



Analysing Spider Web-building Behaviour with Rule-based Simulations and Genetic Algorithms

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We analysed the web construction-behaviour of an ideal orb web-building spider using a computer model that constructed artificial webs with a Rule Based Simulation and optimised them with a Genetic Algorithm (GA). The GA simulated adaptation towards an adjustable ecological niche in a population of artificial (cyber) spiders. Web construction behaviour in each cyber spider was controlled by a set of rule parameters (encoded in artificial genes) resulting in different web shapes. We then statistically compared the best cyber webs from our optimisation runs with real webs of *Araneus diadematus* built under controlled, experimental conditions in the laboratory. Web characteristics like spiral distances, eccentricities and vertical hub location could to a large degree be accurately simulated with the model. In addition, falsification of working hypotheses using the model pointed to incomplete or wrong assumptions about the behaviour under study which became apparent when web geometry adapted poorly.

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Introduction

All spiders produce silk and employ the material in a range of uses. For most spiders the main use is in prey capture by snare or web. Orb-weavers like *Araneus diadematus* or *Zygiella x-notata* build highly specialised types of web (Witt *et al.*, 1968; Shear, 1986). These are flat (two-dimensional), vertical capture nets tailored in shape and mesh dimensions to the environment: vegetation (support), climate (e.g. wind) and prey (insects). This tailoring is the outcome of two types of adaptation: long-term genomic adaptation (evolution) over many generations of selection and short-term behavioural adaptation (modification) in response to local conditions. Although, at first sight, web-building appears to be rather stereotypic, the spider actually seems able to vary its behaviour considerably in order to construct an optimal structure whatever the environmental conditions. Thus, spider webs are ideal objects for studying the evolution of a complex animal architecture resulting

from dynamic interactions of reasonably simple behaviour patterns. The sensory modalities used for orb web-construction are limited. It appears that vision is not used (Witt *et al.*, 1986) and tension only marginally (Eberhard, 1981; Krieger, 1992). Some form of orientation memory stack is likely (Görner & Claas, 1986; Eberhard, 1988) and navigation by path integration not unlikely (Peters, 1937; Krieger, 1992). Thus a major sensory input about limb and body orientation would originate from the kinaesthetic/idiothetic sense via stretchreceptors or lyriform organs (Seyfarth, 1986). It seems to us that, for the purpose of modelling, it is not unreasonable to reduce the orb weaver's building behaviour to a mainly geometrical task allowing simplifications and abstractions. We thus ignore non-spatial cues like tensions and, complex cues like vision, and only allow the spider knowledge about the placement of threads that it had touched a few moves before the present.

Our main reason for computer modelling web-building is the need for a precise, analytical tool in our quest for the spider's own, real construction rules.

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Such a tool (or hypothesis test system) generates data that can be compared with data from real live spiders, be they measurements of geometrical web characteristics or perturbation experiments on the web-building animals. Our present model is based on the *Theseus* approach by Gotts & Vollrath (1991, 1992). In contrast to *Theseus*, our new approach named *NetSpinner III* uses a different set of construction rules as well as a Genetic Algorithm (GA) that incorporates Wright's shifting balance model for the parallel evolution of traits in a subdivided population (Wright, 1970). In this way *NetSpinner III* is able to optimise the variables in its construction rule set for webs that fit best into a range of artificial (modelled) "ecological" niches, pre-set by us.

This approach provides us with a tool to explore behavioural strategies for the (optimal) construction of typical orb web geometry under controlled conditions.

Introduction to Web Construction in Orb Weaving Spiders

Orb web construction differs between spider species in detailed behaviour patterns (Eberhard, 1982). While, for example, *Araneus diadematus* (Araneidae) seems to use mainly its front legs for orientation of a thread placement (Reed *et al.*, 1965; Vollrath, 1987), *Nephila clavipes* and *Zygiella x-notata* (Tetragnathidae) may employ the hind legs for this task (Weissmann, 1987).

Still, all three species built orb webs which share the basic web characteristics of evenly spaced radials overlaid by an evenly spaced spiral. Moreover, even within the same species of spider we can find considerable variation in web morphology (Peters, 1951); *A. diadematus*' webs show structural adaptation to wind, temperature and humidity (Vollrath *et al.*, 1997); and the webs record drug and pesticide application (Peters & Witt, 1949; Witt *et al.*, 1968; Samu & Vollrath, 1992) or experimental perturbation of the normal building procedure (Peters, 1937; König, 1951; Vollrath, 1986). However, even highly modified webs share very specific characteristics (Vollrath, 1988) that can be studied comparatively (Vollrath & Mohren, 1985). After exploration of the web site an orb web spider constructs (1) frame and initial radii, (2) all other radii and the hub, (3) the auxiliary spiral (from the inside out) and finally (4) the capture spiral (from the outside in). Some spider species (such as *Fecinia* sp.) skip the construction of the auxiliary spiral and build the capture spiral

directly from the hub towards the frame (Robinson & Lubin, 1979).

Introduction to Modelling Web Construction

Our model simplifies and divides the web construction stages into construction of (1) first radii, (2) other radii and frame, (3) first spiral loop and (4) following spiral loops.

The spiral loops are built from the inside out and are therefore analogues of the auxiliary spiral in *Araneus diadematus*. However, in some models we will sometimes use them as if they were capture spiral. At this stage of our modelling approach we feel justified in doing so since Zschokke (1993) has been able to demonstrate coiling similarity of auxiliary and capture spiral. Future models using techniques similar to those described below (but obviously more complex) shall attempt to incorporate, in addition to an inside-out spiral, a capture spiral built from the outside; this would be more realistic for comparisons with the behaviour of *Araneus diadematus*.

Our artificial spider has complete freedom where it places the hub and how many initial radii it uses. The length of these radii is only restricted by the shape and size of the given frame wherein to build. The following radii have to be placed between the existing ones and cannot exceed their length.

The frame is simply given by the connection of the end points of the radii. Finally, the artificial spider builds the capture spiral within the given constraints of the previous stages. Unlike the real spider which uses detours (a physical constraint), our cyber spider "jumps" from radius to radius and attaches new capture spiral nodes on each. The parameter controlled rules (Fig. 1) allow the construction of a great variety of different spiral shapes by controlled variation of the spiral distance and optional inversion of the direction of movement.

The Process of Artificial Web Construction

STAGE 1

In stage 1 [Figure 2(a)] the rule system performs the construction of the first radii and the frame. This stage involves the *EqualSpacingRule* and *Length-CrossRule*.

The *EqualSpacingRule* is responsible for the number of first radii (gene 01) and their orientation. The first radius points towards the north direction modified by a phase angle τ (gene 02). The base angle α between all neighbouring first radii is given by

dividing 360 deg by their number. An additional variability factor (gene 03) determines the range of a second random range ρ which is added to the base angle.

