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Confirmation that tension-dependent cues do not guide sticky spiral construction in *Micrathena duodecimspinosa*, and the probable reason why

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Abstract. Sticky spiral construction behavior in orb-weaving spiders is strikingly flexible: 10 to 16 different cues influence the hundreds of decisions that a spider makes while building the sticky spiral in an orb. Several variables that are influenced by radial tensions, including the frequencies and amplitudes of vibrations and the extensibility and tensions of the radii, have been repeatedly mentioned as possible cues guiding sticky spiral placement. Nevertheless, previous studies have suggested that radius tensions do not affect sticky spiral spacing. These tests were complicated, however, by the tight correlations between variables due to the highly regular geometry of orbs, possible context-dependent variation in the use of cues, and the intrinsic difficulty of demonstrating the absence of an effect. Greater certainty regarding tension-dependent cues is crucial for understanding the cues guiding orb construction, so this study extends these experiments, examining the effects of both increasing and decreasing radius tension, and of different sequences and magnitudes of changes. The results confirm previous findings: changes in radius tensions did not influence sticky spiral spacing decisions in consistent ways and generally failed to produce statistically significant effects. I argue that the likely reason why spiders do not use tension-dependent variables to guide sticky spiral placement is that such cues are unreliable because the spider's own weight substantially alters the tensions on nearby web lines in complex and variable ways.

Keywords: orb web construction, radius tensions, sticky spiral spacing
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Orb web construction has long fascinated naturalists because it involves intricate and precisely organized behavior performed by a small animal with limited brain power (Fabre 1912; Hingston 1920; Peters 1939, 1954; Witt et al. 1968; Zschokke & Vollrath 1995; Eberhard 2020). Early observations suggested that orb construction behavior is rigid and highly stereotyped, but this idea has given way to the realization that many aspects of orb construction are highly flexible (Herberstein & Tso 2011; Eberhard 2020). Placement of the geometrically regular, relatively evenly spaced loops of sticky spiral is an especially impressive aspect of orb construction. Sticky spiral construction is surprisingly complex, and a recent summary concluded that orb-weaving spiders are influenced by between ten and sixteen different variables in each of the hundreds of decisions that determine where the spiral is attached to the radii in an orb (Eberhard 2020).

Some stimuli that guide sticky spiral construction are "short-term cues" (Eberhard 2020) that the spider apparently perceives anew just prior to making each attachment to a radius. These cues include the locations of nearby lines, distances and directions travelled since the previous attachment, and the spider's location with respect to the hub (Figs. 1a,b). Others are "longer-term" or "settings" cues that may have been sensed earlier or even prior to sticky spiral construction, such as the spider's supply of silk, recent feeding history, body size and weight, wind velocity on previous days, humidity, the time of the day, and the area of the web (summarized in Eberhard 2020). The fact that different families of orb weavers use several of the same short- and long-term cues in similar ways suggests a monophyletic derivation of orb webs (Eberhard & Barrantes 2015; Coddington et al. 2019; Eberhard 2020, 2022a).

Determining which short-term cues from an orb web are guiding construction is challenging, however, because the behavioral context can influence a spider's responsiveness, and some stimuli can over-ride others when they are in conflict (Eberhard & Hesselberg 2012; Eberhard 2020). Responses to some stimuli are buffered by recent memories of the stimuli sensed on preceding radii, and some effects of an experimental modification are manifested only gradually as the spider moves across her web (Fig. 1b).

Visual stimuli are not used (Eberhard 2020), and instead multiple lines of evidence indicate that the cues guiding orb construction are tactile (summary Eberhard 2020). Several experimental techniques, including removing lines or altering their positions (Hingston 1920; Peters 1939; Reed 1969; Eberhard 1987; Vollrath et al. 2000; Eberhard & Hesselberg 2012), altering the web's position in relation to the spider's perception of gravity (Peters 1939; Eberhard 1987; Vollrath 1988) and moving the supports to which the web is attached (Tilquin 1942; Mulder et al. 2021), have been used to test which variables from the web lines that the spider contacts are used as cues.

The orb itself represents a detailed record of the spatial relationships between many of the lines that the spider contacted during construction. It is sometimes difficult, however, to distinguish among possible cues that co-vary due to the geometrically regular relations between the lines in an orb. In addition, some other variables that the spider might sense by touch are difficult to determine. "Hidden" stimuli that might be used during sticky spiral construction include the tensions, extensibility, and vibrations of radial lines, all of which might allow the spider to indirectly sense other variables such as radius length or the distance to the hub or the frame. Basic physics indicates that these hidden stimuli will vary according to radius tensions, and tension-dependent variables have been mentioned repeatedly in previous studies as possible cues that might guide sticky spiral placement (e.g., Witt et al. 1968; Eberhard 1969; Mulder et al. 2021). Although recent reviews of evidence concluded that tension-dependent cues do not guide sticky spiral construction (Eberhard & Hesselberg 2012; Eberhard 2020; Mulder et al. 2021) or radius construction (Vollrath et al. 2000), some doubt remains.

One source of doubt is that two lines of evidence show that the araneid orb weaver *Micrathena duodecimspinosa* (O. Pickard-Cambridge, 1890) reduces sticky spiral spacing when the spider's

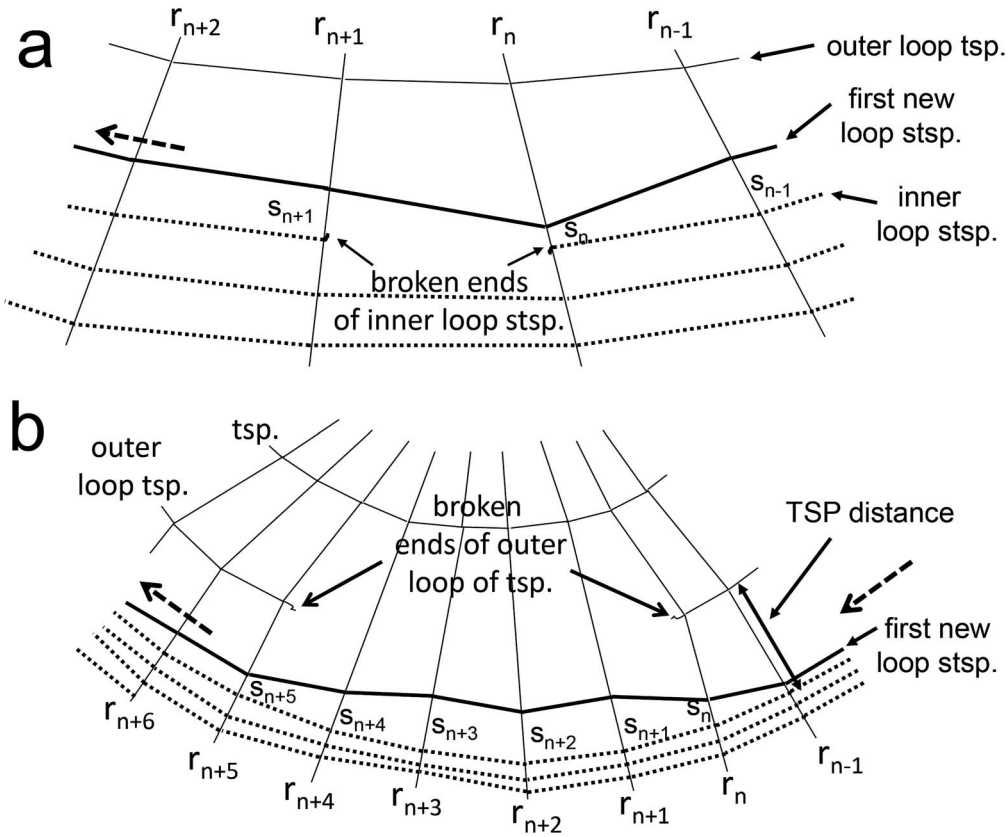

Figure 1.—Diagrammatic illustrations of the lower portion of an orb illustrate how experimental removal of lines in previous studies has demonstrated that the site where the spider attaches the next loop of sticky spiral ("st. sp.") is affected by both the location of the inner loop of sticky spiral (*a*), and by the distance between the outermost intact loop of the temporary spiral ("tsp.") and the inner loop of sticky spiral (the "TSP distance") (*b*). Non-sticky lines are thin; sticky lines laid before the experiment began are dotted; sticky lines laid after the experimental breakage are thick and solid; s = space between sticky spiral loops; the dotted arrow indicates the direction the spider circled the hub. When a segment of the inner loop of sticky spiral was broken experimentally (*a*) (a "Hingston experiment"), the spider attached the next loop of sticky spiral farther outward on r_n (s_n was less than both s_{n-1} and s_{n+1}). When the TSP distance was increased by removing five segments of the outer loop of the temporary spiral (*b*), the spider attached the sticky spiral farther inward on the radii in the experimental sector (spaces s_n to s_{n+5} were greater than s_{n-1} or s_{n+6}). The spider's response to the experimental temporary spiral breakage decreased gradually as she moved across the experimental zone ($s_{n+5} < s_{n+4} < s_{n+3}$), apparently due to memories of recent encounters with experimentally augmented TSP distances (after Eberhard & Hesselberg 2012).

distance from the hub is smaller (Eberhard 2014). Because the spiders do not come close to the hub while laying sticky spiral (Eberhard 2020), it might be that they sense the distance to the hub indirectly, using stimuli such as tension-dependent variables like vibrations, radius extensibility, or radius tensions themselves. In addition, some previous studies whose results argued against tension-dependent cues being used to influence sticky spiral spacing were of limited scope or had small sample sizes. For instance, one type of evidence was that sticky spiral spacing was not altered in several species when radius tensions were experimentally reduced by cutting them experimentally. These experiments involved only a single web in the uloborids *Uloborus diversus* Marx, 1898 (Eberhard 1972) and *Zosis geniculata* (Olivier, 1789) (Eberhard & Barrantes 2015). The most extensive studies, involving the tetragnathid *Leucauge mariana* (Taczanowski, 1881) and *M. duodedimspinosa*, were limited to only the outermost 1–2 loops of sticky spiral (Eberhard & Hesselberg 2012). Although these studies had the advantage of including data on the distances that the spider moved toward and away from the temporary spiral lines (the "TSP distance" in Fig. 1b), there is reason to think that the stimuli guiding the placement of the outermost loops of orbs probably differ in some respects from those guiding the placement of other loops (Eberhard & Hesselberg 2012; Eberhard 2020).

