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Memory of Distances and Directions Moved as Cues During Temporary Spiral Construction in the Spider *Leucauge mariana* (Araneae: Araneidae)

William G. Eberhard[1]

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The spider Leucauge mariana *probably uses the presence of temporary spiral (TSP) lines already in place to determine sites of attachment of currently produced loops of temporary spiral, but less rigidly than has been previously supposed for orb weavers. Memory of distances and directions traveled recently to and from TSP lines is implicated by the fact that adjustments to experimental and natural discontinuities in previous TSP lines occur gradually rather than being abrupt. Distances and directions traveled along both radii and previous TSP lines correlate with relative amounts of adjustment. Body size may also be used as a reference measure, but not in the simple, inflexible way suggested by R. W. G. Hingston (*A Naturalist in Himalaya, *Small, Maynard, Boston, 1920). Tensions on radii are not used as cues in any simple way, and may not be used at all, since experimental changes in tensions produced effects consistent with resulting changes in thread positions but inconsistent with tension differences.*

KEY WORDS: spider behavior; *Leucauge mariana*; web construction; orb weavers.

INTRODUCTION

Orb web construction by spiders is in some ways ideally suited to the analysis of complex behavior. Other than gravity, the external stimuli that guide the spider, at least during the later stages of web construction, probably come exclusively from the lines in the web. These cues can thus be measured and manipulated with precision. The cues and the spider's responses to them are recorded precisely by the positions of the lines in the web, and the planar web

[1]Smithsonian Tropical Research Institute and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica.

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form means they can be photographed easily. In addition, the repetitive motion patterns used during construction along with the predictable occurrence of web building make it easy to accumulate observations.

The usual order of construction of an orb is to make (1) radii and frame lines, then (2) hub loops and (3) the temporary spiral (TSP), and finally (4) the sticky spiral (STSP). The temporary spiral (also known as the provisional, auxiliary, or structural spiral) is a widely spaced spiral of nonsticky silk that starts near the hub and spirals outward. The spider uses it as a bridge when moving from one radius to the next during STSP construction (e.g., McCook, 1889; König, 1951; Witt, 1965). In some groups the TSP also serves to pull the radii into curved patterns that are incorporated into the final web design (Eberhard, 1972, 1974). In most species the TSP is gradually destroyed during construction of the definitive STSP.

Little is known about the cues used to direct TSP placement. Hingston (1920) deduced, from observing leg movements of the Indian araneid "*Araneus nauticus*" (the correct species name is unknown for lack of voucher specimens), that the spider used its own body size and the positions of TSP lines already in place as guides; each successive loop was supposedly laid at one body length (from the tip of the foreleg to the spinnerets) from the previous loop of TSP. König (1951) confirmed, on the basis of similar observations and experimental TSP removal, that TSP already in place serves as a guide for several araneid species. He noted, however, that spacing was variable, being larger in loops farther from the hub. He also found that contact with frame lines (or similarly oriented lines added to the web) caused the spider to terminate TSP construction. Peters (1970) studied the conditions under which *Araneus diadematus* would replace the TSP when it was broken soon after the spider finished it; he found, in addition, that the second TSP is sometimes smaller than the first. His sample sizes were too small, however, to test for significant trends. Gravity influences TSP spacing in *Leucauge mariana* (Eberhard 1987b). The only other published data are scattered photographs of temporary spirals (Savory, 1952; Witt *et al.*, 1968).

The present study reports on observational and experimental studies of TSP construction by *Leucauge mariana* (Keyserling). Experiments included cutting segments of TSP that had just been laid and cutting radii.

THE SPIDER

Leucauge mariana is extremely abundant in many disturbed habitats in Costa Rica. Mature females were used for all observations. Voucher specimens have been deposited at the Museum of Comparative Zoology, Cambridge, Mass. In the field this species generally spins inclined orbs whose angle with the horizontal ranges from about 10 to 80° ($\bar{X} = 39.9 \pm 12.9°$ in 66 webs of as many

different females). The first web of the day is usually built 1 to 2 h before dawn, but if this web is destroyed during the morning, leaving only the frame lines intact, the spider usually makes a second web 1 to 4 h later. Replacement webs are consistently smaller and somewhat different in design (Eberhard, 1987c). All observations were of second webs unless otherwise noted.

METHODS

Spiders were kept in a large (2 × 2 × 5-m) screened cage. The webs built there were taped to circular wire hoops and then destroyed except for the frame lines about an hour later. Hoops were hung so the webs were either horizontal or inclined 45°, thus controlling gravity effects on building (Eberhard, 1987b). Replacement webs that were built in the hoops were photographed after being coated with white talcum powder (Eberhard, 1976).