The length of the radii is determined by the shape of a function of the radius orientation angle γ describing a curve for the radii length in the *LengthCrossRule*. Four genes for the preferred length in north, east, south and west orientation (genes 01–04) are used to set the base points spanning the curve [dashed arrows in Fig. 2(a)]. The shape between these points is then defined by an interpolation function which is either a linear or a sinus/linear overlay function (function type determined by gene 05) specified in the four quadrants north, east, south and west. The pure linear function describes a straight line as a function of radius length over orientation angle (phase transposed to an angle between 0 and 90 degrees within each quadrant). The second one adds a sinus term of two times the phase transposed angle to the linear term which is weighted by an influence factor p (genes 06). The resulting curves for three different values of p are shown in Fig. 2(a).

Finally, the frame is given as a polygon of lines connected with the peripheral points of the radii.

STAGE 2

After the construction of the first radii and the frame, additional radii are filled into the space between them. Figure 2(b) shows the first radii in grey colour and the next radii as black lines. The stage is processed by the *AngleCrossRule* and *LengthToFrameRule*.

The *AngleCrossRule* defines the angle between a new and its previous radius. This angle is described by a set of functions $\alpha_N(\gamma)$, $\alpha_E(\gamma)$, $\alpha_S(\gamma)$ and $\alpha_W(\gamma)$ of the radius angle γ which is spanned by four basic values for the north, east, south and west orientation (genes 01–04). The interpolation of intermediate angles is the same as already described for stage 1, i.e. by a function type (gene 05) and a weighting factor for a sinus overlay (gene 06).

The second rule is not specified by genes and has the only purpose to fix the new radii on the frame,

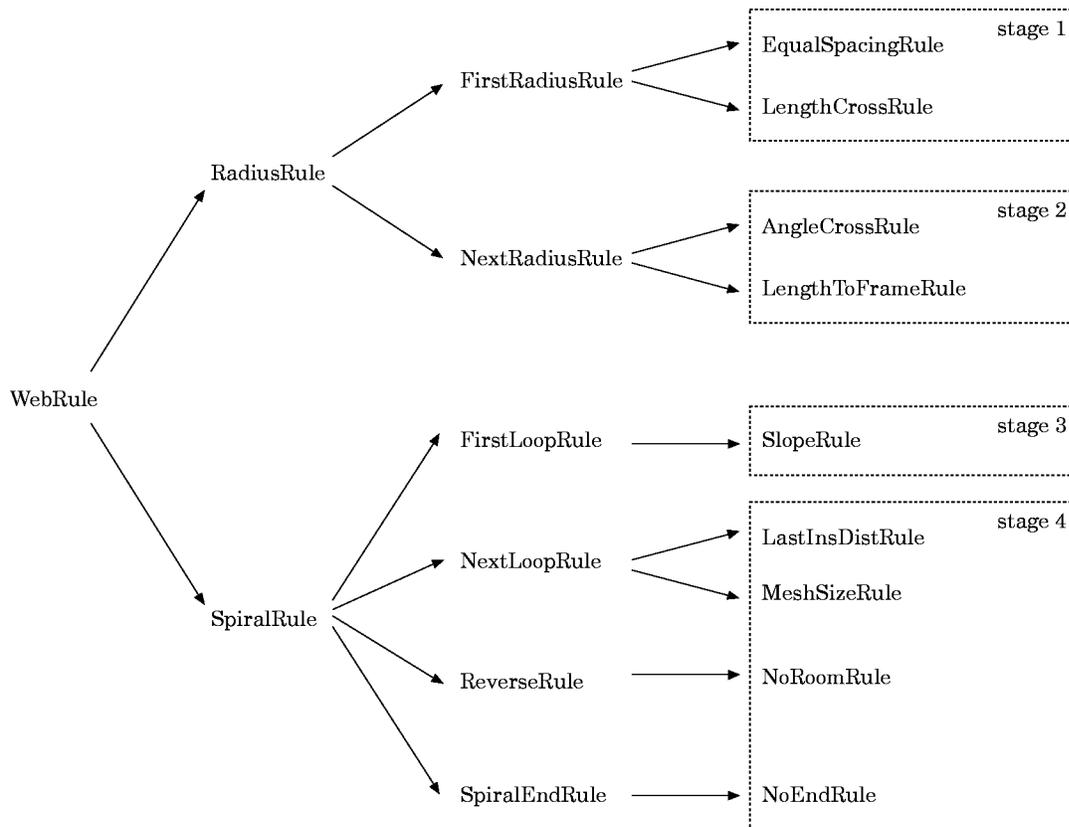


FIG. 1. Structure of the web building rules. The arrows describe an inclusive “is-a” relationship between rule categories, e.g. *FirstRadiusRule* “is-a” *RadiusRule* “is-a” *WebRule*. The nine rules in dashed boxes on the r.h.s. represent the set of rules actually firing in the current approach. They are assigned to one of four web-building stages that are performed in sequential order.

