The influence of the auxiliary spiral on the capture spiral in *Araneus diadematus* Clerck (Araneidae)

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Summary

The relationship between direction of coiling and shape of the auxiliary spiral and that of the capture spiral in orb webs of *Araneus diadematus* Clerck (Araneidae) was investigated. In most webs, the two spirals had the same direction of coiling and a similar shape, indicating that the auxiliary spiral serves as a guide during construction of the capture spiral. Possible causes and mechanisms are discussed.

Introduction

The spider's orb web is a semi-permanent record of the outcome of the application of a series of complex construction rules. These rules are of interest both to the ethologist and the taxonomist in studying the evolution of the orb web. However, looking at the finished web tells us only part of the story; we have to observe the web construction as well. One possible way to observe web construction is to trace the movements of the spider (Zschokke & Vollrath, in prep). When looking at the trace of a spider during placement of the capture spiral, a strong correlation is evident between the path of the spider and the position of the auxiliary spiral (Fig. 1), possibly indicating a stronger influence of the auxiliary spiral than hitherto assumed. This paper describes my research carried out to explore this influence.

Araneus diadematus builds webs in distinct phases (Witt *et al.*, 1968). First, it establishes a frame with the radii. Next, it builds a widely meshed auxiliary (or temporary) spiral from the centre to the periphery of the web. This spiral is usually built without reverses (U-turns). Then it places the finely meshed capture (or sticky) spiral from the periphery to the centre, using the next inner turn of the auxiliary spiral as a bridge to cross from one radius to the next. The auxiliary spiral is removed, bit by bit, as it is encountered during the construction of the capture spiral, leaving small fragments of silk curled up on the radii. The capture spiral usually has several reverses, mainly along the outer edge of the web. Finally, the hub is rebuilt.

Some facts about the geometry of the spirals in the web of *A. diadematus* have been established (Vollrath, 1988a): (i) the auxiliary spiral of *A. diadematus* usually lacks reverses (which is not the case in all orb-weaving spiders), (ii) the spider usually turns around between finishing the auxiliary spiral and starting the capture spiral, and (iii) the two spirals differ in pitch and in type (Vollrath & Mohren, 1985).

The auxiliary spiral is thought to have different functions: to stabilise the radii during capture spiral construction (Foelix, 1982) and to form a bridge to enable the spider to cross from one radius to the next (Peters, 1937). Whether it is also used as a guide during the placement of the capture spiral has been suggested (Foelix, 1982; Witt *et al.*, 1968) and disputed (Hingston, 1920; Vollrath & Mohren, 1985).

The aim of this study was to examine the role of the auxiliary spiral, paying particular attention to its function during the placement of the capture spiral. The observations included: (i) the examination of a large number of photographs of webs constructed in the laboratory without interference, (ii) the examination of webs in which the spider was perturbed during auxiliary spiral construction, and (iii) the observation of webs in which the orientation of the web was altered at several points during spiral construction. The data obtained suggest that the auxiliary spiral serves as a guide for the spider during placement of the capture spiral.

I shall use the following terminology. A spiral is called right-handed if it runs clockwise from the centre outwards, left-handed if it runs anticlockwise. The property of a spiral to be left-handed or right-handed is called "coiling". Any given spiral can be called either left-handed or right-handed, according to the view of the web (back or front). However, the coiling of the capture spiral relative to the coiling of the auxiliary spiral is independent of the view of the web.

Analysis of a large number of webs

Material and methods

A large number of *A. diadematus* were kept under standard laboratory conditions (14L-10D cycle, temperature 24 ± 2°C, humidity 45–55%). They were kept individually in frames 30 × 30 × 5 cm, fed on a diet of *Drosophila* sp. and watered by sprinkling their webs at irregular intervals. Their webs were photographed. Of the photographs of webs with clearly visible remnants of the auxiliary spiral and undamaged capture spiral, a maximum of 2 were taken per spider without any further selection,

