Construction behaviour and the distribution of tensions in orb webs

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Summary

The geometric patterns of most orb webs indicate that the radii in any single web are usually not equally tense. Other things being equal, however, behaviour tending to make radial stresses more rather than less equal will be advantageous because it will improve the mechanical resistance of the web to prey impact and wind. A tendency toward equalisation of tensions in the sticky spiral could also increase the prey capture potential of a given volume of sticky silk. Several behaviour patterns in orb web construction result in changes in radial and sticky spiral tensions, and systematic variations in some of these behaviours seem designed to reduce differences in tensions. Other behaviour patterns appear to be designed to function to locate web lines, economise on time and effort in movements around the web, and avoid entanglement of threads.

Introduction

Spiders build orb webs using a number of complex, relatively stereotyped behaviour patterns. There have been a number of studies, mostly of *Araneus diadematus* Cl., which describe these building movements and the stimuli which release and guide them (Hingston, 1920, 1922; Wiehle, 1927, 1928, 1929, 1931; H. Peters, 1936, 1937, 1939; Tilquin, 1942; Koenig, 1951; Mayer, 1952; Jacobi-Kleeman, 1953; Witt, 1952; Szlep, 1958; Witt & Reed, 1965; Witt *et al.*, 1968; LeGuelte, 1966; Reed, 1969; P. Peters, 1970; Eberhard, 1972). The possible functional significance of these behaviour patterns, and the possibility of alternative behaviours in other species have been largely ignored, however.

This paper presents comparative data from a number of hitherto unstudied species. Taken with the literature data, these observations show a number of clear patterns. Some of the patterns are easily interpretable as adaptations to inform the spider of the locations of lines in its web, and to save time and/or effort as the spider moves about the web; others, however, such as the construction and subsequent destruction of radial and hub lines, seem paradoxical in these terms. These and other behaviours consistently change tensions on web lines in certain ways. Since there are theoretical reasons to expect that certain tension relationships in orbs are selectively superior to others (i.e. result in more effective traps), and since at least some of the changes which the behaviours produce are in the directions predicted by theory, it is argued that these paradoxical behaviours function to adjust the tensions in web lines during construction. Some basic ideas regarding the relative advantages of different tension relationships in orbs are set out below, and then observations of behaviour are described and discussed in the light of these ideas.

Tensions on radial lines in orb webs can modify two functionally important properties of the webs — the transmission of vibrations from the prey to the spider, and the ability of the web to resist loads without rupturing. While more tense lines transmit vibrations with less damping, it is improbable that uniformity or non-uniformity of radial tensions within a given orb is biologically important. Finck *et al.* (1975) showed that webs of *A. diadematus* are not effective transducers of airborne sound, and the behaviour of the spiders on their webs confirms that airborne vibrations are of little biological importance (the spiders almost never respond to prey until they actually hit the web). Transmission of *web-borne vibrations is, on the other hand,* undoubtedly important, but the idea that radial tensions are "tuned" so as to transmit certain frequencies (presumably characteristic of their prey) especially well seems unlikely to be true since (a) there is considerable variability in the web-borne vibrations of prey both within and between species (Suter, 1978; see also Liesenfeld, 1956; Burgess, 1979), and (b) orb weavers (at least 6 of the 9 species for which there are more than 100 prey records) capture a very wide variety of prey (less than 75% of captures in any single order) (Robinson & Robinson, 1970, 1973; Nyffeler & Benz, 1978, 1979; LeSar & Unzicker, 1978; Castillo — unpublished data on prey

of *Metazygia gregalis* (O. P.-C.)) (most of these studies were done in only a single habitat, and thus probably underestimate the variety of prey captured by the species — see Nyffeler & Benz, 1978).

On the other hand, the magnitudes of the differences between tensions on the radii in an orb can be important in the web's mechanical stability (its ability to resist loads applied to it). Langer (pers. comm.) has noted that for an orb of given geometry and consisting of a given volume of silk, the web's ability to resist non-localised loads such as those applied by wind forces perpendicular to the web plane will be greatest when all homologous lines (e.g. all radii) are equally stressed (in an orb with all radii of equal diameters, this would mean equal tensions on all radii, since "stress" = tension/cross-sectional area of the line in its tensed state). This is basically the same idea as that of "Maxwell's lemma" which states (Denny, 1976) that "if every member of a structure built of one substance is under tension such that *the stress in all members is equal* and equal to the breaking stress of the material, the structure is built with the minimum volume necessary to resist the forces causing the tensions in its members" (italics are Denny's).

Webs in nature must also resist localised loads such as the impact of prey and detritus. To stop an object with a mass M, the web must apply a force equal to Ma, where a is the rate of deceleration; the shorter the distance in which the deceleration occurs, the greater the force which must be exerted and the greater the likelihood of rupture (Denny, 1976). Thus the longer of two otherwise equal lines held at equal tensions will stop heavier (or faster moving) objects than the shorter; and if otherwise equal lines are held at different tensions, the less tense one will stop heavier or faster moving objects without rupturing. Although radii in orb webs are generally attached to flexible lines rather than to rigid supports, when loaded the systems of lines to which they are attached (frame at one end, hub lines at the other) are extended much less than the radii, and a loaded radius sags more or less as if its ends were fixed (Liesenfeld, 1956; pers. obs.). Thus the length of a radius will strongly influence its ability to resist localised loads. The functional inferiority of shorter radii could be reduced by installing them under lower tensions, but in fact, as will be shown below, such

radii are usually under *greater* tensions in orb webs.

There are few published data relating to balances of tensions in orb webs. The most important study is that of Denny (1976) on *Nuctenea sclopetaria* (Cl.) (=*Araneus sericatus* Cl.) in which he measured the tension on one anchor line and then used trigonometric relations to calculate the tensions on all radii and frames in the web. He found that the radial tensions varied substantially — between 0.418 and 3.385 $N \times 10^{-4}$ (N = Newtons) in a single web, and that stresses ranged from 8 to 54 MN/m^2. It is not clear however from his descriptions whether the cross-sectional area of each radius was determined (he showed that these vary in unstressed fibres by a ratio of 1 to 2.94, and Work (1977) found coefficients of variation in fibre diameters in webs of four araneids ranging from 15% in *Eriophora fuliginea* (C. L. Koch) to 34% in *Argiope aurantia* Lucas) or whether just the average cross-sectional areas were used for all radii. Eberhard (1972) deduced from angles between the lines in the hubs of *Uloborus diversus* Marx (Uloboridae) that all radii were not equally tense, but the magnitudes of these differences were not determined. LeGuelte (1969a) showed experimentally that *Zygiella x-notata* (Cl.) is capable of sensing radial tension, and lays radii during the early stages of radius construction so as to reduce differences between them. He showed in addition that radii with larger angles between them were under more tension than others in *Z. x-notata* webs.

These data show that in the webs of three species radial tensions are not uniform. A consideration of the effects of the geometry of orbs on the tensions on radii suggests that it is possible to generalise that inequalities in radial tensions occur in nearly all orbs (Fig. 1). Most orb webs have more radii (i.e. smaller interradial angles) in one "half" (180° sector) — generally the lower, larger half. If one considers the tensions at the hub of such an orb, the sum of the forces pulling it in one direction (e.g. the sum of the downward components of the tensions on the radii below the hub — downward arrow in Fig. 1) must be exactly equal to the sum of the forces pulling it in the other direction (upward arrow). Since the downward force is divided among more radii than the upward force, the tension/radius must be smaller in the radii in the half with more radii. This argument applies equally well in horizontal webs with larger angles

between radii in one half than in the other (see Eberhard, 1972).

Another asymmetry is also important. Many spiders rest at the hubs of their webs waiting for prey. In more or less vertical orbs, this means that the spider's own weight increases the tensions on the radii above the hub, and decreases those on the radii below (Langer, 1969). Since there are usually fewer radii in the upper half of non-horizontal orbs (e.g. LeGuelte, 1969b; Witt et al., 1968), the presence of the spider at the hub must increase the differences in tensions on different radii in these webs. For both of these reasons, the geometry of orb webs usually results in substantial differences in tensions on radii.