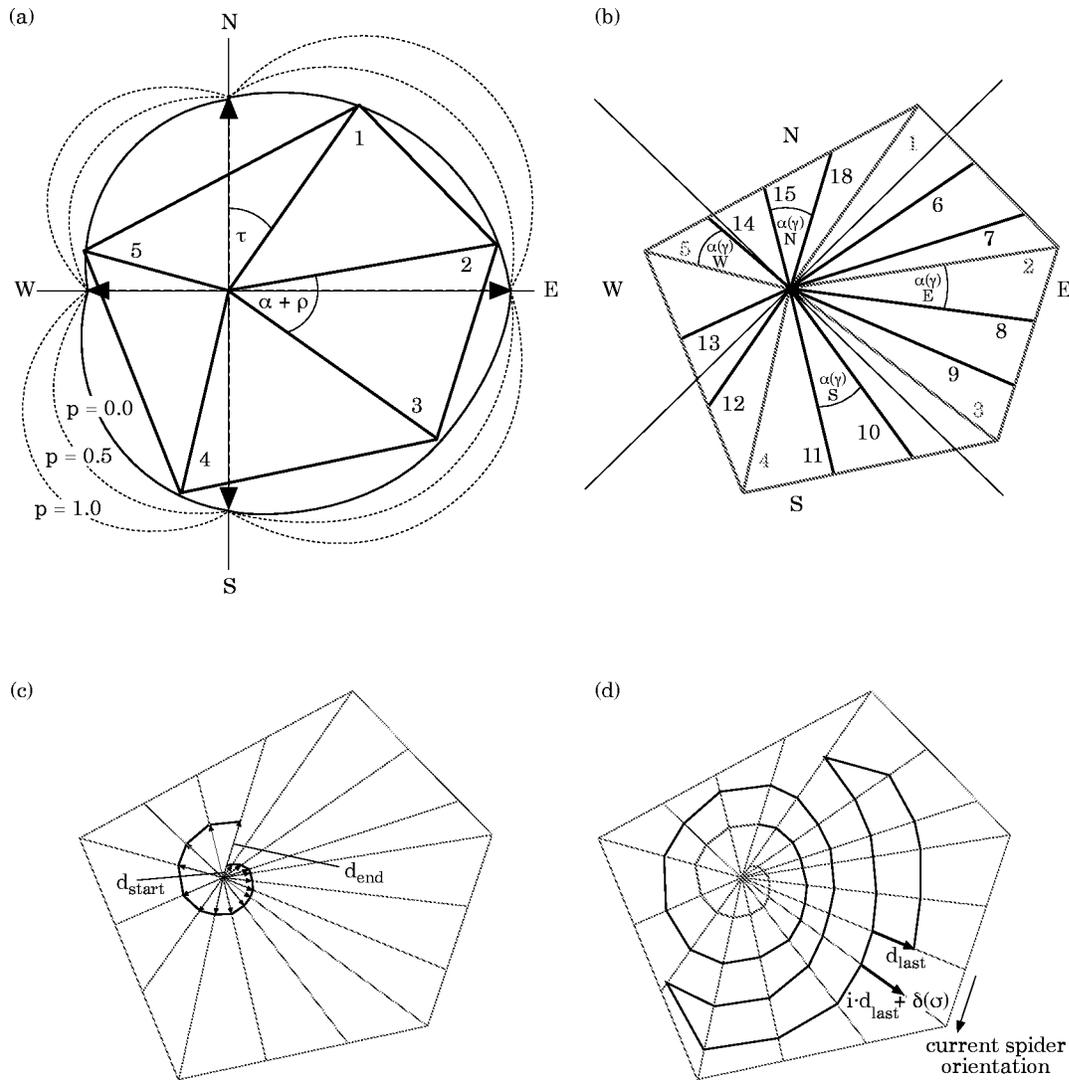


FIG. 2. Graphic description of the web algorithm in action. For extensive explanation see text. Note that in the case presented in this paper we omit the auxiliary/capture spiral duality of the typical orb spider and use only one spiral. (a) Stage 1—construction of first radii and frame. The length of the radii is limited to a curve of a function which is adjusted by a parameter p . Three curves for $p = 0.0$, $p = 0.5$ and $p = 1.0$ are shown, where the solid drawn curve for $p = 0.0$ defines the radii length for this example. The dashed arrows in north, east, south and west orientation represent the basic spanning points for the curve. (b) Stage 2—insertion of next radii between the existing ones. The numbers indicate the sequence of construction. N, E, S and W name the partition of the entire space in four quadrants in north, east, south and west orientation. The angle differences between newly introduced radii and existing first radii α is a function of the radius angle, and is separately defined for each quadrant. (c) Stage 3—first loop of the spiral. The first attachment points are constructed by a linear increase of an initial distance d_{start} from the web centre along the first radius up to a final distance d_{end} of the last radius in clockwise or anti-clockwise orientation. (d) Stage 4—main construction of the spiral. A new distance of an attachment point from the next inner one on the same radius is mainly determined by an increase of the last distance d_{last} by a factor i and can vary by an added value $\delta(\sigma)$ depending on the current body orientation σ of the spider.

i.e. to set their length to the distance of the frame from the centre for a given angle.

STAGE 3

The next stage handles the construction of the first loop of the capture spiral which needs separation from all following actions. This is required because the artificial spider cannot use information coming from existing capture spiral threads before the

construction of the first loop and therefore needs to use a different strategy executed by the *Slope Rule*.

This rule determines the attachment points of the capture spiral on the radii by giving the distance of each new thread junction from the web centre. These distances are given by an initial distance d_{start} for the first radius (gene 01) and equally increased distances for the following ones up to the distance of the last radius d_{end} (gene 02) of the first slope [Fig. 2(c)].

STAGE 4

The final, fourth stage is the most complex involving the four rules *LastInsDistRule*, *Mesh-SizeRule*, *NoRoomRule* and *NoEndRule*. The first two rules represent a subgroup within these four, since they work directly together on the determination of a new attachment point.

The *LastInsDistRule* determines the base location for a capture node on a radius by increasing the last distance of an attachment point to the next inner one on the same radius by multiplying the last distance d_{last} with a factor i (gene 01) greater than one.

The resulting distance is modified by the *Mesh-SizeRule* giving a deviation value $\delta(\sigma)$ which is dependent on the current orientation σ of the spider's body. A deviation value (gene 01) of smaller than 100 enforces smaller meshes (i.e. spiral distances) in horizontal orientation, whereas a greater value leads to smaller meshes in vertical orientation.

This process continues until the remaining space between the next planned attachment point and the frame is becoming too small to fix a new thread. At this point, the reverse rule *NoRoomRule* can fire and reverse the movement direction of the artificial spider.

If there is still no room left for further construction, then the *NoEndRule* stops its continuous firing during this stage and signals the end of the web building. The result is shown in Fig. 2(d).

Optimising the Rule System with Genetic Algorithms

We use Genetic Algorithms in our modelling approach in order to better explore the state space of the model's possible web construction strategies. In the context of our system, GAs have two functions. First, they allow the description and encoding of an optimisation problem as a set of parameters—in this case the parameters of the rule system. Second, they allow us to treat these parameters as if they were genes in an organism; i.e. let them replicate, mutate, recombine and submit to selection. This results in a dynamic-adaptive system where the dynamic is given by changes of the individuals and the adaptation by using natural evolution as a model. Individual spiders are described firstly by their genotype (the syntax, represented by the genetic coding of the parameters in the chromosome) and secondly by their phenotype (the semantics, represented by the interpretation of the genetic information). The evolutionary process consists of the phases: (i) expression (translation from the genotype to the phenotype), (ii) selection (judgement and choice of phenotypes), (iii) replication (generating the offspring-genotypes with the

GA-operators crossing-over and inversion) and (iv) mutation (random changes of the alleles). Following biology, the quality of a solution is given by the fitness of the best individual, which is evaluated by the factor of benefits to costs in web construction. We determine the benefits by “peppering” the webs with artificial prey (Fig. 3) and, following summation of the total amount of prey caught and weighted by its size, exploitable value for the spider and location of the impact. Therefore, the density and size variation of the prey has a major effect on the evaluation of capture efficiency.

