Web construction patterns in a range of orb weaving spiders (Araneae)

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Abstract. We present and compare the spatial and temporal patterns of the capture web-building behaviour in different species from a range of orb weaving and non-orb weaving genera.

INTRODUCTION

The spider's web is an animal creation with a known function that allows in depth studies of its ecology, biomechanics, behaviour and evolution. Of course, a web should never be studied without its builder and operator, but important insights into the animal's biology can be gained even if the spider is temporarily neglected. However, the spider's building behaviour, its web construction, requires detailed studies not only of the structure but also of the moving animal, whether they are descriptive (e.g. Jacobi-Kleemann, 1953; Eberhard, 1990a) or experimental studies (e.g. Peters, 1937a,b; König, 1951; Vollrath, 1988).

The movement pattern of the spider during web construction resembles the final web structure, but does not perfectly match it since during construction the spider walks routes from which it later removes the threads, and it also walks detours which are later bypassed by the threads. Analysis of the pattern made by the moving spider, and its time allocation during web construction, allow us to view the behaviour on a macroscopic (total behaviour pattern) rather than microscopic (step by step action pattern) basis. We have developed a video surveillance system coupled with an image analyser to study the overall pattern in considerable detail (Zschokke & Vollrath, in press). For the observations presented in this paper we use the system for qualitative descriptions of the construction pattern generated by several species from a range of families.

MATERIAL AND METHODS

The web construction of spiders from 14 orb-weaving genera and 2 non-orb weaving genera (following the classification of Brignoli, 1983 and Platnick, 1989) were recorded using the method described in detail elsewhere (Zschokke, 1994). With this method we can automatically track the moves of the spider before, during and after web construction. Although we cannot directly record the positions of the threads we can to some extent infer them from the track of the spider when compared with photographs taken during and after web construction (Zschokke, 1994). Details of building behaviour (such as leg movements) cannot be observed but the recordings can be analysed for speed and timing of movement.

In the results section we briefly describe web construction of one or several typical representatives of each species as we have observed it with our method, and we calculated for most species the activity

patterns (resolution: 1 s) for parts of web construction in order to analyse differences in time allocation. The figures for each species follow the same general pattern: at the top, we show the complete path of the spider for each stage; on the left (A I) the path for the whole of the radius construction [after moving the proto-hub (Zschokke, 1994) until completion of the last radius), in the middle (B I) auxiliary spiral construction (from last loop of hub construction to the end of the spiral) and on the right (C I) capture spiral construction including stabilimentum construction or return to retreat, if any. Biting out the hub has been omitted since the moves of the spider during that final part of the web construction were too small to be recorded in any detail.

At the bottom of the figure (in the same order from left to right) we have extracted one or two parts of each phase and calculated the corresponding activity patterns. The extract of the radius construction shows in most cases the construction of four radii, one primary and three secondary. The activity pattern of the primary radius construction usually has three peaks: first peak: walk out to frame; second peak: make frame (walking via hub); third peak: go back to hub; (the second peak is sometimes split into two sub-peaks). The activity pattern of a secondary radius construction usually has two peaks: first peak, walk out to frame; second peak, return to hub. In some cases, the activity pattern is a series of small peaks (e.g. parts of *Hyptiotes* capture spiral construction); this is an artefact of the recordings (a slowly moving object is recorded in the same way as one moving in small jumps).

For most species we visually analysed a number of focal traits (see below) from the recorded tracks and noted their frequencies. The significance of these traits was tested using a binomial test to find out whether there was a significant preference for each species to do one thing or another. The significance of the focal traits was also tested for species differences against the classic araneid orb weaver *Araneus diadematus* using Fisher's exact test (Abacus Concepts, 1992). Not all traits could be compared even qualitatively for all species, partly because webs differ too much (e.g. *Cyrtophora* has no capture spiral), partly because some of the spiders never built webs from scratch under the conditions necessary to make our recordings (some background light) although they did completely replace existing webs.

Statistics were calculated using StatView 4.01 on a Macintosh computer.

Focal traits

In order to compare with other orb-weavers we analysed seven focal traits in particular (Table 1).

After completing the proto-radii (i.e. provisional radial threads, connecting the proto-hub to the supporting structure), *A. diadematus* moved the hub to its final position whilst constructing the first proper radius (i.e. a radius not attached to the supporting structure) together with the bridge thread (Fig. 1). We analysed (1) whether this hub position was the final one or whether the spider moved it again after the construction of a few additional radii. Note that this trait could only be analysed in vertical webs built de novo.

Frame construction was a highly variable trait, both within and between species (Eberhard, 1990a). We analysed the following parts of this behaviour (Fig. 2): (2) whether the spider attached the new frame to an existing older radius, or, after walking several steps along the frame or supporting structure, to an existing frame thread or to the supporting structure (as in Fig. 2); (3) whether the spider, after construction of the frame thread, walked back out to the end of the first radius or only to the attachment point of the frame thread (as in Fig. 2); (4) whether the spider moved the frame thread on its way back to the hub.

We also analysed (5) whether the spider continued to circle the hub (for at least one full loop) after the last radius had been laid. This trait could not be studied in webs with subsidiary radii.

During spiral construction we analysed (6) whether the spider made any U-turns in the auxiliary spiral; and (7) whether the spider reversed direction between the building of the auxiliary and the capture spiral.

RESULTS AND DISCUSSION

Araneus diadematus (Araneinae, Araneidae)

With our computerised observation method we could observe certain aspects of web construction pattern of *A. diadematus*' in particular detail, resulting in some new information on this behaviour as well as being able to compare it with that of other spiders.

TABLE 1. List of the examined focal traits (see text) of the web construction of each species. On the first line in each box, the number before the slash indicates how often that behaviour was observed, the number after the slash indicates the total number of observations (n). On the second line, the binomial probability for that trait is indicated; on the third line, the probability that the frequency of that trait in that species differed from that of *Araneus diadematus*. n/a: not applicable.

focal trait: species:	1 hub moved	2 attach frame at radius	3 walk to end of radius	4 move frame thread	5 hub loop after last radius	6 U-turn in auxiliary spiral	7 reverse between aux & cap
Araneus diadematus	7 / 32 0.0011	35 / 86 0.0526	12 / 86 <0.0001	0 / 86 <0.0001	32 / 32 <0.0001	2 / 32 <0.0001	30 / 32 <0.0001
Araniella cucurbitina	n/a	27 / 47 0.1909 0.0716	5 / 43 <0.0001 0.7894	0 / 43 <0.0001 0.9999	11 / 11 0.0005 0.9999	2 / 11 0.0320 0.2665	11 / 11 0.0005 0.9999
Larinioides patagiatus	11 / 12 0.0031 <0.0001	12 / 72 <0.0001 0.0015	1 / 72 <0.0001 0.0036	0 / 72 <0.0001 0.9999	14 / 14 <0.0001 0.9999	2 / 14 0.0065 0.5745	12 / 14 0.0065 0.5745
Zilla diodia	2 / 5 0.5000 0.5773	4 / 33 <0.0001 0.0023	0 / 33 <0.0001 0.0354	0 / 33 <0.0001 0.9999	5 / 5 0.0031 0.9999	0 / 5 0.0031 0.9999	5 / 5 0.0031 0.9999
Cyclosa insulana	4 / 4 0.0625 0.0056	9 / 29 0.0307 0.3863	3 / 29 <0.0001 0.7576	0 / 29 <0.0001 0.9999	4 / 4 0.0625 0.9999	4 / 4 0.0625 0.0003	3 / 4 0.3125 0.3053
Argiope bruennichi	n/a	20 / 71 0.0002 0.1304	13 / 71 <0.0001 0.5146	0 / 71 <0.0001 0.9999	15 / 15 <0.0001 0.9999	2 / 15 0.0037 0.5829	14 / 15 0.0005 0.9999
Argiope lobata	5 / 8 0.2045 0.0386	22 / 54 0.1102 0.9999	15 / 54 0.0007 0.0503	0 / 54 <0.0001 0.9999	8 / 8 0.0039 0.9999	5 / 8 0.3632 0.0015	8 / 8 0.0039 0.9999
Gasteracantha cancriformis	n/a	3 / 16 0.0106 0.1576	0 / 16 <0.0001 0.2051	0 / 16 <0.0001 0.9999	0 / 4 0.0625 <0.0001	0 / 4 0.0625 0.9999	4 / 4 0.0625 0.9999
Zygiella x-notata	n/a	4 / 22 0.0022 0.0799	15 / 22 0.6690 <0.0001	0 / 22 <0.0001 0.9999	3 / 13 0.0461 <0.0001	13 / 13 0.0001 <0.0001	12 / 13 0.0017 0.9999
Nephila clavipes	n/a	34 / 62 0.2629 0.0976	40 / 62 0.0150 <0.0001	0 / 62 <0.0001 0.9999	n/a	17 / 17 <0.0001 <0.0001	10 / 16 0.2272 0.0115
Uloborus walckenaerius	n/a	25 / 62 0.0809 0.9999	20 / 62 0.0036 0.0090	51 / 57 <0.0001 <0.0001	10 / 22 0.4159 <0.0001	18 / 22 0.0022 <0.0001	2 / 22 <0.0001 <0.0001
Zosis geniculatus	n/a	14 / 20 0.0590 0.0246	16 / 20 0.0059 <0.0001	15 / 20 0.0207 <0.0001	7 / 8 0.0351 0.2000	6 / 8 0.1445 0.0002	8 / 8 0.0039 0.9999
Hyptiotes paradoxus	n/a	4 / 4 0.0625 0.0322	0 / 4 0.0625 0.9999	4 / 4 0.0625 <0.0001	n/a	0 / 4 0.0625 0.9999	4 / 4 0.0625 0.9999