The differences in the stresses on the radii would depend on the diameters of the fibres and the number of fibres in each' radial line as well as on their tensions, and would be smaller than the differences in tensions if those lines which support larger tensions (those in the upper half) were thicker. As noted above, radial cross-sectional areas vary by a factor of nearly three in one species (Denny, 1976); whether thicker radii were shorter or in the upper portions of orbs was not determined.

The differences in tensions suggest that other selective factors rather than mechanical stability under generalised and localised loads have been important in producing the typical orb patterns with fewer radii in smaller, usually upper parts of the web (see Witt, 1965 and Eberhard, 1972 for selective factors which could have favoured these patterns). However, even in webs whose geometry precludes equalisation of radial tensions, any tendency toward a reduction of the *differences* in tensions on radii will increase the web's resistance to generalised loads, and if it results in the reduction of tensions on shorter radii, will also increase its resistance to localised loads. Such tendencies would be favoured by natural selection.

There is also reason for expecting that differences in tensions on sticky spiral lines will influence the ability of an orb to capture prey. The sticky spiral serves both to stop prey when it hits the web and to hold it there until the spider arrives to attack. In general, as argued by Denny (1976), both functions will be performed better by looser, more elastic lines. Just as with radii, there may be an advantage in laying all sticky spiral lines at more or less equal
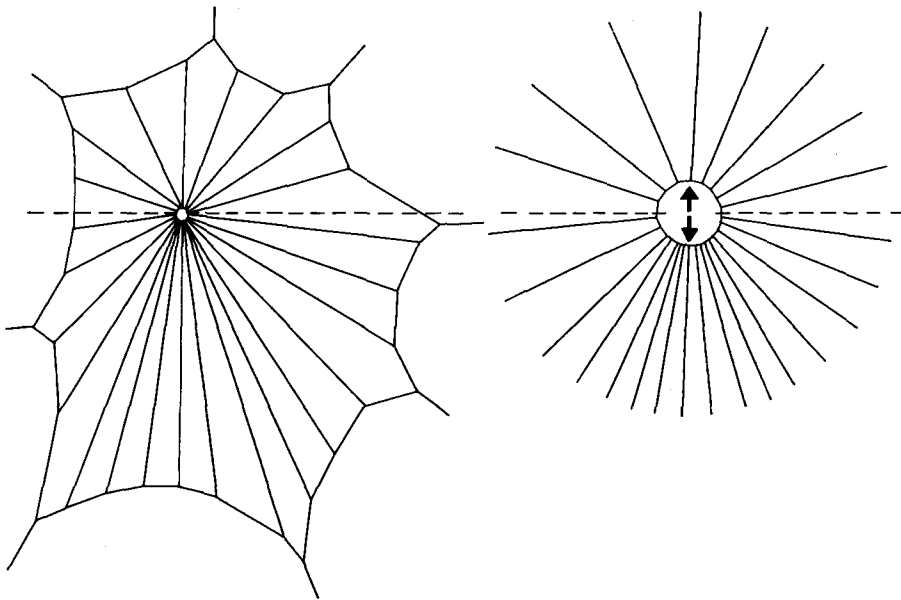

Fig. 1: Balance of radial tensions in a typical orb web. Radii in the part with more numerous radii tend to be under less tension than the others (see text).

tensions, but in this case the advantage is unlikely to be structural since the high extensibility of sticky spiral line (DeWilde, 1943; Liesenfeld, 1956; Denny, 1976) probably makes it relatively unimportant in considerations of tensions on other lines in the web. The spider would, however, maximise the effectiveness of the material it has available for sticky spiral by making it neither too tight, as that would reduce the trapping effectiveness because the line would be more easily broken, nor too loose, since, assuming the spider has a limited supply of silk, investment of too much line in some segments would reduce the total length of sticky line in the web and thus reduce the trapping surface. Also, if the line were excessively loose it would be more likely to sag into contact with neighbouring lines and become entangled, thereby effectively wasting line by creating holes in the web.

The visco-elastic character of spider silks may be important with respect to some of the points made above. The tension in a line of silk decreases gradually when the line is held in an extended position. Thus the tensions on lines in a spider web will gradually decrease somewhat after the lines are installed. Denny's study (1976) of stress-relaxation in *Nuctenea sclopetaria* frame silk suggests that the changes may be substantial, at least at high extensions, and that probably the major part of the relaxation occurs within 20-60 minutes (the length of time the spider usually spends in web construction). Thus the total relaxation of a line extended to $\lambda = 1.2$ (120% of its unstressed length) amounted to 27.5% of the stress present at t_0 (time zero); 48% of this relaxation occurred in the first 30 seconds, and 88% within 16 minutes. Data for lower extensions which would be characteristic of web construction ($\lambda \approx 1.01$ for lines in orbs — Denny, 1976; Fig. 2) are not available however. Probably relaxations are relatively rapid at these extensions also, since Denny notes that for small extensions "while the value of E_t at time zero was accurately measurable, the decay of E_t with time quickly brought the forces involved to a level too low for accurate measurement." Relaxation of sticky spiral silk was much more rapid (67% of final relaxation occurred in 10 sec. when $\lambda = 2.25$). Nevertheless most orb weavers lay each segment of sticky spiral within 1-2 seconds, so much of the relaxation in any given segment probably occurs after the spider has attached both ends to

radii. Again Denny's experiments were with extensions considerably greater than those in normal orbs (DeWilde, 1943, found however that sticky spiral lines were at $\lambda = 5.0$-7.0 in webs of *Meta reticulata* (L.)).

The significance of these relaxations for spiders building webs is not clear. Probably by the time a spider has finished its orb (usually more than 20 minutes' after laying the radii and frames), the tensions on radial and frame lines have diminished appreciably, especially on lines which were laid at especially high tensions. This would mean that during radius construction the spider would not be able to sense the tensions which the radii would be under in the finished web, but by the time it had finished the sticky spiral the radii would have completed most of their relaxation.
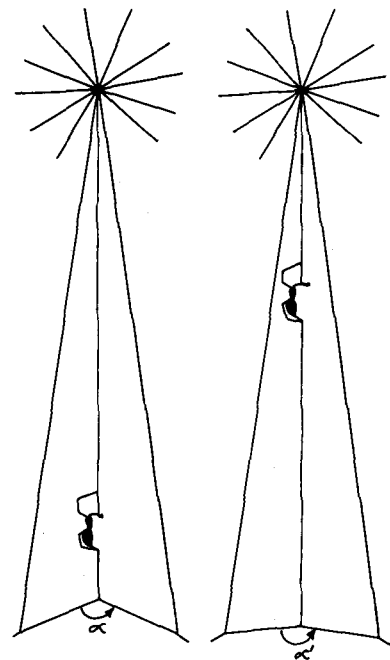

Fig. 2: Method of observing changes in the tension on a radius as it is laid. The more that a vertical radius below the hub pulled the frame out of position (indicated by angle α), the greater the tension (other radii could not be observed in this way because the weight of the spider contributed to the tension exerted by the radius on the frame). The tension is greater in the left hand figure because α is less than α'. Observations of a number of genera indicated that spiders usually reduce tensions on new radii as they return to the hub.