Costs are determined by construction time and the amount of different skills used in a web, subdivided into sticky and non-sticky silk. It is also possible to give the spider a limited silk reservoir and thus restrict its range. In our simulations, all parameters of the artificial ecological niche, including those for benefits and costs, can be adjusted and, if needed, be disabled. Figure 4 shows the fitness calculation in a diagram.

We have extended the GA by allowing it to operate in a more complex environment than is usual for this kind of programming. Our population of cyber spiders is subdivided into subpopulations (demes) that, from time to time, exchange individuals by migration. During the periods of separation, each deme by selection, mutation and recombination evolves its own local optimisation (adaptation). However, the process stops as soon as an optimal solution is reached. Such optimum is not necessarily the global optimum; actually, it is much more likely that only a local solution has been discovered. By sporadic exchange of genetic information between demes, those with “better” general solutions can drive those with worse solutions to incorporate the superior traits, thus spreading the immigrant genes in the deme gene pool. This results in a system of shifting balance of control which is more robust in overcoming local optima than a GA alone. The idea for this realistic complication of a simple GA comes from Sewall Wright's Shifting Balance Model developed for natural evolution in a structured environment (Wright, 1970) and has successfully been used in other modelling approaches to biological phenomena (Sumida *et al.*, 1990).

Materials and Methods

Juvenile spiders (ca. 20 mg) of the garden cross spider *Araneus diadematus* were kept in PVC frames under controlled lab conditions (50% rH, 24°C). Twenty animals were divided into two groups of ten. Members of the control group were kept in 30 × 30 × 5 cm (control) frames; members of the

experimental group in tall, narrow frames ($30 \times 15 \times 5$ cm). After construction, webs were photographed and partly digitised from a slide projection with a Wacom digitisation tablet connected to a Macintosh computer. The computer model was implemented in the object-oriented computing language SMALLTALK with Smalltalk/V from Digitalk on a Power Macintosh 8100/80 Av. The rules we used were derived from (i) observations of orb web spiders in the lab and (ii) the analysis of web characteristics.

Since sampling of individuals from the same simulation run led to non-normal distributed data because of simulated genetic relationships, we decided to take only the overall best cyber spider per simulation run. Therefore, we performed ten simulation runs per frame type (corresponding to those used for the real spiders, i.e. control and vertical) with a population size of 24 individuals over 100 generations in each run. The cyber spider population was subdivided into four semi-separated subpopulations (demes) that exchange emigrants each tenth generation. The total number of migrating cyber spiders was distributed to the demes according to the

mean deme fitness. Three characteristics of (both real and artificial) webs were extracted and analysed (Fig. 5).

First, the distance between the points where successive turns of the spiral meet the same radius (called: spiral distance) was measured for radii with four orientations: north (up), south (down), west and east (sideways). Second, we calculated the eccentricity of the web, i.e. the ratio between the vertical and horizontal extent of the outer sections. Third, we studied the deviation of the hub location in relation to the vertical geometrical centre of the frame.

Real and simulated webs were analysed by a one-way ANOVA for the spiral distance and a two-way ANOVA for the other characteristics after checking that the underlying assumptions for normality and equality of variances held.

In the following sections, webs built in square shaped PVC frames are called "control", those in narrow shapes "vertical". Real and simulated webs are distinguished by the extension "(R)" for real and "(S)" for simulated webs. Sample sizes were $n_{\text{control}}(R) = 10$, $n_{\text{vertical}}(R) = 10$ and $n_{\text{control}}(S) = 10$, $n_{\text{vertical}}(S) = 10$.

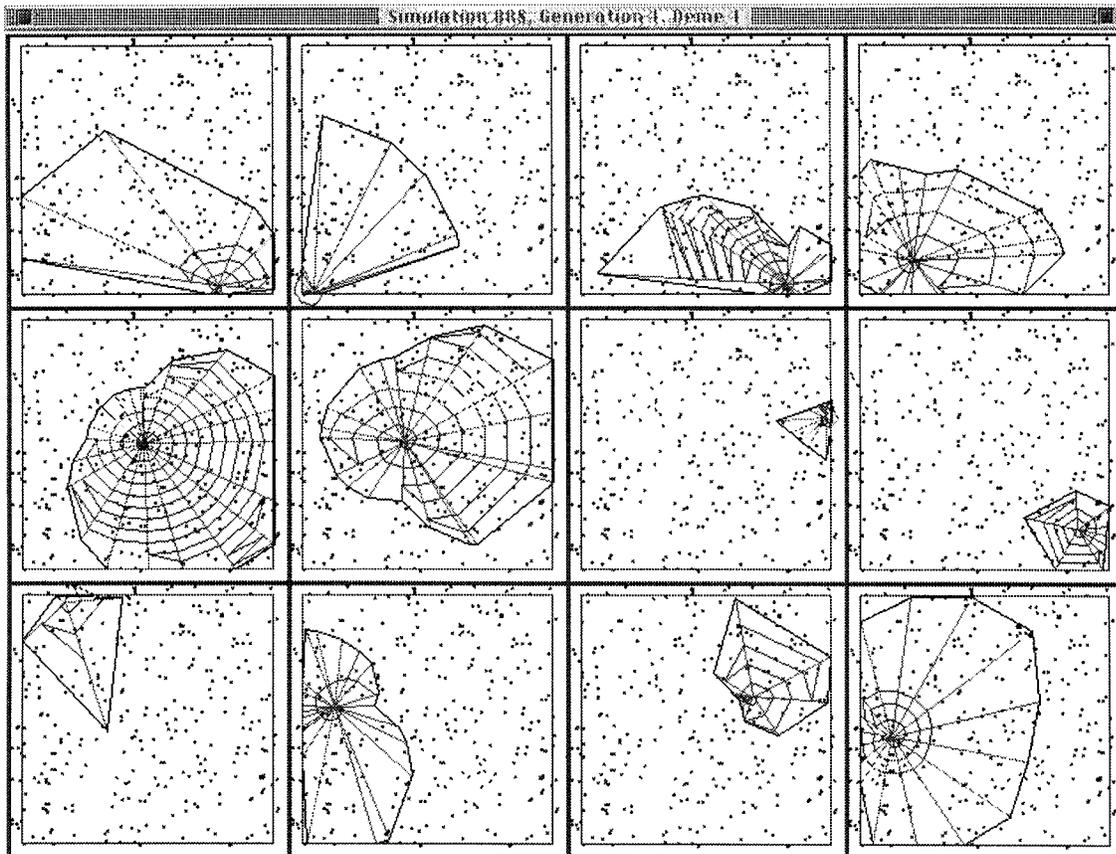


FIG. 3. Fitness evaluation by peppering artificial flies. Example of webs built by 12 spiders of the deme of a start population in the first generation generated with random genes.

