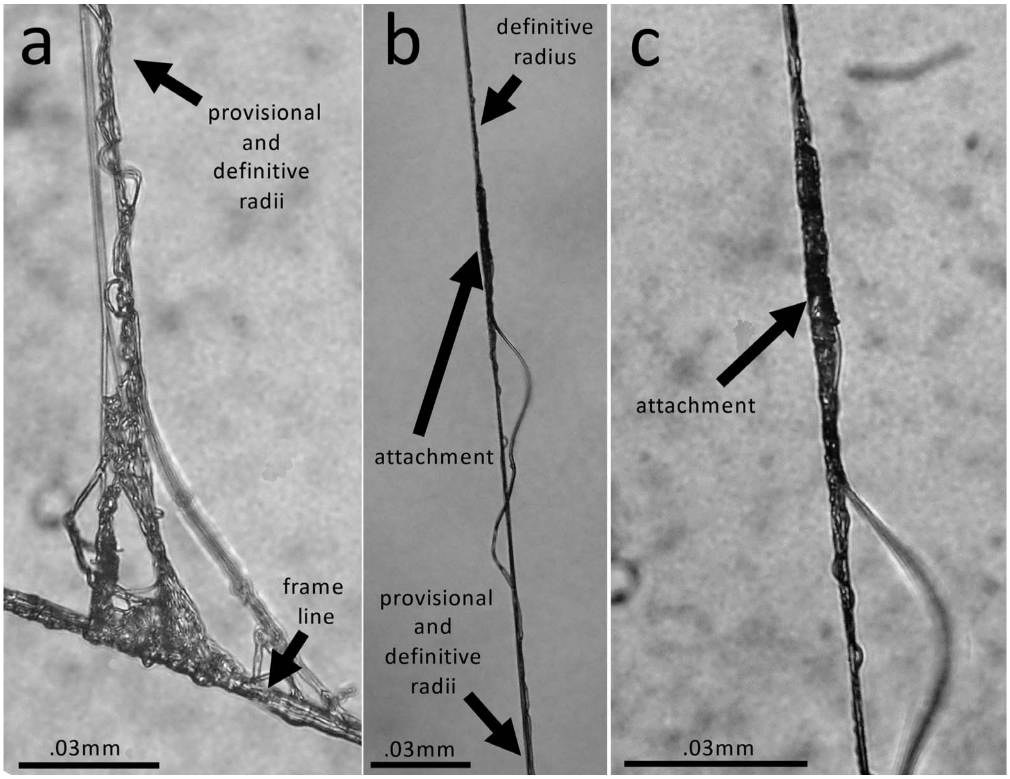

Figure 3.—Close-up views of a piriform attachment of a radius to a frame line (*a*) and a piriform attachment of the definitive radius to the presumed provisional radius (the lax line in *b* and *c*) in a web of a mature female *M. duodecimspinosa* (the direction of the hub is upward in all three photos).

most provisional radii farther from the frame, in the inner half of the orb. The break sites were farther from the frame on radii in the upper half of the orb in *Z. diodia*, but not in *M. duodecimspinosa*. The last radii built by *Z. diodia* had (to a lesser degree) smaller doubled portions (Zschokke 2000), the opposite of the strong trend in *M. duodecimspinosa*.

The significance of these contrasting patterns, and the apparent variation in other species (Eberhard 1981) is unclear. It has been hypothesized that break-and-reel behavior during radius construction functions to allow the spider to adjust the tension on each newly laid radius before attaching it to the hub (Eberhard 1981; Zschokke 2000). Tension changes did indeed occur during radius construction by *M. duodecimspinosa*, with the tension on the definitive radius (judged by the angle between the radius and the frame line; see Eberhard 1981) generally decreasing just before it was attached at the hub, as in other species (Eberhard 1981, in press 2020). But in all of these species, it would seem more advantageous for the spider to wait to make such tension adjustments until she was close to the hub, and thus replace only the innermost portion of the provisional radius. This would leave the radius doubled throughout most of its length, increasing its ability to absorb the kinetic energy of prey striking the orb.

Zschokke's explanation for breaking the provisional radius farther from the frame in the upper portion of the orb was that radii in the upper portion are under greater tensions, and would thus benefit more from having a larger portion doubled. This is logical, but fails to explain the lack of such a pattern in the webs of *M. duodecimspinosa* (which also sits at the hub throughout the day, thus tensing the radii in the upper portion of the orb with its weight). It also fails to explain the trend in *M. duodecimspinosa* for larger portions of the last radii that are attached to a frame line to be doubled. The findings reported here thus do not support this functional explanation.

An additional possible selective factor mentioned by Zschokke (2000) as possibly affecting radius doubling is that when a radius is only partially doubled, it will be less "stiff" (in the sense of being more extensible – S. Zschokke pers. comm.). It is not clear, however, how this presumed advantage would compensate for the major reduction in the line's ability to absorb prey momentum resulting from not doubling it (though it must also be true that prey striking an orb nearer the hub are likely to encounter larger numbers of radii, reducing the forces acting on individual radii nearer the hub – S. Zschokke pers. comm.). Zschokke (2000) mentioned two additional, but apparently minor disadvantages of breaking the provisional radius: breaking the lines involves more complicated behavior; and it increases construction time by about 1s per radius or 1% of the total web construction time (this fraction would be less in *M. duodecimspinosa*).