Our laboratory recordings of *A. diadematus* web construction showed that the proto-hub consisted of several radii – never a simple Y-structure as described by Peters (1937b) – before frame construction began. The first frame thread was always the bridge thread (Fig. 1). After construction of this bridge thread *A. diadematus* moved the hub. This new hub position was usually final (this can be different in other species, see below). The primary radius constructed together with the bridge thread formed the constructional middle of the web. For the construction of both neighbouring secondary radii, this primary radius was used as the exit radius. This was so even when the bridge thread was slanted and the new neighbouring radius being built was actually located above the exit radius. In *A. diadematus* this was the only observed exception to the rule that the exit radius is always above the new radius during frame and radii construction.
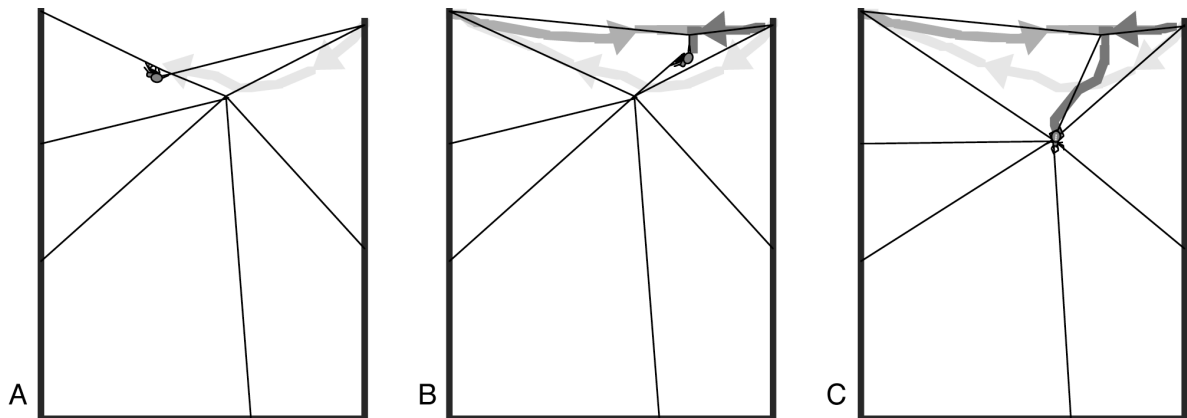
Fig. 1. Construction of bridge thread and first proper radius in *A. diadematus*. The drawings are based on recorded moves of the spider, with the threads reconstructed from those moves. In each picture, the moves of the spider are indicated with grey arrows (light grey – earlier moves; dark grey – later moves). The plain lines show the position of the threads when the "snapshot" was taken.
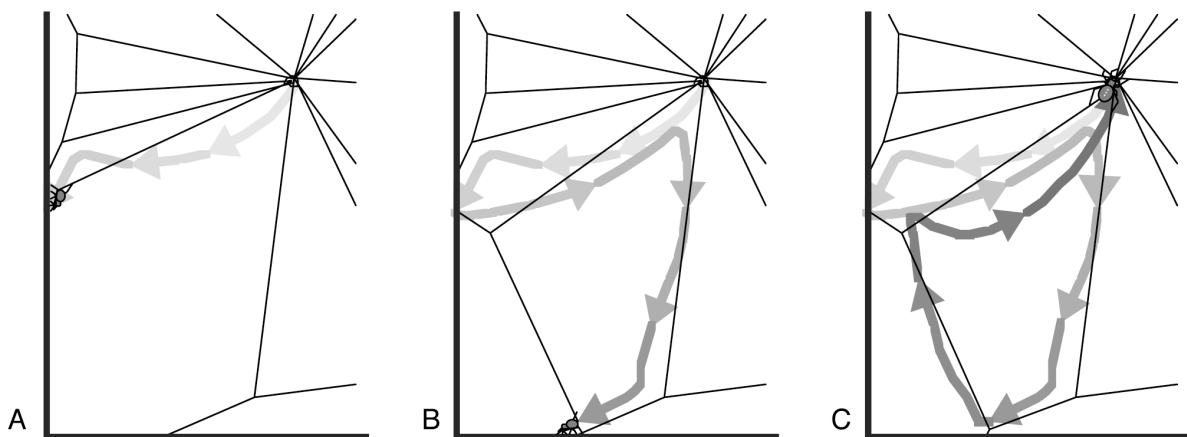
Fig. 2. One possible way of *Araneus diadematus* to construct a frame. The spider first walks out along an existing radius (the exit radius), pulling a dragline behind (A). When it reaches the edge of the web it may walk down a few steps to establish this dragline as a new radius (as shown in this figure). Next it walks back a short distance along this new (or the old) radius and attaches the frame-thread to be (B). Then it walks back to the hub and along the next lower radius to the edge of the web where it attaches the frame thread. Finally it returns to the hub via the newly laid frame thread (C). In this instance of frame construction, the spider attached the new frame on the supporting structure; on returning it did not walk as far as it had walked out the first time and the spider did not move the frame thread on its return to the hub.
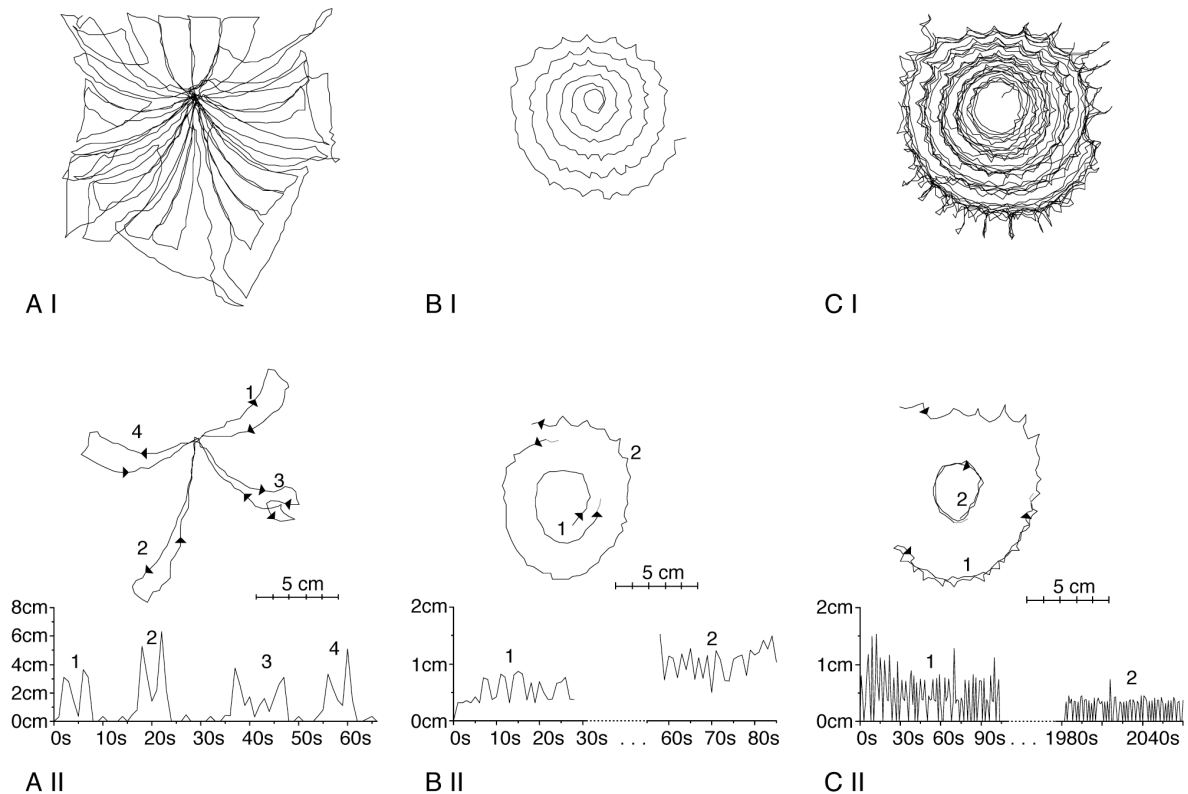
Fig. 3. Path and activity patterns of *Araneus diadematus* during web construction.

During capture spiral construction *A. diadematus* closely followed each individual loop of the auxiliary spiral for several loops of the capture spiral, until finally this auxiliary spiral loop was broken and the next inner loop was used for another set of capture spiral loops (Fig. 3 C I). This resulted in what we called "bundling" of the capture spiral tracks. The observation of this bundling led us to the discovery of the close relationship in terms of coiling and shape of the two spirals (Zschokke, 1993). Since the spider completed most of the capture spiral going in one direction, we were able to observe an interesting asymmetry in the degree of bundling between the left and right sides of the web (east/west). On the side where the spider walked up (left hand side in Fig. 3 C I), the weight of the spider pulled the current radius away from the next, upper radius. This forced the spider to make a detour back to the auxiliary spiral. Consequently the bundling was stronger on this side than on the other side where the spider walked down and where the weight of the spider pulled its present radius towards the next one. In the geometry of the finished web we could not detect any consequences of this behavioural asymmetry, but so far little is known about the local relationships between the two spirals.

The activity pattern during the construction of the capture spiral (Fig. 3 C II) showed a dip each time the spider attached the spiral to a radius. This dip denotes the time (approx. 1 s) the spider took "out" from moving, which indicates the time taken to place thread and joint by orienting the spinnerets as well as the time necessary to apply the cement.