Measurements of photographed webs were made from 8 × 10-in. prints (magnifications of webs in these prints averaged 64% natural size and ranged from 43 to 114%). Thirty repeated measurements of as many distances on prints that averaged 6.25 ± 1.6 cm had a coefficient of variation of 1.3%. Radius lengths were measured from the edge of the hub to the frame.

Lines were eliminated experimentally in webs using sharp scissors (Hingston, 1920). Only one experiment was performed on any given web. Individual spiders were not marked, and it is possible that some experiments were repeated using the same spiders on different days. This must have occurred rarely since the spiders were very abundant, and experiments were done over a span of more than 3 years. The effects of eliminating lines were estimated in a few cases without photographing and measuring webs. In simulations of these experiments using edges of pieces of paper to represent web lines, I found that I could reliably (>95% confidence) perceive differences as small as 0.3 mm. Since the average space between TSP lines was 12.7 mm, this means that, on average, I could perceive changes of about 3%.

Unless otherwise noted, statistical tests of significance were Mann–Whitney *U* tests. Many averages are given ±1 standard deviation. Since there was substantial intraspecific variation in web characteristics, statistical tests of significance were, wherever possible, made using within-web comparisons.

RESULTS

General Description of Construction Behavior

TSP construction behavior was simple and repetitive. The spider began by making an initial loop near the hub and then continued using the previous outer loop of TSP as a bridge between radii as it spiraled outward. It attached the

TSP line to each radius it encountered, moving inward (hubward) and onward to the next radius and then outward on this radius before attaching again. Spiders maintained contact with the previous loop of TSP during the entire process, just as did the araneids observed by Hingston (1920) and König (1951). Leg positions at the moment of attachment were similar to leg positions of araneids during sticky spiral construction (König, 1951; Eberhard, 1982); one leg IV held the line emerging from the spinnerets, while the other leg IV and the ipsilateral leg III held the radius on either side of the point of attachment.

Construction of the first loop of TSP differed from that of later loops. The spider almost always interrupted hub construction abruptly to begin TSP construction. The first loop always continued in the same direction (clockwise or counterclockwise) in which the hub loops were laid. Initially the spider stayed about a body length from the edge of the hub and moved more or less directly from one attachment to the next. Later in the first loop, however, it began attaching farther from the hub's edge and moved inward and then back outward between attachments. Since the spider was large enough to span easily the distance from one radius to the next in this area of the web, these inward and outward movements were "unnecessary" in terms of getting from one radius to the next.

Patterns in Webs with Finished TSP—Start of the Second Loop

When the spider completed the first loop of TSP, it encountered an abrupt change where the first point of attachment of the TSP had been made. The distances shown in Fig. 1 were measured in 22 horizontal and 50 45° webs to determine the effects on TSP placement caused by the first TSP attachment. The patterns were the same in both 0 and 45° webs, and the data are pooled. There was no significant difference when all values of *a*, *b*, and *c* were compared (averages were 18.7, 18.7, and 19.0 mm, respectively); within-web comparisons showed a slight tendency for *c* to be larger than *b* but no consistent difference between *a* and *b*. The spacing of the first segment of the second loop (*d*) was much smaller than *c* in all webs ($\bar{X} = 6.2$ vs 19.0 mm), and subsequent spacings (*e* and *f*) were significantly larger than *d* (averages for *e* and *f* were 8.1 and 8.8; *d* was less than *e* in 67 of 72, and *e* was less than *f* in 52 of 72; both *P*'s < 0.001, chi-square test). The consistency of the *d* vs *c* difference was significantly greater than that of the *e* vs *f* difference ($P < 0.001$, chi-square test). The average for *f* in horizontal webs (9.2 mm) was not far from the average spacing for the rest of the second loop of TSP (10.5 mm) in these webs (direct comparison in nonhorizontal webs was not possible due to the effect of gravity). The overall effect of the spider's placement of the second loop was to smooth over the abrupt discontinuity in the outline of the first loop of TSP which had resulted from TSP initiation.