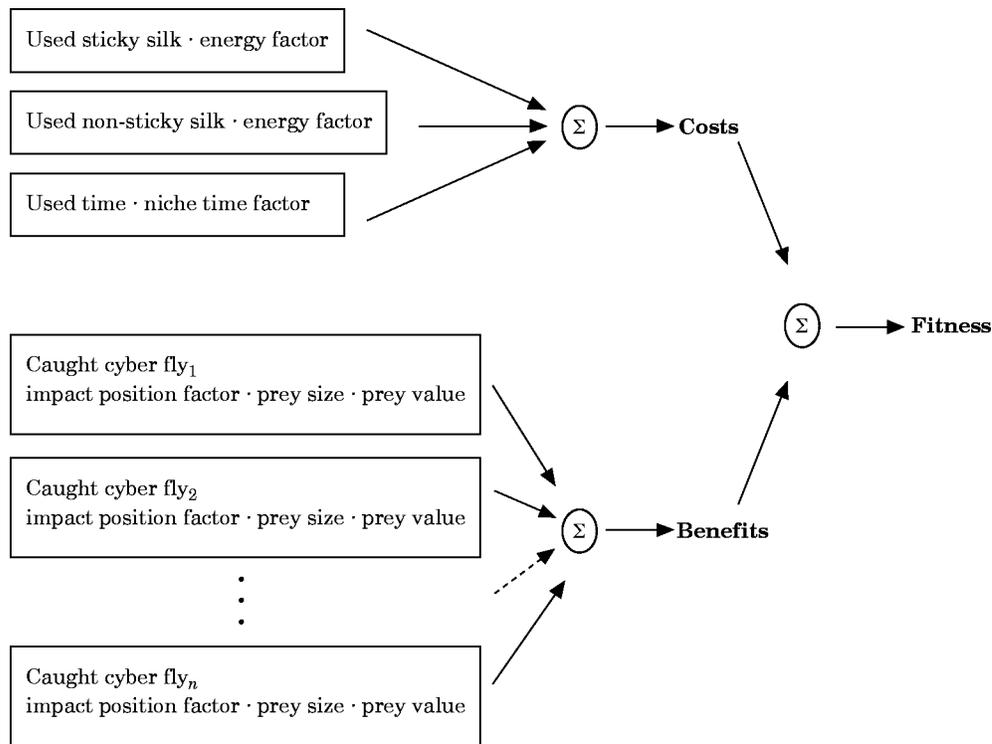


FIG. 4. Calculation of cyber fitness. As the costs for the construction we sum the use of silk weighted by energetic factors and the amount of time for the construction weighted by a time importance factor. As the benefits of the construction we take the amount of prey caught, weighted by the impact position, size and value of each single item. Finally, the cost to benefit ratio gives the fitness of our cyber spider.

Results

SPIRAL DISTANCES

Figure 6 shows the result of the spiral distance analysis, for spiral spacing along one radius each closest to the directions north, south, east and west. A comparison of mean spiral distances (all four orientations pooled) between vertical and control webs of real spiders [Fig. 6(a)] was significant ($F_{\text{real}} = 7.7245$, $P_{\text{real}} = 0.0124$).

In contrast, significance could not be shown for the simulated webs ($F_{\text{simulated}} = 0.0046$, $P_{\text{simulated}} = 0.9465$) [Fig. 6(b)] indicating a failure of a model assumption. In this experimental series the silk reservoir of the artificial spiders for the web construction was limited. Therefore, it turned out to be beneficial for the cyber spiders to keep the overall mean mesh size constant and to use the gain of silk to fill out more space in the oblong frames.

However, real and simulated vertical webs have highly significant smaller meshes [Fig. 6(c + d)] in horizontal (E,W) orientation ($F_{\text{real}} = 40.6677$, $P_{\text{real}} < 0.0001$; $F_{\text{simulated}} = 15.0308$, $P_{\text{simulated}} = 0.0011$). Figure 6 e + f illustrates that neither for real nor simulated webs was there any evidence for spiral distance differences between the north and the south

radii of the web ($F_{\text{real}} = 0.2256$, $P_{\text{real}} = 0.6406$; $F_{\text{simulated}} = 0.0328$, $P_{\text{simulated}} = 0.8584$).

OUTER SECTOR ECCENTRICITY

The outer sector eccentricity [Fig. 7(a)] was analysed with a two-way ANOVA showing that frame shape as source of variation is highly significant ($F_{\text{shape}} = 150.1819$, $P_{\text{shape}} < 0.0001$) whereas simulated and real webs did not differ significantly ($F_{\text{real/sim}} = 0.7166$, $P_{\text{real/sim}} = 0.4029$). Therefore, the simulation accurately imitated the real webs, which supports the model for this characteristic.

HUB DEVIATION

The data output of the analysis of vertical hub location in relation to the web frame is illustrated in Fig. 7(b). A comparison of simulated and real webs and control and vertical frames as second factor resulted in a significant difference between frame shapes ($F_{\text{shape}} = 10.0491$, $P_{\text{shape}} = 0.0031$) and non-significance ($F_{\text{real/sim}} = 1.8945$, $P_{\text{real/sim}} = 0.1772$) between simulated and real webs. However, the effect of frame shape on this characteristic was not as strong as the effects on the outer sector eccentricity. This was reflected in smaller response differences between real and simulated webs which was not as clear-cut as for

the outer sector eccentricity. Moreover, the simulated data show a high degree of variation indicating that selection pressure from the artificial ecological niche to express the characteristic was at best weak.

This was due to our cyber niche specification which counted a cyber prey impact as successfully attacked according to a probability function decreasing with the distance between the impact location and the cyber spider in the web centre. However, a more accurate simulation of the probability to reach struggling prey in time should also include the running direction of the spider, since they run faster downwards than upwards (Ap Rhisiart & Vollrath, 1994). This feature was disabled in our study in order to check for possible treatment effects. Thus (due to full symmetry in our simulation) the cyber spider's

solutions for the vertical hub location were either above or below the geometrical centre.