A further limitation is that the contexts of the tests with the *M. duodecimspinosa* (Eberhard & Hesselberg 2012) were atypical in some respects. The tests compared sticky spiral spacing on cut radii with the spacing on intact radii immediately adjacent to them, where the spider thus experienced relatively large radius tensions that had changed abruptly. Direct measurements of radius tensions in intact orbs indicate that such abrupt changes probably seldom occur in finished orbs (Denny 1976; Wirth & Barth 1992). In addition, abrupt transitions experienced by the spider from tense to lax lines were not distinguished from transitions from lax to tense lines. It is possible that more gradual changes in tension-dependent cues might guide sticky spiral construction in other contexts, such as when the spider spirals inward from the outer portions of the orb and experiences smaller and more gradual changes (Eberhard 2014, 2020). An additional complication is that short-term memories affect sticky spiral spacing (Fig. 1b) (Eberhard 2020), and such memories might buffer the effects of abrupt changes.

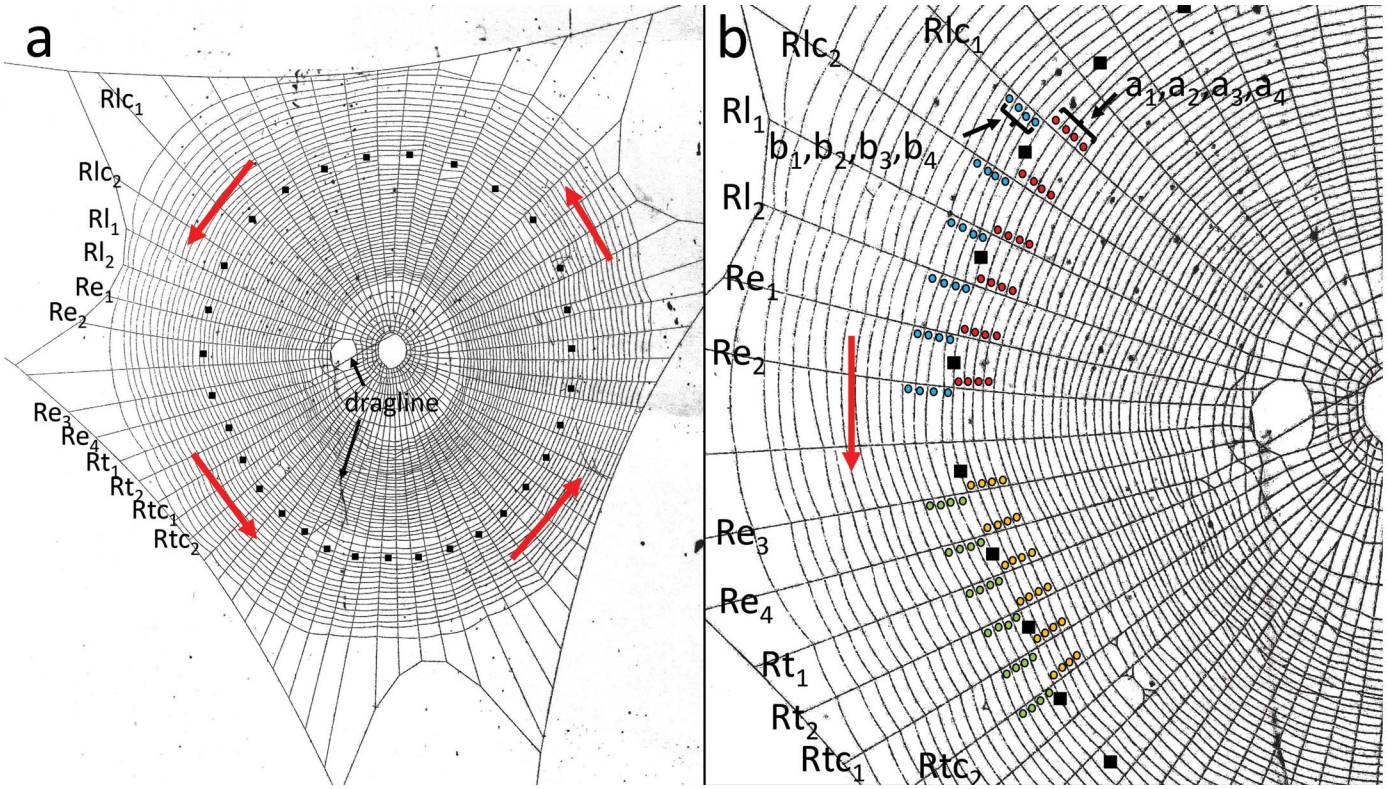

Figure 2.—(a) In Experiment 1 several adjacent radii (N = 5 in this web) were cut near the hub while the spider was building the sticky spiral (the direction the spider was circling the web is indicated by red arrows). The innermost loop of sticky spiral at the moment the radii were cut is indicated by small black rectangles. The radii on which sticky spiral spacing was measured were the following: Rlc (the leading edge control), Rl (the leading edge), Re_1 and Re_2 (the first two experimental radii), R_3 and Re_4 (the last two experimental radii encountered), Rt (the trailing edge), and Rtc (the trailing edge control). The spaces between loops of sticky spiral that were measured are indicated in (*b*). Blue and green dots indicate spaces between loops built immediately before the radii were cut ($b_1 - b_4$); red and orange dots indicate spaces built immediately after ($a_1 - a_4$). The blue and red dots are on the leading side of the experimental zone, while the green and orange dots are on the trailing side. The expected changes in tensions that were experienced by the spider after the radii were cut are the following: Rlc tensions were little modified; Rl tensions were somewhat increased; Re tensions were sharply reduced; Rt tensions were somewhat increased; and Rtc tensions were little affected. The dragline that the spider left when she was removed from the hub in order to photograph the finished web is also labeled in (a).

Further tests of tension-dependent cues are especially important because of the inherent difficulty of proving negative hypotheses, and because ruling out tension-dependent stimuli is necessary to evaluate alternative hypotheses that spiders are guided by other stimuli that do not depend on radius tensions. This study presents additional tests of the conclusion from earlier studies that neither radius tensions nor other cues that depend on radius tensions, such as resonant vibrations, vibration transmission, or radius extensibility, are used to guide sticky spiral spacing. It extends the range of amplitudes and the patterns and contexts of experimental tension modifications, making use of three different experiments in which non-sticky lines in different portions of the web were cut during sticky spiral construction.

Background on orb construction behavior.—Web construction by mature female *M. duodecimspinosa* has been studied intensively (summary in Eberhard 2020). The spider follows the typical sequence seen in other orb weavers: while exploring a potential website, she attaches non-sticky anchor lines to the substrate and builds frame lines and preliminary radii. Then she establishes a hub and builds more radii, adds several tightly spaced spiral hub loops, and builds a widely spaced "temporary" or "auxiliary" spiral while she circles outward from the hub. Finally, starting at the outer edge of the web and slowly circling inward, she builds the sticky spiral, breaking the temporary spiral as she goes (leaving the broken segments of line attached to the radii). To finish, she removes lines in the center of the hub to form a hole. Construction usually occurs in the early morning (about 05:00–09:00), and sticky spiral construction lasts on the order of 30 min. Spiders normally do not turn back while building the sticky spiral, and thus circle the web in either a clockwise or a counter-clockwise direction. Even if the spider is interrupted and moves to the hub, she usually resumes sticky spiral construction circling in the same direction (see Eberhard 2020 for many other behavioral details).

Typical orbs of *M. duodecimspinosa* are relatively symmetrical (Fig. 2a) and more or less vertical (the mean ± standard deviation of the angle of the web plane with horizontal was 74.0 ± 8.6° in 72 webs) (W. Eberhard, unpub.). Webs are built in relatively large open spaces, with the hub far from the substrate; the mean length of the longest frame line was 93 ± 34 cm, and the mean ratio of the longest frame line to the shortest radius was 11.1 ± 4.6 in 71 webs (W. Eberhard, unpub.). Most orbs have only three long, primary frame lines (mean = 3.03 ± 0.17 primary frames in 69 webs) (Figs. 2, 3). The mean space between