Materials and Methods

Most of the observations were made on spiders which have been identified only to genus; the specimens are deposited in the Museum of Comparative Zoology, Cambridge, Mass. 02138, U.S.A. and are referred to in the text by the numbered labels which are included with them in their vials. The inclusion of a given genus in the list for one behaviour and not for another does not necessarily mean that it does not perform the second behaviour, since the ease of observation of different details varied, as did my attention to different details on different occasions. Unless otherwise noted all behavioural observations are believed to be original. References to subfamilies refer to the classification of Simon (1894-5).
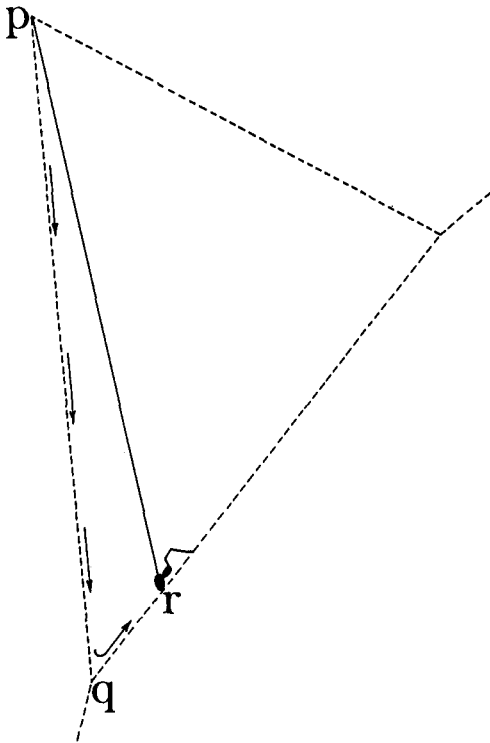

Fig. 3: Path of a spider laying a radius (*p* to *q* to *r*) showing how it must sometimes insert a radius shorter than its outward track (*p* to *q* > *p* to *r*). Since the spider does not gather up silk before attaching the radius to the frame, such movements result in a reduction of tension on the radial line.

Results

Radius Construction

Observations

Spiders lay radii by starting from the hub and moving to the web's edge (frame), then returning to the hub. A line is pulled passively from the spinnerets as the spider moves. Some orb weavers leave the line which is laid on the way to the frame in place in the web, and either reinforce it or make a second radius adjacent to it with the line laid on the return to the hub (Nephilinae, Uloboridae, *Cyrtophora, Mecynogea* and a few other Araneinae — see Eberhard, in press). But most orb weavers (most Araneinae, Tetragnathinae, Metinae and Theridiosomatidae) break the first line, and replace it with the line they lay on the return to the hub (the composition of the original lines is not known for any species, and the composition of the replacement lines is known for only a few species). Why do these spiders perform the seemingly wasteful act of cutting and removing a line which has just been laid?

It was often clear, from observations of angles between frames and radii which were directed downward and thus did not support the spider's weight as it moved upwards towards the hub (Fig. 2), that when a spider broke the first line and replaced it, the tension on the new radius changed as the spider returned to the hub. Such changes were noted in species in the genera *Chrysometa, Cyclosa, Cyrtarachne, Epeirotypus, Eriophora, Eustala, Gasteracantha, Leucauge, Micrathena, Neoscona, Tetragnatha, Theridiosoma* and *Tylorida.* All changes left the finished radius at a lower tension than the tension at the moment when it was broken. In some species, such as *Cyclosa caroli* (Hentz) and *Micrathena sexspinosa* (Hahn), the tensions changed systematically, decreasing when the spider first broke the line, then increasing as it moved towards the hub, and finally decreasing again when the spider reached the hub and attached the new line there. In *Cyclosa* sp. (#2028), *Eriophora* sp. (#2132), *Theridiosoma* sp. (#2184) and *Chrysometa* sp. (#1824) (Araneidae) and the mysmenid *Maymena* sp. (#2168) I saw that the spider made pulling movements with one or both legs IV on the new radius just as it arrived at the hub.

Discussion

The functional significance of this behaviour may be that it allows the spider to make adjustments to the tensions of radii as they are laid. In the first place, as illustrated in Fig. 3, the path taken by a spider from the hub to the site where it will attach a new radial line sometimes involves moving along the frame in a direction partly back towards the hub, with the result that the new radial line is shorter than the exit radius. Since spiders do not reel in the extra silk before attaching to the frame, such movements must slacken the line just laid (LeGuelte, 1966; Eberhard, 1972). Since angles between frames and radii vary widely, it may thus be difficult for a spider to control the tensions on all radii it lays. The return trip to the hub, however, is always direct, so tension control is more feasible.

Secondly, the tension on a given radius in a finished non-horizontal web with the spider resting at the hub is determined partly by the spider's weight. Since many (most) orb weavers rest at the hub and very few orbs are exactly horizontal, this is a very common phenomenon. One consequence is that when a spider attaches a radius to a frame, it is in a particularly poor situation to sense how tense that line will be in the finished web because its own weight is not tensing or relaxing the lines as it will in the finished structure. On the other hand, when the spider reaches the hub on the return trip, its weight is where it will be in the finished web, and it is more feasible to sense tension relationships as they will be when the web is completed.

The consistent lowering of radial tensions observed as a result of breaking the original line and replacing it is in accord with the tension adjustment hypothesis. Since the spiders do not adjust line tensions upward by gathering in silk to tighten slack lines, the most logical behaviour for a spider laying a radial line whose final tension will be determined only when the spider returns to the hub is for the spider to hold the line at a tension sure to be higher than the final tension, then release just enough additional line to bring the tension to the desired value and then attach the radius at the hub. In some species the additional length is apparently pulled from the spinnerets with legs IV; in others which release extra line without moving legs IV, it may result from shifting the grip

which tarsus IV maintains at all times on the new line as it is laid.

Point where radius is broken

Observation

A puzzling detail of radius construction is that the point where the radius is broken varies between species. Some, such as *Araneus diadematus*, *Micrathena schreibersi* (Perty), *M. gracilis* (Walck.), *Eriophora* sp. (#2132), *Leucauge* sp. near *venusta* (Walck.) and #1982, and *Argiope argentata* (Fabr.), break the line near the frame, while others such as *Micrathena sexspinosa*, *Neoscona* sp. (#1947), *Tetragnatha* sp. (#2043) and *Tylorida striata* (Thorell) do not break it until they have moved about one third to one half of the distance to the hub. The behaviour of *Cyclosa caroli* varied even within a single web, and sometimes the line was cut near the frame and other times only after the spider had moved about half the distance to the hub. The radii in the webs of some species are thus doubled in their outer portions.

Discussion

Doubling a substantial portion of the radius would seem to be advantageous since it would strengthen the lines, but the silk which is removed is subsequently ingested by the spider (see below) and is thus not wasted.

"False starts"

Observations

Gasteracantha cancriformis (L.), *Tetragnatha* sp. (#2190) and *Leucauge* sp. near *venusta* occasionally start away from the hub as if to lay another radius, but then break the existing radius which they are on, turn back, and replace the inner portion of the radius as they return to the hub and then continue to lay other radii. The angle which this modified radius made with the frame to which it was attached changed consistently in a way that indicated that the radial tension was reduced as a result of this process. All anapids observed (*Anapis calima* Platnick & Shadab, *A. heredia* Platnick & Shadab, *Anapis* sp. (#2166) and *Anapisona simoni* Gertsch), the mysmenid *Maymena* sp. (#2168) and the symphytog-

nathid *Patu* sp. (#2194) perform analogous operations on all the web radii after the sticky spiral is completed. In all cases the distance between the hub and the innermost sticky spiral line crossing the radius being modified increased — a clear indication that the radius was lengthened and that its tension was thus reduced.

Discussion

These behaviours are so simple, resulting in little other than radius tension modification, that it is difficult to infer any function other than tension adjustment.

Removal of the Hub Centre

Observations

Construction of a centre portion of the hub which is then removed a short while later (usually after the last sticky spiral line is completed) is performed by nearly all orb weavers which have been observed (exceptions among the 119 species in Table 1 of Eberhard (in press) are the Uloboridae and

Nephilinae, *Tetragnatha* sp. (#2043), *Cyrtarachne* sp. (#1994), *Glenognatha* sp. (#0-8), *Cyrtophora nympha* Simon, *Mecynogea* sp. (#1038), *Spilasma artifex* Simon and *Cyrtognatha* sp. (#538)). The centre of the hub is removed when the web is essentially complete, with the radii interconnected both at the centre of the hub and by a series of approximately circular hub loops (Fig. 4). The spider moves to the hub and pulls the centre region to its mouth, usually with its palps and/or legs III. The lines there (mostly rolled up pieces of broken radii that accumulated during radius construction) disappear (probably they are degraded enzymatically and then ingested — see Tillinghast & Kavanaugh, 1977). In some species (those with webs with open hubs) this is the last act of web construction, and the spider settles at the hub to await prey. But in many others (most Araneinae, Anapidae and some Theridiosomatidae — Eberhard, in press) the spider immediately proceeds to replace the lines it has just removed, filling the hole it created with a number of additional lines.