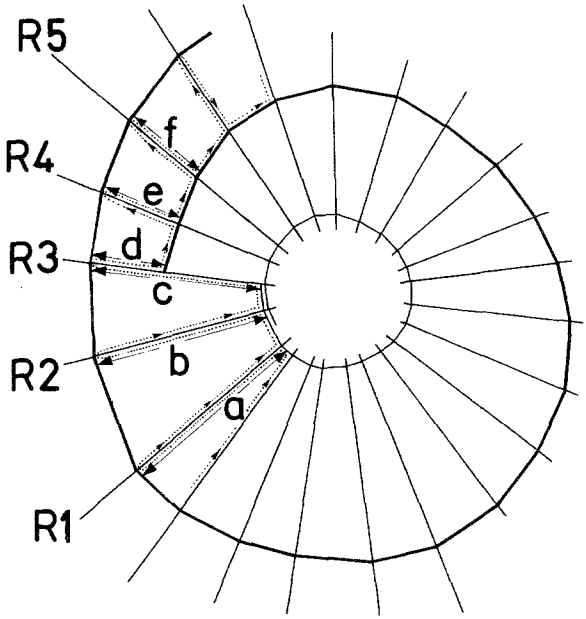

Fig. 1. Diagrammatic representation of the start of the second loop of TSP. The outward distance that the spider moved along the radius on which the TSP began (*c*) was much greater than the inward distance (*d*); placement of the second loop smoothed this abrupt transition.

Experimental Alteration of Webs

Broken TSP Lines

While the spider was spinning TSP on one side of a horizontal web, five segments of the outer loop of TSP on the other side were carefully severed in 18 different webs (Figs. 2 and 3). These gaps consistently affected the spiders' subsequent behavior. The first attachment when a spider reached a gap (r_2 in Fig. 3) was always displaced inward (hubward) with respect to the preceding attachment (i.e., *c* was always greater than *d*); in all cases it was, nevertheless, much farther from the outermost intact loop than the previous attachment had been (i.e., $d > b$) and was farther out than the previous attachment (see broken lines in Fig. 3). Subsequent attachments to r_3–r_5 were progressively farther hubward, gradually coming closer to the original attachment sites, while the attachment to r_6 was displaced slightly outward; averages for the distances *d*–*h* in Fig. 3 were, respectively, 14.8, 13.8, 13.4, 13.3, and 14.4 mm. In some but not all cases the last attachment(s) in the gap was on or very near the original

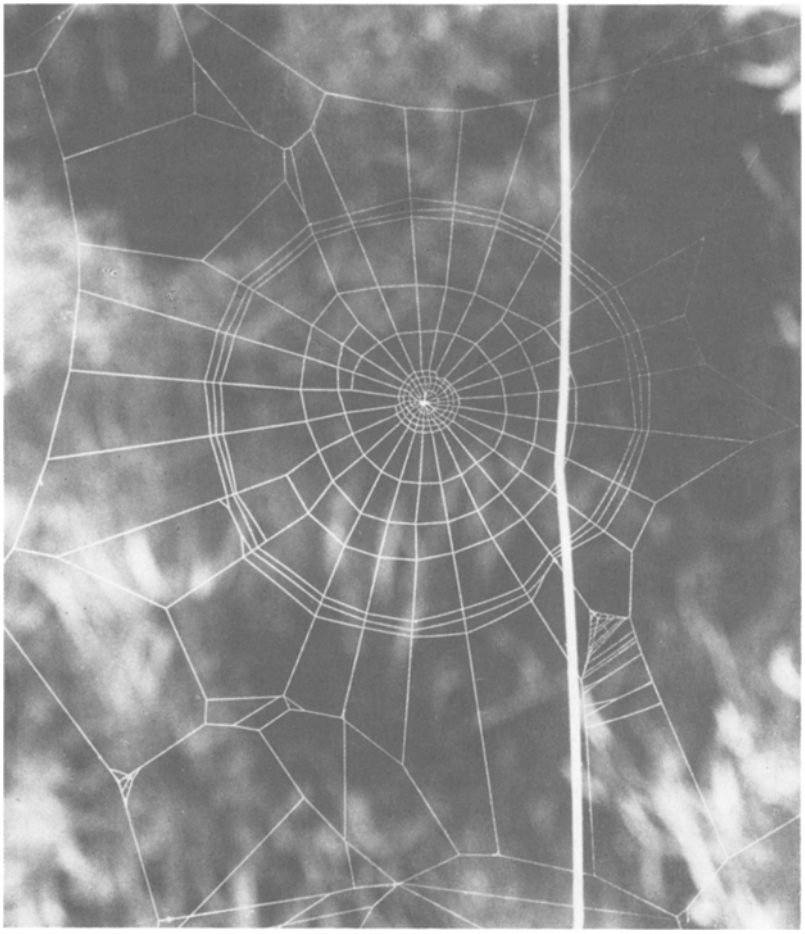

Fig. 2. Horizontal web of *L. mariana* in which five segments of one loop of TSP were severed while the spider was spinning that same loop on the opposite side of the web. The spacing of the next TSP loop in this sector of the web was modified in consistent ways.

attachment site. As can be seen from Fig. 2, the overall result was to smooth over the jagged outline in the TSP that had been produced by cutting lines.