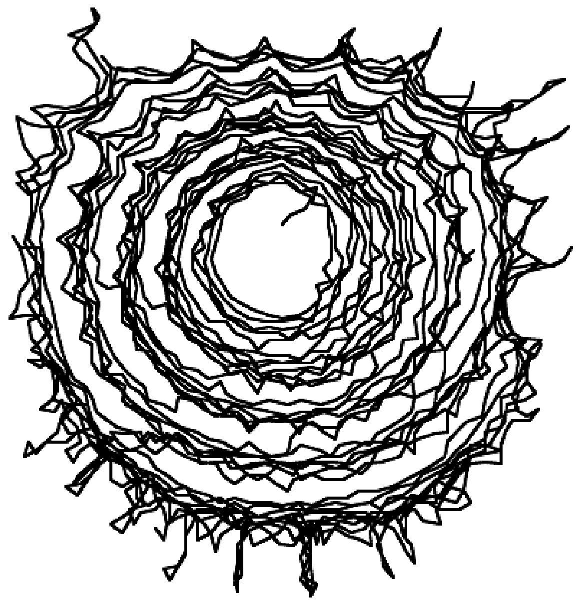

Fig. 1: Trace of the body of *Araneus diadematus* recorded during construction of the capture spiral. The bundle of lines corresponds to the position of the auxiliary spiral.

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giving 100 photographs of webs built by 56 individuals. The following properties were analysed for each of these webs: (i) presence of a reverse between the end of the auxiliary and the beginning of the capture spiral, (ii) presence of reverses within the auxiliary spiral, (iii) number of reverses in the capture spiral, both in the whole web and in the area enclosed by the outermost turn of the auxiliary spiral, and (iv) coiling of the capture spiral compared with that of the auxiliary spiral.

To compare the coiling of the two spirals, the coiling of each of their turns was analysed along two radii in the web, one at the top of the web and one at the bottom. The proportion of turns of the capture spiral within the outermost turn of the auxiliary spiral having the same coiling as the next inner turn of the auxiliary spiral was calculated, giving a percentage that I will call "coiling similarity". If both spirals had the same coiling throughout, then the coiling similarity would be 100%, likewise if they had different coiling, then the coiling similarity would be 0%. A coiling similarity around 50% would imply that there was no correlation between the coilings of the two spirals, whereas a similarity near 100% (or near 0%) would imply a strong correlation.

Results

The analysis showed that there was a reverse between the end of the auxiliary and the beginning of the capture spiral in 97 webs ($n = 100$, $p < 0.001$). Four webs had one reverse in their auxiliary spiral.

The average number of reverses in the capture spiral was 11.0 (sd = 5.6, $n = 100$). Of these reverses, only 2.1 (sd = 2.3) were within the outermost turn of the auxiliary spiral; 73 webs had two or fewer reverses within the outermost turn of the auxiliary spiral, 29 had none.

The coiling similarity of most webs was above 90% (Fig. 2). The average coiling similarity was 94.4% (sd = 10.2, $n = 100$).

To summarise, the capture spiral generally had the following properties: along the outer edge of the web (roughly outside the outermost turn of the auxiliary spiral), it had several reverses. The rest of the capture spiral had the same coiling as the auxiliary spiral and was without any reverse; or if there was one, another reverse occured within less than two turns of the capture spiral.

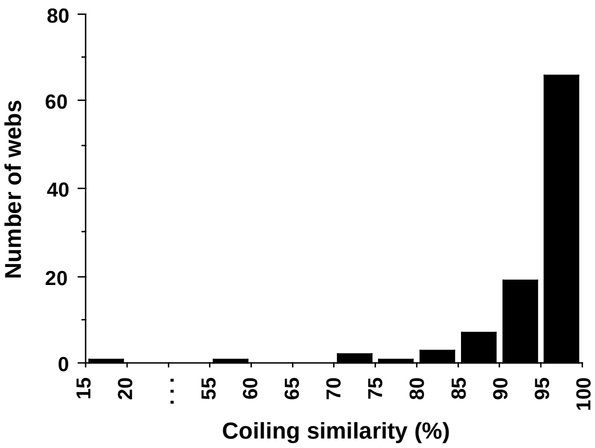

Fig. 2: Distribution of coiling similarities between auxiliary and capture spiral of 100 webs of *Araneus diadematus*. Coiling similarity is the percentage of turns of the capture spiral that have the same direction of coiling as the auxiliary spiral.