Araniella cucurbitina (Araneinae, Araneidae)

This spider built small orb webs with only a few loops of the spirals. The bundling of the path during the construction of the capture spiral was weak (Fig. 4). *A. cucurbitina* built horizontal and vertical webs, the recording shown in Fig. 4 being a recording of a

527

horizontal one. No differences were found for the analysed traits between *A. diadematus* and *A. cucurbitina* (Table 1).
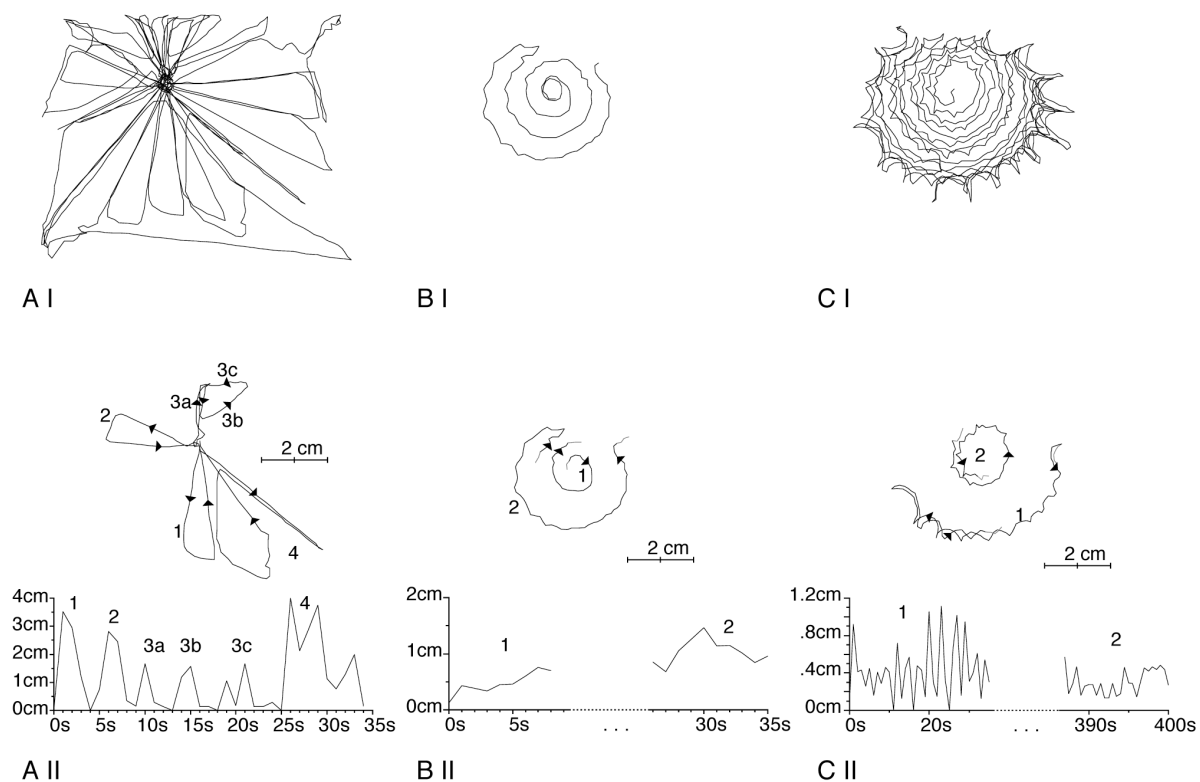

Fig. 4. Path and activity patterns of *Araniella cucurbitina* during web construction.
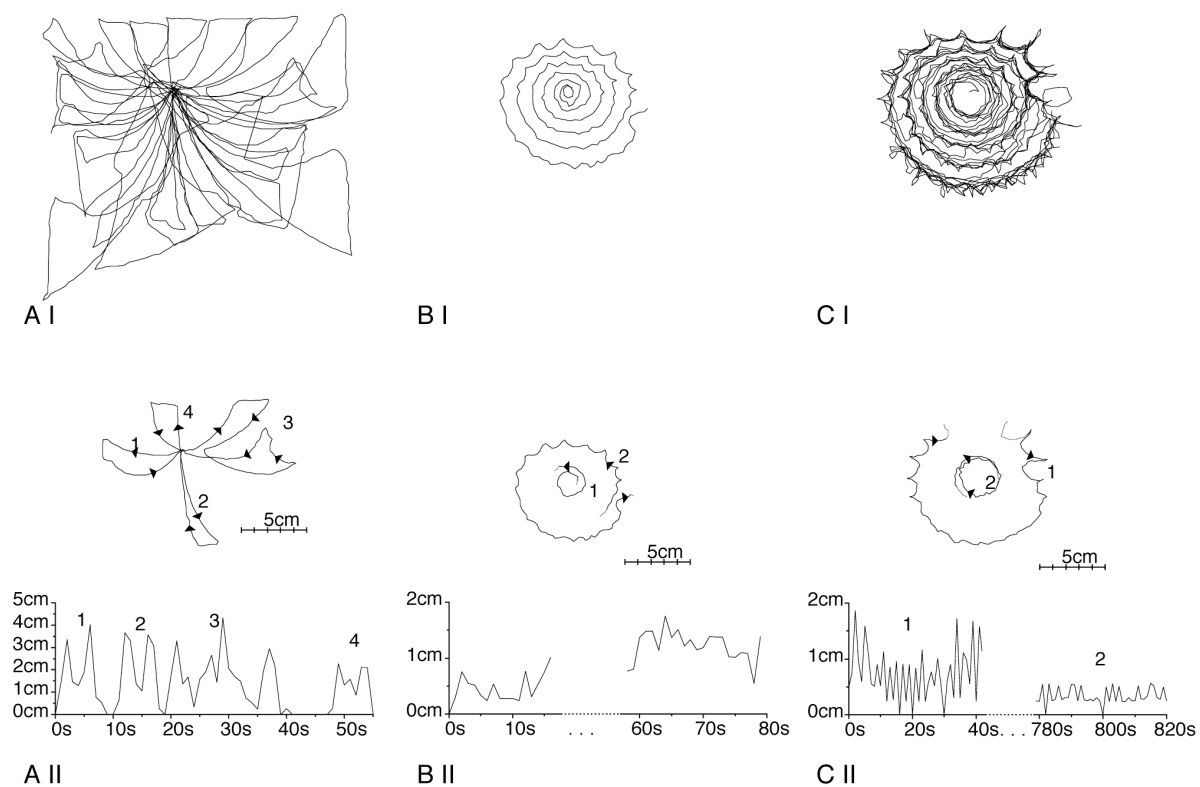

Fig. 5. Path and activity patterns of *Larinioides patagiatus* during web construction.

528

Larinioides patagiatus (Araneinae, Araneidae)

Web construction in this species was also similar to *A. diadematus*. Notable differences were that *L. patagiatus* moved the hub after building the first few radii – in Fig. 5 A I the original position of the hub (above and to the left of the final position) can be clearly seen. Additionally, the hub was often displaced sideways in the web. Frame construction also differed from that of *A. diadematus*. The bundling of the path during the construction of the capture spiral was moderate.

Zilla diodia (Araneinae, Araneidae)

The web of this species was finely meshed and more circular than others. In the recording shown in Fig. 6, the spider moved the hub after constructing a few radii. *Z. diodia* was the only species where the path during radius construction (on the way back to the hub) consistently showed a dip, possibly indicating that the spider had at that point (roughly half way back to the hub) broken the provisional radius (Fig. 6 A II). Araneid (unlike uloborid) spiders are thought always to cut the provisional radius upon returning to the hub (Eberhard, 1982; Coddington, 1986). However, most of them do it at the beginning of the construction of the definite radius, before starting to return to the hub.

We had one observation (out of n = 33) where the lower radius was used as the exit radius for frame construction.

Cyclosa insulana (Araneinae, Araneidae)

The web of this species – like that of *Zilla diodia* – was finely meshed and circular. Construction behaviour was similar to other species from the subfamily Araneinae,
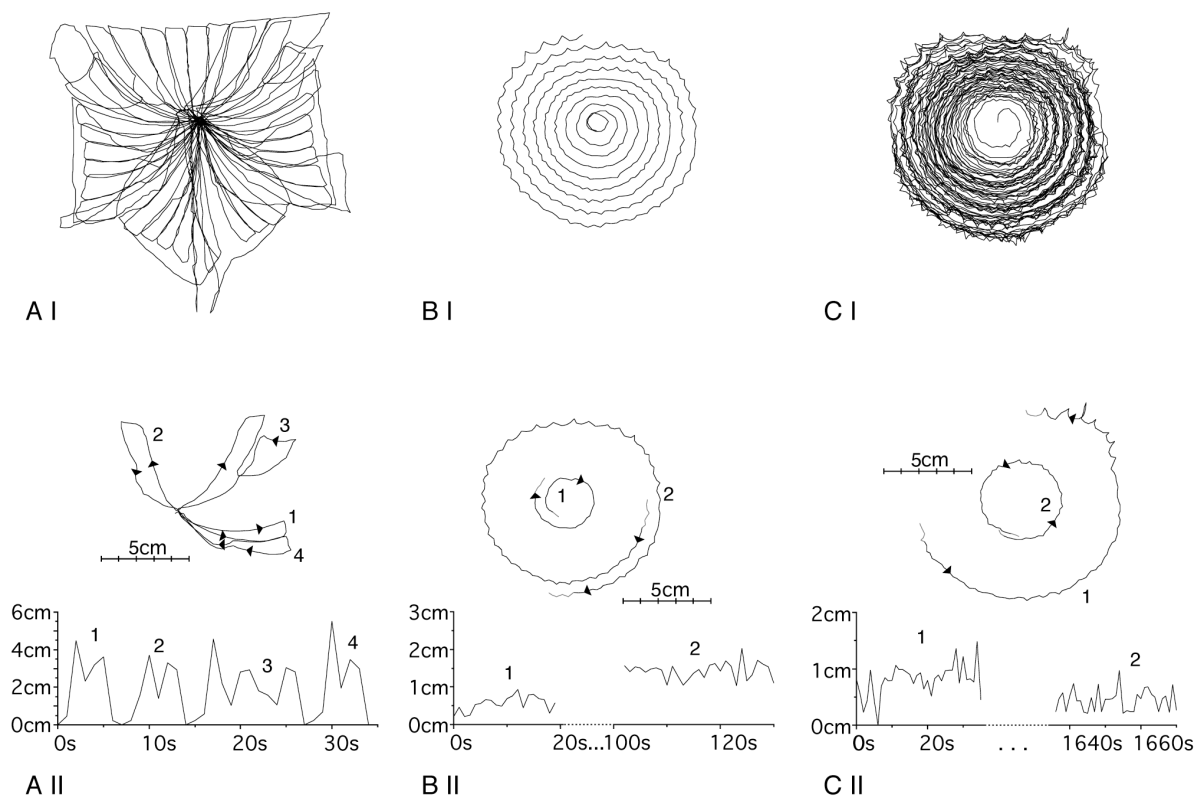

Fig. 6. Path and activity patterns of *Zilla diodia* during web construction. Note how the exit path during radius construction (A II) is smoothly curved, whereas the return path has a bend approximately half way back to the hub.