Photographs of the hubs of *Argiope argentata* webs taken before and after the centre of the hub was
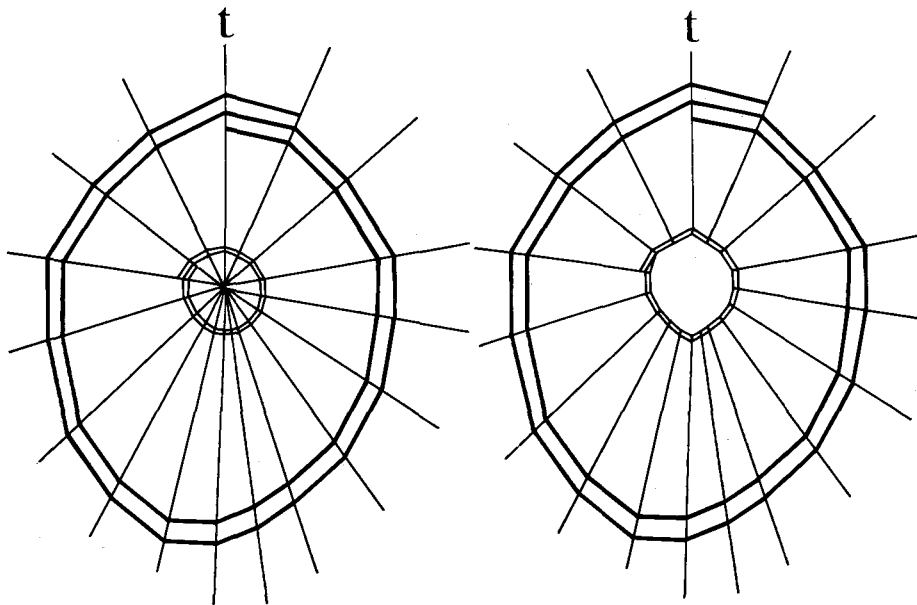

Fig. 4: Schematic representation of a hub before and after the centre is removed. The destruction of the central lines causes the hub to expand, with a consequent relaxation of radial tensions. If some radii (e.g. *t*) are under more tension than their neighbours in the original web, they will pull harder on the hub lines and cause a greater expansion of the hub in their direction and thus a greater reduction in their own tensions.

eaten and replaced (Fig. 5) show that the changes are sometimes complex. Measurements of distances between selected line junctions indicated that the tensions on some radii increased while those on others decreased. This gives clear evidence that tension redistributions such as those being proposed can occur, but of course does not prove that such adjustments are the function of removing the centre of the hub. It should be noted that net increases in radial tensions occurred despite the general loosening effect of sticky spiral placement (Eberhard, 1969); because of the very high extensibility of the sticky spiral (DeWilde, 1943; Liesenfeld, 1956; Denny, 1976) this effect is probably relatively small.

Discussion

Why do spiders perform this apparently unneces-

sary destruction and replacement? Tolbert (1979) speculated that removal of the centre of the hub by *Argiope trifasciata* (Forskal) may serve to increase the spider's exposure to the rays of the sun, but even if this is true it cannot be a general explanation since many nocturnal species remove the centres of their hubs and many others fill in the holes with other lines as soon as they are made. Other possible functions involve tendencies to reduce differences in radial tensions. The removal of tensed central lines will inevitably (*a*) reduce tensions on radii; in addition, it will (*b*) tend to diminish the differences in tensions between radii. It is possible to imagine mechanical advantages for both of these tension modifications. Reduction of tension differences (*b*) would be advantageous for the reasons given above. A general tension reduction (*a*) could be advantageous because
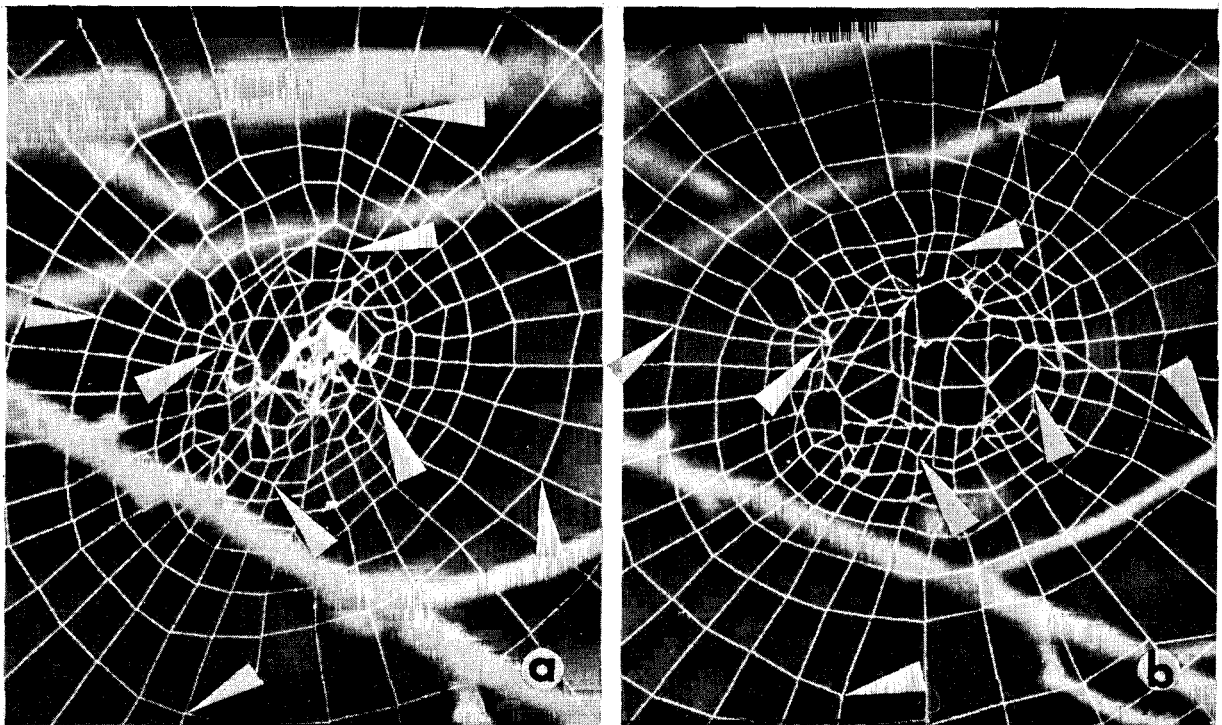

Fig. 5: The hub of a web of *Argiope argentata* before and after the centre was removed and replaced; (a) during temporary spiral construction, (b) after the web was completed. The arrows indicate corresponding line junctions in the two photographs. Measurements of distances between junctions indicate that the horizontal distance across the inner edge of the hub hole increased 30%, and across the outer edge of the hub 2%; corresponding figures for vertical distances were decreases of 16% and 5%. Horizontal radii were thus loosened, and vertical radii tightened. Other webs showed different patterns of change (the photographs are to the same scale).

