Ekológia (Bratislava) Vol. 19, Supplement 3, 307-318, 2000

PLANARITY AND SIZE OF ORB-WEBS BUILT BY *ARANEUS DIADEMATUS* (ARANEAE: ARANEIDAE) UNDER NATURAL AND EXPERIMENTAL CONDITIONS

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Abstract

ZSCHOKKE S., VOLLRATH F.: Planarity and size of orb-webs built by *Araneus diadematus* (Araneae: Araneidae) under natural and experimental conditions. In GAJDOŠ P., PEKÁR S. (eds): Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava), Vol. 19, Supplement 3/2000, p. 307-318.

Orb-weaving spiders build more or less planar webs in a complex, three dimensional environment. How do they achieve this? Do they explore all twigs and branches in their surroundings and store the information in some form of mental map? Or do they at first just build a cheap (i.e. few loops, possibly non-planar) web to test the site and – if this first web is successful (i.e. the web site is good) – later build subsequent improved and enlarged webs, by re-using some of the anchor points and moving other anchor points? The second hypothesis is supported by the fact that the garden cross spider *Araneus diadematus* CLERCK (Araneidae) usually builds several webs at the same site, re-using structural parts of one web for subsequent webs. To further test the second hypothesis, we measured and assessed the planarity of first and of subsequent webs built in the field and in the laboratory.

First webs built at a new site in the field or in the laboratory were less planar and less vertical than subsequent webs. Furthermore, first webs built in the laboratory also had fewer loops in their sticky spiral. Our observations thus support the hypothesis that these orb-weaving spiders follow a risk-minimising strategy of first building a low-investment pilot web which on renewal may be improved and enlarged.

Introduction

The orb-web is a structure built by spiders to catch flying insects. An optimal orb-web is one that captures as many insects as possible for a given construction effort. To maximise the capture rate the spider should – among other considerations like web shape, spiral spacing, etc. (e.g. EBERHARD, 1986; CRAIG, 1987; AP RHISIART, VOLLRATH, 1994; SANDOVAL, 1994; SCHNEIDER, VOLLRATH, 1998) – build the web in a way to cover the largest area possible. This is best achieved when the orb-web is built to lie in a perfect plane, since a planar web has the largest possible projection area per web area (WAINWRIGHT et al., 1976). Another advantage of a planar orb-web is that the forces on the radii are more equally distributed when an insect hits the web (DENNY, 1976; LIN et al., 1995). This equal distribution of forces is important because only a web built in this way makes optimal use of its material; cf. Maxwell's lemma which essentially states (PARKES, 1965) that a structure makes best use of its material if, when loaded to the breaking point, all members break at the same time. Moreover, studies have shown that spiders respond more rapidly in a web with higher regularity (WEISSMANN, 1987; FOX, 1990). Our own observations in the laboratory also suggest that planar webs are visible to the (e.g. human) observer from a small observation angle only, whereas distorted webs are – at least partially – visible from a much wider angle. There are a few spider species of the genera *Theridiosoma* and *Epeirotypus* (Theridiosomatidae) that build webs with a regular distortion. CRAIG (1986) has suggested that these webs may be less visible to insects, since not all parts of the web are in focus at the same time. Since the webs of *A. diadematus* CLERCK do not have a regular distortion, we conclude that for them – as for most orb-weavers – planar webs are optimal.