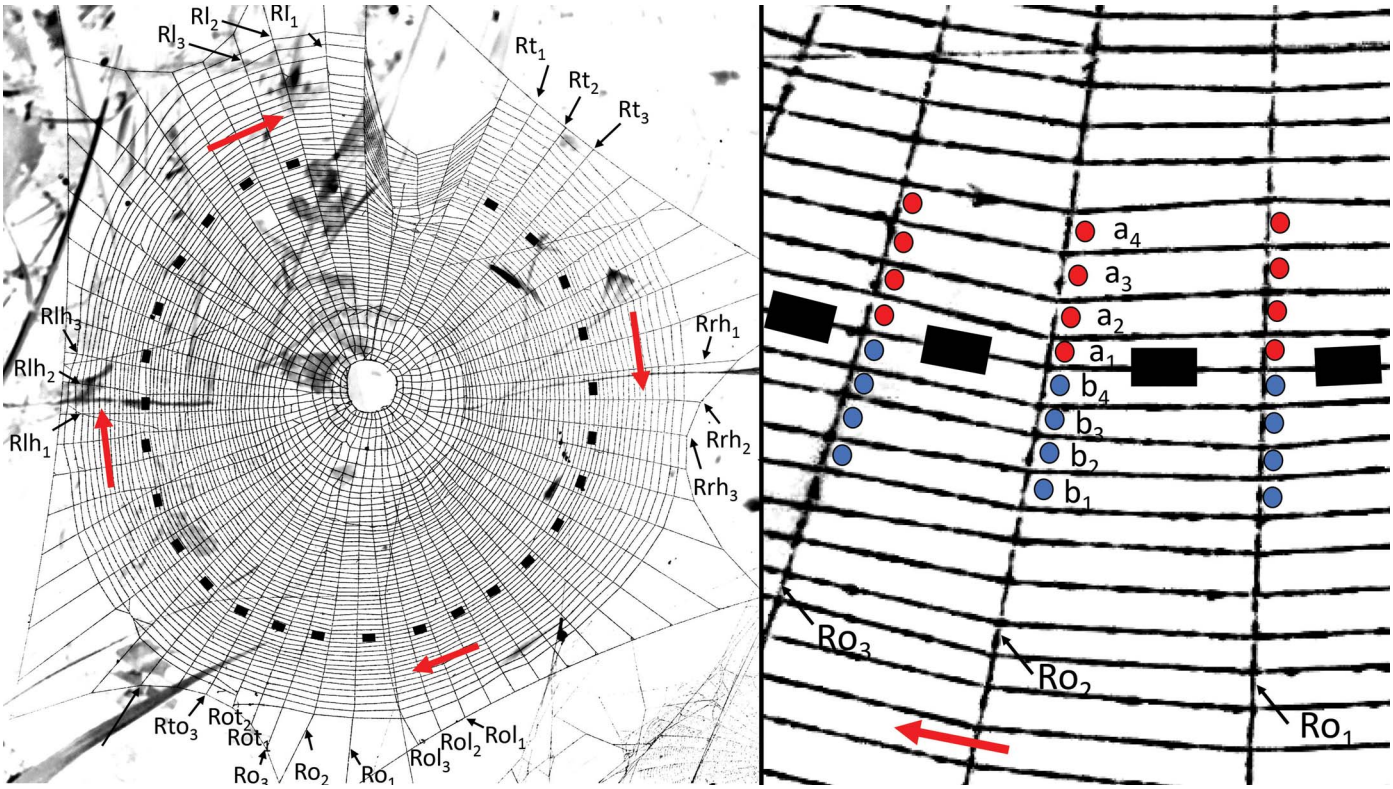

Figure 3.—(*a*) In Experiment 2, several radii were cut near their distal ends where they were attached to the frame line while the spider was building sticky spiral. The innermost loop of sticky spiral at the moment when the radii were cut is marked with black rectangles, and the direction that the spider was moving is indicated with red arrows. The spaces between loops of sticky spiral just before and just after the cuts were made were measured on six sets of radii: the three radii that the spider encountered just prior to encountering the sector that included the radii that were cut and the two bordering radii on the leading side – (Rl); the three radii encountered just after on the trailing side (Rt); the three radii most nearly opposite the cut radii (Ro); the three radii on the leading (Rol) and the trailing sides (Rot) of the Ro radii; the three most nearly horizontal radii on both the left (Rlh) and right (Rrh) side of the orb. The expected tension changes on radii that were encountered by the spider after the experimental cuts were the following: moderate reductions on Ro radii; more moderate reductions on Rol and Rot radii; moderate increases on Rl radii; more abrupt increases on Rt radii; and little if any change on Rlr or Rlh radii. (*b*) On each of the six sets of radii, I measured the four spaces between the loops laid just before the radii were cut (b_1 – b_4, blue circles) and the four spaces between loops laid just after the cuts (a_1 – a_4, red circles).

loops of sticky spiral is greater above the hub than below it (Eberhard 2014), and sticky spiral spacing decreases gradually from the edge of the web to the hub (Eberhard 2014, 2020).

Two tactile cues, the location of the inner loop of sticky spiral already in place, and the "TSP distance" (the distance between the inner loop of sticky spiral and the outer loop of temporary spiral; Fig. 1) influence selection of the site where the sticky spiral is attached to each radius that it crosses (Fig. 1) (Eberhard & Hesselberg 2012). At least the first of these cues is apparently also used by many other orb weavers (Eberhard 1982, 2020; Kuntner et al. 2008; Eberhard & Barrantes 2015).

METHODS

I observed mature female *M. duodecimspinosa* in the field between 05:30 and 09:00 in early second growth near San Antonio de Escazu, San José Province, Costa Rica (9° 53′ 51.41″ N, 84° 08′ 15.99″ W, el. 1325 m) in July–October (wet season) over three years. Spiders were not marked, but I searched for spiders at different places on different days; probably most (and perhaps all) the spiders in any given experiment were observed only once. The spider was usually only slightly disturbed when I cut lines with fine iridectomy scissors; she paused for a few seconds (up to about a minute) and then resuming sticky spiral construction. In a few cases, she went to the hub for 0.5–10 min and then resumed sticky spiral construction; in no case did she re-initiate the sticky spiral in the experimental zone where lines had been cut.

I used field notes, photographs of spiders building, and photographs of webs to determine the direction in which the spider was circling the web (clockwise or counter-clockwise) and the number of loops that were already in place when I made the experimental cuts. I thus distinguished the order in which the spider encountered different radii before and after the experimental cuts (e.g., Fig. 2). After the spider finished building the orb, I removed her from the hub, coated the web lightly with white powder, photographed it, and then returned her to her web. I used these photos and ImageJn1.50i software (W. Rasband, online at https://imagej.net/ij) to make precise measurements of the distances between the attachments of adjacent loops of sticky spiral on each radius. In a test in which I measured the same eight spaces ten times in each of five different webs, the mean coefficient of variation for the 40 distances was 2.4 ± 1.1%. I did not measure radius tensions directly; the probable effects of the experimental web alterations on the relative radius tensions that were experienced by

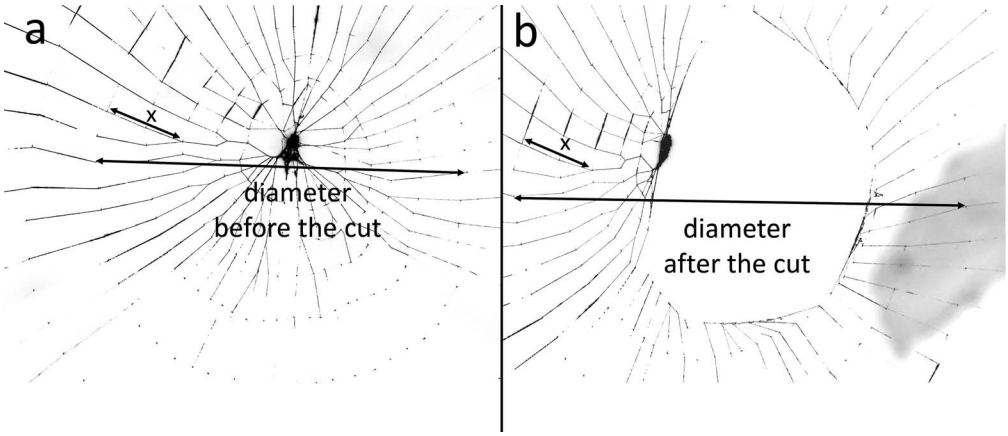

Figure 4.—Photos of a hub just before (*a*) and just after (*b*) lines in the center of the hub were cut in Experiment 3 (the lines are less distinct than in other figures because the web was not coated with powder).

spiders are discussed in the "Limitations of the experiments" section of the Discussion.

Experiment 1: cut radii near the hub to produce both abrupt and gradual changes in radius tension.—I cut four or five adjacent, more or less horizontal radii near the hub while the spider was building sticky spiral on the opposite side of the web. The cut radii formed an "experimental sector" in which radial tensions were sharply lowered (Re_1–Re_4 in Fig. 2). The position of this sector of the orb was generally slightly below the hub (its center averaged 12° below horizontal, and ranged from 7° above to 30° below horizontal (Fig. 2). The tensions were raised somewhat on the intact radii bordering the experimental zone on both the leading radii (those encountered by the spider just before entering the experimental zone; Rl_1 and Rl_2 in Fig. 2) and on the trailing radii (those encountered just after leaving the experimental zone; Rt_1 and Rt_2 in Fig. 2). These tension changes were expected because some of the tension that had been on the radii that were cut (exerted by the lines on the opposite side of the web) was taken up by these intact radii bordering the experimental zone. The tensions were less modified on the leading control radii (Rlc_1 and Rlc_2 in Fig. 2) that just preceded the Rl radii, and on the trailing control radii (Rtc_1 and Rtc_2 in Fig. 2) that followed the Rt radii.

The spider thus experienced the following sequence of experimentally modified radius tensions compared with loops laid just prior to the experimental cuts as she built each loop of sticky spiral: a moderate increase over the previous tensions on Rl_1 and Rl_2 when she arrived at the leading edge of the experimental zone; a sharp decrease from the previous tensions on Re_1 – Re_4 when she entered the experimental zone; and a slight increase over the previous tensions on Rt_1 and Rt_2 at the trailing edge as she left the experimental zone. On all of these radii (from Rlc_1 to Rtc_2) I measured the four "control" spaces between loops of sticky spiral built immediately before the experimental cut ($b_1 - b_4$ in Fig. 2b), and the four "experimental" spaces immediately after the cut ($a_1 - a_4$ in Fig. 2b).

Experiment 2: cut radii near the frame to produce more gradual, less pronounced changes in radius tensions on the opposite side of the web.—I cut three or four adjacent radii near the frame (Fig. 3) while the spider was laying sticky spiral elsewhere in the web. These cuts created experimental zones in which tensions were lowered moderately on the radii opposite the cut radii ("Ro" in Fig. 3). Because of the complex network of hub lines between these radii and the cut radii, these tension changes in the experimental zone were expected to be of lower magnitudes and less abrupt than the tension changes produced in Experiment 1. In addition, the radii on both the leading and the trailing side (Rl and Rt in Fig. 3a) of the experimental zone were increased.

I measured the spaces between the four loops of sticky spiral that were built just before the radii were cut ($b_1 - b_4$ in Fig. 3b), and the four loops laid just after the experimental cuts ($a_1 - a_4$ in Fig. 3b). I measured these spaces on five sets of radii: the three radii most nearly opposite the cut radii (Ro_1–Ro_3 in Fig. 3a); the three radii on the leading side of the experimental zone (Rl_1–Rl_3); the three radii on the trailing side (Rt_1 - Rt_3); and (as controls) the three most nearly horizontal radii on the right and the left side of the orb (Rrh_1–Rrh_3 and Rlh_1–Rlh_3 respectively). I was unable to measure a few spaces because radius-sticky spiral intersections were not distinguishable due to lack of contrast with the background. I did not measure the sticky spiral spacing on the lax radii that had been cut or on the radii on either side because the inner loop of sticky spiral on the lax radii sagged inward dramatically (Fig. 3a), and inward deflections of the location of the inner loop are known to induce substantial changes in sticky spiral spacing (Eberhard 2020).

Experiment 3: cut lines in the center of the hub to produce small, less localized reductions in radius tensions.—I cut the lines in the center of the hub while the spider was building the sticky spiral, causing the hub to expand (Fig. 4). The radii remained interconnected by the hub spiral and the temporary spiral, so these cuts were expected to produce reductions in radius tensions (probably greater on some radii than on others) that had a more uniform, general pattern than the sharper local differences in Experiment 1. On all radii, I measured the "control" spaces between the four loops that the spider had laid immediately before I made the cuts ($b_1 - b_4$ in Fig. 5), and the "experimental" spaces between the next four loops that she laid immediately after the cuts ($a_1 - a_4$ in Fig. 5).