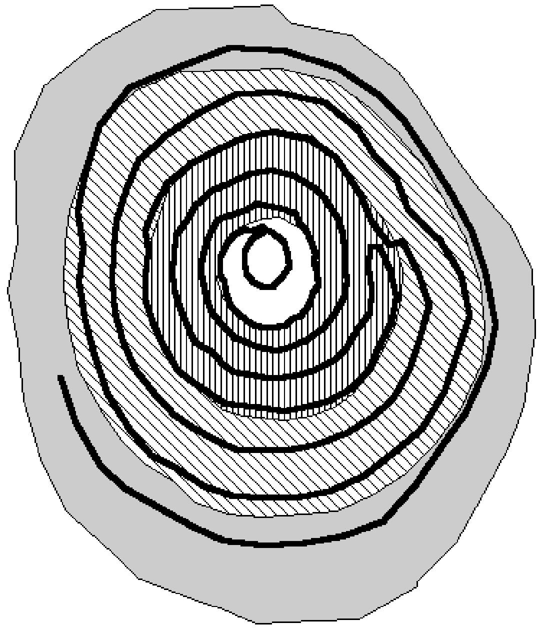

Fig. 3: Diagram of a web with an experimental reverse in the auxiliary spiral. The solid line represents the auxiliary spiral. In the vertically striped area the capture spiral is left-handed; in the diagonally striped area it is right-handed. In the shaded area, the spiral contains a number of reverses and therefore cannot be assigned a coiling (traced from a photograph of the web).

Experimental reverses in the auxiliary spiral

To test the hypothesis that the auxiliary spiral determines the coiling of the capture spiral, spiders were induced to make one or several reverses in the auxiliary spiral.

Material and methods

The spiders were again kept under standard laboratory conditions. During the construction of the auxiliary spiral, when the spider was moving either up or down, the frame was quickly flipped around a horizontal axis. The spider sometimes continued in the same direction as before (up or down) producing a reverse in the spiral. Alternatively, the spider was interrupted during the construction of the auxiliary spiral and induced to go back to the hub, forcing it to build a second auxiliary spiral. If the second auxiliary spiral had a different coiling compared with the first spiral, the first half of the second spiral was burnt away by the experimenter, leaving "one" auxiliary spiral with a change of coiling. The webs in which one of the above treatments had been successful ($n = 5$) were photographed after completion of the auxiliary and again after completion of the capture spiral. For these webs, the coiling similarity was calculated in the same way as above.

Results

The average coiling similarity of the experimental webs was 83.4% (sd = 9.5, $n = 5$), differing significantly from 50% (one group two-tailed t-test, $p < 0.01$). The coiling of the auxiliary spiral did indeed appear to determine the coiling of the capture spiral. Figure 3 shows one of the experimental webs that was perturbed during auxiliary spiral construction. The auxiliary spiral is drawn as a thick black line. The capture spiral was left-handed in the vertically striped area and right-handed in the diagonally striped area. The grey area along the outer edge of the web shows the area where the capture spiral had many reverses and therefore could not be assigned a coiling. The coiling of the capture spiral was indeed the same as the coiling of the auxiliary spiral, and the change from one coiling to the other occurred in both spirals at a similar distance from the centre of the web.

The capture spiral sometimes followed irregularities in the shape of the auxiliary spiral. Note for example in Fig. 3 the bulge in the web on the right-hand side, possibly caused by the similar bulge in the outer turns of the auxiliary spiral.

Influence of shape of auxiliary spiral on the shape of capture spiral

To study further the influence of the shape of the auxiliary spiral, the web was manipulated by changing its orientation during the construction of the spirals. Laying a web horizontally during construction of the auxiliary spiral changes the shape of this spiral (Eberhard, 1987).

Material and methods

Spiders were again kept under standard laboratory conditions, but the experimental webs were laid horizontally during various phases of construction: (i) auxiliary spiral only ($n = 8$), (ii) capture spiral only ($n = 5$), or (iii) both auxiliary and capture spirals ($n = 5$). In all cases the web was in a normal (vertical) orientation before spiral construction. The positions of the spiral attachments to one radius at each side of the web (top, left, bottom and right) were digitised; i.e. their x, y coordinates were entered into the computer for further analysis. Each spiral was then converted into a series of ovals of corresponding shape to compare the auxiliary and the capture spiral; using a method similar to that described in Mayer (1953). Direct comparison of shape was not possible since the two spirals have different pitches. For all ovals, both average diameter (width + height)/2 and the shape were calculated. As a measure for the shape I used the ratio (width – height)/(width + height). A perfectly round web has a shape of 0.0, vertically elongated webs as built by *A. diadematus* have a negative shape. For each web, a range of diameters was determined where the two spirals overlap. Ovals outside that range were discarded, thus eliminating capture-spiral ovals at the periphery of the web and auxiliary-spiral ovals near the centre. From the remaining ovals, the average shape was calculated for both the auxiliary and the capture spirals. The shapes of the auxiliary spirals built in horizontal and vertical orientation were compared using an unpaired two-tailed t-test. The relationship between auxiliary and capture spirals was calculated using regression analysis.