Inclination in the vertical is another aspect of the orb-web that may influence its capture rate. Empirical observations on orb-webs have shown that in most cases vertical or nearly vertical webs are better traps (PETERS, 1933; EBERHARD, 1972, 1989, 1990; VARGHESE, NARENDRAN, 1996). Experiments done with artificial webs also showed higher capture rates for vertical compared to inclined or horizontal webs (CHACÓN, EBERHARD, 1980). The reasons are not quite clear, it is however likely that in vertical webs more web area is projected into the horizontal flight path of the average insect flying in habitats where spiders like *A. diadematus* build their webs. EBERHARD (1972) has also suggested that the sticky threads of most orb-webs are not sticky or strong enough to hold an insect for long and that the web therefore relies on the prey to gather additional strands when tumbling down on the web's face. Whatever it may be, most orb-webs are vertical or slightly inclined (FOELIX, 1996). In the temperate zone, most exceptions are found (1) in the cribellate (uloborid) orb-weavers whose silk and web engineering differs from that of ecribellate spiders (PETERS, 1987; ZSCHOKKE, VOLLRATH, 1995a); (2) in the ecribellate cyrtophorids which build strong dry orb sheets underneath a knockdown web that intercepts flying insects (LUBIN, 1973; ZSCHOKKE, VOLLRATH, 1995b), and (3) in another group of ecribellates (metids and tetragnathids) of which many build widely meshed webs near or over water and other moist areas (WIEHLE, 1939; GILLESPIE, 1987) catching insects flying up from the water surface, which have a large wing length to body mass ratio (DALY et al., 1978) and are therefore easier to catch with a web. In the present study we assume the preference of *A. diadematus* to build planar and vertical or nearly vertical webs to be genetically determined, like all basic web construction patterns (REED et al., 1970).

When we look at real webs in the real world however, nothing is optimal. Most orb-webs deviate more or less from the perfect plane and are twisted in some way or another (Fig. 1) thus possessing less than optimal efficiency. We assume that high planarity and high regularity carry higher construction costs – mainly in the use of time – and that savings and hasty work might cause these twisted webs, which we consider to be sub-optimal.

The two aspects of a web – planarity and inclination – are largely determined by the choice of anchor points, i.e. the points where the anchor threads of the web are attached to the surroundings. The possible choice of anchor points is affected by – and can be limited by – the availability and spacing of twigs and branches in the vegetation. To build a web with perfect planarity and optimal inclination the spider must invest time and dragline material as well as risk predation while clambering around in search for ideal anchor points.

Fig. 1. Example of an experimental first web built in the laboratory. The degree of non-planarity (distortion) can be judged by comparing the distances between radii and between subsequent loops of the sticky spiral. This particular web had a deviation of 23.2°, a waste of 9.0% and an inclination of 17.0° (for a description of these measures see text).

In addition, the spider faces a trade-off between the size of a web and the investment of building time and building material. *A. diadematus* usually renews its web every night (Wiehle, 1927; Breed et al., 1964; Ramousse, 1980), generally in the same place (Janetos, 1982) and typically by re-using some of the anchor points and frame threads (Wiehle, 1927; Nielsen, 1932; Carico, 1986; Wirth, 1988). The main section of the web – spiral and radii – are removed by the spider and ingested (Peakall, 1971; Townley, Tillinghast, 1988) for recycling (Breed et al., 1964). Thus, an existing web is a substantial material (silk) and immaterial (set of anchor points) investment of a spider; an investment, however, which is wholly lost if the web is completely destroyed (Zschokke, 1996). A risk-minimising strategy for a spider constructing a web from scratch might thus be to first build a pilot web to test the site, i.e. to test that the web catches insects and is not destroyed (Riechert, Gillespie, 1986; Nakata, Ushimaru, 1999). This pilot web should best be cheap and may therefore have few loops and be sub-optimal for planarity and inclination. If this pilot web is success-

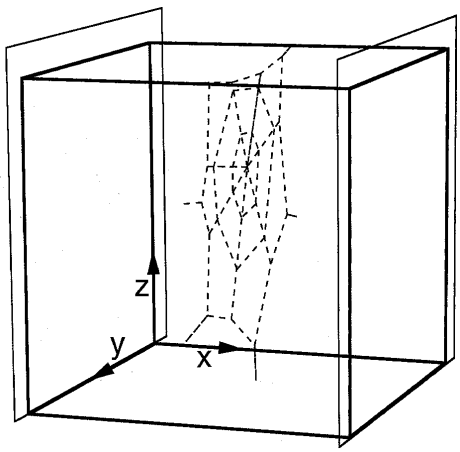

Fig. 2. Cubic box (30 x 30 x 30 cm) used for the experiments. The front, back, top and bottom walls were made out of stiff Plexiglas and the two openings on either side were covered with thin, removable Plexiglas sheets. The thin Plexiglas sheets were smeared with Vaseline to prevent the spiders from attaching threads to them. To measure the position of the anchor points, the corner at the lower left rear of the box was taken as the origin of an x - y - z - grid.