Analyses.—"Within-web" analyses used the signs (positive, negative) of changes in sticky spiral spacing in the same web, regardless of their magnitudes. This was perhaps the most powerful strategy because it held constant several "settings" variables that are known to influence orb web designs (e.g., individual

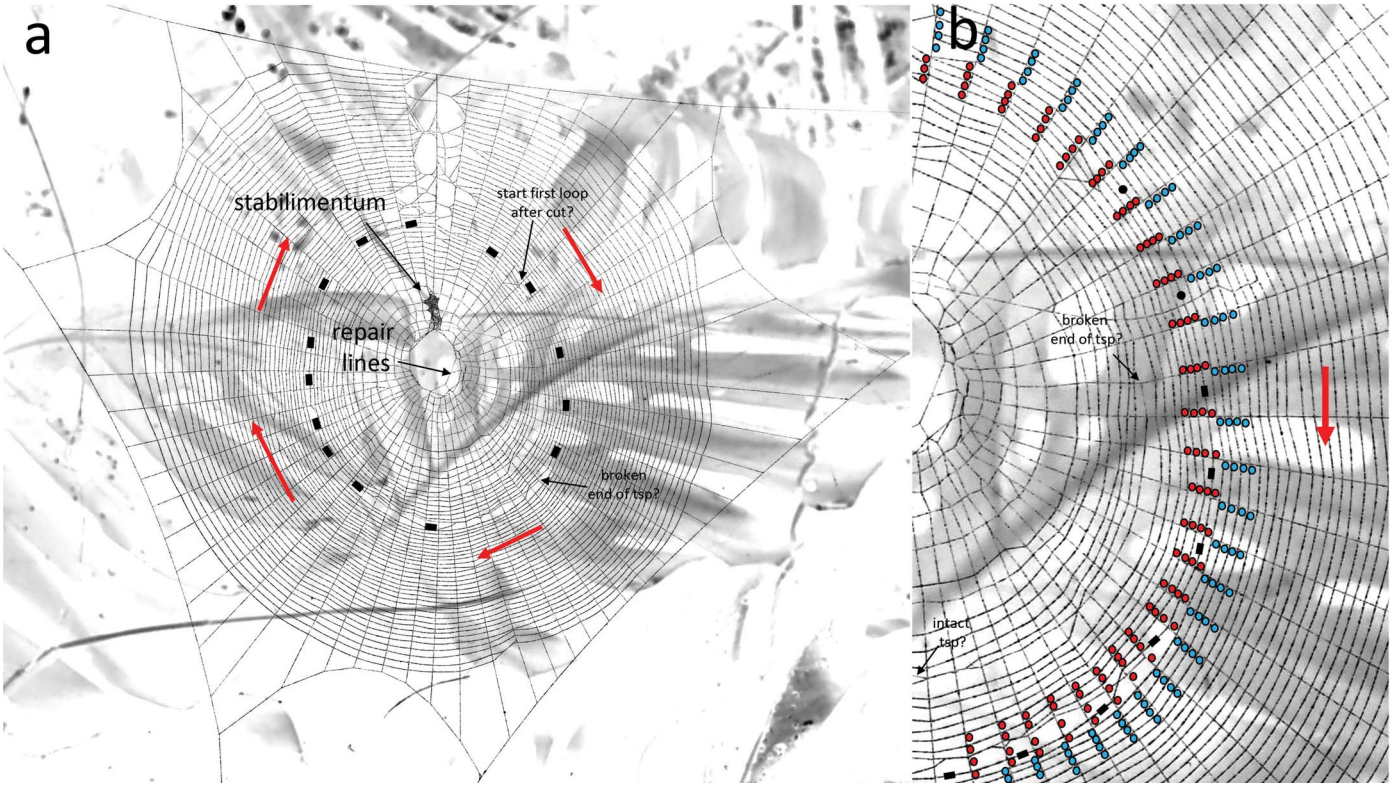

Figure 5.—In Experiment 3, lines in the center of the hub were cut while the spider was building the sticky spiral. The red arrows indicate direction in which the spider was moving, and the black rectangles indicate the inner loop of sticky spiral present when the cuts were made. This spider moved to the hub, added a few repair lines at its inner edge, built a stabilimentum, and then finished the sticky spiral (*a*). The spaces between the four loops of sticky spiral laid just before (blue circles) and just after the cut (red circles) (*b*) were measured on all radii.

identity, size, weight, recent feeding history, silk supply, history of webs at this site, web slant, other possible website variables) (Eberhard 2020). The within-web analyses were especially useful in Experiments 1 and 3, which had large within-web samples. They had the additional advantage of avoiding several suppositions: that the effects of tension were unidirectional: that larger changes in relative tensions would necessarily result in larger changes in sticky spiral spacing; and that, if increased tension was associated with one type of change in spacing (for instance, if it was associated with increased spacing), that a decrease in tension would be associated with the opposite type of change in spacing (e.g., decreased spacing).

Additional, "combined-web" analyses used the magnitudes of the spaces between loops of sticky spiral from multiple webs after the measurements were standardized by dividing by the median spacing in each web, as described by Eberhard & Hesselberg (2012). The response variables in these multi-web analyses included both the magnitudes of the spaces, and the relative magnitudes of changes in spacing on particular radii with respect to the magnitudes of changes in spaces on other radii in the same web whose tensions had been altered in different ways. In some cases, I compared the spaces between loops on the same radius that were laid immediately before and immediately after the experimental cuts. Comparing before and after values had the advantage of maintaining constant several variables associated with the radius, such as its length and angle with vertical. It had, however, the disadvantage that spacing in unmodified webs of *M. duodecimspinosa* gradually deceases in loops nearer the hub (Eberhard 2014). I attempted to deal with this "edge-to-hub" problem by comparing the before and after ratios between nearby spaces (e.g., $(b_3 + b_4)/(a_1 + a_2)$ in Fig. 2) on the same radii. In other cases, I compared the spacing of loops laid after the cuts were made, using radii whose tensions had been modified in different ways by the experimental cuts but that were close to each other in the web. This tactic reduced the edge-to-hub problem, but failed to maintain constant other radius traits such as length and angle with vertical.

I also performed analyses that attempted to account for possible effects of the spider's memory of recent stimuli on her responses to new stimuli. Such memory effects sometimes manifest themselves as slow decays in responses to repeated presentations of stimuli (as in the gradual reduction in the response to an increased "TSP distance" in Fig. 1b), or as slow increases in responses to repeated presentations. I tested for such modulated responses by checking for changes in the spacing on sequential radii in the order in which the spider encountered modified radial tensions. The effectiveness of this test was limited, however, by the possibility that gradual changes in memory might coincide with changes in the strength of the effect of the cut lines.

All tests of statistical significance used the program PAST4.11 (online at https://apps.apple.com/us/app/past4/id1584582394?mt=12). Some variables had non-normal distributions; their means and standard deviations are reported for illustrative purposes only. I used non-parametric tests in order to reduce assumptions regarding the distribution and variance of the data. I used two-tailed Chi^2 Tests (all with df = 1) and Mann-Whitney

Table 1.—Within-web comparisons in the 31 webs in Experiment 1 of the numbers of times in which the medians of sticky spiral spacing increased or decreased when the spider encountered radii with different experimentally modified tensions as she moved across the experimental sector (**Re** in Fig. 2) (labels of radii and spaces are as in Fig. 2). Chi^2 Tests of differences from 50-50 distributions were used to evaluate statistical significance.

Changes in tension differences that the spider experienced on adjacent pairs of radii	Relatively moderate increase in relative tension	Relatively large decrease in relative tension	Equal tensions (lax)	Relatively large increase in relative tension	Relatively slight decrease in relative tension
Comparisons of means of sticky spiral spacing on pairs of radii	$Rlc_{1,2} > Rll_{1,2}$? Yes; No	$Rll_{1,2} > Re_{1,2}$? Yes; No	$Re_{1,2} > Re_{3,4}$? Yes; No	$Re_{3,4} > Rt_{1,2}$? Yes; No	$Rt_{1,2} > Rtc_{1,2}$? Yes; No
Space a_1	14; 17 (NS)	19; 12 (NS)	13; 16 (NS)	14; 15 (NS)	12; 17 (NS)
Space a_2	23; 8 ($P < 0.01$))	14; 14 (NS)	15; 13 (NS)	18; 11 (NS)	13; 16 (NS)
Space a_3	16; 15 (NS)	15; 16 (NS)	12; 16 (NS)	17; 12 (NS)	11; 18 (NS)
Space a_4	16; 15 (NS)	18; 13 (NS)	12; 17 (NS)	15; 13 (NS)	11; 17 (NS)

U Tests (for which I report *z* and *P* values). Differences were judged to be significant when $p < 0.05$. Relatively simple statistical analyses were emphasized rather than more synthetic, general tests such as generalized linear models (Nelder & Wedderburn 1972), because the structure of the experiments: a few types of web manipulation were used to produce multiple patterns of modifications of tensions in different lines. Each pattern of tension changes could have possibly resulted in a different, independent response by the spider. The independent tests also avoided the possibly inappropriate supposition of linear rather than curvilinear responses that is made in some combinatorial tests such as linear models.

Sample sizes varied because a few spaces could not be measured precisely in the photos. "Outward" (or "beyond" or "outside") and "inward" (or "inside") indicate legs or leg movements that were oriented away from or toward the hub respectively.

Voucher specimens were kindly identified by the late H. W. Levi and are deposited in the Museum of Comparative Zoology at Harvard University, Cambridge, MA. Numbers that accompany species names refer to labels included with specimens in this same collection.

RESULTS

Experiment 1 – cut radii near the hub (Fig. 2).—Within-web comparisons in 31 webs showed no clear pattern of changes in the spaces between the sticky spiral loops attached to radii just before compared with just after the experimental cuts had produced tension changes (b_1 to b_4 compared with a_1 to a_4 in Table 1). Only one of twenty comparisons was statistically significant, a decrease in the second space (a_2) on a pair of radii in which the cuts had produced tensions that were moderately increased over their previous values in the intact web (Rlc_1 and Rlc_2 compared with Rl_1 and Rl_2); but comparisons of the other spaces that immediately preceded and followed on these same radii (a_1, a_3, and a_4 on Rlc_1, Rlc_2, Rl_1 and Rl_2) showed no significant differences.

Additional analyses that combined standardized data from all 31 webs also failed to show consistent significant effects of the experimental radius cuts despite substantial variation (Table 2) (the coefficients of variation of the means of spaces ranged from 18% to 32%). There were no significant differences in the spacing when the four loops of sticky spiral ($a_1 - a_4$) were combined on adjacent pairs of radii that suffered similar changes in tensions and then compared with spaces on the preceding adjacent pair of radii whose tensions had been modified in a different way (Table 2B), except for a small decrease in spacing on radii Rt. Control spacing between the loops that were attached to these same radii just prior to the experimental cuts (Table 2B; spaces b_1 to b_4) showed a similar pattern of lack of differences except for Rt, which had increased spacing. This increase in the previous spacing on Rt may have caused the reduction in the subsequent experimental spacing ($a_1 - a_4$), as there is an inverse relation between previous and subsequent spaces between sticky spiral lines in this species (Eberhard & Hesselberg 2012).