An additional possibility is related to the behavior of the web in the wind (Craig et al. 1985; Eberhard in press 2020). The extensibility of the radii, and thus of the central portion of the orb as a whole, under a given, spatially generalized load would be increased by breaking radii; this could increase the distances orbs swung in the wind and possibly their abilities to intercept nearby insects. This would not explain, however, the trend in *M. duodecimspinosa* to break later radii attached to a frame closer to the hub, nor the apparent differences in break sites in different species with similar web designs (e.g., *Leucauge* vs. *Tylorida*, different species of *Micrathena*) (Eberhard 1981, in press 2020). At the moment, none of these hypotheses convincingly explains the strong patterns of provisional radius replacement in *M. duodecimspinosa*.

Equally mysterious is the difference between *M. duodecimspinosa* and *Z. diodia* in whether they attached the definitive radius line to the provisional radius: *M. duodecimspinosa* made a piriform attachment near the tip of the broken end of the provisional radius; but *Z. diodia* failed to make any attachment, and allowed the provisional line to become lax and to adhere to the definitive radius along its length (presumably due to newly spun fibers being slightly sticky). Although the subsequent attachments of temporary and sticky spiral lines to the radius would bind the provisional and definitive radial lines to each other in *Z. diodia*, the failure to make such a piriform attachment would seem to inevitably reduce the mechanical advantage of doubling the radial line by leaving the tension on the provisional radius much lower than that on the definitive radius.

Still another unexplained detail of *M. duodecimspinosa* behavior was the way the spider bounced the web during radius construction, causing her body to move jerkily (Fig. 2b); similar jerky movements did not occur during frame construction. The tracings of spiders' paths in other araneids, including *A. diadematus*, *Z. diodia* and several others, did not include such jerky paths (Zschokke & Vollrath 1995; Zschokke 2000); similar jerkiness was observed, however, during frame (but not radius) construction in the uloborid *Hyptiotes paradoxus* (C. L. Koch, 1834) by Zschokke & Vollrath (1995), who speculated that it might function as a defense against predators. Another, perhaps more likely possibility, given the nocturnal timing of construction by *H. paradoxus* (Marples & Marples 1937), would be to acquire cues from the web, such as, for instance, the resonant frequency of the web as a whole (which would correlate with the tensions on lines and their lengths).

In sum, details of radius construction of araneid spiders are more complex than was previously appreciated. The adaptive significance of some of these details is even less clear than before.

ACKNOWLEDGEMENTS

I thank S. Zschokke for helpful comments on a previous draft, and the Smithsonian Tropical Research Institute for continued financial support.

LITERATURE CITED

Breed, A.L., V.D. Levine, D.B. Peakall & P.N. Witt. 1964. The fate of the intact orb web of the spider *Araneus diadematus* Cl. Behaviour 23:43–60.

Craig, C.L., A. Okubo & V. Andreasen. 1985. Effect of spider orb-web and insect oscillations on prey interception. Journal of Theoretical Biology 115:201–211.

Cranford, S.W., A. Tarakanova, N.M. Pugno & M.J. Buehler. 2012. Nonlinear material behaviour of spider silk yields robust webs. Nature 482:72–76.

Denny, M. 1976. The physical properties of spider's silk and their role in the design of orb-webs. Journal of Experimental Biology 65:483–506.

Eberhard, W.G. 1981. Construction behavior and the distribution of tensions in orb webs. Bulletin of the British Arachnological Society 5:189–204.

Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution 36:1067–1095.

Eberhard, W.G. in press, 2020. Spider webs: Function, Behavior and Evolution. University of Chicago Press, Chicago.

Marples, M.J. & B.J. Marples. 1937. Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica*. Proceedings of the Zoological Society of London, Series A 1937:213–221.

Sensenig, A.T., K.A. Lorentz, S.P. Kelly & T.A. Blackledge. 2012. Spider orb webs rely on radial threads to absorb prey kinetic energy. Journal of The Royal Society Interface 9:1880–1891.

Vollrath, F. 1992. Analysis and interpretation of orb spider exploration and web-building behavior. Advances in the Study of Behavior 21:147–199.

Wirth, E. & F. Barth. 1992. Forces in the spider orb web. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 171:359–371.

Witt, P. N., C.F. Reed & D.B. Peakall. 1968. A Spider's Web: Problems in Regulatory Biology. Springer-Verlag, New York.

Zschokke, S. 2000. Radius construction and structure in the orb-web of *Zilla diodia* (Araneidae). Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 186:999–1005.

Zschokke, S. & F. Vollrath. 1995. Web construction patterns in a range of orb-weaving spiders(Araneae). European Journal of Entomology 92:523–541.

Manuscript received 26 April 2018, revised 10 July 2018.