of the following. If the web lines are under very low tensions while the spider is building, the spider's own weight distorts the lines in its vicinity making it difficult for the spider to sense the relative positions of lines as they will be in the finished web (Fig. 6; see also Witt *et al.*, 1968, fig. 35). Once construction is finished, this is no longer a problem, and the web will be better able to absorb the momentum of impacting prey if it is looser (e.g. Denny, 1976) (too great a loosening, however, probably makes webs less stable under wind stress — see Langer, 1969). The
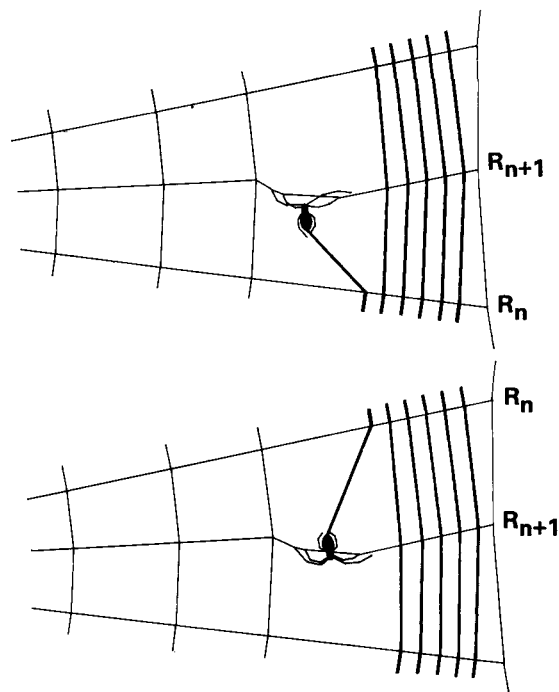

Fig. 6: Diagrammatic illustration of how the weight of a spider laying sticky spiral causes the radii to sag, thereby changing the distances between the points where sticky spiral is attached when the spider is on horizontal radii in more or less vertical webs. As the spider moves upwards (above), its weight causes R_{n+1} to sag *towards* the latest sticky spiral attachment (on R_n); when it moves downwards (below) it causes R_{n+1} to sag *away from* the attachment. Differences in sticky spiral construction behaviour when going up and going down seem to be designed to compensate for the spider's deformation of its web, and reduce differences in tensions on sticky spiral lines.

dramatic tension reductions performed by the mysmenid, symphytognathid and anapids mentioned above, which break and lengthen all radii, probably resulted from selection favouring function (*a*).

It is interesting to note that some spiders behave as if (*a*) may not be important, at least in so far as maintaining the web under tension until sticky spiral construction is completed. These spiders, which include *Cyclosa caroli, Cyclosa* sp. (#1961), *Micrathena triangularis* (C. L. Koch) (?), *Gasteracantha* sp. (#2036) and *Leucauge* sp. (#1936), normally build their webs in the early morning, but I have observed that if it is raining at that time, some individuals build webs with radii, frames, hub loops and temporary spirals, and then wait until the rain stops before laying sticky spiral. Hypothesis (*a*) would predict that spiders would not remove the centre of the hub until after the sticky spiral was finished; but in fact I have observed all of these species to remove the centre on rainy mornings before laying sticky spiral. This does not mean, however, that (*a*) can be discarded with respect to radius and temporary spiral construction; in fact one would expect *a priori* that because of the bracing effect of the temporary spiral on radii, (*a*) would be less important with respect to the placement of sticky spiral than to that of radii and the temporary spiral.

Lack of hub destruction behaviour

Observations

One further point is that the lack of hub destruction behaviour in a few araneid species which are in subfamilies in which it normally occurs (Araneinae, Tetragnathinae, Metinae — it is known to occur in 27 genera in these subfamilies — see Eberhard, in press) seems to be associated with reduction in the number of lines and structural complexity of the orb. It has been lost in species of *Glenognatha, Cyrtognatha, Tetragnatha, Mecynogea, Verrucosa, Cyrtarachne* and *Hypophthalma*. The *Tetragnatha* species (#2043) is a special case since it builds its web with a twig running through the centre of the hub, and removal of the hub centre is thus out of the question (at least six other *Tetragnatha* species whose behaviour is known remove the centres of their hubs). Likewise *Mecynogea* is special because its web does not have sticky silk, the radii are extremely closely

spaced, most radii do not originate at the hub, and the way in which the web functions is different from that of a typical orb (see Lubin, 1973). Of the rest, all except *Verrucosa undecimvariolata* (O. P.-C.) and *Hypophthalma* sp. (#1586) have substantially reduced orbs.

Discussion

This association between simplified orbs and the lack of hub destruction is understandable in terms of the tension adjustment hypothesis since the tensions on radii laid early in web construction are modified by the placement of subsequent radii; the simpler the network of lines, the easier it is to make adequate tension adjustments as the lines are laid instead of later.

These considerations are attempts to answer the question "Why remove the centre of the hub?" There remains the question of "Why replace it immediately with other lines?" A possible explanation again comes from considering the mechanical consequences of the spider's behaviour. When a spider removes and then fills the hub centre, there is first a general reduction and at least a partial equalisation of radial tensions, and then an overall tension increase when the new threads are added (but Fig. 5 shows that the changes can be complex). Perhaps the secondary increase in tension serves to make the web more resistant to generalised loads such as wind.

Sticky Spiral Construction

(a) Pulling silk with legs IV

Observations

As a spider moves between one attachment of the sticky spiral and the next, sticky line is pulled from the spinnerets. In addition, the spider often grabs the sticky line near the spinnerets with one leg IV and then rapidly extends this leg and releases the line, thereby probably (see below) pulling out an additional length of line. This behaviour, involving either alternate pulls with the two legs IV or consecutive pulls with a single leg, has been observed in species of the orb-weaving genera *Tetragnatha, Leucauge, Chrysometa, Argiope, Wagneriana, Cyclosa, Eustala, Araneus* (Jacobi-Kleemann, 1953; pers. obs.), *Alpaida, Eriophora, Metazygia, Neoscona,*

Gasteracantha (Peters, 1954; Robinson & Robinson, 1975; pers. obs.), *Micrathena, Cyrtarachne, Nephila* (Peters, 1954), *Parawixia* and *Hypophthalma* (all Araneidae), *Epeirotypus* (Theridiosomatidae), and *Anapisona* and *Anapis* (Anapidae).

It is conceivable that the tarsus actually slips along the line rather than pulling more thread: I could not convince' myself on this point by direct observations of the tarsi, and Robinson & Robinson (1975) interpret a similar movement by *Pasilobus* sp. to be a sliding movement. Peters (1954) thought the movement served to pull more silk. The pulling hypothesis was confirmed for at least some species (*Alpaida rhodomela* (Taczanowski), *Micrathena* sp. (#1877), *Eriophora* sp. (#1836), *Eustala* sp. (#1841) and *Wagneriana* sp. (#574) by observations of a gradual lowering of tension on the sticky spiral (deduced from sticky spiral-radius angles in the manner illustrated in Fig. 2) while pulling was performed. J. Coddington (pers. comm.) reached the same conclusion regarding pulling vs. slipping from observations made after applying light coats of powder to lines as they were produced by the theridiosomatid *Theridiosoma radiosum* (Emerton).

Uloborus diversus Marx (Eberhard, 1972), *Hyptiotes paradoxus* (C. L. Koch) (Marples & Marples, 1937), *Philoponella vittata* (Nicolet) and *P. vicina* (O. P.-C.) probably achieve similar tension reduction by continuing to comb out "sticky" cribellum silk for several seconds just before they attach the "sticky" spiral to a radius; in these species the "sticky" line is not nearly as extensible as that of the araneids.

The number of pulls clearly decreased as the spider approached the hub in *A. rhodomela, M. sexspinosa, Eriophora* spp. (#1836, 2153), *Cyclosa* sp. (#1832), *Chrysometa* sp. (#1824), *Neoscona* sp. (#1573), *Gasteracantha cancriformis* (Peters, 1954, and pers. obs.) and *G.* sp. (prob. *theisi* Guérin) (Robinson & Robinson, 1975), *Verrucosa* sp. (#2196), *Parawixia* sp. (#2204) and *Metazygia wittfeldae* (McCook). The opposite tendency was observed in three theridiosomatid species in the genera *Theridiosoma* (?) (#984) and *Epeirotypus* (?) (#0-7, 1666) and in the anapid *Anapis* sp. (#2166) which made more rather than fewer pulls as they neared the hub. The webs of these four species differed from those of the other species observed in that the outermost temporary

spiral lines, which the spiders used as bridges between radii, were far from the outer sticky spiral lines but not from the inner sticky spiral lines (Fig. 7) (the anapid had no temporary spiral). A final variation, seen in *Micrathena sexspinosa, M. triangularis* (?), *Cyclosa caroli, Gasteracantha* sp. (#2036), *Cyclosa* sp., *Metazygia wittfeldae* and *Eriophora* spp. (#1836, 1945, 2153), involved making more pulls when the spider was moving upwards in its web than when it was moving downwards (all make more or less vertical webs).