although *C. insulana* did show some peculiarities: this spider usually made U-turns in the auxiliary spiral and it built a linear stabilimentum (Fig. 7 C I), often supplemented by prey remains.
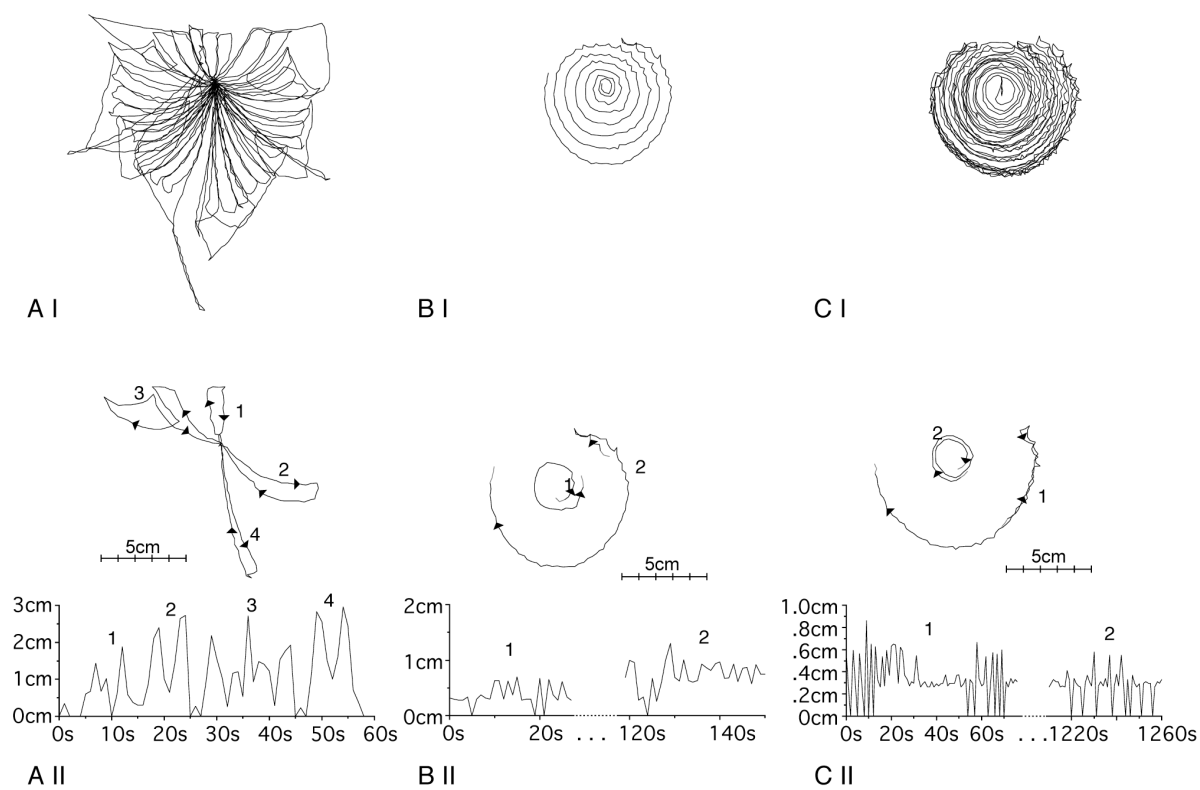

Fig. 7. Path and activity patterns of *Cyclosa insulana* during web construction.
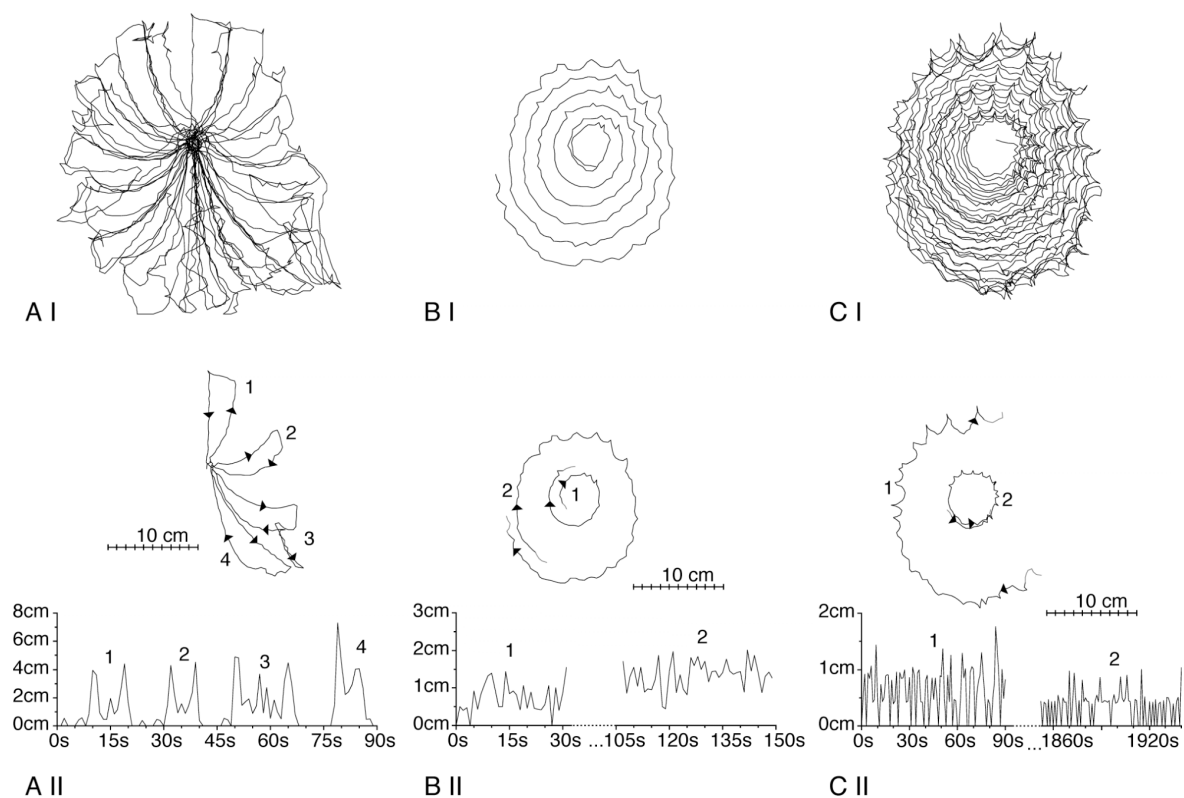

Fig. 8. Path and activity patterns of *Argiope bruennichi* during web construction.
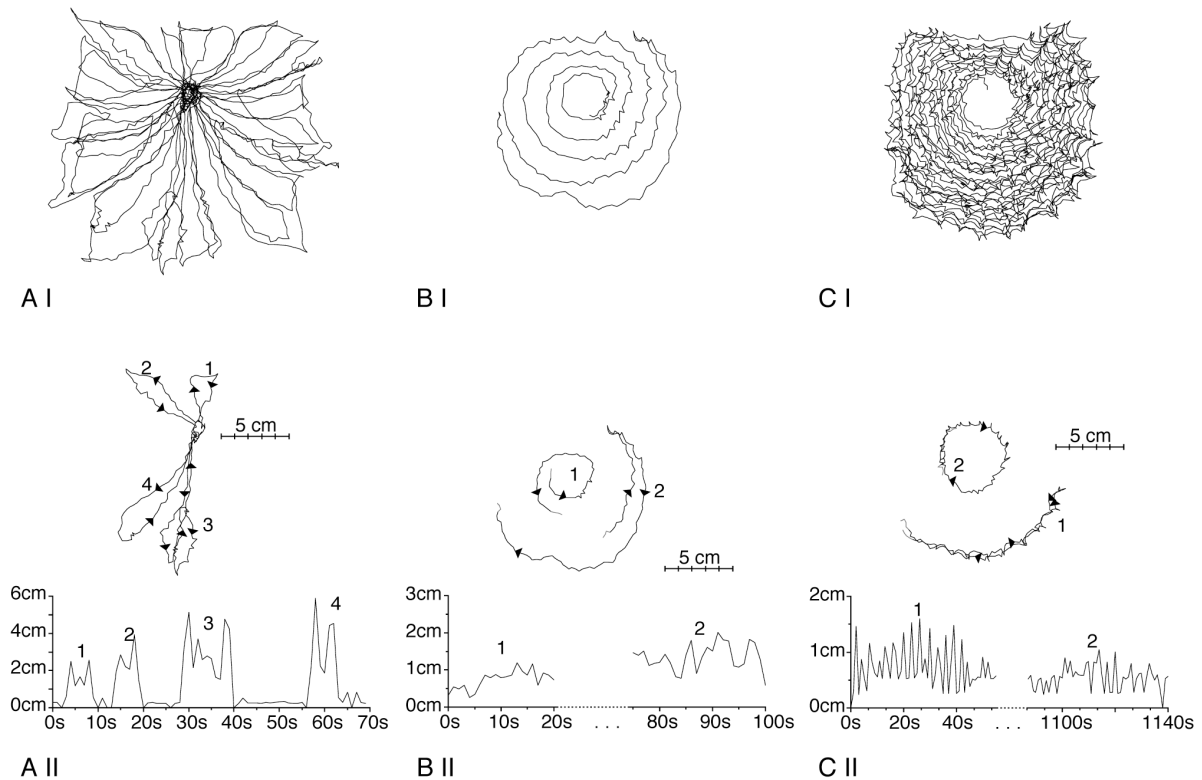
Fig. 9. Path and activity patterns of *Argiope lobata* during web construction.

Argiope bruennichi and *Argiope lobata* (Argiopinae, Araneidae)

There was little difference in web construction between these congeneric species (Figs 8, 9). Their web construction resembled very much the construction behaviour of *A. diadematus*, but the order of radius construction was somewhat different and *A. lobata* often incorporated U-turns in its auxiliary spiral.

The path during frame construction often showed a circle at the upper end of the second loop (Fig. 10) (*A. bruennichi*: 7 of n = 71 *A. lobata*: 8 of n = 54). In *A. lobata*, one frame construction was upside down, i.e. the spider used a lower radius as exit radius. This is noteworthy because this observation (and the one in *Zilla diodia*) were the only observed exceptions to the rule generally strictly followed by araneid spiders that the exit radius is an upper radius (be it for frame or for radius construction).

