REVUE SUISSE DE ZOOLOGIE, vol. hors série: 709-720; août 1996

Early stages of orb web construction in *Araneus diadematus* Clerck

Samuel ZSCHOKKE
Department of Zoology, South Parks Road, Oxford, OX1 3PS, England
and
Zoologisches Institut, Rheinsprung 9, CH-4051 Basel, Switzerland

Early stages of orb web construction in *Araneus diadematus* **Clerck. -** The early stages of orb web construction are the least studied and the most poorly understood, because the behaviour of the spider at that stage lacks the repetitiveness of later stages, the timing is unpredictable and the moves of the spider cannot be deduced from the finished web.
In the present study, all moves of the spider during web construction were recorded using computerised image analysis. The early stages of web construction of several webs were then reconstructed from these recordings and analysed in detail.
The construction leading to the proto-hub was found to be highly variable. It was also found that during its construction, the spider employs a series of fixed behavioural patterns in seemingly random order. These patterns are 'designed' in a way to make it very likely that a proto-hub will emerge. Once the spider had established this proto-hub, its behaviour became more stereotyped and predictable.
The costs to explore a new site were estimated by measuring the distance walked by the spider. These costs were compared to the costs of adapting the framework of an existing web and it was found that re-building and existing web costs much less compared to building a web from scratch.

Key-words: Spider - Web - Construction - Behaviour - Behavioural pattern - Exploration - Behavioural costs - Animal tracking

INTRODUCTION

Many of us have watched with fascination how a spider builds the web, or at least how it builds the spirals and with a little bit of luck on our side, one could also follow the construction of the radii. You need much more than that little bit of luck to

---

Current address: Institut für Natur-, Landschafts- und Umweltschutz, Universität Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.

Manuscript accepted 09.01.1996.
Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8.IX.1995

watch construction from the very start, since the time of the onset of the construction is unpredictable (WITT *et al.* 1968); and even those who were lucky enough to be present when the first threads were laid had problems in actually describing it when they saw it for the first time (EBERHARD 1990), since the spider acts in a seemingly random fashion. Always laying down a new thread (the dragline), it is busy moving and removing threads laid previously until suddenly the proto-hub emerges (MAYER 1952). This proto-hub is then moved to its final position and the construction of the frame threads and the radii starts.

Many published descriptions of the early stages of construction are – as EBERHARD (1990) put it – "probably simply wrong or flawed in ignoring variations". EBERHARD's own description of the early stages of web construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* is very thorough, but hard to understand for the non-specialist and therefore not suitable for publication in popular publications; and it is in these articles where most of the 'simply wrong' descriptions can be found (e.g. CROMPTON 1950, LEVI 1978).

The present paper aims to remedy this situation by depicting the web construction process in, hopefully, an understandable but yet essentially correct way. It also attempts to describe some mechanisms the spider may employ to start a new web. I shall argue that there is no fixed pattern the spider employs to do so, it rather uses one of several possible rules all designed to advance the construction to the point where a knot with several radial lines has emerged. This not may then be used as a proto-hub. The process of building a new web from scratch has not been optimised by natural selection for two reasons. It would not be possible for the spider to rely on a fixed behavioural pattern – as it does for the construction of the rest of the web – since the environment is highly variable and the spider therefore has to react in a flexible manner. In addition, since spiders usually build several webs at the same site, re-using the framework of the previous web, they do not have to build a web from scratch very often.

Along with the description of the early stages of web construction I was also interested in its costs. Since absolute costs are very hard to measure, I attempted to compare the costs of the exploration stage between webs built on supporting structures of different complexity and to compare the exploration costs to the costs of rebuilding an existing web. To get an idea of the order of magnitude of these costs they were also compared to the costs of the rest of the web construction.

MATERIALS AND METHODS

The position of the spider during web construction was monitored continuously with a video camera and an image scanner HVS VP112. The position of the spider was then transferred to a Macintosh computer which recorded the subsequent positions of the spider. For a more detailed description of the method see (ZSCHOKKE 1994). This procedure produced a detailed account of all moves of the spider, but it did not record the positions of the threads. Repeated recordings of the spiders' moves during web construction made it possible to single out spiders that readily built webs.

I managed to video-tape the web construction (from the very beginning) of three webs built by three different spiders. The observations made from studying the thread positions in these recordings – together with pictures of the finished webs – allowed me later to reconstruct the thread positions of some of the other webs of which I had only recorded the moves, giving me a total of 9 recordings with known thread positions.