ful, then the spider should build a larger and better web in the same site; if it is not, then the spider should move and test a different site (cf. TURNBULL, 1964).

There is, however, another reason why the first web might not be planar. The spider may not be able to build a planar web right from the start since the orientation skills required might be too complex (VOLLRATH, 1992). The construction of a new web based on a previous one may be less demanding since the framework – namely the frame and anchor points – of the previous web can be used as a reference platform.

If the spider does indeed build such a pilot web first – either to minimise risks or because it is constrained by its orientation capability – we would expect that the first web built on a new site, or indeed any web built without reusing parts of a previous web, should be a low investment web with fewer spiral loops and probably a non-optimal planarity and inclination compared to later webs. To test these hypotheses, we examined webs in the field and in the laboratory. In the laboratory, series of webs built by the same spider were measured and recorded; each series started with a first web built from scratch and continued with subsequent webs in the same site. In the field we measured (1) first webs, built on the day following a complete and thorough destruction of all webs including anchor threads in a locality and (2) webs without prior manipulation (termed 'other' webs, a mixture of mostly non-first and probably a few first webs).

Material and methods

Laboratory measurements of planarity

In the laboratory, we kept eight immature male and female spiders of similar size in cubic boxes (30 x 30 x 30cm) with top, bottom and two side walls of stiff, roughened Plexiglas and two sides covered with removable smooth sheets (Fig. 2). These sheets were smeared with Vaseline to prevent the spider from attaching threads. The boxes were thoroughly cleaned before a spider was introduced into them. Before the spiders were introduced

into these boxes, they were kept in smaller holding frames (30 x 30 x 5 cm) in the laboratory to accustom them to the laboratory conditions (16L/8D). Once spiders had built webs in the holding frames, they were introduced into the boxes. Frames and boxes were always oriented with the openings facing in the same way.

Boxes were inspected daily for webs. When a web had been built, its anchor points were marked with a waterproof pen on the outside of the box. In a few cases, anchor threads were – often close to the wall – split into two threads. In these cases, the point where the elongation of the thread running to the web intersected with the side wall was marked as the anchor point (Fig. 3). Since the decision whether a certain configuration should be considered as a split thread or as two separate single anchor threads was not always definite, the measures of planarity (see below) were devised in a way that adding another anchor point near an existing one had little or no influence on the result of the analysis. In addition, the position of the centre of the web was determined by measuring its projection onto the top and onto the side of the box. This method is inevitably not very accurate and the position of the centre was therefore adjusted during the data transformation (see below). All webs were also photographed and the number of sticky spiral loops counted on these pictures.

Once a web had been recorded, the spider was fed 2-3 fruit flies, *Drosophila* sp., to make the site 'successful'. Later the web was sprayed with water and its capture area carefully impaired by burning away every other radius, making sure that the frame and the anchor points were left intact for the spider to re-use in subsequent webs. In this way, four webs (one first and three subsequent webs) were recorded in one series. A series was terminated by removing the spider temporarily from the box. The box was then cleaned thoroughly and the spider reintroduced the day after building a web in the holding frame. Each spider thus built several series of webs, each of the total of 18 series starting with a first web (that the spider could not base on the framework of a previous web), followed by subsequent webs, each based on the framework of the preceding web.