When the spider reached the end of the sector with broken TSP lines (r_6), it encountered a situation similar to its encounter with the beginning of the TSP (above), and it responded in a similar manner. The first space (j) was relatively small, and subsequent spaces gradually increased: h was often greater than g (13 of 17 webs) and always greater than j; k was always greater than j.

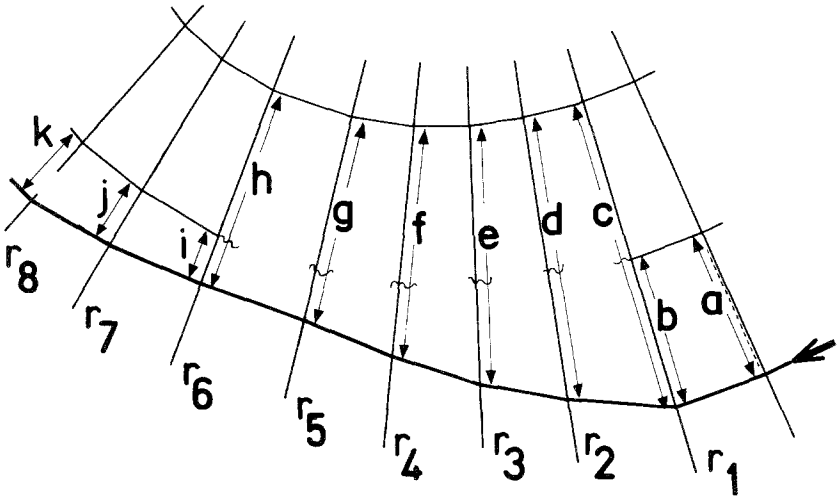

Fig. 3. Diagrammatic representation of a web with broken TSP lines like that in Fig. 2. The next time the spider arrived at the modified sector (heavy arrowhead at right), the new TSP line (heavy line at bottom) was laid with altered spacing.

In effect, at both sides of the gap the spider was forced to travel different distances inward and outward along a given radius, distances which are usually equal; on r_1 the outward trip (b) was shorter than the inward trip (c), while on r_6 the outward trip (h) was longer than the inward trip (i). The average amount of change in the distance traveled was smaller on r_1 ($c - b = 7.3 \pm 2.4$) than on r_6 ($h - i = 10.0 \pm 1.7$), but proportionally the changes were similar [$(c - b)/b = 72 \pm 18\%$ on r_1; $(h - i)/h = 74 \pm 12\%$ on r_6]. The amounts the spiders responded to these changes, when attaching to the next radius, were also similar: the spacing increased $41 \pm 18\%$ from r_1 to r_2 ($d/b - 1.0$) and decreased $44 \pm 11\%$ from r_6 to r_7 ($j/h - 1.0$).

The near-equality of the percentage responses suggests that a relative rather than an absolute measure of change might be used by the spider to adjust the spacing, and further analysis was carried out to test this idea. At the start of the second loop, a similar amount of change [av. $68 \pm 10\% = (c - d)/c$ in Fig. 1] produced a similar response (av. $44 \pm 9\% = e/c$ in Fig. 1). There was a positive correlation ($r = 0.79$, $N = 72$, $P < 0.01$) between the relative distance the spider traveled inward on the radius where the TSP had begun (d/c in Fig. 1) and the relative distance it moved outward for the next attachment (e/c). The analogous correlation in the broken TSP experiment (j/h with i/h in Fig. 3) was also positive and significant ($r = 0.51$, $N = 17$, $0.01 < P < 0.05$).