The spiders used in this study were immature male and female *Araneus diadematus* of similar size, habituated to the laboratory environment (16L/8D, 50% rH, 25°C). They built webs on U– shaped frames (Fig. 1), 18 cm high and 16 cm wide. Each time they had built a web, they were fed with one or two fruit flies Drosophila sp. and the web was sprinkled liberally with water. The web was then removed, the frame wiped clean of remaining silk and the spider re-released onto the right hand stick and the recording was restarted.

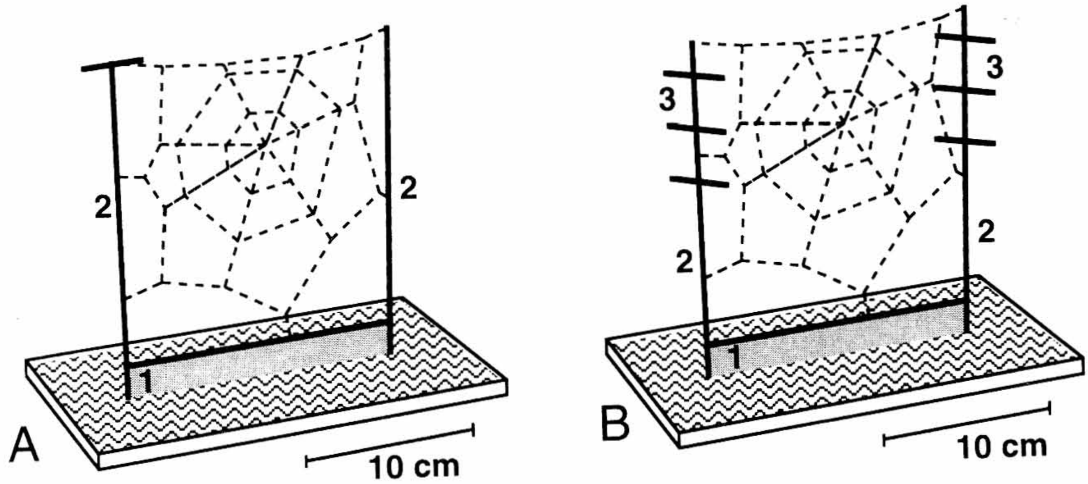

FIG. 1

Supporting structures for the web construction of the spiders. The structures consisted of a perspex plate (1) placed vertically in a tray of water (to prevent escape of spider). On both sides of that plate a transparent drinking straw (2) was fixed with one or several cross-bars (3). Two structures of different complexity were used in this study: a simple one (A) with one cross-bar parallel to the perspex plate and a complex one with six cross-bars (B) turned 45° out of the plane of the perspex plate. The spider was always released on the top of the stick on the right hand side.

From the recordings of the moves of the spider I inferred the positions of the threads. To better visualise the continuity of the web construction process, I divided the web construction into small steps, extracted for each step the moves of the spider from the recordings and added the position of the threads and the frame in different colours (similar to the frames shown in Fig. 2). This gave me a sequence of pictures which I then joined in a Macintosh computer into a QuickTime® movie, allowing me to study the construction of the webs repeatedly.

LABORATORY MEASUREMENTS OF EXPLORATION DISTANCE

Following EBERHARD (1972), the exploration stage (or web removal stage) of the web construction was defined as anything the spider did before it moved the proto-hub.

The costs of exploring a new site were assessed by measuring the distances the spider had walked during the exploration stage. I assumed that the distance the spider had covered was proportional to the energy expenditure of the spider; since the spider always leaves a dragline, the distance covered is the roughly the same as the length of silk produced; the distance covered is also roughly proportional to the locomotory energy used by the spider.

The costs of exploring a new site versus removal of an existing web were assessed by comparing the distances the spiders covered to do these tasks. On the simple supporting structure (Fig. 1A) 37 webs built by 6 different spiders were recorded, and on the complex supporting structure (Fig. 1B) 38 webs built by 5 different spiders. On four occasions I (but not the observing computer) missed the completion of a web and the spider proceeded in due course to remove this web and construct a new one on the same supporting structure. In three out of these four cases, the spider removed the web and proceeded with the construction of the second one without further exploration; in the fourth case, the spider's track after removal of the first web looked similar to tracks typical for the exploration stage, and this web was therefore not used in the analysis.