Gasteracantha cancriformis (Gasteracanthinae, Araneidae)

This species built its webs at an angle of 45° to the vertical. *Gasteracantha cancriformis* also did not make any U-turns in either its auxiliary or its capture spiral. However, it did
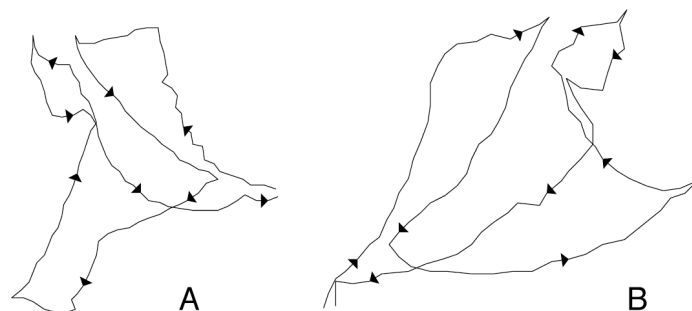

Fig. 10. Path of *Argiope bruennichi* (A) and *Argiope lobata* (B) during construction of a frame thread. Note the circular path at the upper end of the lower loop.
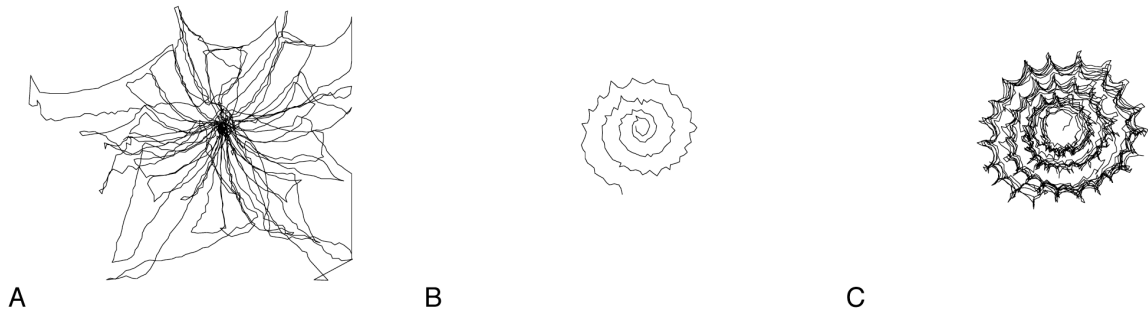
531

Fig. 11. Path of *Gasteracantha cancriformis* during web construction.

turn around between the construction of the two spirals; this resulted in a 100% coiling similarity, i.e. both spirals having the same coiling throughout their full length (Zschokke, 1993). When we looked at the path taken during construction of the capture spiral (Fig. 11 C I), we saw that bundling was very strong.

For technical reasons, we have no recording with accurate timing for this species and are therefore not able to present the activity patterns.

Cyrtophora citricola (Cyrtophorinae, Araneidae)

The horizontal capture sheet in the web of *Cyrtophora* features no capture spiral, but a finely meshed auxiliary spiral with many subsidiary radii; or – looking at it differently – the orb is "just" a greatly enlarged hub, non-sticky, finely meshed and horizontal. Prey are intercepted in mid-flight by vertical threads spun above the orb, and fall down on to it and are caught by the spider which resides below (Lubin, 1973).

Radius construction (be it normal or subsidiary – the distinction is not clear cut in *Cyrtophora* anyway) is unlike that of any other araneid spider; on each trip to the frame, *Cyrtophora* builds two radii attached at the same point to the frame (Fig. 12 A, (Kullmann, 1971). The order of radius construction is – inevitably due to the use of subsidiary radii – different from that of *A. diadematus*. Towards the end of actual web construction, *Cyrtophora* added the vertical strands below and above the web (Fig. 12 C). Construction of these vertical threads alternated with the construction of the last, outermost part of the spiral and radii.

Unlike most other spiders in the family Araneidae which take about one hour (*Nephila* may take up to 4 hours) to build a web which then lasts for one or a few days, *Cyrtophora* takes several nights to build its web which then lasts for many weeks.
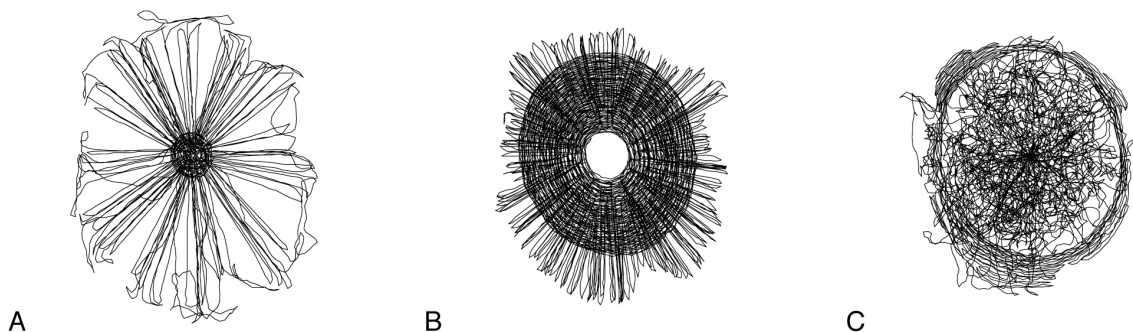

Fig. 11. Path of *Cyrtophora citricola* during horizontal web construction.
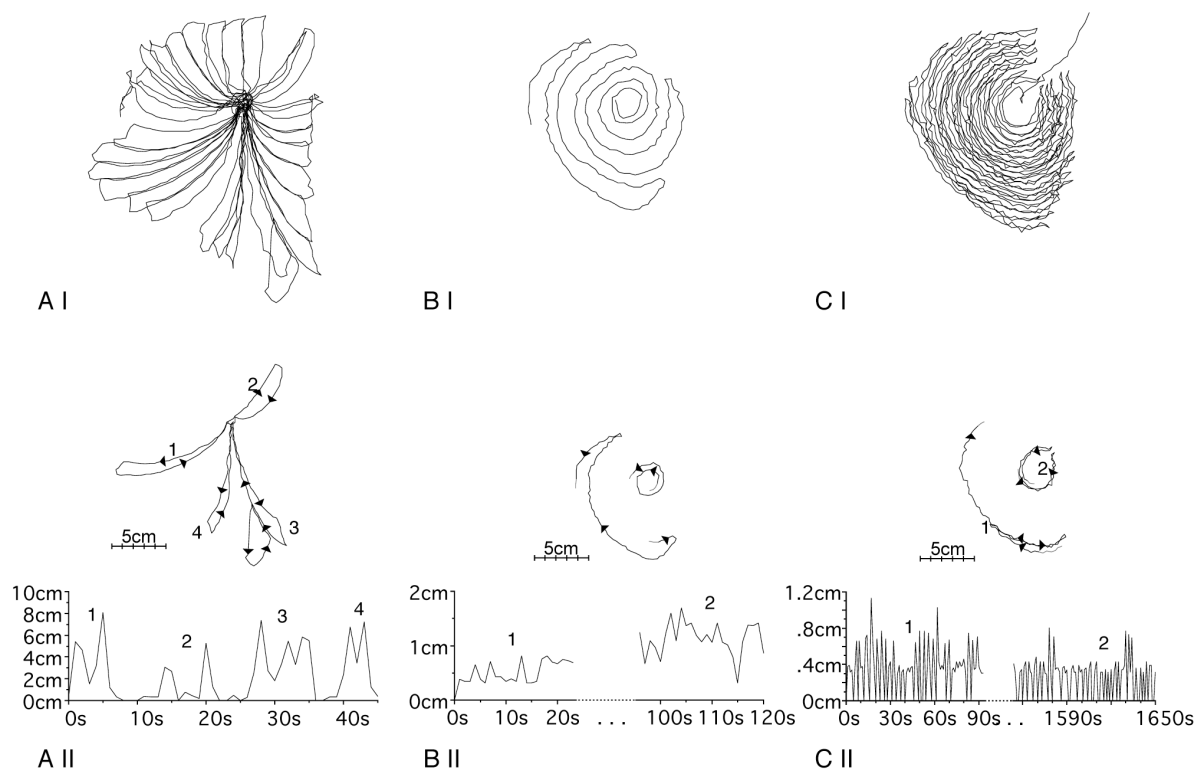
532

Fig. 13. Path and activity patterns of *Zygiella x-notata* during web construction.

For technical reasons, we have no recording with accurate timing for this species and are therefore not able to present the activity patterns.

Zygiella x-notata (Metinae, Tetragnathidae)

The web of this species stands out by having a free sector. In our observations the spider built this free sector sometimes by turning around at its edge (as in Fig. 13 C) and sometimes by removing the spiral threads on either side of the signal thread at the end of web construction. We also found that the first web built by a newly hatched *Z. x-notata* differed from later webs (Fig. 14). Note how this web was more circular and does not have a free sector.

Nephila clavipes (Nephilinae, Tetragnathidae)

Unlike most other orb weavers (with the exception of *Cyrtophora* and its kin) this spider usually constructs more subsidiary than normal radii (Fig. 15 B I). Subsidiary radii are radii that do not to start at the hub (like normal radii) but somewhere further out, attached
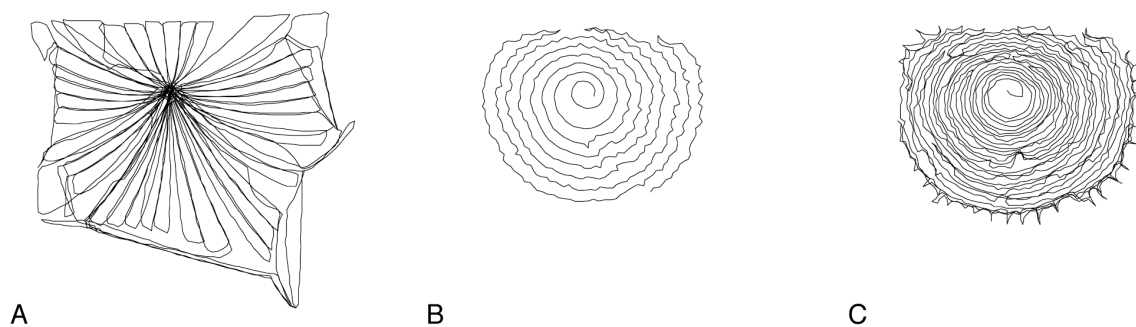