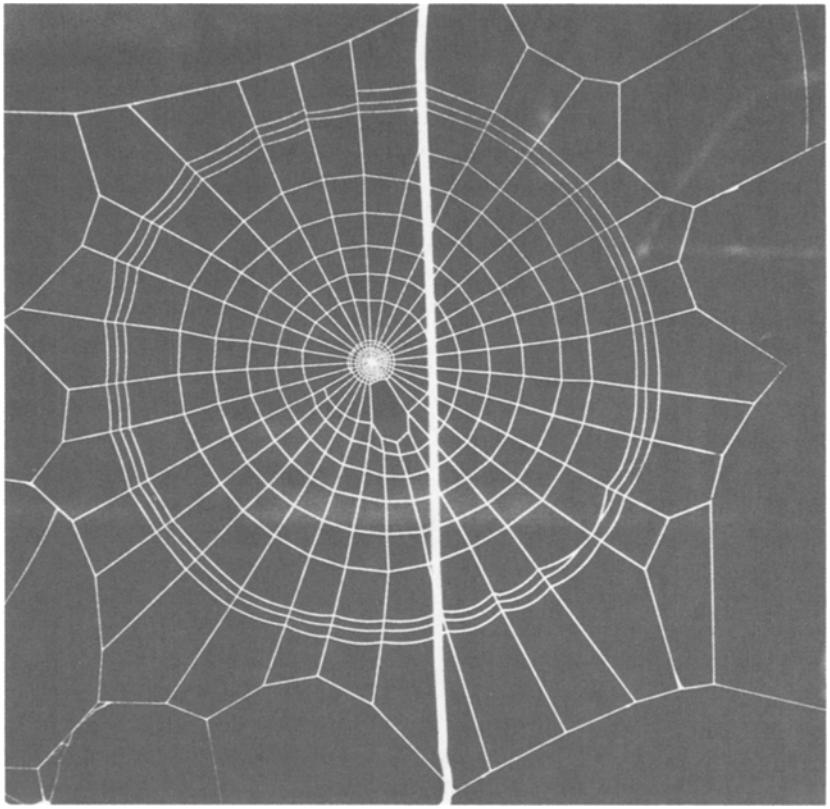

Fig. 4. Horizontal web of *L. mariana* in which three adjacent radii were broken while the spider was on the opposite side of the web laying the first loop of TSP. Spacings of subsequent loops of TSP in the modified sector were changed in consistent ways.

Broken Radii

While the spider was laying TSP on one side of the web, three adjacent radii were carefully cut near the hub on the opposite side in 74 webs (42 photographed), thereby causing the segments of the outer loop of TSP to be displaced outward (Fig. 4). The tensions on the broken radii were reduced, while the tensions on the radii adjacent to the broken radii were probably at least sometimes increased. The relative magnitudes of the tension changes were estimated by calculating the relative tensions on broken and adjacent intact radii in 10 webs in which the TSP had been completed and one to five loops of STSP had been laid (as in Fig. 4). The tension on one was arbitrarily set at 1, and the tensions on the others were calculated using the angles between them and the

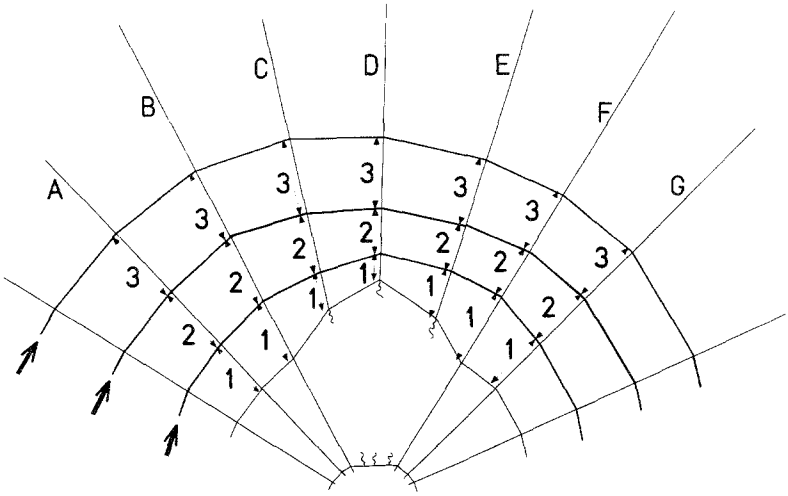

Fig. 5. Diagrammatic representation of a web with radii broken after the first loop of TSP as in Fig. 4. The spider's subsequent arrivals at the experimental sector are indicated by the heavy arrows at left.

frame lines (Denny, 1976). The calculated tensions on broken radii averaged 55% of those on nearby intact radii. Since subsequent TSP and STSP attachments must increase radial tensions near the frame (Eberhard, 1981), the calculated differences probably underestimate the differences encountered by spiders during TSP construction. It seems safe to say that the tensions on broken radii averaged less than half those on adjacent intact radii during these experiments.