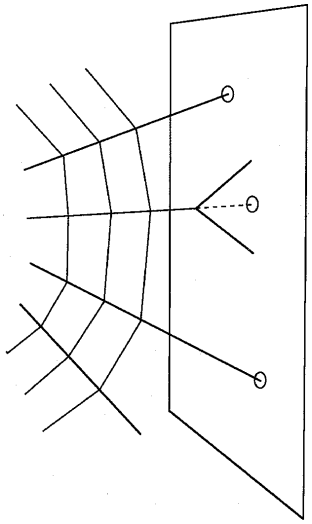

Fig. 3. Method to record the anchor point of split anchor threads. Recorded positions of anchor points are marked with a circle. The one in the middle was extrapolated by elongating (dotted line) the anchor thread running to the web.

Field measurements of planarity

Field data were collected during autumn 1992 from 26 webs built by spiders of various sizes in a hedge along a sports ground in Oxford UK. This hedge had been selected for its abundance of spiders, indicating that it represents a 'good' site for them. Anchor points, frame points and the centres of the webs were recorded using a heavy tripod with a revolving head and a custom-built 3-D measuring device consisting of a pointer sliding on a ruler that could be swivelled (Fig. 4). The position of the measuring pointer in the slider, the position of the slider along the ruler and the angle of the ruler were recorded and later converted into Cartesian (3-D) coordinates. On two evenings all webs along the hedge were destroyed thoroughly to ensure that the following morning all webs were first webs.

Quantification of web planarity

For each web we calculated the median plane, which was defined as the plane where the projection area of the web was largest (Fig. 5). Then the centre of the web was moved perpendicular to that plane to the position where the web area was smallest to correct for inaccuracies during the measurement of its position.

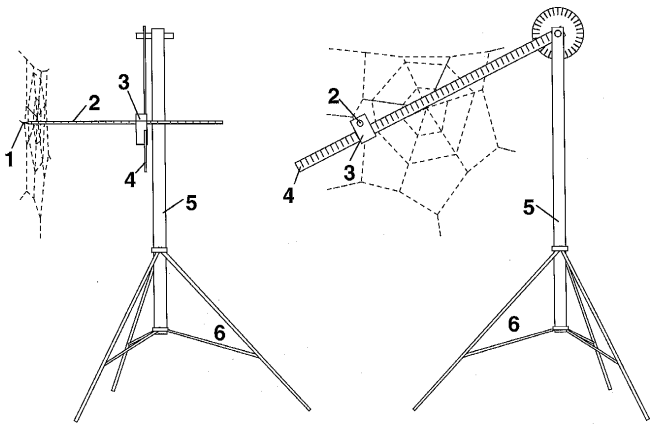

Fig. 4. Side and front view of the tool used to measure webs in the field. The tip (1) of the pointer (2) is on the position to be measured. This pointer can be moved through the slider (3) set onto the ruler (4). The ruler revolves around the top of the vertical post (5) supported by the tripod (6). The position of the tip was determined by the position of the pointer in the slider, the position of the slider along the ruler and the angle of the ruler relative to the (vertical) post.

From a pilot study of this problem (Searle, 1991) we knew that the definition of the measure of planarity quantifying the degree of distortion in a web was critical. For the present study we defined two measures of web planarity. One measure was based on the deviation of the web from the median plane and the other measure on the real area of the web compared to its projection area. Both measures were designed to ensure that a slight change of the position of the centre or the doubling of a point had little or no effect on the result.

With the first measure we assessed the deviation of the web from its median plane (cf. Fig. 5). 360 radial lines separated by one degree were laid from the centre of the web to the connecting lines between the measured points (i.e. either the anchor points or the frame points) and the angles between each radial line and the median plane were calculated. Our first measure, termed 'deviation', was defined as the difference between the upper and lower quartile of these 360 angles.

With the second measure (termed 'waste') we assessed the surplus or waste area of the web. We calculated how much bigger (in %) the real area of the web was compared to its projection onto the median plane. The real area of the web was calculated by summing the areas of the triangles formed by two adjacent measured points and the centre.