Fig. 14. Path of a newly emerged *Zygiella x-notata* during the construction of its first web.
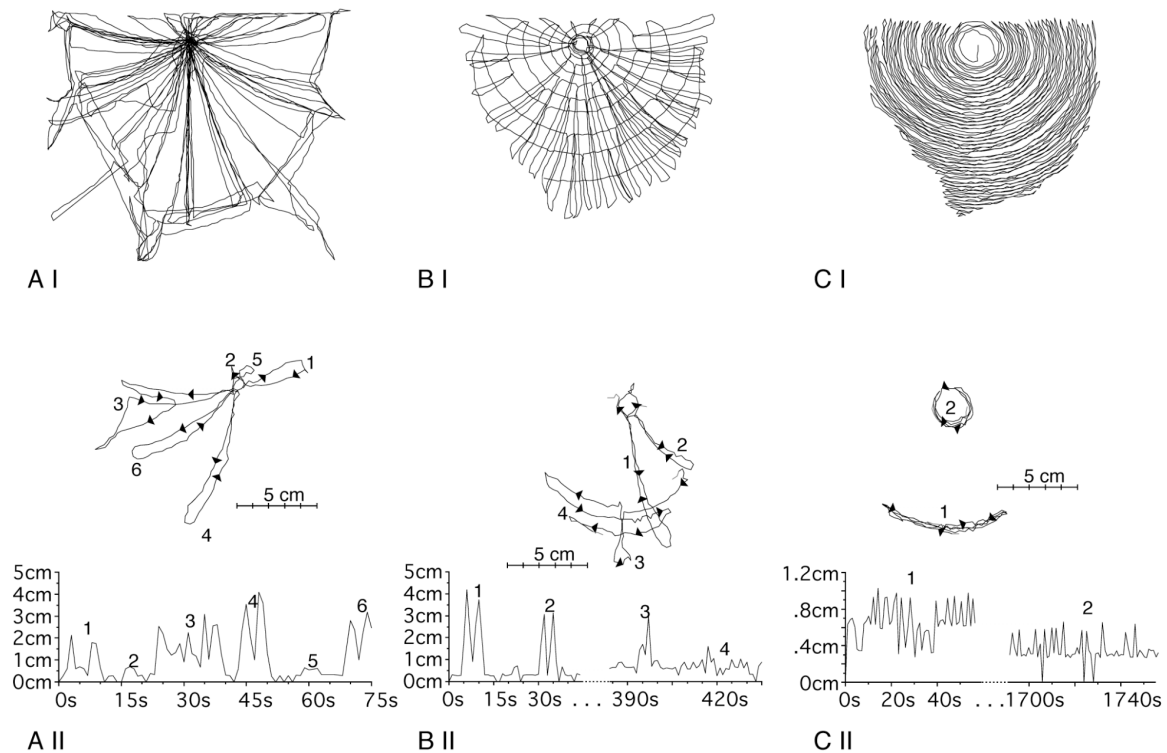
Fig. 15. Path and activity patterns of *Nephila clavipes* during web construction.

either to another radius or to the auxiliary spiral (Zschokke, 1994). Moreover, this species also leaves the auxiliary spiral in the finished web. The web of *N. clavipes* also stands out because it has a surrounding barrier web and the hub is not in the centre; sometimes it is very close to the upper edge of the web. Frame construction was highly variable (Fig. 16). Eberhard (1990a) distinguished 9 different types of frame construction.

The use of subsidiary radii implies an order of construction of the radii which differs from that of *A. diadematus*. From our recordings we distinguished two different types of radius construction: "wide" and "narrow"; the distinction was based on the gap between the exit and the new radius (Fig. 15 A). The wide construction superficially looks like that of *A. diadematus*, but in *N. clavipes* further, narrow radii were added later between the exit radius and the definite radius of a wide radius construction (Fig. 15 A II, B). The first radii that *N. clavipes* built were always wide radii, the last (and all subsidiary radii) were narrow ones.

It was typical for *N. clavipes* to construct most radii leading upwards from the hub as normal radii and a large proportion of the radii leading downwards from the hub as
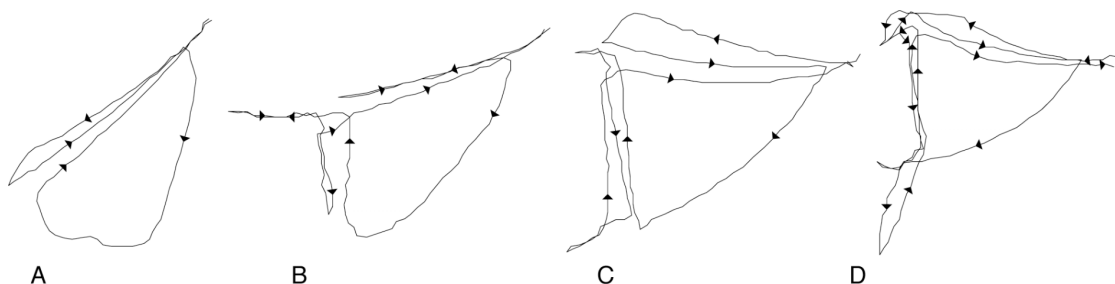

Fig. 16. Path of *Nephila clavipes* during frame construction. The "repertoire" goes from very simple, similar to that of *A. diadematus* (A) to the quite complex (D).
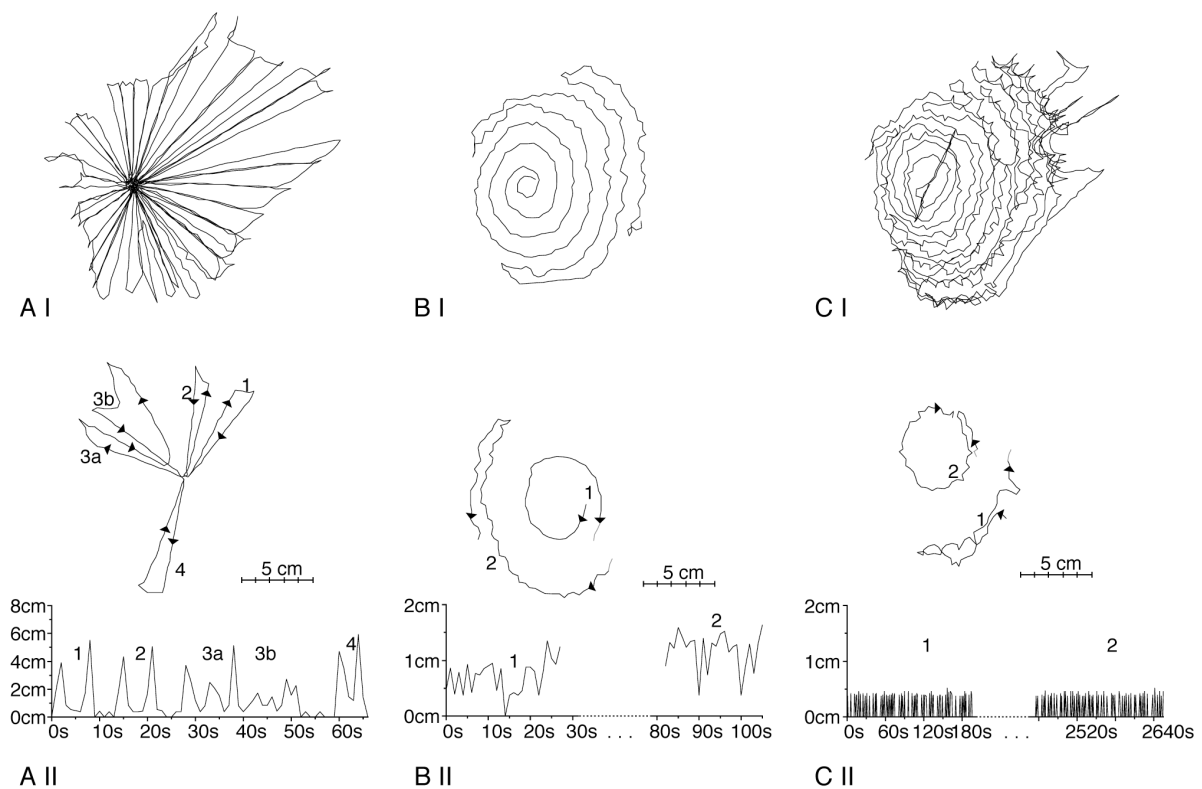
Fig. 17. Path and activity patterns of *Uloborus walckenaerius* during web construction.

subsidiary radii (cf. Figs 15 A, B). The spider's path during capture spiral construction showed "negative" bundling, i.e. instead of following the auxiliary spiral (like e.g. *Gasteracantha cancriformis*, see above) the tracks were spread evenly between the auxiliary spiral loops, leaving a small gap where the auxiliary spiral was (Fig. 15 C I).

Uloborus walckenaerius (Uloboridae)

In our lab, as in nature, this species always built horizontal webs. This caused the recorded paths during radii construction to be straight, since gravity pulled the spider parallel to the axis of the camera, and not orthogonally (like e.g. in *A. diadematus*).

As has been noted before (e.g. Eberhard, 1972, 1982; Coddington, 1986), the basic order of web construction in the Uloboridae is the same as in the Araneidae, leading to the belief that the two webs have the same evolutionary origin; whether this is true is still an open and much discussed problem (Shear, 1986; Eberhard, 1990b). Among the focal traits analysed in the present study, there was only one which showed a consistent difference between cribellate and ecribellate orb weavers (Table 1): cribellates always moved the frame thread on return to the hub during frame construction; ecribellate spiders never moved it.