The distance the spider had covered during the exploration stage was first compared between spiders on the same supporting structure using a Kruskal-Wallis test. Since this comparison gave no differences between spiders (simple supporting structure: $p=0.466$, complex supporting structure: $p=0.340$) and since I have good reasons to believe that the spiders did not learn from one web construction to the next (ZSCHOKKE 1994, see also Fig. 4), the webs of all spiders were pooled for each supporting structure.

I compared the distances the spiders had covered for the removal of a web before building a second one with the exploration distances for both supporting structures. I also compared the exploration distances between the two supporting structures using the Mann Whitney U-test. In addition, I compared the distances for the rest of the web construction.

RESULTS

DESCRIPTION OF ORB WEB CONSTRUCTION IN THE LABORATORY

Bridging the open gap

As a first step, the spider bridges the open space between the two sticks. In the laboratory (where there is no wind) this is done by attaching the dragline at the top of one stick and then walking the detour along the bottom of the supporting structure (Fig. 2A). When it reaches the other stick, it climbs up, sometimes only partly, to a point where it tightens and attaches the dragline to use it to cross back to the top of the first stick (PETERS 1989).

The spider then usually tries to establish a thread as high up as possible; this may be achieved by replacing the original thread or by adding another one (Fig. 2B). During these early steps of web construction, the spider may pause at any time, sometimes for a few minutes, sometimes for several hours.

Establishment of proto-hub and construction of the proto-radii

The spider now establishes the so-called proto-hub, a structure where several threads (the proto-radii) fastened to the supporting structure come together at a single point (Figs. 2C-2E). The establishment of the proto-hub with the construction of the proto-radii is a highly variable process. At first, no pattern can be discovered in the way the spider walks around, constantly laying new threads and sometimes moving or removing older threads. Gradually one point emerges where several proto-radii meet. The spider then continues by constructing a few more proto-radii.

The construction of the proto-radii itself is also highly variable. Most (31 out of 34) proto-radii constructions followed one of six variants of the same basic pattern which is fairly similar to that of the normal radius construction. The spider starts at the proto-hub; then it attaches the dragline at or near the proto-hub. Next it somehow reaches the supporting structure where it attaches the dragline, thus forming the provisional proto-radius. The spider may reach the supporting structure in one of three different ways: it either walks along existing threads (Fig. 2D); or it drops down vertically using the dragline (Fig. 2E); or it uses what I am tempted to call the Tarzan method: the spider – after having attached the thread – walks (usually towards the hub, if the dragline is not originally attached at the hub) a few centimetres and then drops down, swinging around the place where the dragline is attached. When the spider – in full swing – hits another thread or a part of the supporting structure it grabs it and continues the construction from there. Either way, the spider will then return along the provisional proto-radius (reeling it up along the way) back to the hub, inserting the definite proto-radius at the same time.

The spider sometimes performs most of a construction pattern for a proto-radius, but fails to attach a thread when reaching the supporting structure. I could not detect any regularity in the order of the variants used to construct the proto-radii (the variants are distinguished by the place where the provisional radius is attached (at the hub or near the hub) and how the spider reaches the supporting structure).

When the spider has established this proto-hub – usually with four to seven proto-radii (PETRUSEWICZOWA 1938, MAYER 1952, KRIEGER 1992) – it will continue (from now on usually without long rests) by building the first frame thread along the top of the future web. During the construction of the top frame thread, the spider always tightened it whilst sitting in the middle of the top frame thread itself, which seems impractical, since the spider has to lift itself up as well when doing so. It is not known why it does not do it from either end, where the force required would be much smaller. I can only speculate that this position may give the spider better control.