When the spider next came to the sector with broken radii, in 72 of 74 cases it attached the new loop of TSP closer to the old loop on the first two broken radii than it had on the preceding intact radius (C1 and D1 < B1 in Fig. 5). In all of the 42 photographed webs the space on the third broken radius (E1) was larger than that on the second (D1) and was still larger on the next, intact radius (F1); in all but 4 webs F1 was also larger than that on the next intact radius (G1) as well as that on the intact radii on the other side (A1 and B1). As shown in Fig. 6, nearly all pairwise combinations of values in this first loop were significantly different in the 42 photographed webs.

The next loop showed several of the same patterns, but others were changed: B2 continued to be greater than C2 (in 36 of 42 webs), and E2 less than F2 (39 of 42); but C2 was greater than D2 in 39 of 42 webs where no trend was apparent in the first loop, B2 failed to differ from F2 (B2 > F2 in 24 of 42 webs), D2 did not differ from E2 (D2 > E2 in 23 of 42 webs), and F2 was less than

	A1	B1	C1	D1	E1	F1	G1
A1			xxx	xxx		xxx	xxx
B1			xxx	xxx		xxx	xxx
C1					xxx	xxx	xxx
D1					xxx	xxx	xxx
E1						xxx	xxx
F1							x
G1							

	A2	B2	C2	D2	E2	F2	G2
A2				xx	xx		
B2				xx	xx		
C2							
D2						x	xxx
E2						x	xxx
F2							
G2							

	A3	B3	C3	D3	E3	F3	G3
A3					x		
B3					x		
C3							
D3							
E3							
F3							
G3							

Fig. 6. Pairwise comparisons of spaces between TSP lines after radii were broken (letters refer to radii labeled in Fig. 5). Differences were greatly reduced in later loops. xxx, $P < 0.01$; xx, $P < 0.01$; x, $P < 0.05$.

G2 in 37 of 42 webs, showing a reversal of the trend in the first loop. In addition, the sizes of the differences were greatly reduced; for instance, the averages for B1 and C1 in the 22 webs included in Table I were 10.41 and 6.56 (difference is 3.85 or 37% of B1), while the averages for B2 and C2 were 12.62 and 11.78 (difference is only 7% of B2; see also Fig. 4). Further reductions in differences were seen in the third loop.

Table I. Spaces (Averages and Standard Deviations, in Millimeters) Between Loops of TSP in 22 Webs in Which Three Radii (C, D, and E) Were Broken Early in TSP Construction (see Figs. 4 and 5) and the Spider Made at Least Three Subsequent Loops of TSP[a]

	Radius						
Loop	A	B	C	D	E	F	G
1							
$\bar{X}$	10.02	10.41	6.56	6.31	10.13	15.55	13.67
SD	2.30	2.01	1.83	1.98	2.04	2.62	2.40
2							
$\bar{X}$	12.6	12.62	11.78	10.57	10.63	12.27	13.54
SD	2.05	2.35	2.08	2.07	2.28	2.35	2.41
3							
$\bar{X}$	14.66	14.86	14.39	13.61	13.04	13.48	14.83
SD	2.35	2.93	2.74	2.38	2.25	2.96	2.43
4							
$\bar{X}$	15.82	16.35	15.59	15.64	15.74	15.21	15.89
SD	1.6	1.59	1.16	1.56	2.44	1.64	2.83

[a]Only seven of these spiders made a fourth loop. Webs were the first web of the day.

DISCUSSION

The data from the broken TSP experiment and the initiation of the second loop show that the choice of where to attach each segment of TSP is a complex process whose analysis is difficult. Not only must one contend with differences between spiders, possible imprecision in a given spider's behavior (Eberhard, 1987d), and the possibility of multiple spurious correlations that occur in a geometrically regular structure such as an orb, but also the spider's experiences immediately preceding any given attachment have been shown for the first time to cause changes in TSP construction. A spider's response to given stimuli varied according to previous events; as a result, possible stimulus–response correlations were weakened, making it more difficult to determine the effects of different stimuli.