The transition from auxiliary spiral to capture spiral construction was slightly different from that of most other orb weavers. *Uloborus walckenaerius* either made no U-turn at all between the two spirals (8 of n = 18 observations) or continued with the auxiliary spiral for one or two segments (Fig. 17 B I) after a U-turn (8 of n = 18 observations) before pausing and starting capture spiral construction. In only two cases (of n = 18 observations) did we observe the usual pattern for most other species of turning around and pausing at the same place.
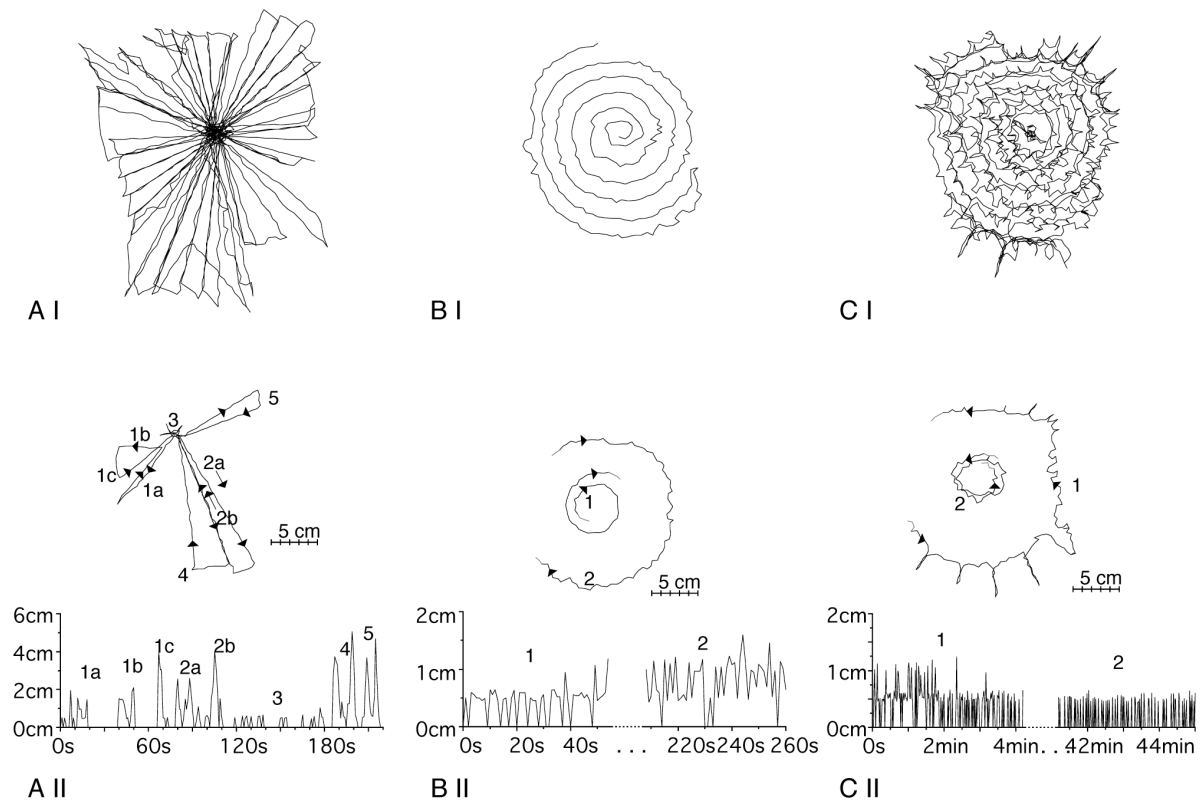
Fig. 18. Path and activity patterns of *Zosis geniculatus* during web construction.

During the construction of the outermost loop of the capture spiral, *U. walckenaerius* sometimes showed the unusual behaviour of using the frame (instead of the auxiliary spiral) to cross from one radius to the next (Fig. 17 C I, between 3 and 5 o'clock). *Uloborus walckenaerius* added a linear stabilimentum at the end of web construction in 9 of 21 observed web constructions (Fig. 17 C I).

Zosis geniculatus (Uloboridae)

Although the webs were very similar, the web construction behaviour of *Z. geniculatus* (Fig. 18) differed from that of *Uloborus walckenaerius*. There was a high rate of aborted radii constructions (no. 3 in Fig. 18 A II) and long breaks between construction of the radii, especially during the early ones. Between the construction of auxiliary and capture spiral we found the same behaviour as in many araneid spiders; pausing and turning at the same place. We also never observed the use of a frame thread to cross from one radius to the next during spiral capture construction. In 6 (of n = 8)webs, *Z. geniculatus* added a stabilimentum with a short linear part (5 of n = 6), followed by the construction of a small disc (5 of n = 6).

Hyptiotes paradoxus (Uloboridae)

H. paradoxus builds a reduced orb web, consisting of only four radii. The basic pattern of frame construction (Fig. 19 A) is the same as in other orb weaving spiders (Fig. 2). After constructing the initial Y-structure, it builds a primary radius (Fig. 19 A II, Nos 1–3; 1a: first peak, 1b + 2 second (split) peak, 3: third peak) and two secondary radii (Nos 4 and 5). Noteworthy, and in this study unique to *H. paradoxus,* is the rapid (4–5 Hz) zigzagging of the path during parts of the frame construction (Fig. 19 A I) caused by the vibrations the
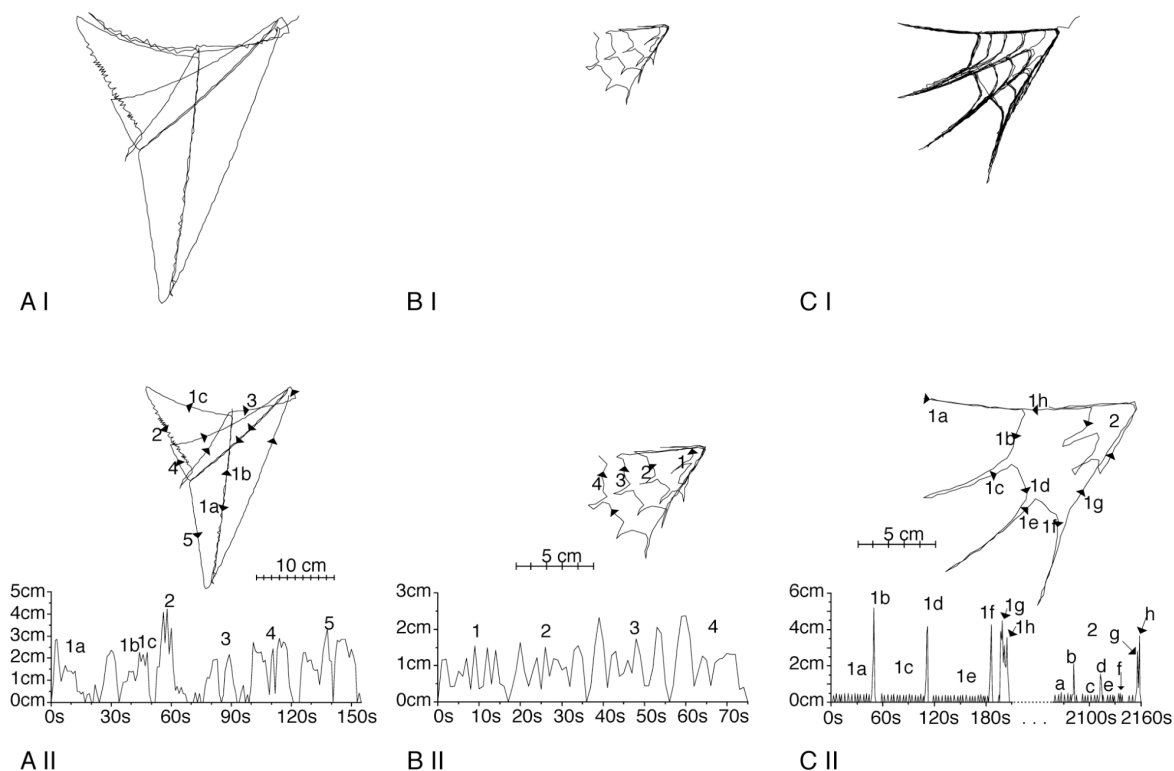
Fig. 19. Path and activity patterns of *Hyptiotes paradoxus* during web construction. In the capture spiral (C II) only the construction of the outer, loop is numbered (1a–1h), the construction of the inner loop followed the same pattern (2a–2h). The seemingly intermittent moves in the activity pattern in C II are an artefact, in reality the spider advanced at a rather steady pace.

spider itself produced, probably to blur its outline as a defence against predators. This zig-zagging was only observed during frame construction.

During the construction of both the auxiliary and the capture spiral, the spider walked back to the hub after laying one "loop" (Fig. 19 B II, C II). For the auxiliary spiral, the spider started each "loop" at the fourth radius (at the bottom) and worked up; for the capture spiral, the spider started at the first radius.

During construction of the capture spiral we were able to distinguish between two different displacement speeds (Fig. 19 C II, Table 2): when actually producing capture silk (Fig. 19 C II, Nos 1a, 1c, and 1e), the spider advanced slowly ($\bar{x}$ =7.0 cm/s); when simply moving (Fig. 19 C II, Nos 1b, 1d, and 1f–1h), it walked much faster ($\bar{x}$ =112 cm/s). The same phenomenon was observed to a lesser degree in other uloborid spiders when they constructed the outermost loops of the capture spiral and had to walk similar detours (cf. Fig. 18 C II). These observations are another indication that uloborid spiders are limited by the speed of silk production (Zschokke & Vollrath, in press). During capture spiral construction, *Hyptiotes* allocated roughly 70% of its time to produce the cribellate sticky silk (Table 2), whereas the detours took less that 15% of the total time. Note that therefore the seemingly wasteful detours during construction of the capture spiral are not very costly in terms of time expenditure.

At this point we would like to correct one misconception about prey capture in *H. paradoxus*. It has often been stated (Wiehle, 1927; Witt et al., 1968; Bellmann, 1992; Foelix, 1992), that the web of *H. paradoxus* can be used only once for prey capture since the spider folds it up completely over the prey. This may be true for larger prey items, but

in our laboratory, when we fed our spiders with fruit flies (or other prey items of similar size), we – like Peters (1938) – never observed a complete collapse of the web.

TABLE 2. Time allocation of *Hyptiotes paradoxus* to different phases of a complete capture spiral construction. "Cribellate silk production" is equivalent to parts a, c and e (Fig. 19 C II); "moving" corresponds to parts b, d, f, g and h; "others" is equivalent to the gaps between the mentioned parts.

	time (s)	%	distance (cm)	%	speed (cm/min)
cribellate silk production	1,443	70.15	168.41	25.60	7.00
moving	257	12.49	479.94	72.95	112.05
others (rests)	357	17.36	9.51	1.45	1.60
total	2,057	100.00	657.86	100.00	

Our observations of the web construction behaviour in *H. paradoxus* showed that there may be an advantage in building a reduced orb web, since the spider can always use exactly the same algorithm (the paths of the spider after establishing the initial Y-structure were structurally identical for all observed webs – but cf. Wiehle, 1927). The web of *H. paradoxus* was also always automatically in one plane since it is fastened to the environment with only three anchor threads.