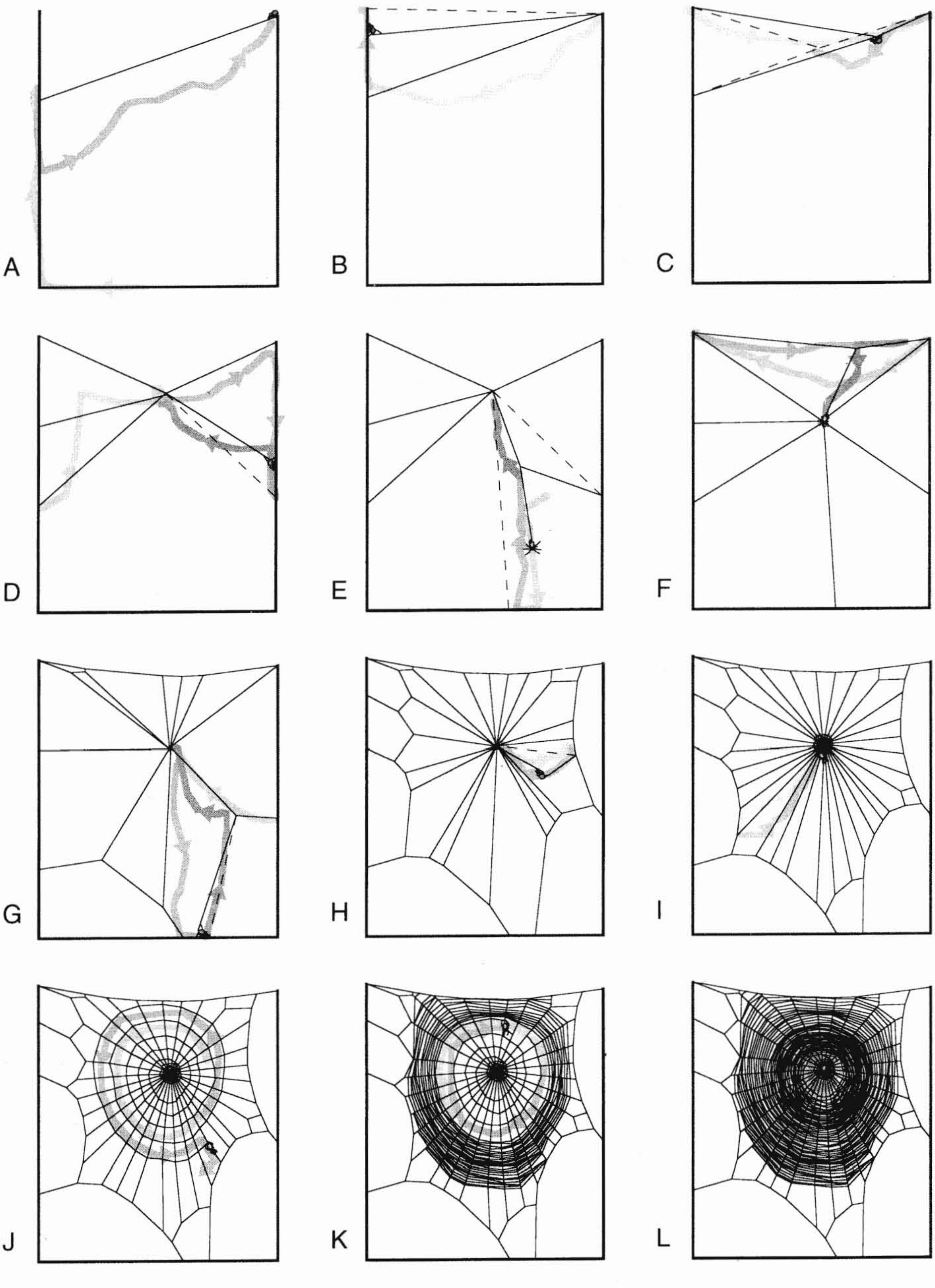

FIG. 2

Outline of orb web construction of *Araneus diadematus* in the laboratory. The drawings are based on recorded moves of the spider, with the threads reconstructed from those moves. It is a slightly simplified account of a web construction selected for its simplicity; early stages (i.e. the

This is immediately followed by moving the proto-hub to its final position, thus turning it into the hub. At the same time the first definitive radius (always between top frame thread and hub) is constructed (Fig. 2F). When the spider has moved the hub it sometimes replaces some of the radii (often only partly), probably to re-adjust their tensions.

Construction of frame and radii

The next stage in the web-building is the construction of the frame and the radii. Primary frame threads (i.e. those attached to anchor threads, MAYER 1952) and secondary frame threads (i.e. those attached to other frame threads) are built using the basic pattern shown in Fig. 2G. The spider walks out along an existing 'exit' radius to attach a thread. Dragging this thread behind, it walks back towards the hub and then along the next lower radius where it attaches that thread to form the frame. It then continues along this newly laid thread back to the upper radius and back to the hub. When the spider builds a secondary radius (i.e. a radius constructed without simultaneous construction of a frame thread, Fig. 2H), it walks out along an existing radius to the frame, then down (always) a few steps along the frame where it attaches the dragline (the 'provisional radius'). The spider then clambers back to the hub, reeling up the provisional radius while simultaneously producing the definitive radius. The remains of the provisional radii can be seen in a web under construction as fluffy white balls of silk in the hub of the web.