Discussion

The pulling movements of legs IV on the sticky line result in a reduction of the tension on sticky spiral lines. Such a reduction will result in an improvement in the line's ability to stop and retain prey, so it is reasonable to suppose that tension reduction may be the function of this pulling behaviour.

Assuming that the force necessary to draw sticky spiral silk from the spider's spinnerets does not change consistently from one part of the web to another, all of the variations observed would also tend to reduce the *differences* in tensions on sticky spiral lines. Fewer pulls near the centre would decrease tension differences since the segments there are shorter and a given percentage lengthening (and thus a given reduction in tension) would result from fewer pulls. The exceptional behaviour of the theridiosomatids is exactly what would be expected if the tension hypothesis is true. In contrast to the other species observed, as the spider moves from radius to radius near the edge of the web by way of the temporary spiral, the length of sticky line drawn from the spider is substantially longer than the final distance between attachment points on the radii. The line drawn while the spider moves from radius to radius near the hub is comparatively shorter because of the proximity of the temporary spiral. Thus the additional silk pulled near the hub would lower the tensions on these inner lines and make them more similar to the tensions on sticky spiral lines near the web's edge. The other orb weavers do not have this problem owing to their larger sizes and/or less distant temporary spirals. The changes in behaviour when going up and going down are also in accord with the tension adjustment hypothesis, since horizontal radii in some webs sag substantially under the spider's weight as it lays the sticky spiral (Fig. 6), and the inequalities in sticky spiral tensions which might result could be reduced by not pulling out extra lengths of sticky line while descending across horizontal radii.

(b) "Pushing" the sticky spiral just before attaching it

Observations

All araneoid orb weavers which have been observed laying sticky spiral place one leg IV on the sticky line and push it ventro-posteriorly just before attaching it to a radius (Eberhard, in press). Savory (1952) and Robinson & Robinson (1975) thought that this behaviour served to break the adhesive on the lines into balls, but I have shown (Eberhard, 1976 — also see below) that the formation of balls does not result from this behaviour.

Discussion

Pushing behaviour probably represents a pulling movement similar to those described above but performed just before the attachment to the radius. I have not been able to confirm by direct observation that additional line is pulled, but observations of variations in pushing behaviour support the tension adjustment hypothesis.

(c) Variations in pushing behaviour

Observations

Two species of *Neoscona* (#1947, 2054), *Micrathena sexspinosa, M.* spp. (#1877, 0-13a), *Cyclosa caroli* and *Gasteracantha* sp. (#2036) were all observed to cease making pushing movements as they laid sticky spiral while descending in more or less vertical webs, then resume it as they circled onward. In addition, *Neoscona* sp. (#1947) pushed consistently near the edge of the web but ceased entirely as it laid sticky spiral near the hub. In none of these cases did the omission of pushing behaviour affect the tendency of the adhesive to break up into balls (ball formation probably results from physical properties of the adhesive; other viscous materials such as Tack Trap® also break up into balls

spontaneously when applied to nylon threads in appropriate quantities).

Discussion

These variations are similar to those seen in pulling behaviour (above), and, for the same reasons discussed there, suggest that variations in pushing behaviour serve to reduce differences in the tensions on sticky spiral lines.

(d) Localisation of innermost sticky line

Observations

Orb weavers begin laying sticky spiral lines at the edge of the web and work inwards. As they move

they use some of their legs (legs I in Uloboridae, Araneinae, Tetragnathinae, Metinae, Theridiosomatidae and Anapidae, legs IV in Nephilinae — see Eberhard, in press) repeatedly to touch the innermost sticky line already in place ("inner loop" in Fig. 7). The movements occur just before each attachment of the sticky spiral as the spider moves outwards along the radius; they often involve apparently exploratory tapping movements in the air; and as soon as the leg contacts the sticky line (or occasionally after two contacts), the spider ceases both its movement along the radius and the tapping, and turns to make the attachment.

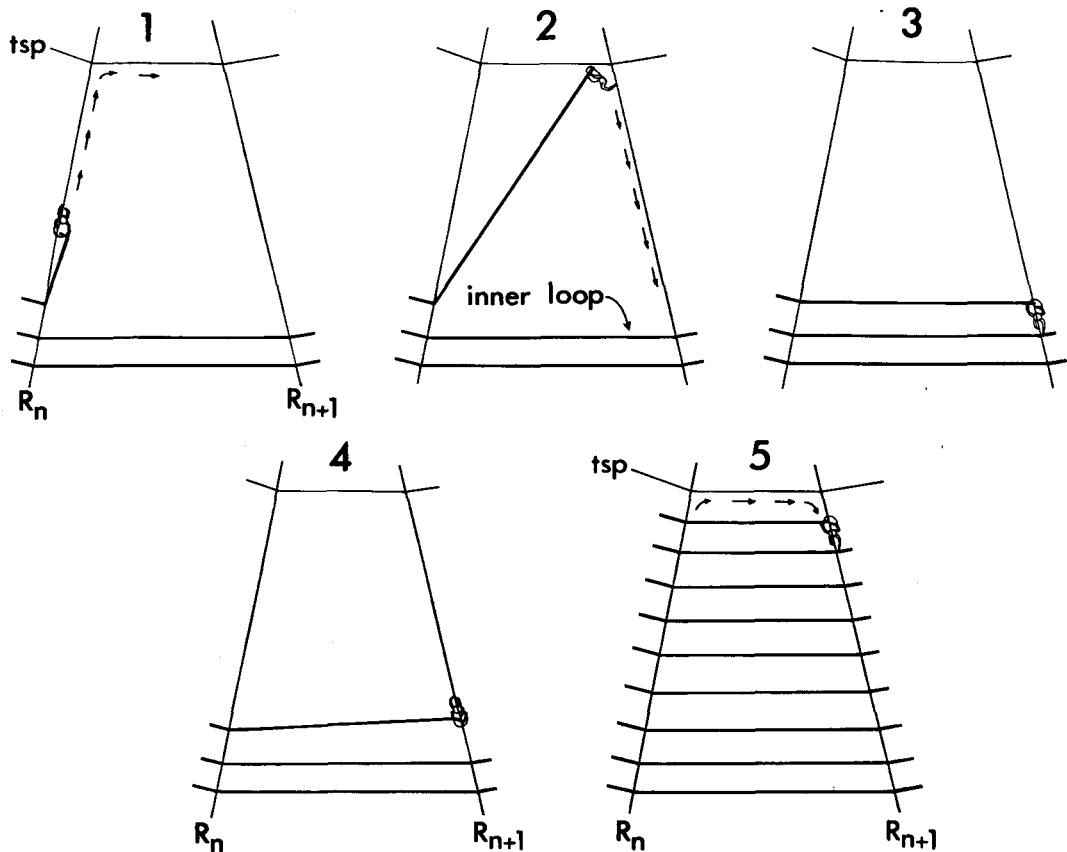Although nephilines did not tap with their legs IV but instead moved them directly from one radius to

Fig. 7: Movements (diagrammatic) of *Epeirotypus* (?) sp. (#1863) as it laid sticky spiral from one radius (R_n) to the next (R_{n+1}) near the edge of its web (1-4) and near the hub (5). Near the edge the spider's path by way of the temporary spiral (tsp) took it farther from the point of attachment to R_n than the final distance to be spanned; near the hub this was not true, and spiders apparently compensated for this near the hub by pulling extra lengths of silk with their hind legs.

the next, it was clear in both *Nephila clavipes* (L.) and *N. maculata* (Fabr.) that the leg often slid along the radius just before gripping it until contact was made with the innermost sticky spiral line (or the outermost temporary spiral line). One individual of *Nephilengys malabarensis* (Walck.) which had one leg IV damaged (it was held stiffly aloft and did not grip lines) moved too rapidly for me to distinguish details of its behaviour, but when this leg was in position to grip the radius, the sticky spiral was laid with very irregular spacing from the innermost line, while when the spider moved in the opposite direction on the web so that the other, intact leg IV was in position to grip the radius, the spacing was normal. Hingston (1922) also observed that the sticky spiral spacing became irregular when the tips of legs IV of *Nephila maculata* were removed.