Discussion

Modelling of orb web construction allows reasonable simplifications (outlined in the introduction) which can give a good image of the aspects to be investigated, so that results of the simulations can be transferred to the investigated system. However, highly complex systems, like animals interacting with their environment, make it difficult to justify conclusions drawn from a simulation. Former work with computer simulations of spider web construction by Gotts & Vollrath (1992) already mention these general simulation problems for web building behaviour and identify the problem of finding

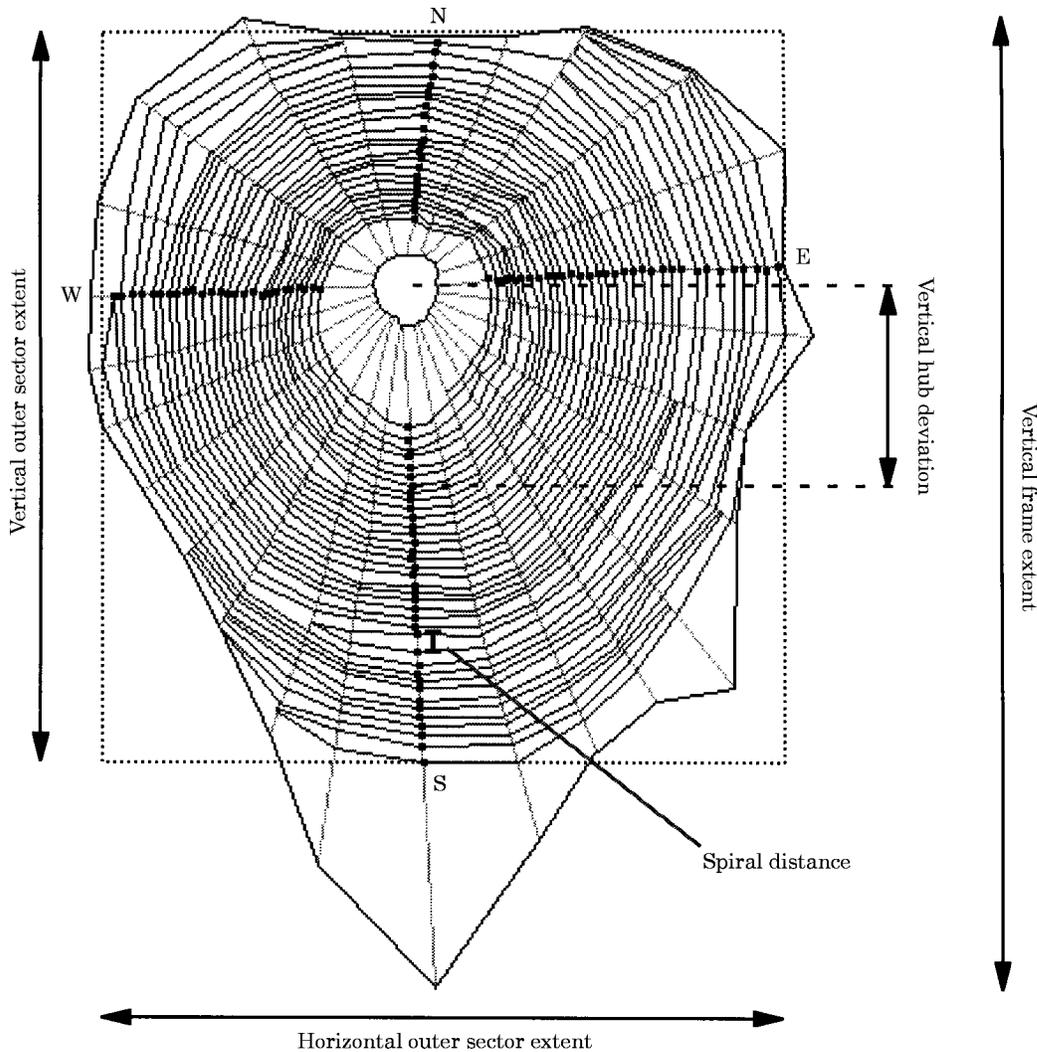


FIG. 5. Analysis of web geometry: (i) Spiral distance measurement along the four spokes N, S, W and E. (ii) Outer sector eccentricity as the ratio of vertical to horizontal outer sector extent (the outer sector is given by the most peripheral capture spiral threads). (iii) Deviation of the vertical hub location in relation to the vertical geometrical centre of the web frame.

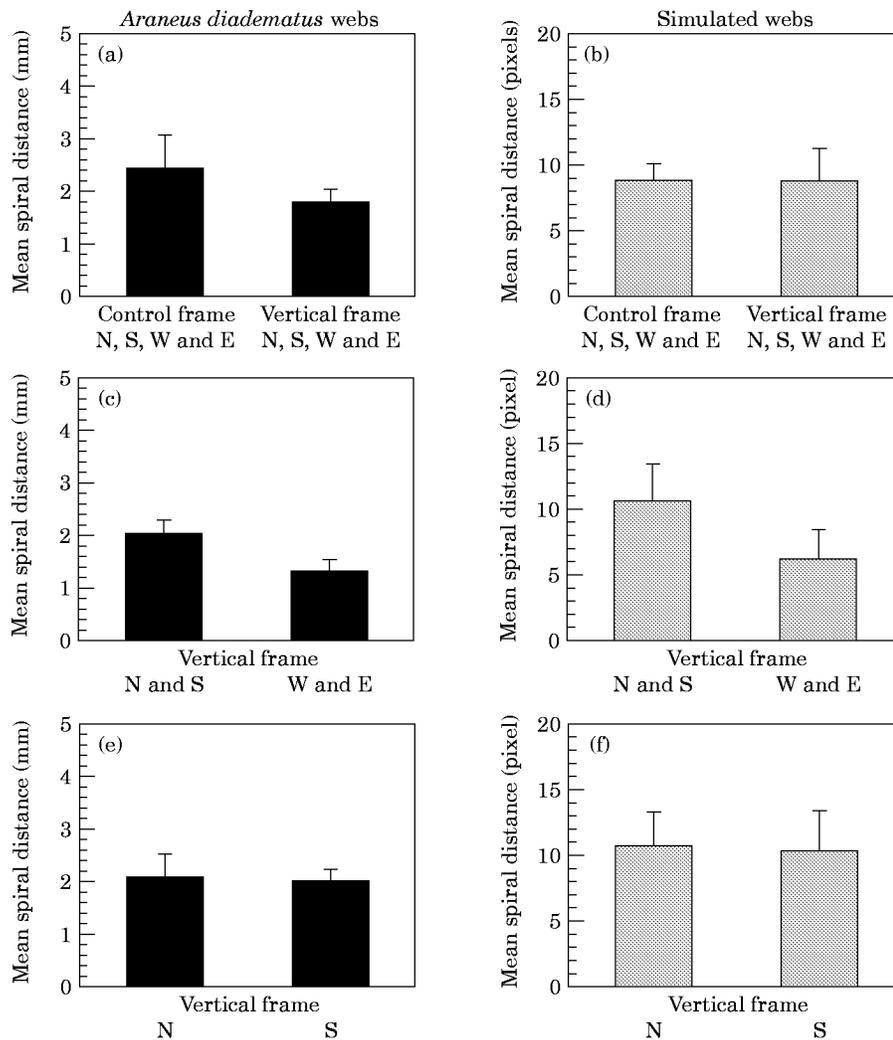


FIG. 6. Comparison of mean spiral distances. (a), (c) and (e) are data from real webs of *Araneus diadematus*; and (b), (d) and (f) are data from artificial webs evolved by simulation. (a) and (b): mean spiral distances in all four orientations (N, S, W and E) between webs built in square control and experimental tall narrow frames; (c) and (d): mean spiral distances for webs built in tall narrow frames between spiral distances in vertical (N and S) and horizontal (W and E) orientation; (e) and (f): mean spiral distances for webs built in tall narrow frames between spiral distances in the northern (N) and southern (S) orientation.

appropriate abstractions and simplifications. In addition, Gotts & Vollrath describe the problem of a large number of possible model solutions and the problem of recognising the “right” one.