The order of the radii construction follows certain patterns; the spider always puts in the new radius immediately below an existing one; never above and never with a large gap where it would later on add another radius (PETERS 1937, REED 1969). It tends to build the radii above the hub before those below it (KRIEGER 1992). Additionally, it adds the radii in an order apparently to balance the forces in the hub (MCCOOK 1881, KÖNIG 1951, EBERHARD 1981, WIRTH & BARTH 1992).

---

ones represented in A-E) are highly variable and usually more complicated than the ones shown here (cf. Fig. 4B). In each picture, the moves of the spider are indicated schematically 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, the dashed lines show the position of the threads when the spider had completed the moves shown in the picture (only where the position of the spider shown differs from the final one). To keep the sequence of pictures lucid, all moves of the spider not resulting in new permanent threads have been omitted in this representation. Remember that the spider always leaves a dragline; in A for instance, it first attached the dragline at the top of the right hand stick and walked down and around the bottom of the supporting structure, always trailing this dragline behind. When it had reached about one third of the height of the left hand stick, it tightened and attached that dragline, thus establishing a first thread across the open space (not shown in the figure). Then it proceeded to walk up to two thirds of the height of the stick, attached the dragline again, walked down and used the thread it had just before laid across the open space to go back to the top of the right hand stick, at the same time removing this thread and still (as always) pulling a dragline behind. Having reached the top of the right hand stick, it tightened and attached the dragline again, thus establishing the thread shown in the figure.

The first frame thread is always the one at the top of the future web, the top frame thread; the other frame threads are only laid after moving the hub.

Frame construction follows quite a rigid pattern (ZSCHOKKE & VOLLRATH 1995). In the 9 webs analysed in detail, I observed few secondary frame-threads (8 of 55). Of the 47 primary frames, 19 were built without inserting a new radius at the same time and not as described by CODDINGTON (1986): "*Uloborus walckenaerius* and *Araneus diadematus* both construct a radius each time they construct a frame line".

Construction of the spirals

When the spider builds the radii it keeps circling the hub to find a gap to place the next radius. This circling then continues after the insertion of the last radius, thus forming the hub structure (Fig. 2I). Circling of the hub changes suddenly without interruption into the construction of the auxiliary spiral (Fig. 2J). The spider finally completes the web by building the capture spiral (Fig. 2K) before going to the centre of the web and remaining there motionless, waiting for prey to fly into the web (Fig. 2L).

The spider usually replaces the web every night (WIEHLE 1927). When it stays at the same place it re-uses large parts of the anchor and frame threads, but it replaces all radii and the capture spiral (CARICO 1986). The old web is ingested and the silk recycled.

ORB WEB CONSTRUCTION IN THE FIELD

In a natural environment outdoors bridging an open space (the equivalent of the step shown in Fig. 2A) is usually achieved by letting a thread fly with the wind (TERBY 1867, HINGSTON 1920, WIEHLE 1927, PETERS 1989); this thread may then become entangled on the opposite side of the open space and enables the spider to cross it. In the laboratory, attempts of the spider to let a thread fly were often observed, but almost never produced results, and when they did, it was to my misfortune because it allowed the spider to leave the field of vision of the camera, often enough to build a web just next to it, leaving me with a blank recording of the moves.

In the laboratory, I never observed web construction based on an initial Y-structure as described by PETERS (1939). This may be due to my relatively small supporting structure or – as suggested by MAYER (1952) – due to the use of spiders of different age-classes or due to the limited space available. Outdoors, the webs of *A. diadematus* often span gaps of several metres (WIEHLE 1927, own observations).

DISTANCES WALKED BY SPIDERS TO CONSTRUCT A WEB

The distances the spiders covered during the exploration stage varied greatly (Fig. 3). For the simple supporting structure it lay between 2.79 and 63.21 m (median=5.61 m, MAD (median absolute deviation)= 1.79 m); for the complex supporting structure it lay between 6.55 and 212.53 m (median=27.60 m, MAD=13.35 m). Even the exploration stages of two consecutive web constructions by the same