Discussion

The form and timing of tapping behaviour and the behaviour which immediately follows contact with the innermost line all indicate that it is a sensory movement whose function is to locate the innermost line of sticky spiral; this was also the conclusion reached by Hingston (1920, 1922) from his observations of *N. maculata* and *"Araneus nauticus* (L. Koch)" and by Peters (1954) from observations of *Araneus* and *Gasteracantha*. The effects of damage to legs IV of *Nephila* and *Nephilengys* and legs I of *"Araneus nauticus"* support this interpretation. The probable adaptive significance of localisation of the innermost line is that in order to spin a web with an orderly array of sticky spirals, the spider must determine the location of the sticky lines already in place so as to be able to space the line it is spinning at some standard distance from those already in place. Hingston (1920, 1922) and Eberhard (1969) have shown that spiders use the position of the innermost sticky line to guide their movements.

(e) One leg "following" another

Observations

Most orb weavers build in darkness, and it is clear that they locate lines in their webs mainly if not exclusively by touch. Often, as described above, they execute probing movements with leading legs

which seem to serve this function. Sometimes other, more posteriorly located legs do not probe but instead move directly forward to seize lines which have already been located and are being held by other legs. Usually such a "following" leg grabs the line near the point where the probing leg holds it, and often the probing leg then releases its hold immediately and probes ahead again. In some cases one following leg is followed by yet another leg. The spider thus passes lines it has located "from leg to leg", and does not have to search anew with each leg. As shown in Table 1, following behaviour involving a number of different combinations of legs has been seen in a variety of species.

Discussion

Following behaviour clearly reduces the effort needed to locate lines to be held by different legs, and is probably an adaptation to enable the spider to move on its web more rapidly and efficiently.
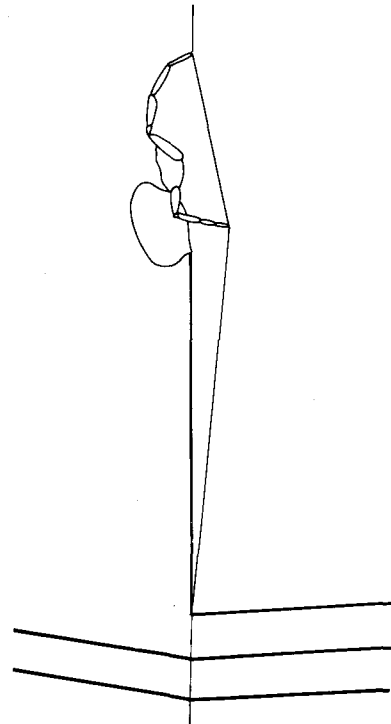

Fig. 8: Diagrammatic illustration of *Epeirotypus* (?) sp. (#1863) holding the radius (thin line) away from the sticky spiral (thick line) with its leg IV as it moves towards the hub during sticky spiral construction.

(f) One leg IV holds radius away from sticky spiral

Observations

When some spiders moved towards the hub after attaching the sticky spiral to the radius, they held the radius away from their bodies with one leg IV (Fig. 8), apparently letting the radius slide through the tarsal claw as they moved (the spiders were too small to allow certainty on this point). This behaviour was observed only in the theridiosomatids *Theridiosoma* (?) sp. (#984), *Ogulnius* (?) sp. (#1292) and *Epeirotypus* (?) spp. (#1566, 1863, #2170) and the anapids *Anapisona simoni* and *Anapis* sp. (#2166), although I also looked for it in many of the araneid species mentioned above.

Discussion

The function of this behaviour is probably to avoid having segments of the sticky line adhere to the radius. In all of these species the temporary spiral is far from the outer sticky spiral lines (e.g. Fig. 7) (in *A. simoni* and *Anapis* sp. (#2166) webs there was no temporary spiral) so the small spider must go a long distance along the radius to which it has just attached *the sticky line before moving away towards the next* radius; as is clear from Fig. 7, this means that the angle between the current segment of the sticky spiral and the radius becomes very small as the spider moves inwards, making it easy for the sticky line to adhere to the radius (in fact I saw this happen twice).

	Legs involved						
	oIV follows oII	oIV follows oIII	iIII follows iII	oII follows oI	oIII follows oII	iIV follows iIII	iII follows iI
Araneidae							
Alpaida rhodomela (Taczanowski)	+	−	+	−	+	−	−
Araneus bogotensis (Keyserling)	−	−	−	−	+	−	−
Argiope argentata (Fabricius)	+.	−	−	−	+	−	−
Argiope sp. (#1904)	+	−	−	−	+	−	−
Chrysometa sp. (#0-6)	+	−	+ˣ	−	+	−	−
Chrysometa sp. (#1824)	+.	−	−	+	+	−	+
Cyclosa sp. (#1832)	+	−	−	−	+	−	−
Cyclosa sp. (#0-10)	−	−	−	−	+	−	−
Cyclosa sp. (#1867)	+.	−	−	−	+	−	−
Eriophora sp. (#1836)	+.	−	no	−	+	−	−
Eustala sp. (#1841)	+.	−	−	−	−	−	−
Gasteracantha sp. (#2036)	−	−	−	−	−	+	−
Leucauge sp. (#0-4)	+	−	no	−	+	−	−
Metazygia sp. (#1865)	+	−	−	−	+	−	−
Micrathena sexspinosa (Hahn)	+.	−	+	−	+	−	−
Micrathena sp. (#1877)	+.	−	−	−	+	−	−
Micrathena sp. (#0-13a)	−	+	+	−	+	−	+
Nephila maculata (Fabricius) (pers. obs. and Hingston, 1922)	−	+	−	−	+	−	−
Tetragnatha sp. (#1819)	−	−	−	−	+	−	−
Tetragnatha sp. (#1823)	−	−	−	+	−	−	−
Tetragnatha sp. (#2043)	−	−	−	−	+	−	−
Uloboridae							
Uloborus diversus Marx (Eberhard, 1972)	no	−	+ˣ	−	+	−	−
Zosis geniculatus (Olivier)	−	+	−	−	−	−	−

Table 1: Following behaviour of legs of orb-weaving spiders during sticky spiral construction. ("−" = not ascertained; "." = leading leg left line before following leg arrived; "x" ≈ at least sometimes; "i" = leg on side of spider closest to the hub; "o" = leg on side of spider closest to the edge of the web).

The uloborid *Hyptiotes paradoxus,* which also has the temporary spiral far from the "sticky" lines (Marples & Marples, 1937) and the araneids *Pasilobus* sp. (Robinson & Robinson, 1975), *Poecilopachys australasia* (Griffith & Pidgeon) (Clyne, 1973), and *Cyrtarachne* sp., which spin webs without any temporary spiral, appear to solve the same problem in a different manner — by holding the abdomen away from the radius at right angles so that the spinnerets are as far from the radius as possible.

References

BURGESS, W. 1979: Web-signal processing for tolerance and group predation in the social spider *Mallos gregalis* Simon. *Anim.Behav.* **27**: 157-164.

CLYNE, D. 1973: Notes on the web of *Poecilopachys australasia* (Griffith and Pidgeon, 1833) (Araneida: Argiopidae). *Aust.entomol.Mag.* **1**(3): 23-29.