In order to hold variables such as the length of the radius and its angle with vertical constant in the comparisons and to reduce the "edge-to-hub" effect, I calculated for each radius the ratio of the sum of the two spaces between the loops laid just before and just after the cut (b3 + b4)/(a1 + a2); I then combined these ratios for pairs of adjacent radii that had suffered similar relative tension changes (Rlc1 and Rlc2; Rl1and Rl2; Re1 and Re2, Re3 and Re4; Rt1 and Rt2; and Rtc1 and Rtc2) (Table 2C). Only the ratio on Rt differed significantly from the ratio on the preceding pair of radii (Table 2C). This change was in the opposite direction of three of the four other (all non-significant) differences in intra-web comparisons (Table 1). Hand-over-Spacing was significantly smaller on most of the radii when the four sticky spiral spaces immediately prior to the cut were compared with the four spaces immediately after the cut (($b_1 + b_2 + b_3 + b_4$) vs. ($a_1 + a_2 + a_3 + a_4$)) on each pair of radii. These changes, however, occurred on nearly all, regardless of relative tension changes ($P < 0.001$ for all but $Re_{3,4}$). They resembled the "edge-to-hub" pattern typical of unmodified orbs in this species (Eberhard 2014) and thus cannot be confidently attributed to the experimental tension changes.

Additional radius-by-radius analyses (Table 3) also failed to reveal differences associated with experimental changes in radius tensions. When all values following the cut ($a_1 - a_4$) were combined in each of the 31 webs, there was no case in which the spacing changed significantly when pairs of adjacent radii with and without relative tension modifications were compared (column B in Table 3). The change between last two loops before ($b_3 + b_4$) and the first two loops after ($a_1 + a_2$), quantified as ($b_3 + b_4$)/($a_1 + a_2$), also failed to show any significant differences between adjacent radii whose tensions had been modified in different ways (column D in Table 3).

I performed further tests on the combined standardized data (Table 4) to test the possibility that the spider's responses to the abrupt changes in tensions produced by the experimental cuts were buffered by memories of stimuli that she had perceived on

Table 2.—Analyses combining data from different webs in Experiment 1, using the means and medians of the standardized spaces between loops of sticky spiral on pairs of adjacent radii whose tensions were modified in different ways when the radii were cut. The pairs of radii are presented in the order in which the spider encountered them (see Fig. 2) along with the tension changes produced when the radii were cut. A) The four spaces between loops built immediately after radii were cut ($a_1 - a_4$) did not differ significantly on sequential pairs of radii. B) The four spaces between the loops built immediately before the radii were cut also did not differ significantly except when comparing Re_3 and Re_4 with Rt_1 and Rt_2. C) The change in the ratio of before/after was significant (only barely) in only one comparison, between the same pair of radii that differed before the cut. D) The four spaces on most of the radii decreased significantly after the cut, showing the typical "edge-to-hub" reduction in spacing nearer the hub in the intact webs of this species (Eberhard 2014).

A. Spaces $a_1 - a_4$ after cuts						
Experimentally induced changes in the tensions on pairs of radii that the spider experienced as she moved from one pair of radii to the next	Rlc_1, Rlc_2 little or no change	Rl_1, Rl_2 moderate increase in relative tension	Re_1, Re_2 sharp decrease in relative tension	Re_3, Re_4 little or no change (both pairs are lax)	Rt_1, Rt_2 sharp increase in relative tension	Rtc_1, Rtc_2 moderate decrease in relative tension
Mean of median space (a_1 to a_4)	0.96 ± .19	0.94 ± .20	0.92 ± .18	0.96 ± .20	0.94 ± .32	0.97 ± .27
Compare median spaces with those on the preceding pair of radii (Student's t, *P*)		No change (0.98, 0.33)	No change (0.21, 0.84)	No change (1.66, 0.10)	No change (0.90, 0.37)	No change (1.47, 0.14)
N	310	310	305	290	289	279
B. Spaces before cuts ($b_1 - b_4$) (controls)						
Mean of median space (b_1 to b_4)	1.03 ± .21	1.02 ± .20	1.00 ± .18	1.00 ± .18	1.04 ± .16	1.05 ± .18
Compare means of median spaces with those on the preceding pair of radii (Student's t, *P*)		No change (0.46, 0.64)	No change (1.19, 0.24)	No change (0.13, 0.90)	Increased (3.00, 0.003)	No change (0.54, 0.59)
C. Compare ratio just before cut/just after cut (mean of $b_3 + b_4/a_1 + a_2$) with that on preceding pair of radii (Student's t, *P*)	1.05 ± .21	1.02 ± .17 No change(0.47, 0.64)	1.04 ± .10 No change (0.44, 0.66)	0.96 ± .17 No change (1.77, 0.08)	1.06 ± .19 Increased(2.05, 0.045)	1.06 ± .18 No change (0.05, 0.96)
D. Compare spaces on same pair of radii before vs. after experimental cuts (b_1 to b_4 vs. a_1 to a_4 (the "edge-to-hub" pattern) (Student's t, *P*)	Decreased (4.54, <0.001)	Decreased (5.20, <0.001)	Decreased (3.89, <0.001)	No change (1.22, 0.22)	Decreased (3.95, <0.001)	Decreased (3.39, <0.001)

Table 3.—Two types of comparisons of standardized spacing on adjacent radii in Expt. 1, at the leading and the trailing edges where modifications of tensions were relatively large. Column A presents the standardized spaces between the four loops built on each radius immediately after the radii were cut (a_1, a_2, a_3, and a_4 in Fig. 2); column B tests the statistical significance of differences in the spacing on adjacent radii. Column C presents the change in spacing on each radius comparing the two spaces before and the two spaces after ($(b_4 + b_5)/(a_1 + a_2)$); column D tests the statistical significance of the differences between adjacent radii in column C. Means are followed by ± one standard deviation. Each comparison in column B and D is with the space on the previous radius; the values are Student's t, followed by the corresponding probability that the means are equal.

Radius	A. Mean space for $a_1 - a_4$	B. Compare with mean space on previous radius (Student's t, *P*)	C. Mean $(b_4+b_5)/(a_1+a_2)$	D. Compare with ratio on previous radius (Student's t, *P*)
Leading side				
Rlc_1	0.98 ± 0.22		1.07 ± 0.25	
Rlc_2	0.98 ± 0.17	0.07, 0.95	1.03 ± 0.22	0.55, 0.58
Rl_1	0.99 ± 0.21	0.45, 0.65	1.01 ± 0.19	0.45, 0.66
Rl_2	0.95 ± 0.20	1.49, 0.14	1.04 ± 0.20	0.67, 0.50
Re_1	0.95 ± 0.17	0.095, 0.92	1.06 ± 0.18	0.44, 0.66
Re_2	0.97 ± 0.20	0.80, 0.42	1.03 ± 0.24	0.77, 0.44
Trailing side				
Re_3	0.99 ± 0.19		1.04 ± 0.40	
Re_4	1.00 ± 0.24	0.13, 0.89	0.96 ± 0.21	0.87, 0.39
Rt_1	0.90 ± 0.34	0.87, 0.39	1.09 ± 0.32	1.84, 0.07
Rt_2	0.97 ± 0.36	0.22, 0.82	1.10 ± 0.27	0.07, 0.95
Rtc_1	0.99 ± 0.30	0.44, 0.66	1.14 ± 0.53	0.27, 0.79
Rtc_2	1.03 ± 0.28	0.93, 0.36	1.11 ± 0.41	0.27, 0.79

immediately preceding radii (see Fig. 1b). At the transition where the cuts produced a radius such as Rl_2 with a small increase in tension followed by a radius with an abrupt decrease in tension (Re_1), I tested two differences: Re_1 compared with Re_2, Re_3, and Re_4 combined; and $Re_1 + Re_2$ compared with $Re_3 + Re_4$ (Table 3A). I made a similar set of comparisons at the transition where an abrupt decrease (Re_4) was followed by a small increase (Rt_1) (Table 3B). Memory effects of the sort in Fig. 1b would predict that in these cases the spacing on the first radius that the spider encountered at the transition would differ from the spacing on subsequent, similarly modified radii. Table 4 presents the results of analyses of the sizes of the spaces (A1, A2, B1, B2), and of the ratios of spaces on the same radius just before and just after the experimental cuts $(b_3 + b_4)/(a_1 + a_2)$ (Table 4A3, B3) on successive radii. In none of the 28 comparisons was the difference significant. These results suggest that buffering effects of memory did not occur.

Experiment 2 – cut radii near the frame (Fig. 3).—In the 11 experimental webs, I used as "controls" the sticky spiral spacing on the six horizontal radii (Rh), whose tensions were probably little affected by the experimental cuts, to check for possible changes in spacing induced by the cuts. I compared the controls with the following: Ro (radii that experienced a moderate reduction of tensions produced by the cuts); Rl (radii that experienced a slight increase in tensions); Rt (radii that experienced a slight increase in tensions) (this resulted in a sharper modification for the spider, from moderately lowered to slightly increased tensions); and both Rl and Rt combined (in both types of radii the tensions were increased experimentally) in order to increase the sample size for radii with experimentally increased tensions.

Ro (tension moderately reduced) vs. Rh.—In within-web comparisons, I compared the numbers of cases in which the spacing of the first loop that the spider attached to the relaxed radius (Ro in Fig. 3b) increased or decreased when compared with the space immediately preceding the experimental cuts (that is, space b_4 compared with space a_1 on the same radius), as compared with the corresponding numbers for the spaces between the same loops on the control, horizontal radii (Rh radii in Fig. 3a). There were 18 increases and 15 decreases on three Ro radii, and 38 increases and 28 decreases on the six Rh radii; this difference was not significant ($Chi^2 = 0.08$, $P = 0.77$). In a similar analysis that combined the two spaces just prior to the cut ($b_3 + b_4$) and compared them with the two spaces immediately following the cut ($a_1 + a_2$), the spaces on Ro radii prior to the cut were larger on 18 radii and smaller on 14 others; the respective numbers for Rh radii were 31 and 34 ($Chi^2 = 0.63$, $P = 0.43$).