Gotts & Vollrath’s *Theseus* approach attempted to study auxiliary spiral construction by describing the web with geometrical rules instead of simulating the spider and its behaviour patterns generating the web (Gotts & Vollrath, 1991). This approach by its very nature could only lead to simulations fitting web geometry after considerable manual parameter tweaking without giving conclusive insights into the real animal’s behavioural rule set. Nevertheless, in our approach (outlined above) we followed their basic interpretation of the spider’s rules after they had been clarified, improved and re-implemented in a more

realistic approach by Peter Fuchs (Fuchs, 1993; Krink & Fuchs, 1994). However, the main purpose of our new approach is very different. Here, the central idea is to explore and optimise graph solutions of a complete orb web-like structure to fill out a given space as well as possible with limited resources under specific environmental conditions. In its automatic parameter exploration and optimisation the Genetic Algorithm of *NetSpinner III* turned out to be a powerful tool for studying a real spider’s web-building algorithm. The artificial ecological niche allowed us to define different types of prey, different shapes of sites for web construction and adjustment of benefit/cost weights.

However, even this new approach still has some problems. The construction of the capture spiral from

inside to outside makes it difficult to compare our artificial webs with real webs of an orb spider like *Araneus diadematus*. For *Araneus diadematus* the previous construction of an auxiliary spiral could be crucial since it is thought to be involved in the spatial orientation processes of the capture spiral construction (Zschokke, 1995). Simulations indicated that it was difficult to find a rule description which approximated correct capture spiral characteristics without an auxiliary spiral. In fact the parameter variety had to be artificially restricted to achieve this, suggesting that the auxiliary spiral does indeed function as a guide for the construction behaviour (Zschokke, 1995) as well as a scaffold for web engineering (Wirth & Barth, 1992).

An important aspect of our model is the ability to adjust the artificial ecological niche which determines the spider fitness. Although estimates exist on energy consumption during web construction, e.g. (Peakall & Witt, 1976; Lubin, 1986), it is not all clear how to combine and weight in a model all different energetic factors related to web construction (Lubin, 1986).

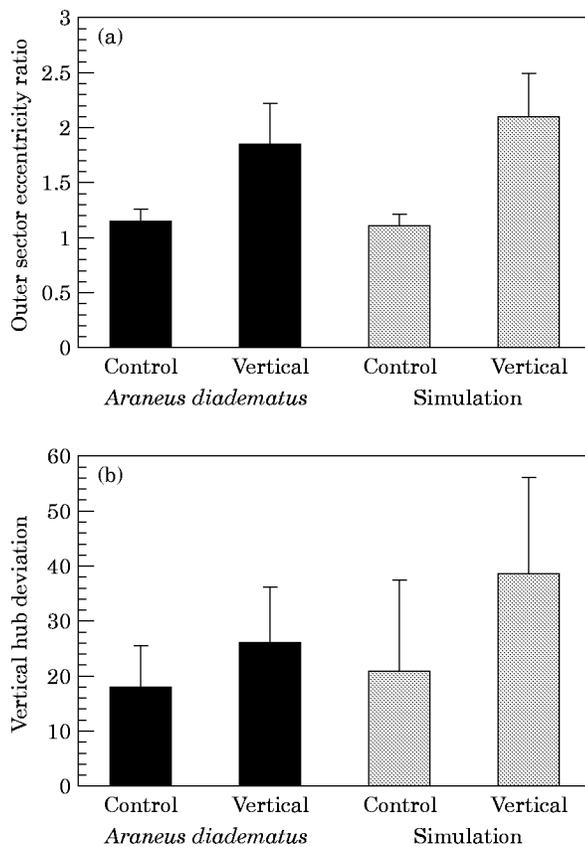


FIG. 7. Comparison between real and artificial webs. These webs were built in control as well as vertical frames. (a) Comparison of outer sector eccentricity ratios. (b) Comparison of vertical hub location deviation from the vertical geometrical centre of the frame.

In conclusion, we can say that the web-building simulation approach *NetSpinner III* seems to be a powerful tool to explore the space of geometrical possibilities to fill out a given structure based on a two-dimensional radii/spiral construction.

The artificial (simulated) spiders constructed a circular structure in the square control frames and a more elliptic structure in vertical frames. We assume that in both cases this was done in order to fill out the frame as well as possible. Moreover, both real and artificial webs built in the narrow frames were significantly more eccentric than webs constructed in the square control frames.

Real webs in narrow frames had overall (i.e. in all four orientations) significantly smaller mesh than real control webs whereas the simulated webs did not have significantly different meshes. However, similarity between simulated and real webs was found for local differences of mesh sizes: real and artificial webs had significantly smaller mesh in the horizontal (E/W) compared with the vertical (N/S) orientation in the web.

A comparison of real and simulated webs built in control and narrow, vertical frames showed that the vertical hub-location deviation from the geometrical centre of the web was significantly different for the two frame shapes. In contrast, no significant differences could be shown between simulated and real webs. However, these simulation results did not fully confirm the model for this web characteristic. While the hub of the real webs was always found above the geometrical web centre, the simulated hubs were located on both sides of the centre. In addition, the conspicuous variation of the data indicated only a weak selection pressure on this web aspect. Therefore, the vertical location of the hub must have been determined by environmental factors other than the shape of the building site alone. One possible explanation would be based on the observation that the spider runs down faster than up, resulting in isoclines of equal speed that are oval with the hub eccentric and in the upper half (Ap Rhiart & Vollrath, 1994). Accordingly the spider has a better chance to catch an insect trapped further below the hub before it escapes from the web.