For all webs we also calculated their inclination, i.e. the angle between the median plane of the web and the vertical. For webs built in our experimental boxes in the laboratory we additionally counted the number of sticky spiral loops on the photographs of the web. The number of loops was defined as the average number of loops above and below the hub.

Statistical analyses

For the laboratory webs we compared the deviation, the waste, the inclination and the number of sticky spiral loops using a nested ANCOVA with the number of the web within a series as covariate and the spider and the number of the series nested in spider as factors. For the field webs we compared first webs and other webs with a one-tailed unpaired t-test. This comparison was done twice; once for the measures from the anchor points and once for the measures from the frame of the web.

We also compared the deviation, the waste and the inclination (based on the anchor points) between the field and laboratory webs using a two-factor ANOVA with the place as one factor (field vs. laboratory) and the kind (first vs. other) as the second factor. Since subsequent webs built in one series in the laboratory were not independent, their measures were averaged for each series and were used as one data point for 'other' webs in the analysis.

All data handling and transformation were performed using our own software. The statistical analysis was performed using StatView v5.0 on a Macintosh computer and SAS v. 6.08 on a VAX mainframe computer. Nomenclature of orb-web elements follows Zschokke (1999).

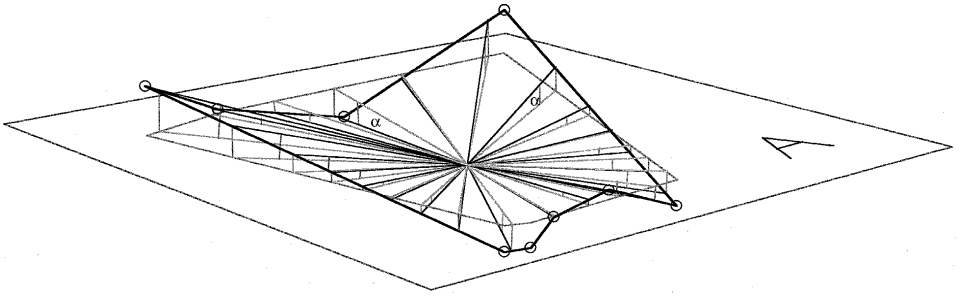

Fig. 5. Quantification of web planarity. The thick black outline is the frame of the web; it is drawn by connecting the measured frame (or anchor) points (marked with small circles). The median plane is indicated by the rectangle A with the projection of the web onto the median plane drawn in grey. To calculate the deviation of the web, radial lines (shown here as thin black lines) were laid between the centre of the web and the connections between the measured points (for illustrative purposes only 24 of the 360 lines used in the calculations are shown here). Deviation was defined as the difference between the lower and upper quartile of all angles (?) between these radial lines and the median plane.

Results

Within each series of webs built in the laboratory, deviation (ANCOVA, P=0.016), waste (ANCOVA, P=0.045) and inclination (ANCOVA, P=0.012) decreased significantly and number of sticky spiral loops increased significantly (ANCOVA, P<0.001). There were no differences between individual spiders for deviation, but there were differences for waste, inclination and number of sticky spiral loops. Furthermore, there was a non-significant difference between series for deviation (Table 1, 2).

For the field webs we calculated deviation, waste and inclination for both frame and anchor points. The comparison of first webs and other webs gave mixed results (Table 3). There was no difference in deviation between first webs and other webs. Waste calculated from the anchor points (but not from the frame) was significantly (t-test, P=0.035) larger for the first webs. The inclinations (calculated from the anchor points and from the frame) of the first webs were larger (t-test, p=0.048 and p=0.049, respectively) than inclinations of the other webs.

The comparison between field webs and laboratory webs showed that deviation, waste and inclination were all significantly larger for the laboratory webs (ANOVA, P?0.001, Table 4). Waste (ANOVA, P=0.050) and inclination (ANOVA, P=0.018) were smaller in first webs whereas deviation was only non- significantly (ANOVA, P=0.079) so. No significant interactions between the two factors were found.