Tests using the mean values of standardized data combined from the different webs also failed to reveal differences produced by the experimental cuts. The mean of the median value of b_4/a_1 for Ro radii (0.97) did not differ significantly for the corresponding value (0.94) for Rh radii ($z = 0.26$, $P = 0.79$). Similarly, the mean of the medians of the sum of the last two spaces before ($b_3 + b_4$) divided by the sum of the first two spaces after the cut ($a_1 + a_2$) did not differ significantly between Ro radii (0.99) and Rh radii (0.98) ($z = 0.65$, $P = 0.51$).

Rl (tension slightly increased) vs. Rh.—In within-web comparisons of the spacing on Rl radii with that on Rh radii, the numbers of Rh radii on which the spaces increased or decreased immediately following the cuts (space b_4 compared with space a_1 in Fig. 3) were 18 and 14. The corresponding numbers on Rh radii were 38 and 28; the difference between the radii was not significant ($Chi^2 = 0.15$, $P = 0.90$). Similarly, $b_3 + b_4$ was larger than $a_1 + a_2$ on 18 Rl radii, and smaller on 14 others. The corresponding numbers for Rh radii were 31 and 34 ($Chi^2 = 0.63$, $P = 0.43$).

Tests that employed mean values of standardized data combined from the different webs also failed to show an effect of altered radius tensions. The mean values of b_4/a_1 in Rl and Rh radii in all webs were, respectively, 1.04 and 1.03 ($z = 0.1.03$, $P = 0.30$). Comparing the means of the medians of pairs of spaces

Table 4.—Tests for the possibility of memory effects in Experiment 1 in which short-term memories mask the spider's first response to abrupt decreases and increases in modified radius tensions (as in Fig. 1b). Standardized spaces produced immediately following radius cuts are compared with the subsequent spaces on which the modifications of radius tension were similar. Each statistical test compares the mean standardized space with that on the following line of the table.

	Radius	Mean ± std. Deviation	Student's *t*	*P*
	A. A relatively abrupt decrease in tension			
A1. Spaces				
a_1	Re_1	0.93 ± 0.12	1.38	0.17
	$((Re_2 + Re_3 + Re_4)/3)$	1.00 ± 0.27		
	$(Re_1 + Re_2)/2$	0.94 ± 0.12	1.22	0.23
	$(Re_3 + Re_4)/2$	1.01 ± 0.28		
a_2	Re_1	0.99 ± 0.17	0.36	0.72
	$(Re_2 + Re_3 + Re_4)/3)$	1.00 ± 0.17		
	$(Re_1 + Re_2)/2$	0.98 ± 0.15	0.94	0.35
	$(Re_3 + Re_4)/2$	1.02 ± 0.12		
a_3	Re_1	0.99 ± 0.19	0.06	0.95
	$((Re_2 + Re_3 + Re_4)/3)$	0.99 ± 0.21		
	$(Re_1 + Re_2)/2$	0.99 ± 0.18	0.15	0.88
	$(Re_3 + Re_4)/2$	1.00 ± 0.20		
a_4	Re_1	0.91 ± 0.17	1.29	0.20
	$((Re_2 + Re_3 + Re_4)/3)$	0.96 ± 0.18		
	$(Re_1 + Re_2)/2$	0.93 ± 0.18	0.84	0.40
	$(Re_3 + Re_4)/2$	0.96 ± 0.12		
A2. Spaces a_1 to a_4 combined	Re_1	0.95 ± 0.17	1.47	0.14
	$(Re_2 + Re_3 + Re_4)/3$	0.98 ± 0.16		
	$(Re_1 + Re_2)/2$	0.97 ± 0.34	0.71	0.48
	$(Re_3 + Re_4)/2$	0.99 ± 0.19		
	$(Rt_1 + Rt_2)/2$	0.97 ± 0.34	1.08	0.28
	$(Rtc_1 + Rtc_2)/2$	1.01 ± 0.25		
A3. Ratio $(b_3 + b_4)/(a_1 + a_2)$	Re_1	1.06 ± 0.18	1.75	0.09
	$((Re_2 + Re_3 + Re_4)/3)$	0.98 ± 0.17		
	$(Re_1 + Re_2)/2$	1.06 ± 0.35	0.53	0.60
	$(Re_3 + Re_4)/2$	1.03 ± 0.34		
	B. A relatively abrupt increase in tension			
B1. Spaces				
a_1	Rt_1	1.06 ± 0.59	0.014	0.99
	$(Rt_2 + Rtc_1 + Rtc_2)/3$	1.06 ± 0.47		
	$(Rt_1 + Rt_2)/2$	1.06 ± 0.63	0.04	0.97
	$(Rtc_1 + Rtc_2)/2$	1.06 ± 0.39		
a_2	Rt_1	0.93 ± 0.13	1.59	0.12
	$(Rt_2 + Rtc_1 + Rtc_2)/3$	0.98 ± 0.10		
	$(Rt_1 + Rt_2)/2$	0.93 ± 0.13	1.62	0.11
	$(Rtc_1 + Rtc_2)/2$	.99 ± 0.13		
a_3	Rt_1	0.92 ± 0.26	0.95	0.35
	$(Rt_2 + Rtc_1 + Rtc_2)/3$	0.97 ± 0.18		
	$(Rt_1 + Rt_2)/2$	0.92 ± 0.18	1.29	0.20
	$(Rtc_1 + Rtc_2)/2$	1.00 ± 0.22		
a_4	Rt_1	0.94 ± 0.14	0.54	0.59
	$(Rt_2 + Rtc_1 + Rtc_2)/3$	0.96 ± 0.18		
	$(Rt_1 + Rt_2)/2$	0.93 ± 0.13	1.39	0.17
	$(Rtc_1 + Rtc_2)/2$	0.99 ± 0.21		
B2. Spaces $a_1 - a_4$ combined	Rt_1	0.90 ± 0.36	0.22	0.82
	Rt_2	0.97 ± 0.36		
	Rtc_1	0.99 ± 0.30	0.44	0.66
	Rtc_2	1.03 ± 0.28		
B3. Ratio $(b_3 + b_4)/(a_1 + a_2)$	Rt_1	1.09 ± 0.32	0.07	0.95
	Rt_2	1.10 ± 0.27		
	Rt_2	1.10 ± 0.27	0.40	0.64
	Rtc_1	1.14 ± 0.53		
	Rtc_1	1.14 ± 0.53	0.25	0.80
	Rtc_2	1.11 ± 0.41		
	Rt_1	1.09 ± 0.32	0.06	0.95
	$(Rt_2 + Rtc_1 + Rtc_2)/3$	1.10 ± 0.41		
	$(Rt_1 + Rt_2)/2$	1.11 ± 0.35	0.28	0.78
	$(Rtc_1 + Rtc_2)/2$	1.12 ± 0.47		

before and after the cut (the median of b_3 and b_4 vs. the median of a_1 and a_2) on Rl and Rh yielded the same conclusion: the means of the medians on the two sets of radii were and 1.03 and 1.01 ($z = 0.17$, $P = 0.86$).

Rt (tension slightly increased) vs. Rh.—The spider encountered radii that had experienced moderate increases in tensions when she left the lax, cut radii (Re) and reached the trailing radii (Rt in Fig. 3) that had experienced slightly increased tensions. Within-web comparisons of the changes in sticky spiral spacing on the Rt radii before and after the cuts with those on the control Rh radii showed no significant difference. The number of cases in which the spaces on Rt increased or decreased immediately following the cuts (b_4 compared with a_1) were compared with the comparable numbers for the spaces between the same loops on the six control, horizontal radii (Rh radii). There were 21 increases and 12 decreases on the Rt radii, and 38 and 28 on the Rh radii; the difference is not significant ($Chi^2 = 1.65$, df = 1, $P = 0.20$).

Tests that combined the mean standardized values from all webs led to a similar, though slightly less confident conclusion. The difference between the median b_4/a_1 on Rt radii (0.89) and on the six Rh radii (0.97) was not significant ($z = 1.28$, $P = 0.20$). On combining the pair of spaces just before and the pair of spaces just after the cut, however, the median of $(b_3 + b_4)/(a_1 + a_2)$ on the three Rt radii (0.89) was slightly less than that on the six Rh radii (0.99) ($z = 1.95$, $P = 0.051$). When one more loop before and one more after the cut was included in the comparison $(b_2 + b_3 + b_4)/(a_1 + a_2 + a_3)$, however, the difference disappeared: the mean for the three Rt radii was 0.97 ± .19, and that for the Rh radii was 1.00 ± .14;($z = 0.42$, $P = 0.67$). I conclude that the decrease in spacing after the cut did not differ on Rt compared with Rh radii.

Rl_2 and Rt_1 (both with tension slightly increased) vs. Rh.—Because the spider encountered increased radius tensions at both the leading and trailing edges of the experimental zone, I performed an additional analysis that combined the data for the "adjacent" radii (Rl_2 and Rt_1), thus providing replicates of when spiders experienced an increase in radius tension. The results supported the same conclusion that tension-dependent cues did not influence sticky spiral spacing. In within-web comparisons, the number of cases in which the spaces on Rt_2 and Rl_1 radii increased or decreased immediately following the cuts (space b_4 compared with space a_1 on each) were compared with the corresponding numbers for the spaces between the same loops on the control, horizontal radii (Rh radii). There were 36 increases and 29 decreases on these "adjacent" radii, and 38 and 28 on the Rh radii; this difference was not significant ($Chi^2 = 0.06$, $P = 0.80$).

Tests using mean standardized values combined from different webs led to the same conclusion. The difference between the median on the "adjacent" radii of b_4/a_1 (0.95) and the corresponding median on Rh radii (0.97) was not significant ($z = 0.16$, $P = 0.87$). When the sums of the pair of spaces just before $(b_3 + b_4)$ and the pair of spaces just after the cut $(a_1 + a_2)$ were compared, median of (b3 + b4)/(a1 + a2) on the "adjacent" radii (0.94) and that on Rh radii (0.99) was also not significant ($z = 1.10$, $P = 0.27$). Thus, the Rt–Rh difference noted in the previous section was not repeated when both of the sites where radius tensions had been raised by the experimental cuts were combined.

Summary for Experiment 2.—In sum, when the spaces between sticky spiral loops laid before and after experimental cuts were compared in 11 webs, three different analyses on the three radii most nearly opposite the radii that had been cut near the frame and thus had moderately reduced tensions (Ro_1–Ro_3 in Fig. 3a) showed no significant differences in within-web comparisons, nor did they show consistent significant differences in analyses of standardized data combined from different webs. The slight increases in tensions on the radii bordering the experimental zone (Rl_1 and Rl_2, Rt_1 and Rt_2) also failed to result in consistent changes in sticky spiral spacing.