Leucauge mariana is evidently guided by multiple cues as it lays the TSP. Data from the broken TSP and broken radii experiments, from intact webs, and from direct observations of the spiders' behavior all strongly imply that, as suggested by Hingston (1920) and König (1951), spiders use the positions of previously laid TSP lines as guides for the placement of current TSP lines. The most convincing evidence on this point is that when the outermost previous TSP lines are experimentally modified, the locations of subsequent attachments in this area change in consistent ways (König, 1951; this study). Patterns in the changes in *L. mariana* webs, however, show that additional factors are in-

volved. For instance, when a spider comes upon an abrupt change in the location of the outermost previous loop of TSP in either intact or modified webs, it only gradually adjusts the location of the new loop of TSP over the course of several subsequent attachments. This happens whether the sudden change is outward, as occurs once in every normal *L. mariana* web at the start of the second loop (Fig. 1) and in the broken TSP experiments (r_6 in Fig. 3), or inward in the broken TSP experiments (r_1 in Fig. 3), a pattern that rarely, if ever, occurs in normal webs.

The function of the spider's gradual response to abrupt changes is probably to smooth the TSP outline and, thus, make the eventual outline of the sticky spiral smoother (Eberhard, 1987e). This in turn results in a more regular and presumably more efficient array of sticky lines. How the spider achieves the smoothing is less certain. Correlations between distances traveled and adjustments made in spacing suggest that the spider remembers distances and directions it has traveled recently. Such a kinesthetic memory is apparently widespread in spiders [LeGuelte (1969) on an araneid, Barth and Seyfarth (1971) on a ctenid, Görner (1973) on an agelenid, Görner and Zeppenfeld (1980) on a lycosid, and Buchli (1969) on a ctenizid]. Memory of distances traveled is also implicated indirectly as a cue in web construction in orb weavers of the families Anapidae, Mysmenidae, and Theridiosomatidae (Eberhard, 1987a). An accurate kinesthetic sense may in fact be a primitive trait in arachnids, as some scorpions are also able to judge short distances traveled (<10 cm) quite accurately (Brownell, 1984).

A simple version of the "kinesthetic memory" hypothesis is that when there is an excessive difference between the distance traveled outward along a radius from the previous TSP and the distance traveled back inward to reach the next segment of TSP (e.g., b vs c or i vs j in Fig. 3), the spider should adjust the spacing on the next radius. If the inward distance was longer ($b < c$ in Fig. 3), then the next space (d in Fig. 3) should be increased in proportion to the relative difference ($c - b/b$); if the inward distance was less ($i < h$ in Fig. 3), then the next space (j) should be decreased proportionally ($h - i/h$). Alternatively, the spider may compare the distance it moves inward to reach the TSP with some "reference" distance. This might be related to the spider's own body, as originally hypothesized by Hingston (1920), but it would have to be a "sliding reference" that was modified during construction (see König, 1951; Eberhard, 1987b; below). If the inward distance is less than the reference, the next space should exceed the inward distance by an amount proportional to the difference. If the inward distance exceeds the reference, the next space should be proportionally less than the inward distance. Both hypotheses account equally well for attachments such as those to r_2 and r_7 in the broken TSP experiment. Only the second hypothesis is able to explain the continued

reduction in TSP spacing that consistently occurred on r_3–r_6 in this experiment because the distances in and out on each of these radii did not differ.

Another possible explanation involves TSP-radius angles, with spacing being more reduced when the angles deviate more from perpendicular. This could explain the data from the experiment with the broken radii (Fig. 4) but not those from the experiment with broken TSP lines (Fig. 2), since the angles of the remaining lines are unchanged, but nevertheless, the spider changes the TSP spacing dramatically.

Radial tensions do not appear to affect TSP spacing. In the broken radius experiment tensions on some radii were reduced by at least 50% compared to those on adjacent intact radii, but the changes in spacing of the next loop of TSP on loosened radii were inconsistent: some loosened radii consistently had smaller spacing, and others larger. In addition, some differences in spacing changed in later loops, and most eventually disappeared in the outermost loops (Fig. 6), even though the radii were still substantially looser than neighboring intact radii. Visual cues have recently been implicated in araneid orientation (Crawford, 1984), but the structure and placement of the eyes make it highly unlikely that they are used to direct fine details of web construction (Land, 1985).