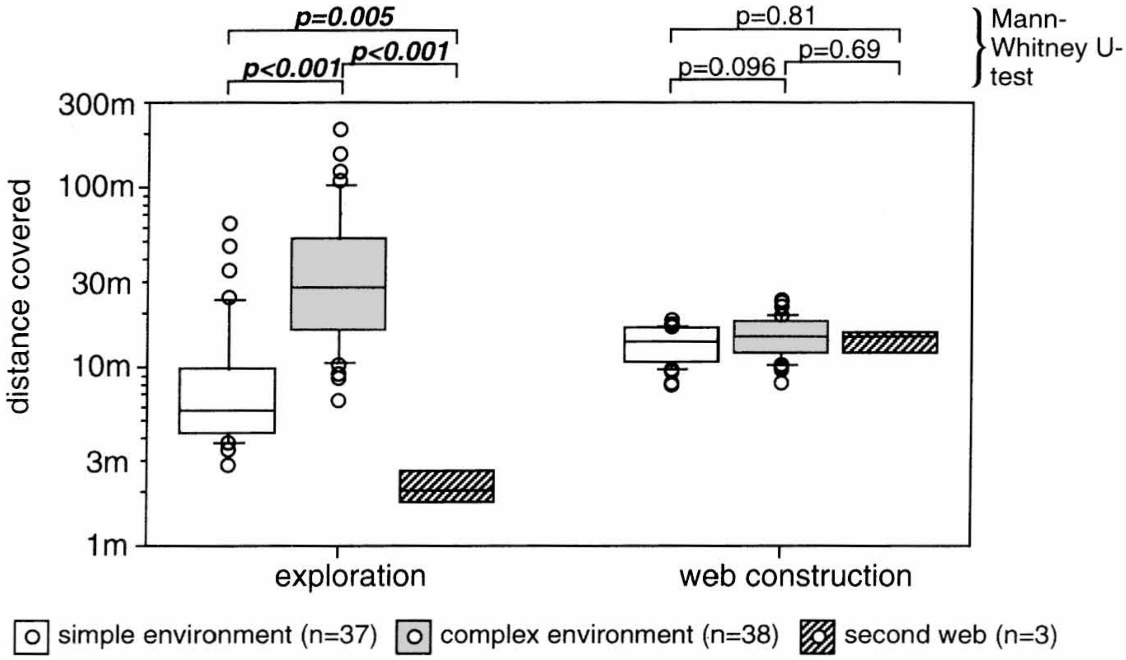

FIG. 3

Box plot of the distances covered by the spider to explore the environment (left) and to build the web (right) on the simple supporting structure (n=37), the complex supporting structure (n=38) and also for second webs (and therefore web removal in the left graph, n=3). The distances were compared using Mann-Whitney U-tests, giving significant ($p<0.01$) p-values between all three groups for the exploring distances but not for the web-building distances.

spider sometimes showed a huge difference (Fig. 4). The distances the spider walked to actually build the web (constructions of radii, auxiliary and capture spiral) varied much less. For webs built on the simple supporting structure they lay between 7.86 and 18.46 m (median=13.64 m, MAD=2.61 m) and for those built on the complex one between 8.24 and 24.09 m (median=14.37 m, MAD=2.72 m).

The distance the spider had moved to remove the old web before constructing a new one (Fig. 3), was significantly smaller than the distance covered to explore the simple supporting structure ($U=1$, $p=0.005$) or to explore the complex supporting structure ($U=0$, $p<0.001$). The distance to explore the simple supporting structure was also smaller than the exploration distance on the complex supporting structure ($U=156$ $p<0.001$). The distances of the actual web construction (Fig. 3) did not differ between the three groups (second web vs. simple: $p=0.81$; second web vs. complex: $p=0.69$; simple vs. complex: $p=0.096$).

DISCUSSION

WEB CONSTRUCTION PATTERNS

I observed large variations in the behaviour of the spiders during the exploration stage of orb web construction. It is not possible for the spider to use a rigid