Experiment 3.—cut lines in the center of the hub (Figs. 4, 5).—When the lines in the center of the hub were cut in 11 webs, the outer edges of the hub and all radii sagged outward. The tensions on all radii were thus reduced, though the magnitudes of the reductions probably varied for different radii. The within-web comparisons in this experiment had the advantage of large numbers of measurements in each web, allowing robust within-web analyses. They also largely eliminated variations in several features that are known to affect sticky spiral spacing, including the orientation of the radius with respect to gravity, the relative distance to the hub, and the spider's silk reserves (Eberhard 2020). They were complicated, however, by the "edge-to-hub" decrease in spacing (mentioned above) that was documented in previous studies of unmanipulated webs of this species (Eberhard 2014). I thus emphasized comparisons between adjacent and nearly adjacent loops in evaluating the effects of the experimental tension reductions.

Within-web analyses of the mean spaces between the four loops laid immediately preceding the experimental cuts and the four loops built immediately following the cuts showed that cutting neither consistently increased or decreased these changes comparing "control" $(b_1 - b_4)$ and "experimental" $(a_1$–$a_4)$ spaces in web-by-web analyses: median spacing decreased immediately following the cut ($b_4 > a_1$) in 64% of 11 webs; this frequency did not differ significantly from corresponding frequencies three similar comparisons prior to the cut ($b_1 > b_2$; $b_2 > b_3$; and $b_3 > b_4$) (67% of 33 comparisons) ($Chi^2 = 0.03$, $P = 0.85$). This lack of difference suggests that the experimental reduction in radius tensions did not affect sticky spiral spacing.

Further analyses in which the standardized data from the eleven webs were combined, using the means of medians (Eberhard & Hesselberg 2012), suggested the same conclusion. There was no significant change when the means of medians of spaces produced just before and just after the cuts were compared: for $(b_3 + b_4)/2$ versus $(a_1 + a_2)/2$, ($z = 0.20$, $P = 0.84$).

I performed an additional analysis of the combined data from the eleven webs to take into account that the tensions the spider experienced as a result of the experimental cut were undoubtedly affected in different ways by her own weight in different parts of the web (Eberhard 2020). For instance, the spider's weight increased the tension on the outer portion of the radius and decreased that on the inner portion while she was above the hub; in contrast, her weight had the opposite effect while she was on radii below the hub, increasing the tension on the inner portion and decreasing that on the outer portion (see below for further discussion). I compared the spacing on the seven radii that were oriented most nearly upward with the spacing on the seven radii that were oriented most nearly downward. Cutting out the center of the hub produced no significant differences in the sticky spiral spacing on radii above the hub compared to those below the hub in two different comparisons. The mean values for b_4/a_1 above

and below the hub were, respectively 1.38 and 1.08 ($z = 1.11$, $P = 0.26$); the mean values above and below the hub for $(b_3 + b_4)/(a_1 + a_2)$ were 1.10 and 1.06 ($z = 1.12$, $P = 0.26$).

Another, inadvertent experiment.—The exceptional adjustments to web damage that are illustrated and described in Fig. 6 demonstrate that even when the tensions on radii were severely reduced when the spider herself collapsed a large sector of her orb, she subsequently built regularly spaced sticky spiral loops. The tensions on the radii that ended on the broken frame were severely reduced, and many radii (at least ten) were completely lax. Nevertheless, even these severe tension reductions did not prevent the spider from laying highly regular sticky spiral spacing in the damaged sector and in other parts of the orb. She encountered the damaged sector on 40 occasions during sticky spiral construction after having broken the frame line, but many of the spaces between the loops that she laid in this sector were highly uniform (Fig. 6), and this relatively uniform spacing was repeated many times (over 200 attachments of 23 loops).

This experiment was not repeated (when I broke frame lines experimentally, the spiders responded by repairing them) (Eberhard 2022b). Nevertheless, it demonstrates that the spider made relatively uniform spaces between sticky spiral attachments to radii whose tensions were drastically reduced (Fig. 6). This regularity reinforces the conclusions from the previous experiments that tension cues do not guide sticky spiral placement.

The uniform spaces between these sticky spiral attachments to the lax radii in this web also demonstrate that the spider was able to modify and coordinate her leg and spinneret movements so as to produce highly regular spacing, even when the positions of the radii relative to each other were substantially altered when they sagged dramatically under her weight. The fact that the spider's progress during sticky spiral construction slowed each time she crossed the damaged sector suggests that this behavioral adjustment may have been challenging.

DISCUSSION

Within-web analyses.—Most analyses indicated that the different magnitudes and patterns of changes of radius tensions in the experiments in this study did not result in consistent changes in sticky spiral spacing. Probably the most powerful results were the within-web comparisons because they held several potentially important variables constant and did not rely on attempts to standardize data. No within-web comparisons showed significant differences in Experiments 2 and 3. The lone significant difference was in the second loop (a_2) of Experiment 1 on radii whose tension had been increased slightly; but the other loops (a_1, a_3 and a_4) on these same radii showed no significant changes (Table 1).

Combined-web analyses.—Analyses that combined standardized data from different webs also failed to show convincing effects of experimental tension changes. In Experiment 1, there was only a single significant before-after difference: the ratio $(b_3 + b_4)/(a_1 + a_2)$ increased on the two Rt radii (whose tensions were expected to have been moderately increased by the cuts) compared with the ratio on the preceding pair of radii (Re_3 and Re_4) (whose tensions had been sharply lowered by the cuts)(Table 2C). But on these same Rt radii, the spaces b_3 and b_4 (built just before the experimental cuts) also showed a difference (an increase) compared with the spaces on the previous pair of radii (Table 2A). This relative increase in the spacing prior to the cuts may have caused the reduction in the subsequent spacing because there is, in general, an inverse relation between previous and subsequent spacing on a radius (Eberhard & Hesselberg 2012). In addition, a radius-by-radius analysis (Table 3) failed to show a significant difference between Re_4 and Rt_1 with respect to the four spaces that were built immediately following the cuts ($a_1 - a_4$). In sum, there were few differences, and none could be confidently attributed to the tension changes.

In Experiment 2, there were no differences comparing radii whose tensions had been substantially reduced (Ro) with control radii (Rh). There was again only a single significant difference: the value of $(b_3 + b_4)/(a_1 + a_2)$ was lower on Rt (where tensions had been slightly increased) than on Rh. This difference was not confirmed, however, when the second set of radii with slight tension increases (Rl) was combined with Rt.

There were no significant differences in the analyses using combined data from Experiment 3, indicating an absence of short-term memory effects on possible responses to tensions changes.

In sum, there was little or no evidence that the experimentally produced changes in radius tension caused changes in the spacing between sticky spiral loops. While it is difficult to prove a negative, the general conclusion from these data, combined with those from previous studies of this and other species of orb weavers (summary Eberhard 2020), is that tension-dependent cues seem not to influence sticky spiral spacing. At the very least, changes in radius tensions did not seem to influence sticky spiral spacing decisions in consistent ways.

Why tension-dependent variables are probably unreliable cues to guide sticky spiral construction.—At first glance, it might seem surprising that spiders did not use tension-dependent cues, because such cues could provide potentially useful information about various web traits, including radius length and the distances to the hub and to the frame. Further reflection reveals, however, that tension-dependent cues are likely to be very unreliable indicators of these web variables.

Probably the most important drawback is that spiders are likely to suffer from arachnological "observer artefacts" in sensing radius tensions during sticky spiral construction. This is because the spider's own weight will cause substantial changes in tensions on the lines in her immediate vicinity (Eberhard 2020). For example, the force exerted by a 48 mg *Araneus diadematus* Clerck, 1757 at sea level would be 471 μN, substantially greater than the tensions (60 to 255 μN) on the radii in an unoccupied orb of this species (Wirth & Barth 1992). In addition, the magnitudes and distributions of the local tension changes caused by the spider's weight must vary substantially within an orb, especially in large, more-or-less vertical orbs. In an approximately vertical orb, the spider's weight will increase tensions on lines above her, in the outer portion of the radius to which she is about to attach the sticky spiral; in contrast, it will reduce tensions on the inner portion of this same radius that is below her. When she is below the hub, the situation is reversed; her weight will decrease the tension on the outer portion and increase that on the inner portion of the radius. Both the magnitudes and the patterns of tension changes will vary on different lines when she is in other parts of the web.

In addition, the magnitude of her effects on radial tensions will also vary with the spider's own weight, which can vary substantially according to her recent feeding history. Tensions will also