Finally, we stress the ability of the new approach to point to problems during the process of model validation. Failures of the simulations to comply with reality guided our research by allowing us to track down improperly described, incomplete or contradictory knowledge. One example shown in this article is the model's failure to construct correct (i.e. naturally occurring), overall (i.e. in all four orientations) mean spiral distances. This response showed a falsification

of the model's assumption that the spider's silk reservoir for the capture spiral construction is limited. The model's optimal solution for this constraint was to keep the overall mean spiral distance constant. One reason for this might be that the meshes were adapted to the mean prey size of the given artificial ecological niche. Moreover, the system optimised the webs in such a way that the capture area covered the given frame with silk as completely as possible. Therefore, a decrease of the overall mean spiral distance (using the same amount of silk) would have resulted in a smaller capture area when the silk reservoir was tightly limited.

Thus, model validation and falsification of models using computer simulations assists our research into elucidating the rules of web-building in real spiders and the evolution of these rules.

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REFERENCES

- AP RHISIART, A. & VOLLRATH, F. (1994). Design features of a spider's orb web. *Behav. Ecol.* 280–287.
- EBERHARD, W. G. (1981). Construction behaviour and the distribution of tensions in orb webs. *Bull. Br. arachnol. Soc.* 6, 189–204.
- EBERHARD, W. G. (1982). Behavioural characters for the higher classification of orb-weaving spiders. *Evolution*, 36, 1067–1095.
- EBERHARD, W. G. (1988). Memory of distances and directions moved as cues during temporary spiral construction in the spider *Leucauge mariana* (Araneae: Araneidae). *J. Ins. Behav.* 1, 51–66.
- FUCHS, P. (1993). *Computerunterstützte Analyse und Simulation des Netzbaus von Radnetzspinnen*. Studienarbeit: Informatik Hamburg.
- GÖRNER, P. & CLAAS, B. (1986). Homing behaviour and orientation in the funnel-web spider, *Agelena labyrinthica* Clerck. In: *Neurophysiology of Spiders*. (F. W. Barth, ed.) pp. 275–297. Berlin: Springer.
- GOTTS, N. M. & VOLLRATH, F. (1991). Artificial intelligence modelling of web-building in the garden cross spider. *J. theor. Biol.* 152, 485–511.
- GOTTS, N. M. & VOLLRATH, F. (1992). Physical and theoretical features in the simulation of animal behaviour: the spider's web. *Cybernet. Syst.* 23, 41–65.
- KÖNIG, M. (1951). Beiträge zur Kenntnis des Netzbaus orbiteler Spinnen. *Z. Tierpsychol.* 8, 462–492.
- KRIEGER, M. (1992). Radien im Netz der Radnetzspinne. Diploma Thesis, University of Basel, Switzerland.
- KRINK, T. & FUCHS, P. (1994). Modellierung als Mittel zur Analyse räumlichen Orientierungsverhaltens. Gegenüberstellung zweier Modellansätze am Beispiel des Netzbaus der Kreuzspinne. Diploma thesis, Hamburg University.
- LUBIN, Y. D. (1986). Web building and prey capture in the uloboridae. In: *Spiders: Webs, Behavior and Evolution*. (W. A. Shear, ed.) pp. 132–171. Stanford: Stanford University Press.
- PEAKALL, D. B. & WITT, P. (1976). The energy budget of an orb web-building spider. *Comp. Biochem. Physiol.* 54A, 187–190.
- PETERS, H. (1951). Untersuchungen über die Proportionierung im Spinnen-Netz. *Z. Naturforsch.* 6b, 90–107.
- PETERS, H. & WITT, P. (1949). Die Wirkung von Substanzen auf den Netzbau der Spinnen. *Experientia*. 5, 161–162.
- PETERS, H. M. (1937). Studien am Netz der Kreuzspinne (*Aranea diadema* L.). II. Über die Herstellung des Rahmens, der Radialfäden und der Hilfsspirale. *Z. Morphol. Ökol. Tiere.* 33, 128–150.
- REED, C. F., WITT, P. N. & JONES, R. L. (1965). The measuring function of the first legs of *Araneus diadematus* Cl. *Behaviour*, 25, 98–119.
- ROBINSON, M. H. & LUBIN, Y. D. (1979). Specialists and generalists: The ecology and behavior of some web-building spiders from Papua New Guinea. II *Psecchus argentatus* and *Fecinia* sp. (Aracae: Psecchridae). *Pac. Insects.* 21, 133–164.
- SHEAR, W. A. (1986). *Spiders: Webs, Behavior and Evolution*. Stanford: Stanford University Press.
- SAMU, F. & VOLLRATH, F. (1992). Spider orb webs as bioassays for agrochemicals. *Entomologia exp. appl.* 62, 119–126.
- SEYFARTH, E.-A. (1986). Spider proprioception: receptors, reflexes and control of locomotion. In: *Neurophysiology of Spiders*. (F. W. Barth, ed.) pp. 230–248. Berlin: Springer.
- SUMIDA, B. H., HOUSTON, A. I., MCNAMARA, J. M. and HAMILTON, W. D. (1990). Genetic algorithms and evolution. *J. theor. Biol.* 147, 59–84.
- VOLLRATH, F. (1986). Gravity as orientation guide during web-construction in the orb spider *Araneus diadematus*. *J. Comp. Physiol. A.* 159, 275–280.
- VOLLRATH, F. (1987). Altered geometry of webs in spiders with regenerated legs. *Nature*, 328, 247–248.
- VOLLRATH, F. (1988). Spiral orientation of *Araneus diadematus* orb webs built during vertical rotation. *J. Comp. Physiol. A.* 162, 413–419.
- VOLLRATH, F., DOWNES, M. & KRAKOW, S. (1997). Design variables in a Spider's orb web. *Physiol. Behav.* (in press).
- VOLLRATH, F. & MOHREN, W. (1985). Spiral geometry of the garden spider's orb web. *Naturwissenschaften.* 72, 666–667.
- WEISSMANN, M. (1987). Web-building and prey capture in two orb weavers. MSc. thesis, Oxford.
- WIRTH, E. & BARTH, F. G. (1992). Forces in the spider orb web. *J. Comp. Physiol. A.* 171, 359–371.
- WITT, P. N., REED, C. F. & PEAKALL, D. B. (1968). *A Spider's Web: Problems in Regulatory Biology*. Heidelberg: Springer.
- WRIGHT, S. (1970). Random drift and the shifting balance theory of evolution. In: *Mathematical Topics in Population Genetics*. (K. Kojima, ed.) pp. 1–31. Berlin: Springer-Verlag.
- ZSCHOKKE, S. (1993). The influence of the auxiliary spiral on the capture spiral in *Araneus diadematus* Clerck (Araneidae). *Bull. Brit. Arachnol. Soc.* 9, 169–173.
- ZSCHOKKE, S. (1995). The coiling of the spirals in the orb web of *Araneus diadematus*. *Newslet. Brit. Arachnol. Soc.* 74, 9–10.