Thus, of the hypotheses considered, the "gradual adjustment to a sliding standard" is in best accord with the data. A modification is needed, however, to account for some of the results of the broken radii experiment. When the radial distances transversed by the spider as it moved along the TSP (u, v, x in Fig. 7) as well as those along the radii (t, w, y in Fig. 7) were measured in 38 experimental webs, consistent patterns emerged. In all cases, s was less than $t + u$, and in all but one, t was less than $v + w$; there was an extremely strong correlation between s and $t + u$ ($r = 0.85$, $t + u = 0.94s + 3.69$) and between t and $v + w$ ($r = 0.84$, $v + w = 1.1t + 2.92$) (both P's < 0.001). The change in spacing made by the spider, for example, from s to t when moving from radius B to radius C, correlated with the radial distance (toward or away from the hub) moved along the TSP (e.g., u in going from B to C). The r values were 0.51 for u vs $s - t$, 0.48 for v vs $t - w$, and -0.44 for x vs $w - y$ ($P < 0.01$ in all cases) (log transformations did not improve correlations, suggesting that the relationships are linear). In other words, when the spider moved farther outward as it moved along the TSP prior to making an attachment on radius C, the reduction in TSP spacing on this radius was greater. Similar reductions occurred on radius D, and in fact the slopes of the regression lines were nearly equal (0.39 on C, 0.42 on D; $d = 0.196$, $P > 0.5$). The spacing on radius E was greater, rather than smaller, than that on the previous radius, and the same correlation occurred: the farther inward the spider went as it moved along the TSP, the greater was the increase in spacing on E. These data suggest

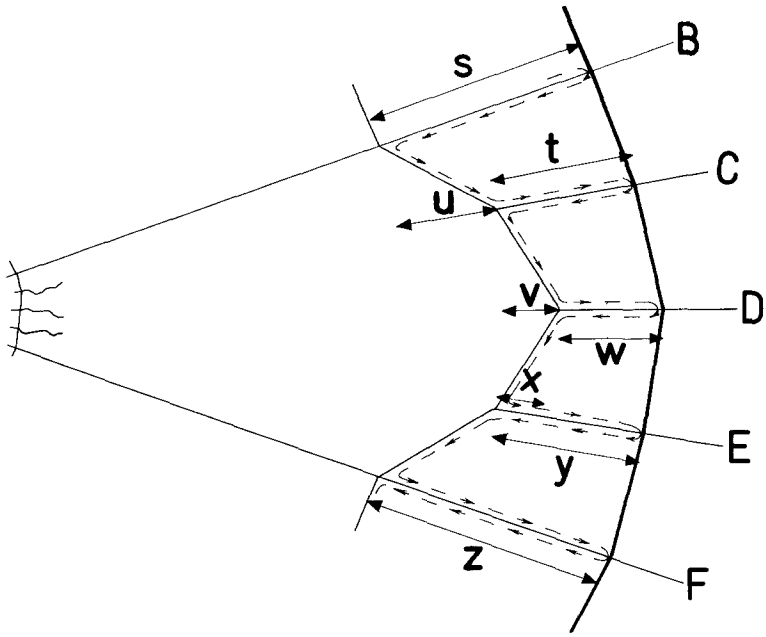

Fig. 7. Diagrammatic representations of radial distances traveled while the spider moved along radii (s, t, w, y, z,) and while it moved along TSP bridges (u, v, x) (dashed line indicates the path of the spider).

that the spider uses both distances and angles with respect to radial directions (i.e., it does simple trigonometry) as it travels. This is not unreasonable, as similar kinesthetic abilities exist in other spiders (references above).

The influences of several other factors are probably superimposed on the basic cues from positions of previous TSP lines and memories of distances in determining TSP spacing. Correlations have been noted with radius length, position above vs below the hub in nonhorizontal webs, and stage of TSP construction (Eberhard, 1987b), and these may modify the "sliding reference" discussed above.

Orb web construction behavior is unusual in that the web provides an extremely precise and complete record of the spider's decisions. If there is a certain degree of imprecision or stochasticity in animal behavior [Eberhard, 1987d; Dawkins and Dawkins, (1973) and Bell (1985) for possible cases], it would presumably be manifest in such precise records. It may be that some of the residual variation not explained in this study is the result of such imprecision.

I have assumed throughout this study, as is usual in behavioral studies, that simpler explanations are more likely to be correct than more complex explanations. For instance, I have not considered extreme hypotheses such as the

possibility that the spider uses different sets of cues to guide each different TSP attachment, that the spider recognizes each radius individually and remembers its position relative to all the others, etc. In general such parsimony is probably the best approach for understanding the behavior of an animal such as a spider because of the probable restrictions imposed by its limited nervous system. It is, however, a dangerous assumption (Griffin, 1984) and is probably not always true for *L. mariana*. This spider's ability to abandon apparent spacing and termination rules when a large sector in another part of the web has not yet been filled with TSP (Eberhard, 1987b) suggests that external stimuli and/or memories that give a more general overview of the web also influence the spider. This may also have contributed to the observed residual variation.

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