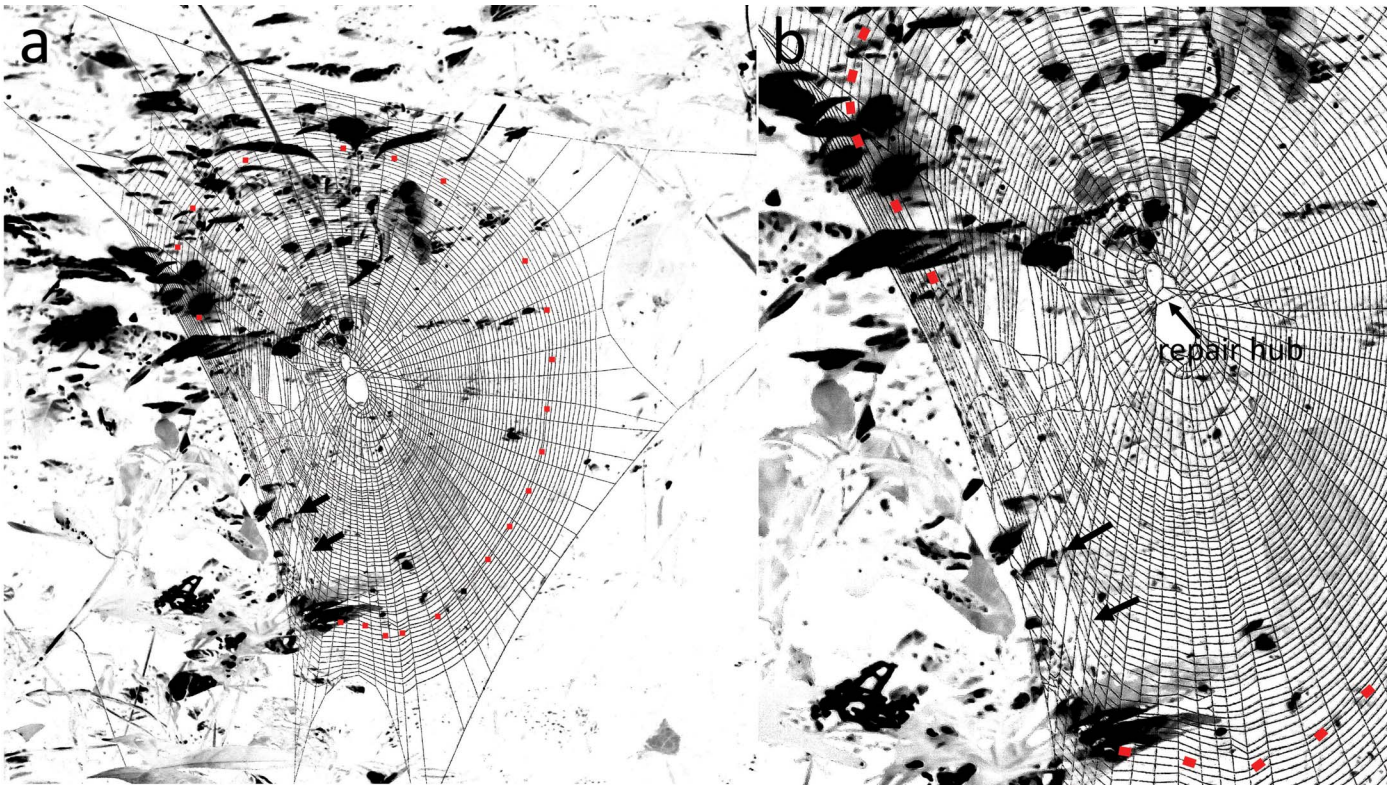

Figure 6.—This web illustrates how even a severe reduction in radius tensions that resulted from a broken frame line did not prevent a spider from laying sticky spiral lines with strikingly regular spacing. The history of this web was as follows. I inadvertently jarred the web when 12 loops of sticky spiral had been built (the red rectangles in *a* and *b* mark the innermost loop at this moment) (adhesions between lines precluded confident identification of the innermost loop in the central portion of the damaged sector). The spider interrupted sticky spiral construction, moved to the hub and waited there several (< 5) minutes. When she resumed sticky spiral construction, I immediately cut the hub lines. She responded by moving to the nearest major frame line (on the left in figure 6b) and breaking it, partially collapsing the entire left side of her web. She paused briefly after breaking the frame, wandered briefly between the frame line and the hub (perhaps re-establishing her memory of location of the hub?), and then resumed sticky spiral construction without repairing the frame. I recorded her construction behavior during her 40 subsequent encounters with the collapsed sector (6:30 to 10:00), in field notes. In 17 cases she turned back near the edge of this sector, reversing the direction of the sticky spiral (black arrows mark two possible turnback sites; many other turnback sites are obscured by adhesions between lines). The other 23 times that the spider encountered the damaged sector she moved across it, attaching the sticky line to each of the lax radii. The sequence in which turnbacks ("tb") and no turnbacks ("no tb") occurred when the spider arrived at the sector where she had broken the frame (with the approximate sites where the turnbacks occurred in terms of clock face positions) was the following: eight tb at 7:00, 10:00, 9:30, 8:00, 9:00, 7:30, 9:30, 6:30; three no tb; two tb at 10:00, 8:00; one no tb; one tb at 7:30; one no tb; four tb at 9:30, 8:00, 9:30, 8:30; eight no tb; two tb at 9:00, 9:00; and ten no tb. Finally, after finishing the sticky spiral, the spider repaired the hub hole. The spider's rate of progress slowed substantially each time she moved across the damaged sector, and this sector sagged deeply under her weight. Nevertheless, the spaces between many of the loops she laid there were relatively uniform (note, for example, those in the sector 7:30–8:30 in *b*).

vary in complex ways depending on the exact sites and lines (radii or temporary spiral lines) that the spider happens to grasp with her tarsi. For instance, grasping a temporary spiral line will reduce the magnitudes of the changes in tension on the attachment radius, because more of her weight will be supported by other, nearby radius and temporary spiral lines. The tensions exerted by her legs must vary between sites in the orb because they more often grasp other nearby radii rather than the attachment radius when she is nearer the hub. In addition, the spider's own movements will also alter the effects exerted by her weight. Still another source of variation is that some of the effects of her weight on radius tensions will be greater when the plane of the orb is more nearly vertical.

Even further complications may arise from movements of the substrates to which anchor lines are attached (Mulder et al. 2021), causing variable, unpredictable changes tensions in web lines. Even in webs that are attached to rigid supports, changes in the properties of the silk in radial lines when exposed to different humidity, especially "super-contraction" that occurs under higher humidity (e.g., Boutry & Blackledge 2013), could result in changes in radius tensions. Finally, previous studies using direct measurements and analyses of angles between lines show that the tensions on unloaded radial lines in finished orbs vary substantially: radius tensions varied by a factor of about 8 in an *Larinioides sclopetarius* (Clerck, 1757) orb (Denny 1976), and by a factor of 4.25 in an *A. diadematus* orb (Wirth & Barth 1992). Radii in the upper portions of *Zygiella x-notata* (Clerck, 1757) web were under more tension than others (LeGuelte 1966). The tension on a radius even varies along the length of the radius itself, because the spiral lines attached to it pull it inward (Eberhard 1969; Zschokke 2000).

In sum, a spider would need to make many complex corrections in order to translate tension-dependent cues such as extensibility, resonant vibrations, and radius tensions themselves into

reliable estimates of the distance to the frame or to the hub during sticky spiral construction. Thus, the reason why tension-dependent cues are apparently not used to guide sticky spiral construction may be because they are unreliable.

This discussion of the distorting effects of the spider's weight illuminates a previously unexplained detail of the sticky spiral construction behavior of some heavy-bodied, stubby-legged araneids such as *Gasteracantha cancriformis* (Linnaeus, 1758) (Eberhard 1982, 2020). A mature female *G. cancriformis* differs from other araneids such as *Araneus diadematus* (Zschokke & Vollrath 1995) when building sticky spiral in the outer portion of her orb, in that when she prepares to attach the sticky spiral to a radius, she does not move outward along this radius, but instead maintains contact with the outer loop of temporary spiral (Eberhard 2020). She reels in the radius using "hand-over-hand" movements of her legs, first with legs I and II and then with legs II and III. At the same time, she taps outward with her outer leg I toward the inner loop of sticky spiral to eventually touch it (fig. 3.25 in Eberhard 2020). The temporary spiral thus helps sustain the spider's weight during these "reeling-in" operations and reduces the downward displacement of the attachment radius caused by the spider's weight. This reduction in the amount that her weight deforms her web would be especially pronounced when the spider reels in a more-or-less horizontal radius in an approximately vertical orb. Similar "reeling in" movements with legs I and II, or with II and III occurred in several other araneid species that also have relatively stubby legs; *G.* sp (#2036); *Witica crassicauda* (Keyserling, 1865); *Alpaida* sp. (#2189); *Bertrana* (?) sp. (#1669); *Hypophthalma* sp. (#1586); *Neoscona* sp. nr. *nautica* (#2058); *Eriophora edax* (Blackwall, 1863); *Eustala* sp. (#1841); and *Araneus bogotensis* (Keyserling, 1864) (W. Eberhard, unpub.).

An additional, unrelated implication of the conclusion that tension-dependent cues are unreliable indicators of web variables is that it gives reason to doubt the importance of one of the 20 putatively phylogenetically informative orb construction traits that are shared by deinopoid and araneoid orb weavers. I have argued (Eberhard 2022a) that this similarity (not using tension-dependent cues during sticky spiral construction) was unlikely to be the result of convergence, and that it could thus be interpreted as an indication of orb web monophyly. But the realization that there is an adaptive advantage in not using these cues weakens the argument favoring the monophyly of this trait.

Tension-dependent cues in other contexts.—It is important to emphasize that even though spiders probably do not use tension-dependent cues to guide sticky spiral construction, such cues may be used during other stages of orb web construction. For example, the uloborid *U. diversus* apparently uses radius extensibility, a tension-dependent trait, to guide selection of an especially short radius that ends near an anchor line on which to place a stabilimentum line (both radius length and proximity to an anchor are negatively correlated with radius extensibility) (Eberhard 1973). The spider's apparent searching behavior while at the hub immediately preceding stabilimentum construction (after the web was otherwise complete) suggested that she used radius extensibility to make this choice. She performed repeated series of slow flexes and sharp jerks, especially with legs I, and also gently bounced the web with her entire body; jerks were often preceded by a series of slow flexes. At first, the spider turned substantially (90° or more) between the bursts of jerking and bouncing, but gradually her turns became smaller and smaller until finally all jerks were directed toward the same small sector of the web where she ultimately placed the stabilimentum line. The positions of legs I also "zeroed in" on a particular radius; early in the process they usually gripped adjacent or nearly adjacent radii; but later in the series, both gripped the same radius. During this process, the spider's weight was largely sustained by the densely meshed lines in the hub that were held by legs III and IV; her weight was thus less likely to mask differences in radius tension and radius extensibility than during sticky spiral construction. Protection from predation was the likely function of choosing a short radius ending near an anchor. The spider faced directly toward the stabilimentum while resting at the hub of her finished orb, probably to camouflage her outline; her choice of stabilimentum radius facilitated rapid escapes to the edge of the web and the substrate when disturbed; here she was more difficult to see (Eberhard 1973).

Tension-dependent cues may also be used during the earlier, less-studied exploration and radius construction stages of orb construction, although currently available data argue against their use in at least one stage of radius construction (Vollrath et al. 2000). Further data are needed to evaluate other possibilities.

Limitations of the experiments.—One important variable that I did not take into account even though it is known to have substantial effects on sticky spiral spacing, was the distance from the inner loop of sticky spiral to the outermost intact loop of temporary spiral (Fig. 1b). This distance (which cannot be determined in photos of powdered webs such as those in this study) affects the placement of early loops of sticky spiral in *M. duodecimspinosa* (Eberhard & Hesselberg 2012); its omission could have been responsible for inconsistencies in responses.

A second major limitation is that I did not measure the tensions on radii directly. All analyses concerned only the effects of increases and decreases in relative tensions, rather than the effects of differences in tensions per se. The absolute tensions on radii likely varied substantially in the intact web before the lines were cut (Denny 1976; Wirth & Barth 1992) and they may have been of sufficient magnitude to mask at least some of the experimental tension changes. In addition, tension changes due to the spider's weight and her movements were undoubtedly substantial, and probably masked some (and perhaps many) experimental changes. In sum, it is probable that at least some of the changes that were produced by the experimental modifications (e.g., those listed in Table 1) were not the same as the changes in absolute tensions that were experienced by the spider. The effects of the spider's weight, of course, are the very reason that tension-dependent cues are likely to be poor indicators of web variables.

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