Two previous detailed descriptions of *H. paradoxus* web construction differ with regard to the question of exit radius for the second (middle) radius. Marples & Marples (1937) described the use of the first (upper) radius, whereas Peters (1938) described the use of the third (lower) radius. [The description by Wiehle (1927) is not detailed enough to allow
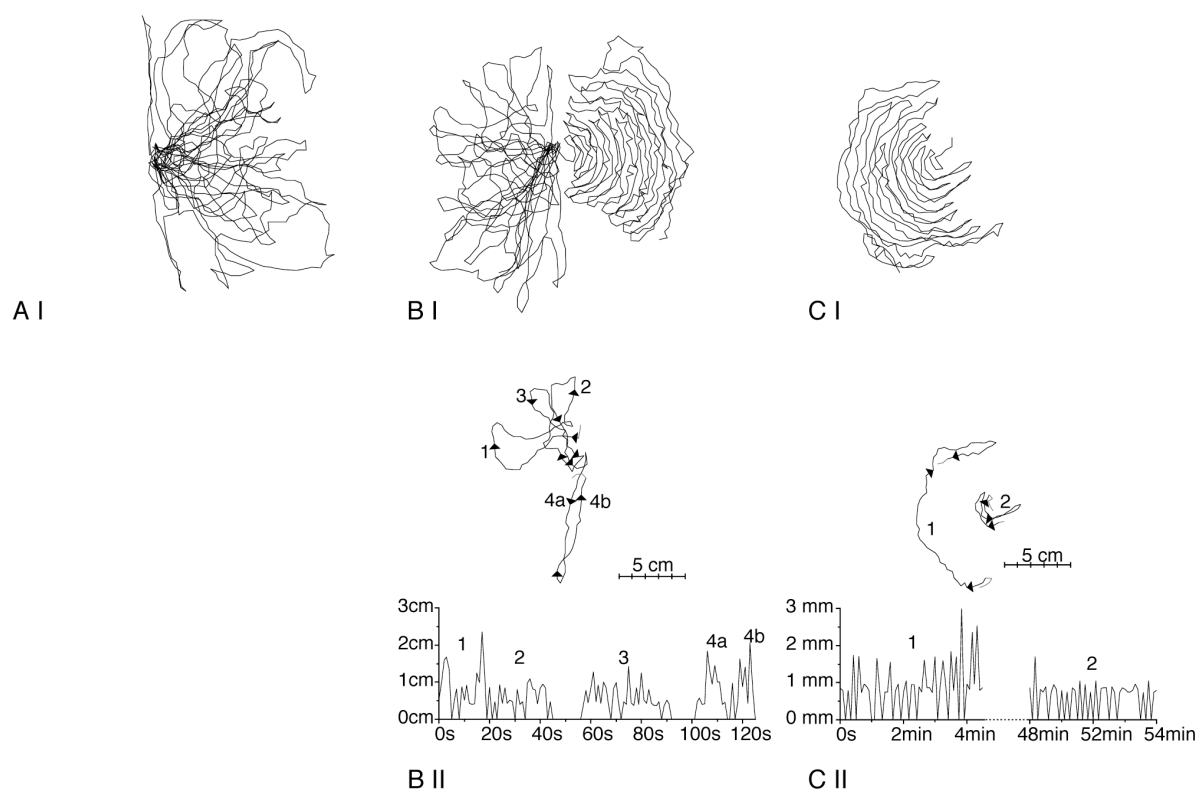

Fig. 20. Path and activity patterns of *Fecenia singaporiensis* during web construction. The temporal resolution for the activity pattern for the spiral construction is 5 s, the y-axis is cm/s.
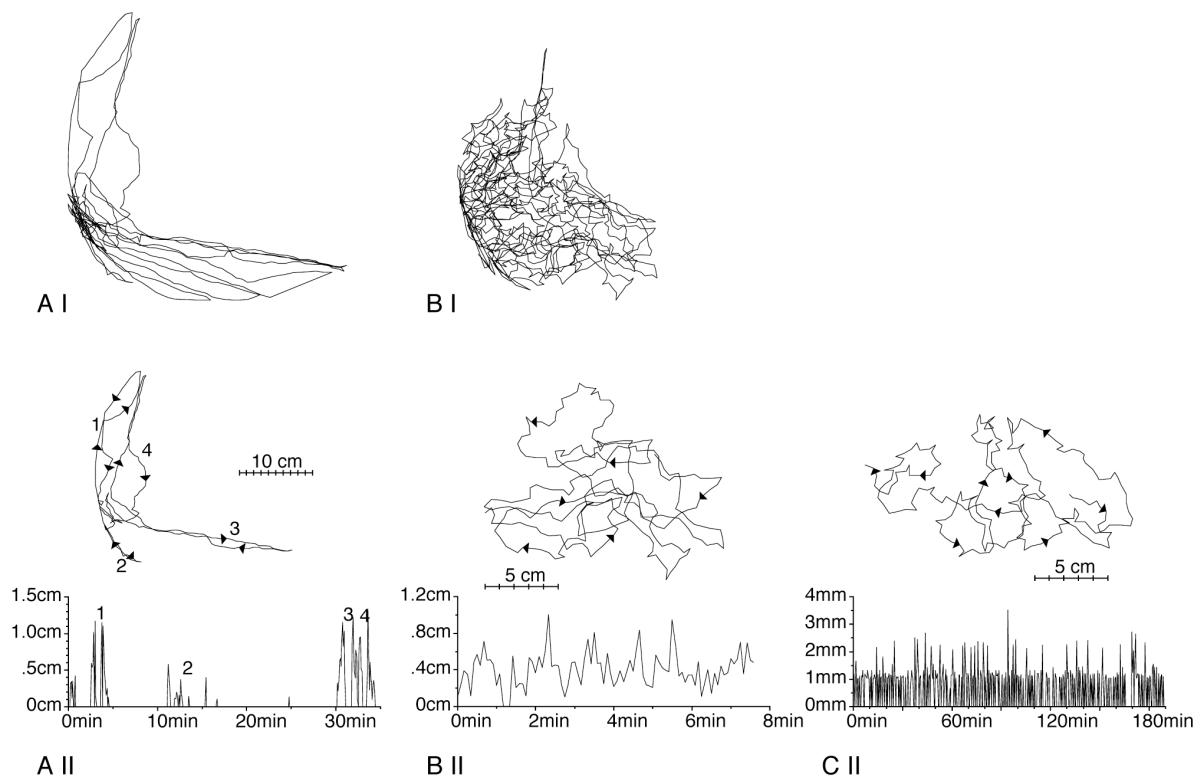
Fig. 21. Path and activity patterns of *Psechrus* sp. during web construction. The temporal resolution for all three activity patterns is 5 s, the y-axis is cm/s.

comparison.] Our observations agree with those of Peters. This is noteworthy because the construction of this radius – as we observed it – is different from that found in most araneid spiders where the radius above the newly constructed one always serves as exit radius.

Fecenia singaporiensis (Psechridae)

The genus *Fecenia* belongs to a family usually not considered to be orb weavers. How ever, the web construction of this spider has some surprising similarities to that of an orb web (Robinson & Lubin, 1979).

In this recording *Fecenia* built first the radii equivalents (Fig. 20 A) and the spiral on the right hand side (Fig. 20 B), and later it built the left hand side of the web in the same order (Fig. 20 B, C). The capture "spiral" was always built from the outside inwards, without the aid of any auxiliary "spiral". There was a noticeable difference between the displacement speed of the spider during "radius" construction (29 cm/min) and "spiral" construction (4 cm/min). It took a spider about two and a half hours to build this kind of web.

Psechrus sp. (Psechridae)

The genus *Psechrus* belongs to the same family as *Fecenia*, but its web construction shows fewer similarities to orb weavers. *Psechrus* sp. showed a tendency to walk first in more or less straight lines (Fig. 21 A, "radius" construction?) and then to walk in more circumvented paths (Figs 21 B, C) which do not resemble any spiral construction at all. When walking in more circumvented paths, two distinct speeds could be distinguished

without any obvious difference in the path itself. The spider alternated between two periods of higher speed ($\bar{x}$ = 21.8 cm/min, as in Fig. 21 B II) and two periods of lower speed ($\bar{x}$ = 4.27 cm/min, as in Fig. 21 C II).

CONCLUSIONS

The main new result of this descriptive study is the observation that capture spiral tracks, rather than being evenly spaced, are bundled around the auxiliary spiral; moreover, this bundling was pronounced to different degrees in the different species studied. Bundling seems to provide some indication of the extent to which the auxiliary spiral is used as a "handrail" during capture spiral construction (Zschokke, 1993), and it may be an indication of differences in the web-building algorithm (Vollrath, 1992). Our data show an apparent relationship between the degree of bundling and the coiling similarity. Only two species of those analysed in our study showed strong bundling, namely *Gasteracantha cancriformis* and *Hyptiotes paradoxus* – and both displayed a coiling similarity of 100%. The bundling and coiling similarity in other species was markedly weaker (e.g. *Araneus diadematus*, *Larinioides patagiatus*) or non-existent (e.g. *Zygiella x-notata*, *Uloborus walckenaerius*), but no species showed strong bundling and low coiling similarity or vice versa. Obviously bundling would be expected to be more pronounced in webs where both spirals are widely spaced.

A lesser result, but possibly interesting for detailed analysis of web construction, is the observation that all our spiders – with the remarkable exception of *Hyptiotes paradoxus*, – always used the upper radius as exit radius during radius construction. We had two isolated observations where a spider broke that rule during frame construction; one in *Argiope lobata* , the other in *Zilla diodia*. Clearly this is a good rule that can sometimes be broken. This finding serves as another indication of the spider's "rule of thumb" (rather than mathematical) approach to web-building (Vollrath, 1992).

Last but not least, our study showed that the orb of *Cyrtophora citricola* with its fine mesh consists of a frame of normal and subsidiary radii interlocked with a tightly wound auxiliary spiral – if we assume any auxiliary spiral to begin at the laying down of the first few radials. Otherwise, if we assume the auxiliary spiral to begin at the sudden widening of its spacing, we must consider the *Cyrtophora* web as one gigantic hub structure. Both interpretations allow us to accept without any problems this rather unusual capture area as a highly specialised orb web. *Nephila* with its many subsidiary radii (at the end more than normal radii) might serve as an intermediate step; in *Nephila* the transition from hub to auxiliary spiral is also not clearly marked with a sudden widening, although some widening does occur. But note that *Nephila* is emphatically not a missing link between *Cyrtophora* and a more "normal" orb weaver such as *Araneus* or *Zygiella*.

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