Results

All spiders completed their webs after the disturbance of changing the orientation of the frame, although some waited at the hub for several minutes before continuing.

The shape of the auxiliary spiral was influenced by the orientation of the web during its construction. The average shape of auxiliary spirals built in vertical (normal) orientation was –0.0627 (sd = 0.0190, $n = 13$), which differed significantly ($p < 0.001$) from the average shape of auxiliary spirals built in horizontal orientation which was 0.0087 (sd = 0.0435, $n = 13$).

The shape of the auxiliary spiral largely determined the shape of the capture spiral (Fig. 4). If the shape of the capture spiral were identical to the shape of the auxiliary spiral, the slope of the regression line would be 1.0. In reality, the slope was less than 1.0 ($p < 0.01$), but the regression line went through the point (0.0, 0.0). This means that the capture spiral tended to be closer to a “round” (shape = 0.0) spiral than the auxiliary spiral. This finding was independent of the shape of the auxiliary spiral and independent of the orientation of the web during placement of the capture spiral.

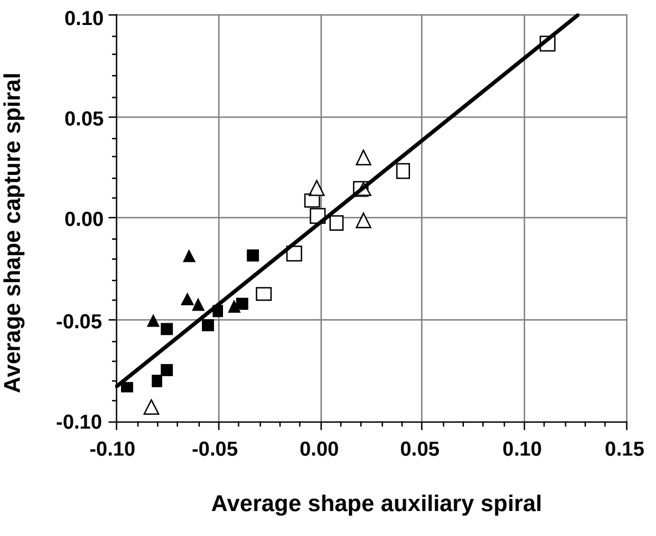

Fig. 4: Regression between the shapes of auxiliary and capture spirals ($y = -0.002 + 0.802x$, $r^2 = 0.898$, $p < 0.001$). Each symbol represents one web. Solid symbols represent webs that were in a normal (vertical) orientation during construction of the auxiliary spiral. Open symbols represent webs that were in a horizontal orientation. The shape of the symbol indicates the orientation of the web during construction of the capture spiral (triangle = horizontal, square = vertical).

General discussion

The coiling and shape of the auxiliary spiral of *A. diadematus* largely determined coiling and shape of the capture spiral. Vollrath & Mohren (1985) claim that the two spirals have fundamentally different forms, the auxiliary spiral being logarithmic, the capture spiral arithmetic. My results do not contradict this idea, since the type of spiral is defined by the distance from one turn to the next, whereas the shape as used in my work is defined as the deviation from a “round” spiral.

The shape of the auxiliary spiral depended on the orientation of the web during its construction. Eberhard (1987) demonstrated that the auxiliary spiral in non-horizontal webs of *Leucauge mariana* (Keyserling) (Araneidae) showed consistent up-down asymmetries in spacing between loops that were not present in horizontal webs. My results go further than that and show that the overall shape of the auxiliary spiral is affected by the orientation of the web.

The shape of the capture spiral did not depend on the orientation of the web during its construction. This would suggest that gravity plays no role during the placement of the capture spiral. On the other hand, we know from Vollrath (1988b) that capture spirals are greatly disturbed when they are built under rotation around an axis perpendicular to the web plane, i.e. when the vector of gravity is continuously changing, indicating that the spider uses gravity somehow.

Which clues does the spider use to sense the coiling of the auxiliary spiral while it is building the capture spiral, and what do these results tell us about the possible rules the spider applies during the placement of the capture spiral? Three possible explanations of how the spider "knows" the coiling of the auxiliary spiral are that: (i) the spider "remembers" how it built the auxiliary spiral, (ii) the spider can somehow detect the direction in which the silk was laid down, or (iii) the spider uses the position of the auxiliary spiral with respect to the capture spiral as the latter is constructed.