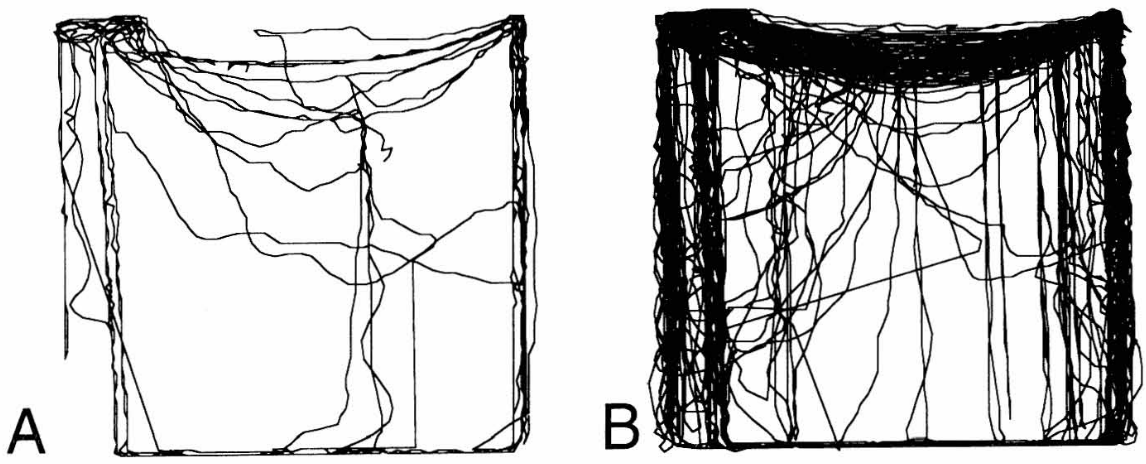

FIG. 4

Recorded tracks of the exploration stage of two consecutive web constructions by the same spider on subsequent days. During the exploration stage of the first web (A), the spider walked 7.28 m and for the second one (B) 63.21 m.

pattern, since the environment is highly variable. With the establishment of the proto-hub with the proto-radii, the spider then laid the foundation for the construction of the rest of the web. This foundation showed less variation and enabled the spider to use a more rigid pattern for the subsequent construction of radii, frame and the spirals. The fact that the spider rested only rarely after the establishment of the proto-hub also indicates the use of a more fixed neural program at this stage.

I had also expected the early stages to be less optimised than later ones, because the spider usually re-uses many anchor threads and frame threads when rebuilding a web (CARICO 1986, WIRTH 1988, own observations). This implies that the early stages of orb construction are not done as often as the later stages and have therefore been under weaker selection pressure.

I have recorded a great number and great variety of web constructions; they however have one flaw in common: they were all recorded in the laboratory. Under natural circumstances, conditions are different; the spider has more space available and it may employ wind currents to establish the first thread. The combination of these two factors certainly influences the behaviour of the spider; to what extent we can only know when detailed and repeated observations have been carried out in the field.

When looking at the results presented in this study, we must remember that most early stages are more complicated than the one presented here (cf. Fig. 4B). The spider often lays threads which serve no apparent purpose and are later removed.

EXPLORATION DISTANCE

My analysis of the exploration distances showed clearly that it is much cheaper for the spider to rebuild an existing web rather than building a web at a new site, even when disregarding (as I did in the present study) the risks and costs of moving to and finding a new web-site (RYPSTRA 1984, VOLLRATH 1985, VOLLRATH 1987). The distances travelled for exploring and the distances travelled for building the web were on average about the same. However, the real costs differed, since some of the investment for the actual web building (i.e. the production of the silk) can be recovered when the spider eats the web and thus recycles the silk. I could not observe recycling of silk laid down during exploration.

One aspect of the exploration stage I could not study satisfactorily was how the spider ascertains that the area intended for web construction is indeed free of obstacles. In this study, the spider may have known this after establishing the first thread across the gap; this thread – dragged across the open space – would have been caught by any obstacle if there had been one. Due to the different mechanism of establishing the first thread in nature; the spider may need an additional step to ascertain that nothing interferes with the web to be.

Looking at the overall pattern during the exploration stage, it can be seen that the spider always first established a horizontal thread as high up as possible and then built the web working down from that thread. This automatically ensured an approximately vertical and planar web, at least in my simple environment – but see also (ZSCHOKKE & VOLLRATH in press).

ACKNOWLEDGEMENTS

This study was carried out in partial fulfilment of the PhD Thesis of Samuel Zschokke and was financed by a research grant from the Swiss National Science Foundation to Fritz Vollrath. I would like to thank Christoph Jäggi for statistical advice and Bruno Baur and an anonymous referee for their helpful comments on the manuscript. I am deeply indebted to my supervisor Fritz Vollrath for his advice and help throughout my PhD thesis. Figure 1 was drawn using the freeware program 'Rotater' by Craig Kloeden.

REFERENCES

CARICO, J.E. 1986. Web Removal Patterns in Orb-Weaving Spiders, pp. 306-318. *In:* Spiders: Webs, Behavior and Evolution (W.A. SHEAR, ed). *Stanford University Press, Stanford.*

CODDINGTON, J. 1986. The Monophyletic Origin of the Orb Web, pp. 319-363. In: Spiders: Webs, Behavior and Evolution (W.A. SHEAR, ed). *Stanford University Press, Stanford.*

CROMPTON, J. 1950. Life of the Spider, *William Collins Sons & Co, Glasgow*, 249 pp.