Examining the numerical values of the measures (Table 5) we found that field-webs were generally quite planar. The waste of undisturbed field webs was on average less than 4%. The inclination of some laboratory webs on the other hand was quite large, e.g. one web was nearly horizontal at 88.9°, and another one had an inclination of 74.4° to the vertical.

T a b l e 1. Nested ANCOVA of the measurements taken from webs built in the laboratory. The spider and the number of the series nested in spider were used as factors and the number of the web within a series (no. of web) was used as a covariate. The deviation, waste and inclination decreased with the number of the web.

Source		Deviation			Waste			Inclination		
	df	MS	F	P	MS	F	P	MS	F	P
Spider	7	54.6	1.26	0.289	390.7	4.63	**<0.001**	1168.6	3.43	**0.004**
Series (spider)	10	78.3	1.80	0.082	103.9	1.23	0.293	400.4	1.18	0.327
No of web	1	270.4	6.23	**0.016**	356.3	4.23	**0.045**	2294.5	6.74	**0.012**
Residual	53	43.4			84.3			340.3		

Discussion

The results from our laboratory study suggest that the first webs built in a new site were usually more distorted, less vertical and relatively small, i.e. had fewer loops of the sticky spiral. When given the chance to build subsequent webs at the same site – reusing the frame and anchor points of the old web – the spiders built webs that were more planar, more vertical and had more sticky spiral loops. These results support the hypothesis that an orb-weaver like *A. diadematus* first builds a low investment pilot web and, if the first web was successful, will then build 'better' webs at the same site. The results from the field webs were not so clear, probably because some webs we assumed to be other webs, were at least partially first webs, because a part or the whole of the previous web had been destroyed by other causes like wind or dropping leaves or because the spiders that built a web the day after our thorough destruction of all webs may have been a non-random sample of the spiders at that location (e.g. only small spiders) which may have built differently.

We suggest that *A. diadematus* builds this first pilot web either to minimise risks or because it is incapable of building a perfect web from scratch. Because *A. diadematus* is virtually blind and primarily uses tactile information for orientation (e.g. VOLLRATH, 1992), it can use its first web as a reference plane and working platform to build a subsequent, improved web.

T a b l e 2. Nested ANCOVA of the numbers of sticky spiral loops of the webs built in the laboratory. The spider and the number of the series nested in spider were used as factors and the number of the web within a series (no. of web) was used as a covariate. For this analysis some data were missing because the sticky spiral loops could not be counted on all photographs. The number of sticky spiral loops increased with the number of the web.

Source	Sticky spiral loops			
	df	MS	F	P
Spider	7	362.3	6.22	**<0.001**
Series (spider)	9	93.4	1.60	0.146
No of web	1	1088.6	18.69	**<0.001**
Residual	42	58.3		

The inclination angles we measured were similar to those measured by other researchers. PETERS (1937) measured webs built in his house and gives an average inclination angle of 8.6° to the vertical. Horizontal or nearly horizontal webs of *A. diadematus* were repeatedly observed in the laboratory (SZLEP, 1958; own observations) and have

T a b l e 3. Comparison between the first (n=9) and the other (n=17) webs measured in the field. The table on the left is based on the measurements of the anchor points, the table on the right is based on the measurements of the frame of the webs.

Anchor	t (unpaired)	P (1–tail)	**Frame**	t (unpaired)	P (1–tail)
Deviation	0.379	0.354	Deviation	0.122	0.452
Waste	1.894	**0.035**	Waste	0.546	0.295
Inclination	1.735	**0.048**	Inclination	1.721	**0.049**

T a b l e 4. Two-factor ANOVA comparing laboratory webs with field webs (where) and first webs with other webs (kind). The interaction where * kind was omitted when its p-value was larger than 0.25.