DENNY, M. 1976: The physical properties of spider's silk and their role in the design of orb-webs. *J.exp.Biol.* **65**: 483-506.

DEWILDE, J. 1943: Some physical properties of the spinning threads of *Aranea diademata.* *Archs néerl.Physiol.* **28**(1): 118-131.

EBERHARD, W. G. 1969: Computer simulation of orb-web construction. *Am.Zool.* **9**: 229-238.

EBERHARD, W. G. 1972: The web of *Uloborus diversus* (Araneae: Uloboridae). *J.Zool.,Lond.* **166**: 417-465.

EBERHARD, W. G. 1976: Physical properties of sticky spirals and their connections: sliding connections in orb webs. *J.nat.Hist.* **10**: 481-488.

EBERHARD, W. G. in press: Behavioural characters for higher classification of orb-weaving spiders. *Evolution, Lancaster, Pa.*

FINCK, A., STEWART, G. M. & REED, C. F. 1975: The orb-web as an acoustic detector. *J.acoust.Soc.Am.* **57**(3): 753-754.

HINGSTON, R. W. G. 1920: *A naturalist in Himalaya.* Small, Maynard & Co., Boston.

HINGSTON, R. W. G. 1922: The snare of the giant wood spider (*Nephila maculata*). Part II. *J.Bombay nat. Hist.Soc.* **28**(4): 911-917.

JACOBI-KLEEMANN, M. 1953: Ueber die Locomotion der Kreuzspinne *Aranea diademata* biem Netzbau (nach Filmanalysen). *Z.vergl.Physiol.* **34**: 606-654.

KOENIG, M. 1951: Beitrage zur Kenntnis des Netzbaues orbiteiler Spinnen. *Z. Tierpsychol.* **8**: 462-492.

LANGER, R. M. 1969: Elementary physics and spider webs. *Am.Zool.* **9**: 81-89.

LEGUELTE, L. 1966: *Structure de la toile de* Zygiella *x*-notata *Cl. (Araignées, Argiopidae) et facteurs que régissent le comportement de l'araignée pendant la construction de la toile.* Thése Pub.Univ.Nancy.

LEGUELTE, L. 1969a: Comportement de construction de l'araignée et tension des premiers rayons de sa toile. *Revue Comport.Anim.* **3**(1): 27-32.

LEGUELTE, L. 1969b: Peut-on expliquer la spécificité de la toile des araignées? *Revue Comport.Anim.* **3**(4): 6-12.

LE SAR, C. D. & UNZICKER, J. D. 1978: Life history, habits, and prey preferences of *Tetragnatha laboriosa* (Araneae: Tetragnathidae). *Environ.Entomol.* **7**(6): 879-884.

LIESENFELD, F. J. 1956: Untersuchungen am Netz und ueber den Erschutterungsinn von *Zygiella x-notata* (Cl.) (Araneidae). *Z.vergl.Physiol.* **38**: 563-592.

LUBIN, Y. D. 1973: Web structure and function: the non-adhesive orb-web of *Cyrtophora moluccensis* (Doleschall). *Forma et Functio* **6**: 337-358.

MAYER, G. 1952: Untersuchungen ueber Herstellung und Struktur des Radnetzes von *Aranea diadema* und *Zilla x-notata* mit besonderer Beruecksichtigung des Unterschiedes von Jungend- und Alternetzen. *Z. Tierpsychol.* **9**: 337-362.

MARPLES, M. & MARPLES, B. J. 1937: Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica.* *Proc.zool.Soc.Lond.* (A) **107**: 213-221.

NYFFELER, M. & BENZ, G. 1978: Die Beutespektren der Netzspinnen *Argiope bruennichi* (Scop.), *Araneus quadratus* Cl. und *Agelena labyrinthica* (Cl.) in Ödlandwiesen bei Zürich. *Revue suisse Zool.* **85**(4): 747-757.

NYFFELER, M. & BENZ, G. 1979: Zur ökologischen Bedeutung der Spinnen der Vegetationsschicht von Getreide- und Rapsfeldern bei Zürich (Schweiz). *Z.angew.Ent.* **87**(4): 348-376.

PETERS, H. 1936: Studien am Netz der Kreuzspinne (*Aranea diadema*). *Z.Morph.Ökol.Tiere* **32**: 613-649.

PETERS, H. 1937: Studien am Netz der Kreuzspinne (*Aranea diadema*). *Z.Morph.Ökol.Tiere* **33**: 128-150.

PETERS, H. 1939: Probleme des Kreuzspinnennetzes. *Z. Morph.Ökol.Tiere* **36**: 179-266.

PETERS, H. 1954: Estudios adicionales sobre la estructura de la red concentrica de las arañas. *Comun.Inst.trop. Invest.cient.S.Salv.* **3**(1): 1-18.

PETERS, P. 1970: Orb web construction: interaction of spider (*Araneus diadematus* Cl.) and thread configuration. *Anim.Behav.* **18**: 478-484.

REED, C. 1969: Cues in the web-building process. *Am.Zool.* **9**: 211-221.

ROBINSON, M. H. & ROBINSON, B. 1970: Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. *Zool.J.Linn.Soc.* **49**(4): 347-357.

ROBINSON, M. H. & ROBINSON, B. 1973: Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithson.Contrib.Zool.* **149**: 1-76.

ROBINSON, M. H. & ROBINSON, B. 1975: Evolution beyond the orb web: the web of the araneid spider *Pasilobus* sp., its structure, operation and construction. *Zool.J.Linn.Soc.* **56**(4): 301-314.

SAVORY, T. H. 1952: *The spider's web.* Frederick Warne & Co., New York.

SIMON, E. 1894-5: *Histoire naturelle des araignées* **1**(3-4): 489-1084. Roret, Paris.

SUTER, R. 1978: *Cyclosa turbinata* (Araneae, Araneidae): prey discrimination via web-borne vibrations. *Behav. Ecol.Sociobiol.* **3**: 283-296.

SZLEP, R. 1958: Influence of external factors on some structural properties of the garden spider (*Aranea diademata*) web. *Folia biol., Kraków* **6**: 287-299.

TILLINGHAST, G. & KAVANAUGH, E. J. 1977: The alkaline proteases of *Argiope* and their possible role in web digestion. *J.exp.Zool.* **202**: 213-222.

TILQUIN, A. 1942: *La toile géométrique des araignées.* Presses Universitaires, Paris.

TOLBERT, W. 1979: Thermal stress of the orb-weaving spider *Argiope trifasciata* (Araneae). *Oikos* **32**: 386-392.

WIEHLE, H. 1927: Beitrage zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden, und Uloboriden. *Z.Morph.Ökol.Tiere* **9**: 468-537.

WIEHLE, H. 1928: Beitrage zur Biologie der Araneen, inbesondere zur Kenntnis des Radnetzbaues. *Z.Morph. Ökol.Tiere* **11**: 115-151.

WIEHLE, H. 1929: Wietere Beitrage zur Biologie der Araneen, inbesondere zur Kenntnis des Radnetzbaues. *Z.Morph.Ökol.Tiere* **15**: 262-306.

WIEHLE, H. 1931: Neue Beitrage zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae, und Theridiidae. *Z.Morph.Ökol.Tiere* **22**: 348-400.

WITT, P. N. 1952: Ein Einfaches Prinzip zur Deutung einiger Proportionen im Spinnennetz. *Behaviour* **4**: 172-189.

WITT, P. N. 1965: Do we live in the best of all possible worlds? Spider webs suggest an answer. *Perspect.Biol. Med.* **8**(4): 475-487.

WITT, P. N. & REED, C. 1965: Spider-web building. *Science, N.Y.* **149**: 1190-1197.

WITT, P. N., REED, C. & PEAKALL, D. B. 1968: *A spider's web.* Springer-Verlag, New York.

WORK, R. W. 1977: Dimensions, birefringences, and forceelongation behavior of major and minor ampullate silk fibers from orb-web-spinning spiders — the effects of wetting on thread properties. *Text.Res.J.* **47**(10): 650-662.