EBERHARD, W.G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). *Journal of Zoology, London*, 166: 417-465.

EBERHARD, W.G. 1981. Construction behaviour and the distribution of tensions in orb webs. *Bulletin of the British Arachnological Society* 5: 189-204.

EBERHARD, W.G. 1990. Early stages of orb-construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. *Journal of Arachnology* 18: 205-234.

HINGSTON, R.W.G. 1920. A Naturalist in Himalaya. *H. F. & G. Witherby, London*, 300 pp.

KÖNIG, M. 1951. Beiträge zur Kenntnis des Netzbaus orbiteler Spinnen. *Zeitschrift für Tierpsychologie* 8: 462-492.

KRIEGER, M. 1992. Radienbau im Netz der Radnetzspinne. *Diplomarbeit, Universität Basel.*

LEVI, H.W. 1978. Orb-weaving spiders and their webs. *American Scientist 66*: 734-742.

MAYER, G. 1952. Untersuchungen über die Herstellung und Struktur des Radnetzes von *Aranea diadema* und *Zilla x-notata* mit besonderer Berücksichtigung des Unterschiedes von Jugend- und Altersnetzen. *Zeitschrift für Tierpsychologie* 9: 337-362.

MCCOOK, H.C. 1881. How orb-weaving spiders make the framework or foundations of webs. *Proceedings of the Academy of Natural Sciences of Philadelphia* 33: 430-435.

PETERS, H.M. 1937. Studien am Netz der Kreuzspinne (*Aranea diadema*). II. Über die Herstellung des Rahmens, der Radialfäden und der Hilfsspirale. *Zeitschrift für Morphologie und Ökologie der Tiere* 33: 128-150.

PETERS, H.M. 1939. Probleme des Kreuzspinnen-Netzes. *Zeitschrift für Morphologie und Ökologie der Tiere* 36: 179-266.

PETERS, H.M. 1989. On the structure and glandular origin of bridging lines used by spider for moving to distant places. *Acta Zoologica Fennica* 190: 309-314.

PETRUSEWICZOWA, E. 1938. Beobachtungen über den Bau des Netzes der Kreuzspinne (*Aranea diadema* L.). *Travaux de l'Institut de Biologie Générale de l'Université de Vilno* 13: 1-24.

REED, C.F. 1969. Cues in the web-building process. *American Zoologist* 9: 211-221.

RYPSTRA, A.L. 1984. A relative measure of predation on web-spiders in temperate and tropical forests. *Oikos* 43: 129-132.

TERBY, M.F. 1867. Sur le procédé qu'employent les araignées pour relier des points éloignés par un fil. *Bulletin de l'academie royale des sciences, des lettres et des beaux-arts de Belgique*, Ser. 2, 36: 274-297.

VOLLRATH, F. 1985. Web spider's dilemma: a risky move or site dependent growth. *Oecologia (Berlin)* 68: 69-94.

VOLLRATH, F. 1987. Growth, Foraging and reproductive success, pp. 357-370. *In:* Ecophysiology of Spiders (W. NENTWIG, ed). *Springer, Berlin.*

WIEHLE, H. 1927. Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden. *Zeitschrift für Morphologie und Ökologie der Tiere* 8: 468-537.

WIRTH, E. 1988. Sensorische und mechanische Grundlagen des Netzbauverhaltens. *PhD Thesis, Goethe Universität Frankfurt am Main,* 85 pp.

WIRTH, E. & BARTH, F.G. 1992. Forces in the spider orb web. *Journal of Comparative Physiology, A* 171: 359-371.

WITT, P.N., REED, C.F. & PEAKALL, D.B. 1968. A Spider's Web: Problems in Regulatory Biology. *Springer, Berlin*, 107 pp.

ZSCHOKKE, S. 1994. Web construction behaviour of the orb weaving spider *Araneus diadematus* Cl. *PhD Thesis, Universität Basel*, 177 pp.

ZSCHOKKE, S. & VOLLRATH, F. 1995. Web construction patterns in a range of orb weaving spiders. *European Journal of Entomology* 92: 523-541.

ZSCHOKKE, S. &VOLLRATH, F. in press. Planarity of orb webs built by *Araneus diadematus* under natural and experimental conditions. *Journal of Arachnology*.