Source	**Deviation**				**Waste**			**Inclination**			
	df	MS	F	P	MS	F	P	df	MS	F	P
Kind	1	110.4	3.19	0.079	277.4	4.01	**0.050**	1	1715.9	5.91	**0.018**
Where	1	1157.7	33.49	**<0.001**	824.0	11.91	**0.001**	1	4055.3	13.96	**<0.001**
Where* kind								1	646.2	2.22	0.141
Residual	60	34.6			69.2			59	290.5		

T a b l e 5. Averages, Standard Error, minimum and maximum of the deviation, waste and inclination of the webs. The values are given separately for first and other webs and laboratory webs and field webs (measurements based on anchor points). Sample sizes were: laboratory: 18 first webs, 54 other (= subsequent) webs; field: 9 first webs, 17 other webs.

	Deviation [°]		**Waste [%]**		**Inclination [°]**	
	Laboratory	Field	Laboratory	Field	Laboratory	Field
First	18.2±1.8 (6.9–32.5)	6.4 ±0.8 (2.1–8.8)	16.3 ±2.8 (2.7–39.8)	7.4 ±2.2 (0.8–18.9)	35.4 ±6.8 (0.1–88.9)	13.0 ±2.2 (5.1–23.3)
Other	14.9 ±1.0 (2.8–31.6)	5.9 ±0.9 (2.1–15.3)	13.8 ±1.5 (0.6–43.2)	3.9 ±0.7 (1.0–12.1)	24.2 ±2.4 (1.0–74.2)	8.8 ±1.4 (0.9–20.7)

also been observed in the field, i.e. over the top of a rainwater-barrel (BENNET-CLARK, pers. com.).

A surprising result of this study was that laboratory webs were consistently less planar and had a larger inclination to the vertical than field webs, even though the spiders had a seemingly 'perfect' environment for choosing anchor points, as the Plexiglas walls of the box were available on four sides for attaching threads, as opposed to a limited number of branches and twigs in the field. We suggest that the Plexiglas boxes might not have provided enough structural diversity, either for the spider to orient itself or to easily clamber to a desired place and that the spiders lacked the wind currents often employed during the early stages of web construction. In some instances we observed that the spiders had problems walking along the side walls or the top of the boxes, even though the walls had been roughened.

Breed et al. (1964) has shown an increase in web size when spiders were left undisturbed and could ingest their old webs. He has also shown that this increase is smaller when the web was destroyed but still left for the spider to ingest. He hypothesised that the existence of the web or its remnants constitutes a signal for spiders to build a larger web the following day. In the present study, the frame of the web had been left intact, but a large part of the material had been burnt away. The number of loops in the web nevertheless showed an increase. It seems that both the possibility to recycle material from the previous web *and* the possibility to reuse the frame of the previous web induce the spider to invest more into the web. Other studies (Eberhard, 1988; Zschokke, 1997) have also shown that the size of the web is strongly influenced by the availability of material in the silk-glands of the spider.

The orb-web of ecribellate orb-weavers (like *A. diadematus*) is considered to be a low-investment web (Vollrath, 1985; Janetos, 1986; Tanaka, 1989) and much of the energy invested into building a web is thought to be recycled when the web is removed and ingested (Peakall, 1971; Townley, Tillinghast, 1988). We would therefore expect that *A. diadematus* can cheaply (and often) change its web-site. This is, however, not the case (Wiehle, 1927; Janetos, 1982), because the risks and costs of travelling to and of exploring a new site are costly (Vollrath, 1987; Zschokke, 1996) which makes it often more economical (and safer) for the spider to stay, even at low benefit sites. The present study shows that changing a web site may carry additional costs through a sub-optimal first web.

Acknowledgements

This study has been carried out as a partial fulfilment of Samuel Zschokke's Ph. D. Thesis and has been financed by a grant of the Swiss National Science Foundation to Fritz Vollrath. Annemarie Fränkl and Helene Bracht Joergensen helped with data collecting. We would like to thank Alun ap Rhisiart and several reviewers for critical comments on earlier drafts of the manuscript and Peter Duelli for his help in entomological matters. Figures 2 and 5 were drawn using the freeware program 'Rotater' by Craig Kloeden.

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