The most parsimonious explanation is that the spider uses the position of the auxiliary spiral as a guide to place the capture spiral. Since constructing a highly regular capture spiral from the periphery to the centre of the web would seem to be a difficult task, the spider probably requires points of reference to place the capture spiral. It has been established that spiders use the distance to the previous turn of the capture spiral (Vollrath, 1987). However, distances between consecutive turns of the capture spiral vary by 30% (unpublished data). If a spider uses the previous turn of the capture spiral only, this variation would—starting with a nearly round first turn—lead to a distorted shape in the capture spiral near the hub. It follows that the spider requires another guide or reference. Possible guides include the angle between the spiral segment and radius or the distance between capture spiral and auxiliary spiral. Neither of these guides would be easy to use since the angle between capture spiral and radius changes depending on the position in the web (Vollrath & Mohren,1985). This is inherent from the fact that the web is not a perfectly round structure. The distance between the two spirals changes as the spider builds the capture spiral, either increasing or decreasing depending on the relative coiling of the two spirals (Fig. 5).

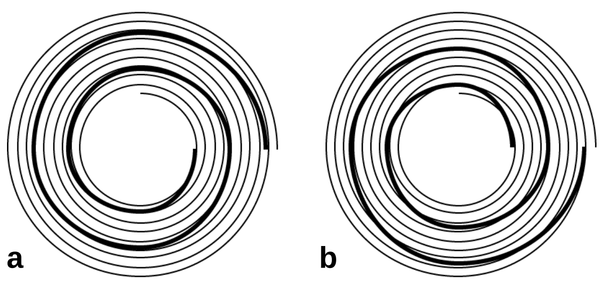

Fig. 5: Schematic representation of auxiliary (bold line) and capture (thin line) spiral in a web. In (**a**), both spirals have the same coiling, in (**b**) they have opposite coiling. If the two spirals have the same coiling, the distance to the next inner auxiliary spiral increases as the spider advances with the construction of the capture spiral from the periphery to the centre. If they have opposite coiling, the distance decreases.

My results showing that both spirals have a similar shape suggest that the spider *does* use the auxiliary spiral as a guide. However, any rule relating the distance between the two spirals would need to take into account whether the capture spiral has the same coiling as the auxiliary spiral, since the change of distance between the two spirals depends on the relative coiling. A simple rule might be that the spider builds the capture spiral mainly with the same coiling relative to the auxiliary spiral, so that the change of distance between the spirals would be constant. In fact, my results show that this is exactly what the spider does! I suggest that the reason the two spirals usually have the same coiling over a large part of the web is merely a manifestation of the use of the auxiliary spiral as a guide.

The results of my study do not allow conclusions about whether the angle between radius and capture spiral is also used by the spider as a guide when placing the capture spiral.

The other two explanations of why the two spirals have the same coiling seem less likely. Neither can give a satisfactory reason why the spider should build most of the capture spiral in the same coiling as the auxiliary spiral. The third series of experiments also showed that the spider built the capture spiral in the same coiling as the auxiliary spiral, even when the spider was disturbed and went back to the hub between construction of the auxiliary and the capture spiral. This fact renders the explanation that the spider remembers the coiling of the auxiliary spiral even less likely.

There is also no known clue about how the spider could detect the direction in which the silk was produced, even though some male lycosid spiders seem to be able to detect the direction in which a female dragline was laid (Tietjen, 1977), but then only with a probability of at most 67%. Threads of *A. diadematus* do not seem to have any surface structures indicating the direction (SEM analysis by T. Köhler, pers. comm.). However, at present the possibility cannot be excluded that the spider may somehow be able to recognise the direction in which the auxiliary spiral was constructed.

My experiments and observations were done on *Araneus diadematus*. Other species have different coiling similarities, ranging from around 50% (e.g. *Zygiella x-notata* (Clerck) (Araneidae) and *Uloborus walckenaerius* Latreille (Uloboridae)) to 100% in a species of the genus *Gasteracantha* (Araneidae) and *Hyptiotes paradoxus* (C. L. Koch) (Uloboridae) (unpublished data, small sample size). This suggests that different species use different rules for their capture spiral construction.

The coiling similarity is quite easy to determine from a good photograph of a web and it gives us some indication of the rules the spider uses to place the capture spiral. Comparing coiling similarities between species would therefore be a good and easy way to help find answers to questions concerning the evolution of the orb web.

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